Université Montpellier II

Ecole Doctorale « Systèmes Intégrés en Biologie, Agronomie,

Géosciences, Hydrosciences, Environnement »

Mémoire présenté en vue d'obtenir l'Habilitation à Diriger des Recherches

Les Tribulations d'un Chercheur en Agroécologie

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"Je déclare avoir respecté, dans la conception et la rédaction de ce mémoire d'HDR, les valeurs et principes d'intégrité scientifique destinés à garantir le caractère honnête et scientifiquement rigoureux de tout travail de recherche, visés à l'article L.211-2 du Code de la recherche et énoncés par la Charte nationale de déontologie des métiers de la recherche et la Charte d'intégrité scientifique de l'Université de Montpellier. Je m'engage à les promouvoir dans le cadre de mes activités futures d'encadrement de recherche."

Avant-propos

J’imagine que chaque chercheur a sa propre façon d’appréhender et de rédiger son mémoire d’HDR. C’est après tout un recul sur son passé professionnel impliquant une certaine part d’introspection. Si j’ai trouvé que ce regard en arrière était plutôt intéressant, plaisant et même enrichissant, j’avoue avoir eu du mal à trouver sous quelle forme rédiger le mémoire. Quelles activités j’évoquais ? Devais-je faire une rétrospective complète ? Faire des choix ? Si oui sur quels critères ? Parler uniquement de ce qu’on voit comme une réussite ou bien s’attarder également sur les ratés, les erreurs de parcourt. Il a y ces questions sur le fond mais je m’interrogeais également sur la forme. J’ai pu lire ou, pour être honnête, parfois survoler, les mémoires d’HDR de collègues Ciradiens et de chercheurs d’autres organismes pour me faire une idée de ce qui devait ou pouvait être fait.

J’ai choisi dans le présent mémoire de faire un focus sur seulement une partie de mes activités depuis que je suis chercheur au Cirad, et de me limiter à mentionner le reste dans une annexe. Pourquoi cela ? J’avais envie de raconter ces activités comme une histoire, une chronologie de recherches qui s’imbriquent dans un ensemble cohérent. Enfin j’espère que c’est ce que vous éprouverez en lisant... En faisant ce choix, je voulais aussi pouvoir poser un regard critique, avec un minimum d’objectivité, sur le choix des questions abordées, des méthodes utilisées et des résultats obtenus au cours des dix dernières années.

J’espère que le ton que j’ai mis dans mon écriture, volontairement léger dans la forme, ne sera pas pris pour le reflet d’une légèreté dans la démarche scientifique que j’ai. La déclaration de la page précédente prouve de toute façon que ce n’est pas le cas... Comme écrit plus haut, c’est un travail d’introspection et ces choix personnels, je le pense, me correspondent bien. Travailler dans le monde de la recherche c’est aussi travailler avec et pour un collectif. Dans mon expérience de management, transversal ou vertical, j’ai noté que les relations humaines sont finalement le cœur d’un projet scientifique, que le collectif et l’individu gagnent, et donc le projet, à être dans un environnement agréable, humain et où la communication est fluide et sereine. Et cette certaine "décontraction" n’implique pas qu’on ne fait pas les choses rigoureusement et dans les règles déontologiques que nécessite le travail de chercheur. Sinon encore une fois vous n’auriez pas trouvé la déclaration de la page précédente… enfin si peut-être puisque c’est obligatoire de l’inscrire dans le mémoire.

Par ailleurs, et puisqu’un mémoire d’HDR est rédigé pour l’obtention d’un diplôme permettant de diriger les thèses, je dirai que, s’il faut évidemment veiller à la bonne formation scientifique et professionnelle de doctorants, il est aussi crucial de le faire avec une certaine bienveillance pour guider l’étudiant jusqu’à son autonomie professionnelle en maintenant toute sa motivation et sa créativité.

Remerciements

Comme dans bien d’autres aspects de la vie, les chemins que l’on prend et l’histoire personnel que l’on construit sont la résultante de nos choix face à des opportunités, que l’on provoque parfois soi-même, qui sont d’autres fois le fruit du hasard ou encore là grâce aux personnes rencontrées. Dans ce dernier cas, il faut savoir les remercier.

En premier lieu et par soucis de chronologie, je remercie les différentes personnes dont l’encadrement, alors que j’étais encore étudiant, a permis de tracer une route qui m’a mené au métier de chercheur. Je pense ici à Denis Poinsot dont la capacité à éveiller la curiosité n’a d’égal que sa pédagogie à enseigner les statistiques. Je remercie également Régis Ferrière, qui accepta de diriger ma thèse et de m’initier aux équations différentielles, aux matrices jacobiennes et autres outils de la dynamique adaptative. Je remercie Stéphane Legendre qui m’a donné le goût de la programmation informatique et apporté si souvent son soutien.

Il me faut aussi remercier tous les étudiants et jeunes recrutés que j’ai eu la chance d’encadrer. J’espère vous avoir apporté autant que vous l’avez fait pour moi. Merci donc à Rémi, Martin, Cathleen, Amélie, Camille, Charlotte, Sacha, Kévin, Blanche, Paul, Lola, Chloé, Constant et Antoine.

Je remercie Luc de Lapeyre de Bellaire, mon directeur d’unité, pour la confiance qu’il m’accorde et pour avoir su me tirer de ma zone de confort en me confiant de nouvelles responsabilités dans mes activités.

Un énorme remerciement à Philippe Tixier qui a toujours été présent pour me soutenir, depuis mon recrutement jusqu’à la rédaction de ce mémoire. Merci pour la motivation, la bonne humeur constante, ton soutien à ma famille au Costa Rica, les partages d’idées, le co-encadrement de doctorants et surtout, oui surtout, pour tous ces jeux de mots échangés !

Un très grand merci à William Puech qui a sauté dans la barque avec nous pour louvoyer aux frontières séparant alors l’agroécologie et l’informatique. J’espère que nous tirerons prochainement de nouveaux bords ensemble et qu’ils te mèneront jusqu’à l’île de la Réunion !

Je ne saurais manquer de remercier Leïla Bagny Beilhe d’être venu me chercher il y a quelques années pour travailler ensemble et pour les projets que nous avons depuis menés ensemble. Et merci évidemment pour ce travail conjoint pour la rédaction de nos mémoires respectifs. C’était motivant, stimulant et surtout marrant !

Un grand merci à Dave Bohan, Anne-Marie Cortesero, Aude Vialatte, Bastien Castagneyrol et Thibaud Decaens pour avoir accepté d’être rapporteurs de ce mémoire.

Je remercie mes collègues du quotidien à la Réunion, ceux de Bassin Plat comme ceux de Ligne Paradis, avec qui j’ai plaisir de travailler depuis près de 3 ans maintenant. Merci à zot tout !

Un merci tout particulier à Mathilde Hoarau, ou la pa fine antand amoin koz kreol ! Merci aou dalon Waro !

Et pour terminer, un incommensurable merci à ma meute qui m’a aidé à finir ce mémoire dans les temps grâce à leur soutien inconditionnel. Merci Violaine, Siméon, Blaise, Gaspard, Stooges et Luciole !

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Mon CV

Curriculum Vitae

Etat-Civil	
Nom	Carval Dominique
Nationalité	Française
Date et lieu de naissance	10 avril 1981 à Pont L'Abbé (Finistère)
Adresse professionnelle	Bâtiment A - Bureau 003 Station de Bassin Plat - BP 180 97455 Saint-Pierre Cedex Réunion dominique.carval@cirad.fr +262 2 62 49 26 38
Fonction	Chercheur en Agroécologie
Organisme	**CIRAD** - Centre de Coopération Internationale en Recherche Agronomique pour le Développement
Département	**PERSYST** – Performances de Systèmes de Production et de Transformation Tropicaux
Unité	**GECO** – Fonctionnement écologique et gestion durable des agrosystèmes bananiers et ananas
Compétences linguistiques	Français (langue maternelle) Anglais (scientifique), Espagnol (notions), Créole (notions)
Diplômes	**Doctorat en Ecologie** - Université Pierre & Marie Curie (Paris VI) - **2009** **Master 2 Biologie, Ecologie et Evolution** - Université Pierre & Marie Curie (Paris VI), INA-PG & Ecole Normale Supérieure – **2005**
Expériences Professionnelles	**Depuis 2011 Chercheur en Agroécologie** UPR GECO (2011-2016 Martinique, 2016-2019 Montpellier, 2019-Présent Réunion)
	Octobre 2010-Décembre 2010 Post-Doctorat ONCFS - Office National de la Chasse et de la Faune Sauvage - CNERA - Petite faune sédentaire de plaine - Estimation de la perméabilité de l'environnement à la propagation de l'hépatite virale (EBHS) chez le lièvre d'Europe (*Lepus europaeus*)
	Octobre 2009-Septembre 2010 Post-Doctorat Université Claude Bernard Lyon 1 Laboratoire de Biométrie et Biologie Évolutive (UMR CNRS 5558) -Modélisation spatialement explicite de la propagation d'une épidémie virale (EBHS) dans des populations d'hôtes (*Lepus europaeus*)

Projets

DPP SADUR 2022-2024 Système Alimentaire Durable en milieu insulaire
Fonction : Chef de projet (en binôme avec Layal Dahdouh UMR Qualisud Réunion)
Montant total du projet (année 2022) : 2843 k€ (FEDER & FEADER Réunion)

CosmoCount – Application smartphone utilisant l'IA pour la détection et le dénombrement des arthropodes piégés dans les agrosystèmes, cas du charançon du bananier 2022
Fonction : Chef de projet
Montant : 15 k€ (Crési CIRAD)

easyPM: Embedded Automated SYstem for Pest Monitoring 2022
Fonction : Participant (Chef de projet : L. Bagny Beilhe UMR PHIM, CIRAD)
Montant : 13 k€ (INPP CIRAD)

MahoSinza Préservation de la production de la bananeraie mahoraise face aux bioagresseurs actuels et émergents 2022-2023
Fonction : Participant (Chef de projet : T. Lescot, UR GECO, CIRAD)
Montant : 273 k€ (FEADER Mayotte)

Structuration de filière banane dessert à Mayotte 2022-2023
Fonction : Participant (Chef de projet : Oumbaïdi Sidi M'Colo, AVM)
Montant : 198 k€ (FEADER Mayotte)

Quantification de la régulation des ravageurs par les prédateurs généralistes, utilisation de l'analyse d'images pour déterminer et quantifier les réseaux d'interactions 2018-2020
Fonction : Participant (Chef de projet : P. Tixier, UR GECO, CIRAD)
Montant du projet : 20 k€ + ½ bourse de thèse (#Digitag)

PredaTV : Identifier les prédateurs généralistes ayant un rôle dans la régulation des ravageurs des cultures : mise au point d'une méthodologie standard basée sur la vidéo. 2018
Fonction : Participant (Chef de projet : L. Bagny Beilhe UMR PHIM, CIRAD)
Montant du projet : 14k€ (Crési CIRAD)

STRADIV : System approach for the TRAnsition to bio-DIVersified agroecosystems, from process analysis to multi-scale co-conception with actors **2015-2019**
Fonction : Participant (Chefs de projet : P. Tixier, UR GECO & Eric Scopel, UR AIDA, CIRAD)
Montant du projet : 1300 k€ (Agropolis Fondation)

Valorisation économique de la biodiversité de la Martinique pour améliorer le fonctionnement des agrosystèmes 2014-2015
Fonction : Chef de projet
Subvention : 776 k€ (FEDER Martinique)

Conception de systèmes de cultures innovants à faibles impacts environnementaux 2013-2014
Fonction : Chef de projet
Subvention : 283 k€ (FEDER Martinique)

Bilan des publications dans les revues à comité de lecture

h-index : 11

21 articles parues dans des revues à facteur d'impact

- 20 articles de résultats originaux de recherche
- 1 revue bibliographique
- 6 articles en premier auteur
- 8 articles avec des doctorants co-encadrés

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Table 1. Récapitulatif des revues à comité de lecture. Les métriques des revues sont issues du Journal Citation Report 2020.

Journal	IF 2020	Catégorie	Rang	Quartile	Nombre d'articles
Methods in Ecology and Evolution	7.781	Ecology	9/166	Q1	1
Proceedings of the Royal Society B	5.349	Biology	13/93	Q1	1
Applied Soil Ecology	4.046	Soil Science	11/37	Q2	1
Evolution	3.742	Ecology	45/166	Q2	1
Biological Control	3.687	Entomology	10/102	Q1	3
Basic and Applied Ecology	3.414	Ecology	53/166	Q2	1
IEEE Access	3.367	Computer Science	65/161	Q2	1
Phytopathology	3.234	Phytopathology	46/235	Q1	1
Ecological Modelling	2.974	Ecology	69/166	Q2	1
Ecology & Evolution	2.910	Ecology	72/166	Q2	3
PeerJ	2.984	Multidisciplinary Sciences	27/72	Q2	1
Journal of Applied Entomology	2.603	Entomology	21/102	Q1	2
Crop Protection	2.571	Agronomy	26/91	Q2	1
Int. Journal of Pest Management	1.907	Entomology	39/102	Q2	1
Bulletin of Entomological Research	1.750	Entomology	43/102	Q2	2

N.B. Les auteurs dont le nom est ci-dessous souligné sont les doctorants que j'ai co-encadrés.

Publications dans des revues à comités de lecture avec facteur d'impact

[ACL21] **Carval D.**, Resmond R., Dassou A. G., Cotté V., Achard R. & Tixier, Philippe. 2022. Influence of a cover crop on ants and dermapterans in banana plantations: consequences for the regulation of the banana weevil. *International Journal of Pest Management* (online). https://doi.org/10.1080/09670874.2022.2029972

[ACL20] Tresson P., Tixier P., Puech W. & **Carval D.** 2021. The challenge of biological control of *Cosmopolites sordidus* Germar (Col. Curculionidae): A review. *Journal of Applied Entomology* 145 (3) 171-181. https://doi.org/10.1111/jen.12868

[ACL19] Tresson P., **Carval D.**, Tixier P. & Puech W. 2021. Hierarchical classification of very small objects: Application to the detection of arthropod species. *IEEE Access* 9: 63925-63932. https://doi.org/10.1109/ACCESS.2021.3075293

[ACL18] Bagny-Beilhe L., Roudine S., Quintero Perez J.A., Allinne C., Daout D., Mauxion R. & **Carval D.** 2020. Pest-regulating networks of the coffee berry borer (*Hypothenemus hampei*) in agroforestry systems. *Crop Protection* 131: 105036, 10 p. https://doi.org/10.1016/j.cropro.2019.105036

[ACL17] Dassou A.G., Vodouhé S.D., Bokonon G.A., Goergen G., Chailleux A., Dansi A., **Carval D.** & Tixier P. 2019. Associated cultivated plants in tomato cropping systems structure arthropod communities and increase the *Helicoverpa armigera* regulation. *Bulletin of Entomological Research* 109 (6): 733-740. https://doi.org/10.1017/S0007485319000117

[ACL16] Tresson P., Tixier P., Puech W., Bagny-Beilhe L., Roudine S., Pagès C. & **Carval D.** 2019. CORIGAN: Assessing multiple species and interactions within images. *Methods in Ecology and Evolution* 10 (11): 1888-1893. https://doi.org/10.1111/2041-210X.13281

[ACL15] Collard B., Tixier P., **Carval D.**, Lavigne C. & Delattre T. 2018. Spatial organisation of habitats in agricultural plots affects per-capita predator effect on conservation biological control: An individual based modelling study. *Ecological Modelling* 388: 124-135. https://doi.org/10.1016/j.ecolmodel.2018.09.026

[ACL14] Poeydebat C., **Carval D.**, Tixier P., Daribo M.O. & De Lapeyre de Bellaire L. 2018. Ecological regulation of black leaf streak disease driven by plant richness in banana agroecosystems. *Phytopathology* 108 (10): 1184-1195. https://doi.org/10.1094/PHYTO-12-17-0402-R

[ACL13] Dassou A.G., Tixier P., Depigny S. & **Carval D.** 2017. Vegetation structure of plantain-based agrosystems determines numerical dominance in community of ground-dwelling ants. *PeerJ* 5: e3917, 13 p. https://doi.org/10.7717/peerj.3917

[ACL12] Poeydebat C., Tixier P., Chabrier C., De Lapeyre de Bellaire L., Vargas R., Daribo M.O. & **Carval D.** 2017. Does plant richness alter multitrophic soil food web and promote plant-parasitic nematode regulation in banana agroecosystems? *Applied Soil Ecology*, 117-118: 137-146. https://doi.org/10.1016/j.apsoil.2017.04.017

[ACL11] Poeydebat C., Tixier P., De Lapeyre de Bellaire L. & **Carval D.** 2017. Plant richness enhances banana weevil regulation in a tropical agroecosystem by affecting a multitrophic food web. *Biological Control* 114: 125-132. https://doi.org/10.1016/j.biocontrol.2017.08.009

[ACL10] **Carval D.**, Cotte V., Resmond R., Perrin B. & Tixier P. 2016. Dominance in a ground-dwelling ant community of banana agroecosystem. *Ecology and Evolution* 6 (23): 8617-8631. https://doi.org/10.1002/ece3.2570

[ACL9] **Carval D.**, Resmond R., Achard R. & Tixier P. 2016. Cover cropping reduces the abundance of the banana weevil *Cosmopolites sordidus* but does not reduce its damage. *Biological Control* 99: 14-18. https://doi.org/10.1016/j.biocontrol.2016.04.004

[ACL8] Dassou A.G., Depigny S., Canard E., Vinatier F., **Carval D.** & Tixier P. 2016. Contrasting effects of plant diversity across arthropod trophic groups in plantain-based agroecosystems. *Basic and Applied Ecology* 17 (1): 11-20. https://doi.org/10.1016/j.baae.2015.09.003

[ACL7] Poeydebat C., **Carval D.**, De Lapeyre de Bellaire L. & Tixier P. 2016. Balancing competition for resources with multiple pest regulation in diversified agroecosystems: a process-based approach to reconcile diversification and productivity. *Ecology and Evolution* 6 (23): 8607-8616. https://doi.org/10.1002/ece3.2453

[ACL6] **Carval D.**, Cotte V., Notaro M., Ryckewaert P., Tixier P. 2015. Spatiotemporal population dynamics of the banana rind thrips, *Elixothrips brevisetis* (Bagnall) (Thysanoptera: Thripidae). *Journal of Applied Entomology* 139 (7): 510-518. https://doi.org/10.1111/jen.12190

[ACL5] **Carval D.**, Perrin B., Duyck P.F. & Tixier P. 2015. Local and neighboring patch conditions alter sex-specific movement in banana weevils. *Ecology and Evolution* 5 (23): 5735-5743. https://doi.org/10.1002/ece3.1818

[ACL4] Dassou A.G., **Carval D.**, Depigny S., Fansi G. & Tixier P. 2015. Ant abundance and *Cosmopolites sordidus* damage in plantain fields as affected by intercropping. *Biological Control* 81: 51-57. https://doi.org/10.1016/j.biocontrol.2014.11.008

[ACL3] Duyck P.F., Dortel E., Vinatier F., Gaujoux E., **Carval D.** & Tixier P. 2012. Effect of environment and fallow period on Cosmopolites sordidus population dynamics at the landscape scale. *Bulletin of Entomological Research* 102 (5): 583-588. https://doi.org/10.1017/S0007485312000089

[ACL2] **Carval D.** & Ferrière R. 2010 A unified model for the coevolution of resistance, tolerance, and virulence. *Evolution* 64 (10), 2988-3009. https://doi.org/10.1111/j.1558-5646.2010.01035.x

[ACL1] Lizé A., **Carval D.**, Cortesero A.M., Fournet S. & Poinsot D. 2006. Kin discrimination and altruism in the larvae of a solitary insect. *Proceedings of the Royal Society B: Biological Sciences* 273 (1599): 2381-2386. https://doi.org/10.1098/rspb.2006.3598

Article issu de communication à congrès international

[CP1] Tresson, P., Tixier, P., Puech, W., **Carval, D.** 2019. Insect interaction analysis based on object detection and CNN. IEEE 21st International Workshop on Multimedia Signal Processing, 8901798.

Communication à congrès international

[CI11] Tresson, P., Tixier, P., Puech, W., **Carval, D.** 2019. Insect interaction analysis based on object detection and CNN. IEEE 21st International Workshop on Multimedia Signal Processing, Kuala Lumpur, Malaysia, 27-29 September.

[CI10] Coulis M., Achard R., **Carval D.** 2018. Effect of mulch physical properties on soil invertebrate communities. Sfécologie 2018 : International Conference on Ecological Sciences, Rennes, France, 22-25 Octobre 2018.

[CI9] Poeydebat C., **Carval D.**, De Lapeyre de Bellaire L., Tixier P. 2016. Effect of plant diversity on above and below ground food webs, perspectives to enhance pest regulations in agroecosystems. Sfécologie 2016 : International Conference on Ecological Sciences, Marseille, France, 24-28 Octobre 2016.

[CI8] Poeydebat C., **Carval D.**, De Lapeyre de Bellaire L., Tixier P. 2016. Disentangling the impact of plant diversity on the regulation of multiple pests in banana agroecosystems. International Symposium on Banana: ISHS-ProMusa Symposium on Agroecological Approaches to Promote Innovative Banana Production Systems. Montpellier, France, 10-14 Octobre 2016.

[CI7] **D. Carval,** R. Resmond, R. Achard & P. Tixier. 2016. Cover cropping enhances banana weevil regulation by affecting biological control agents. International Symposium on Banana: ISHS-ProMusa Symposium on Agroecological Approaches to Promote Innovative Banana Production Systems. Montpellier, France, 10-14 Octobre 2016.

[CI6] **D. Carval,** R. Resmond, R. Achard & P. Tixier. 2016. Cover cropping reduces the abundance of the banana weevil Cosmopolites sordidus but does not reduce its damage to the banana plants. ecoSummit – *Ecological Sustainability*, Montpellier, France, 29 August-1 September 2016.

[CI5] **Carval D.**, De Lapeyre de Bellaire L., Tixier P. 2013. La modelización como apoyo de SdC sin fungicidas. Séminaire international sur les cercosporioses et la production de banane durable, Guadeloupe, France, 25-27 juin 2013.

[CI4] **Carval D.**, De Lapeyre de Bellaire L., Tixier P. 2013. La modelización como apoyo de SdC sin fungicidas. Seminario internacional sobre el manejo de la Sigatoka negra en el Caribe, La Habana, Cuba, 19-20 marzo 2013.

[CI3] Ferrière R. & **Carval D.** 2008. Six coevolutionary transitions in the ecological landscape of competition, antagonism, and mutualism. 93rd ESA Annual Meeting, Milwaukke, Wisconsin, USA.

[CI2] **Carval D.**, Ferrière R. and Legendre S. 2007. Evolution of the switch threshold from infectious to reproductive forms in intracellular parasitic bacteria: an individual based simulation model. 3rd Meeting of Ecology and Behaviour, Montpellier, France.

[CI1] Lizé A., **Carval D.**, Fournet S., Cortesero A.M. and Poinsot D. 2005. Kin recognition in parasitoid larvae of the coleopteran *Aleochara bilineata* (Staphylinidae). 9th European workshop on insect parasitoids "community ecology", Cardiff, Great Britain.

Communication à congrès national

[CN11] Tresson, P., Tixier, P., Puech, W., **Carval, D.** 2021. Caractérisation des interactions écologiques autour du charançon du bananier. 42èmes Journées des Entomophagistes, Rennes, France.

[CN10] Collard B., Tixier P., **Carval D.**, Lavigne C. & Delattre T. 2018. Effet d'habitats hétérogènes sur le comportement de prospection d'un arthropode prédateur généraliste : analyse des déplacements nocturnes en microcosme expérimental du dermaptère *Euborellia caraibea* de la Martinique. Colloque SFECA, Rennes, France, 19-21 juin 2018.

[CN9] Collard B., Delattre, T., **Carval D.** Lavigne C. & Tixier P. 2017. La parcelle comme un paysage pour la prospection des ennemis naturels : modélisation de l'effet de l'organisation spatiale intra-parcellaire sur la lutte biologique par conservation. Colloque réseaux PAYOTE, Paris, France, 4-5 octobre 2017.

[CN8] **Carval D.** & Grechi I. 2013 Modélisation pour une gestion durable de la santé des cultures : Activités de recherche au CIRAD. Séminaire Réseau PIC INRA-CIRAD, Paris, France, 4-6 Février 2013.

[CN7] **Carval D.**, De Lapeyre L.., Tixier P. Etudes spatiales des bioagresseurs des cultures bananières. Ecole chercheur M3D d'Oléron, France, 7-11 mai 2012.

[CN6] **Carval D.**, Tixier P. & Duyck P.F. 2011. "Cosmodrome": an experimental design to study movements and behavior of the banana weevil, *Cosmopolites sordidus*, using RFID. Workshop "Towards a Multi-Scale approach for Improving Pest Management", Montpellier, France, October 4-5 2011.

[CN5] Duyck P.F, Tixier P., Ryckewaert P., **Carval D.**, Ripoche A., Djigal D. & Mollot G. 2011. Étude des relations entre réseaux trophiques et régulation des bioagresseurs. Séminaire "Agroécologie des systèmes multi-espèces", Le lamentin, Martinique, 16-17 Juin 2011.

[CN4] **Carval D.** and Legendre S. 2007. Individual based model of within-host parasites. Centre de Mathématiques Appliquées, Centre de Mathématiques, Ecole Polytechnique, Palaiseau, France.

[CN3] Lizé A., **Carval D.**, Fournet S., Poinsot D. and Cortesero A.M. 2005. Reconnaissance de parentèle chez les larves du coléoptère *Aleochara bilineata* (Staphylinidae). 13èmes Journées des Entomophagistes, Gif-sur-Yvette, France.

[CN2] Lizé A., Cortesero A.M., **Carval D.**, Fournet S. and Poinsot D. 2005. Les larves du parasitoïde *Aleochara bilineata* ont l'esprit de famille ! 2ème réunion du GDR Ecologie Chimique, Tours, France.

[CN1] **Carval D.**, Guitton J.S., Fouchet D., Pontier D. 2010. Analyse spatiale de l'épizootie du syndrome hémorragique du lièvre européen (EBHS) en 2004. Réunion nationale annuelle CNERA "Lièvre". Le Bouchet, France.

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[PO6] Vilchez Mendoza S. J., Bagny-Beilhe L., Bommel P., Cilas C., Ronin A. & **Carval D.** 2021. Detection and counting of coffee berry borer (*Hypothenemus hampei*) using computer vision algorithm. Conference of Association for the Science and Information on Coffee (ASIC 2021), Montpellier, France, 28 Juin-1er Juillet 2021.

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[PO1] **Carval D.**, Ferrière R. & Legendre S. 2005. From parasitism to symbiosis: how host life cycle influences the joint evolution of interaction and transmission. 10th Congress of the European Society for Evolutionary Biology, Krakow, Poland. 2005

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[CO2] Tixier P., **Carval D.**, Kamenova S., Martin J.F., Vinatier F. & Rusch A.. 2019. Les réseaux d'interactions dans les paysages agricoles. In : Paysage, biodiversité fonctionnelle et santé des plantes. Petit Sandrine (ed.), Lavigne Claire (ed.). Versailles : Ed. Quae-Educagri, 131-144. (Sciences en partage) ISBN 978-2-7592-3013-6

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English version : http://www.quae.com/fr/r5192-living-territories-to-transform-the-world.html

Version française : http://www.quae.com/fr/r5066-des-territoires-vivants-pour-transformer-le-monde.html

Data papers, datasets & codes

Codes et données pour [ACL16] :

https://github.com/PTres son/Corigan/tree/v1.0 https://zenodo.org/recor d/3357305 https://doi.org/10.5281/zenodo.3357305 https://doi.org/10.5061/dryad.t03b7b8

Poeydebat C., Tixier P., De Lapeyre de Bellaire L. & **Carval D.** 2017. Dataset on the regulation of banana weevil abundance and corm damage associated with plant richness and the ground-dwelling arthropods' food web. *Data in Brief*, 15: 208-212. https://doi.org/10.1016/j.dib.2017.09.003

Carval D., Resmond R., Achard R. & Tixier P. 2016. Data on the abundance of the banana weevil *Cosmopolites sordidus* and of the earwig *Euborellia caraibea* in bare oil and cover crop plots. *Data in Brief*, 7: 1565-1569. https://doi.org/10.1016/j.dib.2016.04.056

Gbèblonoudo A.D., **Carval D.**, Depigny S., Fansi G. & Tixier P. 2016. Dataset on the abundance of ants and *Cosmopolites sordidus* damage in plantain fields with intercropped plants. *Data in Brief*, 9: 17-23. https://doi.org/10.1016/j.dib.2016.08.027

Données pour [ACL5] :
http://knb.ecoinformatics.org/knb/metacat?action=read&qformat=knb&docid=knb.341.1
http://knb.ecoinformatics.org/knb/metacat?action=read&qformat=knb&docid=knb.345.1

Doctorants

Thibault Nève De Mevergnies (Janvier 2022 - Décembre 2024). Pest0p: Biodiversité et amélioration de la régulation naturelle des arthropodes ravageurs - Cas des agroécosystèmes horticoles diversifiés à La Réunion
Directrice de thèse : Pr. Marie-Stéphane Tixier (L'Institut Agro)
Co-encadrants : Anaïs Chailleux (UR Hortsys, CIRAD), Joël Huat (UR Hortsys, CIRAD), Julien Haran (UMR CBGP, CIRAD)
École Doctorale GAIA (ED 584) – Biodiversité, Agriculture, Alimentation, Environnement, Terre, Eau

Paul Tresson (Octobre 2018 - Décembre 2021). Quantification du rôle des prédateurs généralistes dans la régulation du charançon du bananier grâce à l'analyse d'images prises *in situ*.
Directeurs de thèse : Dr. Philippe Tixier (UR GECO, CIRAD) & Pr. William Puech (ICAR, LIRMM, CNRS-UM2)
École Doctorale GAIA (ED 584) – Biodiversité, Agriculture, Alimentation, Environnement, Terre, Eau
Thèse de l'Institut de Convergence #Digitag
3 publications ([ACL20], [ACL19], [ACL16]) et 1 papier de conférence ([CP1])
Position actuelle : Chercheur deep learning et agroécologie (CDI de projet), UMR AMAP, CIRAD, Montpellier

Blanche Collard (Décembre 2015 - Mars 2019). Effet de l'organisation spatiale intra-parcellaire des habitats sur le contrôle biologique par conservation : étude et modélisation des déplacements de dermaptères dans les bananeraies.
Directeurs de thèse : Dr. Philippe Tixier (UR GECO, CIRAD) & Dr. Claire Lavigne (PSH, INRAE)
Co-encadrant : Dr. Thomas Delattre (PSH, INRAE)
École Doctorale Agrosciences et Science (ED 536)
1 publications ([ACL15])
Dernière position : Post-doctorat Analyse des variations interannuelles des ventes de produits phytosanitaires et de l'indicateur NODU basée sur la base de données nationale française BNV-d, mai 2019 - décembre 2020, INRAE, THIVERVAL-GRIGNON

Charlotte Poeydebat (Janvier 2014 - Décembre 2016). Régulations écologiques d'un complexe de bioagresseurs du bananier dans un gradient de complexité végétale des agroécosystèmes.
Directeur de thèse : Dr. Philippe Tixier (UR GECO, CIRAD)
Co-encadrant : Dr. Luc de Lapeyre de Bellaire (UR GECO, CIRAD)
École Doctorale GAIA (ED 584) – Biodiversité, Agriculture, Alimentation, Environnement, Terre, Eau
4 publications ([ACL14], [ACL12], [ACL11] [ACL7])
Position actuelle : Enseignante-chercheure (CDD) Bordeaux Sciences Agro

Master 2

Simon Carlier (Février-Août 2022). Qualité sensorielle de nouvelles variétés de bananes à La Réunion.
Co-encadrant : Christian Soria (UMR QUALISUD, CIRAD)

Mathilde Cyprien (Mars-Septembre 2022) Diagnostic participatif de la filière Banane à la Réunion, caractérisation des pratiques post-récolte des acteurs de la production et de la commercialisation.
Co-encadrant : Claire Cerdan (UMR INNOVATION, CIRAD)

Sacha Roudine (Janvier-Juin 2018). Regulatory service of the coffee berry borer (*Hypothenemus hampei*) in complex agroforestry systems in Nicaragua.
Master 2 of Écologie Végétale & Environnement, Université de Toulouse 3 Paul Sabatier
Co-encadrant : Dr. Leïla Bagny Beilhe (UMR PHIM, CIRAD)
1 publication ([ACL18])
Position actuelle : Thèse en préparation. Impact des plantes de services sur le contrôle des ravageurs des grandes cultures céréalières (Direction de thèse : Pr. Joan Van Baaren et Dr. Cécile Le Lann)

Camille Montégu (Février-Juillet 2015). La diversité végétale présente dans les agroécosystèmes influence-t-elle les prédateurs généralistes ? Ces derniers peuvent-ils réguler la population de *Cosmopolites sordidus* (Gemar, 1824), le charançon du bananier ?
M2 Expertise Ecologique et Gestion de la Biodiversité, Université Aix-Marseille.
Position actuelle : Chargée d'étude Pôle Protection de la Nature, LPO Occitanie, Villeveyrac

Cotté Violaine (Mars-Août 2013). Analyse statistique des interactions des fourmis et modélisation multi-agent de l'agrosystème bananier.
Master 2 Bioinformatique, Université de Nantes.
1 publication ([ACL6])
Position actuelle : Responsable qualité produits chez Logipren, Saint-Pierre, Réunion

Master 1 / Bac +4

Chloé Tellier (Mars-Juillet 2020). Développement d'un modèle multi-agents des agrosystèmes.
Position actuelle : Ingénieur (CDD), modélisation des stocks de sole dans le golfe de Gascogne, Ifremer, Nantes

Martin Notaro (Septembre 2012-Janvier 2013). Suivi démographique, étude du cycle de vie et barcoding du thrips *Elixothrips brevisetis*, responsable de la rouille argentée sur bananier.
1 publication ([ACL6])
Position actuelle : Chercheur, Agronome, systèmes agroforestiers tropicaux (CDI), UMR ABSys, CIRAD, Abidjan, Côte d'Ivoire

L3

Constant Leroy (Septembre-Décembre 2021). Le freckle, bioagresseur majeur de la banane à la Réunion : Etude des facteurs et des pratiques influençant sa dynamique
Position actuelle : 3e année Bachelier Agronomie des régions chaudes (L3), HEPH-CONDORCET, Ath, Belgique

Kevin Plessis-Fraissard (Juillet-Août 2018). Mise au point d'une méthode d'identification et de détection d'organismes vivants à travers des méthodes de d'apprentissage automatique (deep learning, CNN, ...).
Dernier diplôme : Ingénieur AgroParisTech - Spécialisé en data science, machine learning & deep learning, 2020, Massy.

Cathleen Mirande-Ney (Juillet 2013). Le Barcoding : vers une régulation du *Cosmopolites sordidus* plus écologique.
Position actuelle : Post-Doctorante, Laboratoire GlycoMEV UR 4358, Université de Rouen

DUT

Marguerite Boyer (Avril-Juillet 2022). Qualité sensorielle de nouvelles variétés de bananes à La Réunion.
Co-encadrant : Mathilde Hoarau (UMR INNOVATION, CIRAD)

Volontariat Service Civique

Paulin Lenclu Mars 2022-Férvrier 2023. Evaluation variétale pré- et post-récolte au sein de la filière de la banane

Antoine Wyvekens Mars 2020-Septembre 2021. Evaluation variétale de bananiers à la Réunion.
Position actuelle : Ingénieur en protection des plantes pour améliorer la lutte contre la cercosporiose noire du bananier (VIE), GECO, CIRAD, Abidjan, Côte d'Ivoire

Amélie Février (VSC) Avril 2013-Décembre 2013. Suivi de populations des communautés de fourmis, des dermaptères et du charançon du bananier à l'échelle parcellaire.
Position actuelle : Ingénieure en expérimentation agronomique, ERCANE, Saint-Denis, La Réunion

Rémi Resmond (VSC) Février 2012-Janvier 2013. Etude de l'association d'une plante de couverture en bananeraie.
2 publications ([ACL6], [ACL21])
Position actuelle : Ingénieur expérimentation en agroécologie, EGI, IGEPP, Le Rheu

Benjamin Perrin (VSC). Etude du mouvement chez le charançon du bananier *Cosmopolites sordidus*.
1 publication ([ACL5])
Position actuelle : Ingénieur d'étude expérimentation et production végétales, UE Maraîchage, INRAE, Perpignan

Mon parcours

Si l'on doit remonter au tout début, je ne vous raconterai pas que depuis tout petit j'ai eu la vocation d'être un chercheur en biologie. Bien que grand amateur des documentaires naturalistes aux voix des grandes stars françaises de l'époque, je n'appréciais guère la biologie que nous apprenions au collège et au lycée, mise à part les maigres parties sur l'évolution des hominidés et sur les dinosaures. Mais force est de constater que le choix de s'inscrire en biologie à l'université m'a paru naturel. Mon premier contact avec la recherche me vient d'un stage effectué sur la mégafaune benthique du golfe de Gascogne après ma première année à l'université de Brest Occidentale. J'ai réalisé ce stage au LEMAR (Laboratoire des sciences de l'environnement marin) sous la responsabilité de François Le Loc'h. C'est là que mon intérêt pour la recherche en écologie a vraiment débuté.

Mais le premier stage qui m'a amené à travailler dans les recherches liées à l'agriculture était au laboratoire d'Ecobiologie des Insectes Parasitoïdes (Université de Rennes 1). Cette équipe de recherche travaillait sur la mouche du chou, *Delia radicum*, et sur son interaction avec un parasitoïde, le staphylin *Aleochara bilineata*. Mon maître de stage, Denis Poinsot, nous motivait à réfléchir et à proposer une question de recherche que nous pourrions prendre en main. J'ai proposé de travailler sur l'effet de la parentèle sur l'hyperparasitisme, en proposant à des larves de staphylins le choix d'hyperparasiter une pupe de mouche déjà parasitée par une larve non-apparentée et une pupe déjà parasitée par une larve apparentée. Les résultats étaient prometteurs et Anne Lizé, dans une partie de sa thèse, mena par la suite des expériences supplémentaires sur ce sujet qui démontrèrent, pour la première fois chez un insecte parasitoïde solitaire, l'existence d'une capacité de discrimination de parentèle (Lizé et al., 2006)[ACL1]. Je retenais alors de ce stage que l'écologie de l'évolution c'est vraiment cool !

Par la suite, mon parcours s'est plus orienté vers la composante théorique du domaine de l'écologie et de l'évolution. C'est ainsi, que je finis par travailler sur une thèse en écologie sur la coévolution de systèmes hôte-parasite. Pendant cette thèse, j'ai notamment travaillé sur la coévolution des défenses de l'hôte (résistance et tolérance) et de la virulence du parasite en développant des modèles d'éco-évolution mathématique de dynamique adaptative (Carval and Ferriere, 2010)[ACL2].

C'est en 2011 que j'intègre le Cirad, au sein de l'unité Geco, pour mener des recherches sur les bioagresseurs du bananier.

Je suis alors affecté en Martinique où je découvre le climat tropical et les systèmes de cultures bananiers. Dans la prochaine section, je vais revenir en détail sur les activités réalisées sur la régulation des bioagresseurs du bananier en Martinique, au Costa Rica et à la Réunion, où je suis actuellement en poste. Je ferai un focus sur la régulation du charançon noir du bananier, *Cosmopolites sordidus*, et le contrôle biologique par conservation.

Mes recherches passées

Intensification écologique : ce qui a été fait, ce qu'il faudrait faire

L'intensification écologique se base sur l'hypothèse que dans les systèmes "conventionnels" avec une utilisation d'intrants importante les services écosystémiques fournis sont sous-optimaux (Bommarco et al., 2013; Doré et al., 2011; Kremen et al., 2002; Pretty et al., 2011; Tittonell, 2014) et que la gestion de la biodiversité maintenue ou introduite dans les agrosystèmes permettrait de compléter, voire remplacer, l'usage d'intrants tout en maintenant ou en améliorant la productivité et en réduisant le coût environnemental (Bommarco et al., 2013).

Cette intensification écologique peut se faire par de nombreuses manières. L'intensification de la biodiversité végétale dans le temps et ou l'espace au travers de rotations culturales (Rusch et al., 2013), de plantes de couverture (Lavigne et al., 2010), de bandes fleuries (Serée et al., 2022), de plantes pièges (Shelton and Badenes-Perez, 2006), de l'introduction d'arbres (Ivezić et al., 2021), de la mise en place de systèmes agroforestiers (Poeydebat et al., 2018, 2017a, 2017b) [ACL11, 12, 14], de cultures associées (Dassou et al., 2019) [ACL17], ou encore de haies. (Garratt et al., 2017). Elle peut aussi se faire au travers des pratiques plus respectueuses de l'environnement comme par l'absence de travail du sol ou par l'utilisation de fertilisants organiques (Kleijn et al., 2019). Un grand nombre d'études se sont intéressées à ces systèmes écologiquement intensifiés et, plus particulièrement, à cette relation entre biodiversité et auxiliaires que ce soit à l'échelle parcellaire ou du paysage. Ces études montrent généralement les effets positifs de la biodiversité sur un ou plusieurs services écosystémiques (voir par exemple Dainese et al., 2019; Dassou and Tixier, 2016; Letourneau et al., 2011; Poveda et al., 2008).

C'est sur cette thématique d'intensification écologique et de service de régulation de ravageurs par le contrôle biologique par conservation que j'ai mené une part de mes activités et que je présente ci-après.

Le charançon du bananier

Le bananier durant son existence doit faire face à tout un cortège de bioagresseurs. Parmi ceux-ci, le charançon noir du bananier *Cosmopolites sordidus* est le ravageur principal. La femelle pond un œuf au niveau du bulbe ou à la base du pseudotronc du bananier. La larve se nourrit ensuite de la plante en creusant des galeries à l'aide de ses puissantes mandibules avant de nymphoser (Figure 1). Une de mes premières missions au Cirad était de continuer les études sur ce coléoptère, robuste et discret, aux mœurs nocturnes.

Figure 1. De gauche à droite : *Cosmopolites sordidus*, galeries de larves de charançon dans un bulbe de bananier, nymphe et bananier versé en raison des nombreux dégâts liés aux charançons. (Crédit Photos : P. Tresson, CIRAD)

Mais que fait-il de ses nuits ?

Des études sur le mouvement et la dispersion avaient été réalisées au sein de l'UR GECO avant mon arrivée (Vinatier et al., 2010, 2009). Ces études ont utilisé des méthodes RFID (Radio Frequency IDentification) pour appréhender et modéliser les déplacements à l'échelle parcellaire en réponse à la répartition spatiale des bananiers. Afin de mieux comprendre les facteurs influençant le mouvement du charançon, j'ai réalisé une expérimentation en laboratoire. Le mouvement, défini comme un changement dans la localisation spatial d'un individu (Schellhorn et al., 2014), est nécessaire pour la survie, la reproduction et la dispersion de nombreux organismes. Les bananeraies de Martinique étant un environnement plutôt homogène dans le temps et l'espace, je me suis intéressé aux possibles effets de facteurs propres aux charançons : le sexe, le sex-ratio et la densité de conspécifiques (Carval et al., 2015) [ACL5]. Globalement, les résultats indiquent que plus il y a d'individus conspécifiques où il se situe et moins il y a d'individus conspécifiques dans le voisinage, moins il bouge du patch où il se situe, et *vice versa*. Plus il y a de monde partout, plus ça bouge. Ceci suggère que les charançons perçoivent la densité de conspécifiques localement comme un proxy de la compétition interspécifique et celle du voisinage comme un proxy de la qualité de l'environnement voisin. Le charançon répond aussi au sex-ratio : si le sex-ratio est biaisé en faveur des femelles, la probabilité que celles-ci partent pour le patch voisin est plus grande. On peut en conclure que les femelles perçoivent la densité locale de femelles comme un proxy pour la compétition pour l'oviposition, et donc la compétition entre leurs progénitures. De même, les mâles ont tendance à partir pour le patch voisin lorsque le sex-ratio est biaisé en faveur de mâles. Ceci reflète la compétition entre mâles pour l'accouplement.

C'est joli tout ça, mais qu'est-ce que ça apporte à la gestion du bioagresseur ? Pour un contrôle du charançon par des prédateurs, il faut déjà qu'il y ait une rencontre entre eux. Le charançon est un animal cryptique et nocturne. Il s'enterre facilement, se cache dans des anfractuosités ou sous des résidus, et ne se déplace pas du tout le jour. Le type de prédateur va importer, et on y reviendra un peu plus tard en détail. Par exemple, si le prédateur est diurne, il faut qu'il prospecte activement le jour en fouillant le sol. Une poule par exemple. Si le prédateur est nocturne, il peut profiter des déplacements du charançons, alors susceptible, pour le manger. Or, on a vu que le charançon, en environnement homogène, ne se déplaçait que très peu lorsque la densité de charançons est faible et que sa propension à se déplacer augmentait avec la densité d'individus. Ainsi, une régulation par des prédateurs nocturnes en début d'infestation devrait être faible. Celle-ci interviendrait plus lorsque la population est déjà bien établie. On y reviendra un peu plus tard. Mais peut-être rendre l'environnement hétérogène aiderait… On y reviendra là aussi un peu plus tard…

Par ailleurs, il faut que le timing soit le bon : selon cette expérience en conditions contrôlées et d'autres données issues du terrain (non publiées), le charançon est actif et se déplace surtout dans les premières heures de la nuit (Figure 2). Il faut donc que le prédateur ait un cycle d'activité compatible à celui du charançon. On y reviendra également, soyons patients…

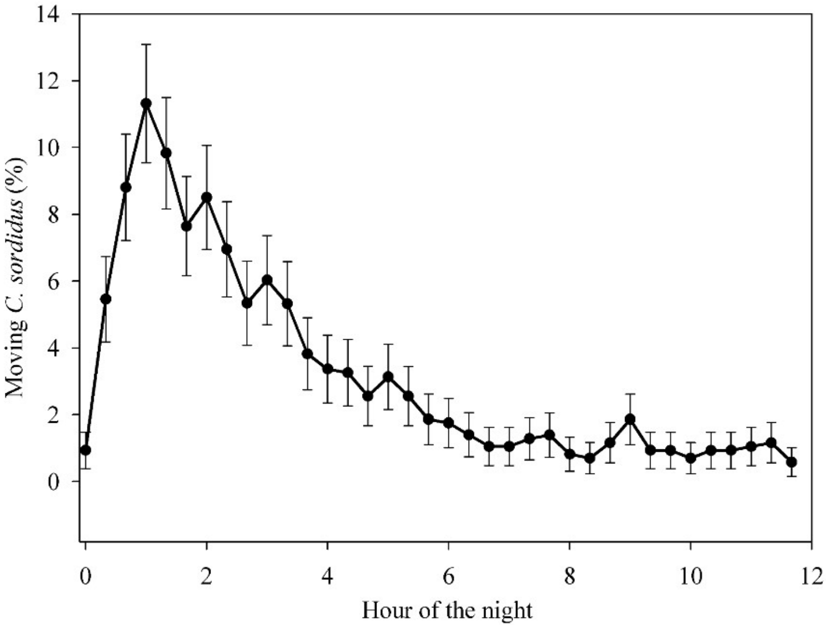

Figure 2. Rythme d'activité du charançon noir du bananier *Cosmopolites sordidus* (Carval et al., 2015) [ACL5].

Devine qui vient dîner ?

L'unité GECO s'est intéressée avant mon arrivée à identifier les ennemis naturels du charançon, notamment en Martinique. Plus particulièrement, le contenu stomacal de différents arthropodes a été analysé par metabarcoding (Mollot et al., 2014). Parmi les espèces chez lesquelles de l'ADN de charançon a été retrouvé, on trouvait le dermaptère *Euborellia caraibea*. S'agit-il d'une prédation primaire ou secondaire ? De nécrophagie ? De quel stade de vie ? Il faut suivre la piste pour essayer d'en savoir plus et notamment voir si *E. caraibea* a un effet sur la régulation du charançon. J'ai mis en place une expérimentation sur le terrain visant à voir l'effet d'une plante de couverture, *Paspalum notatum*, sur la régulation des populations de charançon et d'autres arthropodes, dont notre cher dermaptère *E. caraibea*. Premier constat : on observe plus de charançons dans les parcelles au sol nu que dans les parcelles enherbées (Carval et al., 2016) [ACL9]. C'est le résultat escompté… Sous l'hypothèse que notre dermaptère est responsable de cela et donc présent en plus grand nombre dans les parcelles enherbées… Perdu ! (Figure 4) C'est exactement l'inverse. Ce dermaptère aurait finalement qu'un rôle anecdotique dans la prédation du charançon ?

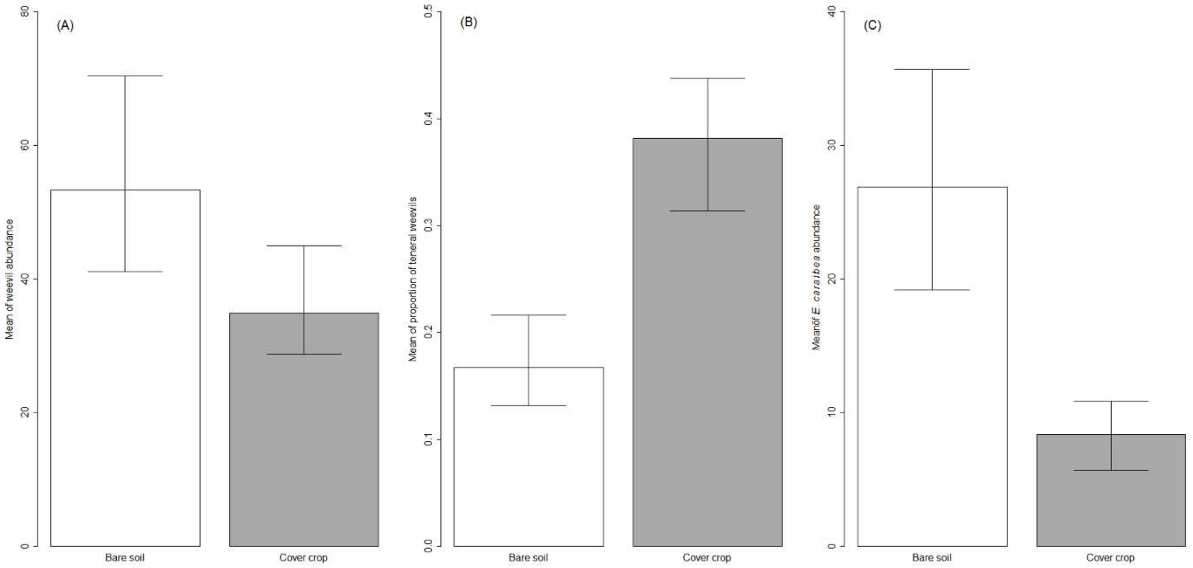

Figure 3. A : Abondance de charançons. B : Proportion de charançons au stade ténéral. C : Abondance de *E. caraibea* (Carval et al., 2016) [ACL9].

Revenons à notre question de déterminer le stade cible de ce prédateur. Un dermaptère de cette taille n'est pas en mesure de s'attaquer à un charançon adulte vivant. Mais il est peut-être capable de s'attaquer aux autres stades, comme l'œuf ou les stades larvaires. L'œuf peut être accessible un certain moment après la ponte, avant d'être recouvert par le latex de la plante. Les larves, elles, creusent dans le bulbe en s'en nourrissant et sont donc difficilement atteignables dans un bulbe encore vivant. Quoiqu'il en soit, si le dermaptère arrivait à se nourrir de l'un ou de l'autre de ces stades, ne devrait-on pas observer moins de charançons adultes quand il y a plus de dermaptères ? Les agrosystèmes, qui plus est tropicaux, sont complexes même lorsqu'ils sont simplifiés à outrance par l'homme comme dans les bananeraies. Autrement dit, il y a beaucoup de facteurs que je n'ai pas observé dans cette expérimentation et qui pourraient expliquer ce résultat. Mais revenons à nos charançons noirs du bananier. Cet insecte est un coléoptère holométabole et une fois la nymphose terminée, un jeune et magnifique charançon noir va émerger du bananier. Sauf qu'il est rouge … (Figure 5). Cet adulte au stade ténéral n'a pas un exosquelette complètement fini : celui-ci doit se durcir et il prendra au fur et à mesure sa couleur noire définitive, dans les 30 jours après émergence environ en zone tropicale (Gold et al., 2001). Si l'on compare la proportion de "jeunes" charançons et des plus "vieux", on constate qu'il y a moins de jeunes en proportion dans la parcelle au sol nu, où, rappelez-vous, il y a plus de dermaptères. En outre, il y a moins de dégâts au niveau du bulbe. Les dermaptères auraient finalement bien un impact positif sur la régulation du charançon et de ses dégâts en s'attaquant aux stades d'œuf et/ou larvaires (Figure 5). La plus forte régulation globale des charançons observée dans les parcelles enherbées serait dû à une ou plusieurs autres causes.

Figure 4. Jeune adulte *C. sordidus* au stade ténéral. Son tégument est encore mou et de couleur rougeâtre. (Crédit Photo : Alexis Delaplace, GECO, CIRAD)

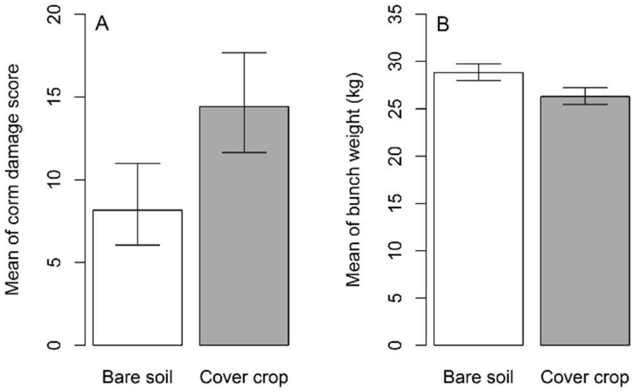

Figure 5. A : Dégâts causés par le charançon (% de surface du bulbe). B : Poids du régime.

L'enfant modèle : le dermaptère

Lors de sa thèse, Blanche Collard (2019) a modélisé le déplacement d'un prédateur de type dermaptère dans une bananeraie. L'objectif de ce modèle individu-centré était d'étudier l'influence des habitats à une échelle intra-parcellaire fine sur le comportement de fourragement d'un prédateur. Je ne vais pas reprendre ici les détails techniques du modèle, pour cela je vous invite à lire son article (Collard et al., 2018) [ACL15], mais uniquement en donner une description simplifiée et faire le focus sur une partie des résultats de cette étude, en lien avec ce que j'ai écrit dans les paragraphes précédents. Le modèle considérait 3 types d'habitats : un habitat défavorable à notre dermaptère digital - par exemple un sol nu ; un habitat alternatif lui étant favorable - par exemple une plante de couverture ; un habitat cultivé lui aussi favorable à ce prédateur- allez ! prenons tout à fait par hasard l'exemple du bananier… Dans ce paysage intra-parcellaire, Blanche a fait varier différentes métriques au niveau du bananier (nombre d'habitats favorables adjacents, distance au plus proche habitat favorable) et à l'échelle de la parcelle (pourcentage de surface d'habitats favorables, zone de contact moyenne entre habitats favorables et les bananiers, niveau d'agrégation des habitats favorables) (Figure 6). Elle a analysé l'effet de la valeur de ces métriques sur la fréquence et la durée des visites des bananiers par le prédateur. Son modèle a montré que la durée des visites par le prédateur diminuait d'autant plus que le pourcentage d'habitat favorable alternatif était élevé à l'échelle de la parcelle (Figure 7). Rappelez-vous que dans l'essai précédent, je comparais une parcelle au sol nu, c'est-à-dire 0% d'habitat favorable alternatif, à une parcelle enherbée, c'est-à-dire 100% d'habitat favorable alternatif. Rappelez-vous aussi que j'avais plus de dermaptères et une proportion moindre de charançons au stade ténéral dans la parcelle au sol nu. Comme suggéré par le modèle de Collard et al. (2018), l'habitat alternatif aurait créé un effet de dilution divertissant le prédateur de la culture et des ravageurs. Cet effet de dilution expliquerait les résultats observés sur le terrain.

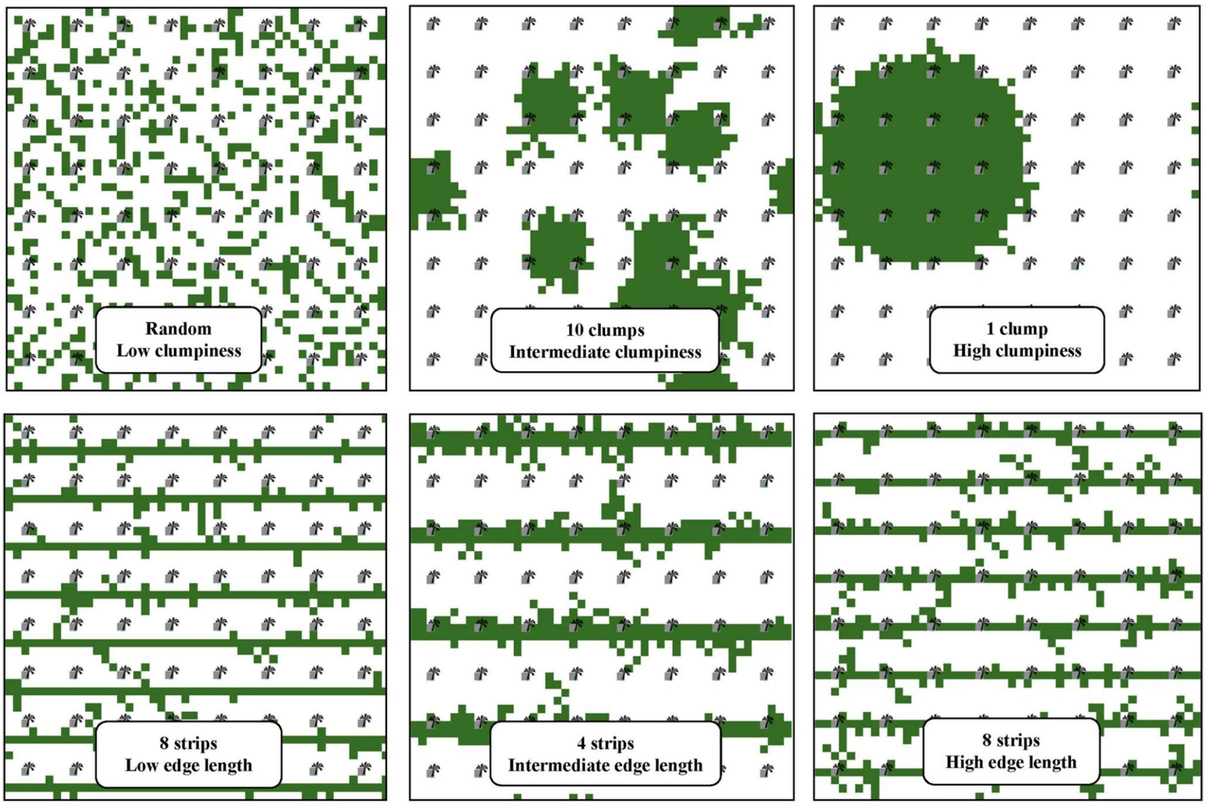

Figure 6. Type de configuration de l'habitat favorable alternatif. Les bananiers sont en noir, l'habitat alternatif en vert et le sol nu en blanc.

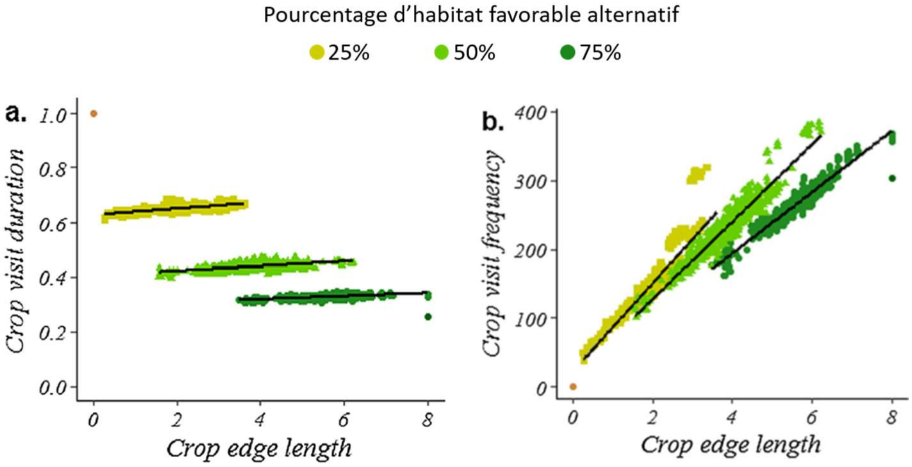

Figure 7. Effet de la longueur de bord sur a : la durée des visites du bananier par le prédateur et b : la fréquence des visites du bananier par le prédateur. La longueur de bord correspond aux nombres de voisins (modèle de type lattice) du bananier constitués d'habitat favorable alternatif.

Quand c'est trop, c'est tropicaux !

Allongeons-nous un moment sur ce tapis vert de plantes de service pour marquer une pause et faire le point à l'ombre d'un bananier. Si nous résumons ce que nous ont appris ces études et leurs résultats. L'hypothèse sous-jacente d'intensification écologique d'une culture de bananier par l'ajout d'une plante de couverture était que les prédateurs généralistes, dont les dermaptères, bénéficieraient directement ou indirectement des habitats alternatifs et en retour accroîtraient le service de régulation du charançon. On a pu voir que la population de charançons était effectivement plus faible dans les parcelles enherbées, dans lesquelles Les dermaptères étaient piégés en moindre nombre. Mais est-ce réellement exact de conclure que cet habitat alternatif ne favorise pas l'abondance du dermaptère ? Le modèle de Blanche Collard nous apprend qu'une couverture importante d'habitat alternatif résultait en une faible durée des visites des bananiers par un prédateur tel qu'un dermaptère, du fait d'un effet dilution. Autrement dit, trop c'est comme pas assez !

Mais le modèle de Blanche nous apporte d'autres éléments intéressants quant à l'organisation spatiale des habitats. Ainsi, il ressort des simulations que la longueur de bord entre les bananiers et l'habitats alternatif, c'est-à-dire la zone de contact entre ces habitats, peut compenser cet effet de dilution en diminuant la durée pour laquelle les prédateurs sont absents au niveau des bananiers (Figure 7). A l'échelle de la parcelle, la configuration qui maximise la longueur de bord entre les bananiers et l'habitat alternatif est celle de parcelles avec des bandes d'habitats alternatifs situées sur les rangs de bananiers. Ainsi, l'agencement spatial de la diversité végétale de la strate herbacée doit être choisi judicieusement pour favoriser un service de régulation.

Et les fourmis dans tout ça ?

Quand on arrive en milieu tropical, il est un genre animal que nul ne peut ignorer : les fourmis. Diversifiées, présentes en abondance, dans les agrosystèmes, dans les forêts, sur les plages, dans votre maison, sur vous… aïe ! Dur de les ignorer. Ne restons pas allongés là plus longtemps. Ces superbes créatures sont partout et en nombre, représentant une part substantielle de la biomasse animal dans les écosystèmes tropicaux (Hölldobler and Wilson, 1990). Mais quel peut-être leur impact dans la régulation des ravageurs, et plus particulièrement dans celle du charançon ?

C'est à cette question que j'ai par la suite cherché des réponses (Carval et al., 2022) [ACL21]. Premièrement, je me suis intéressé à l'identification des espèces présentes dans les agrosystèmes en Martinique. On compte sur cette île une centaine d'espèces différentes (publication en préparation). Dans les parcelles expérimentales évoquées plus haut, j'ai suivi 14 espèces sur plusieurs années en mesurant leur occurrence et leur abondance en utilisant un appât constitué d'un mélange de thon et de miel. D'autres méthodes (*e.g.* pièges à fosses, chasse à vue) auraient permis de suivre d'autres espèces (telles que *Gnamptogenys striatula*, *Ectatomma ruidum* ou *Strumigenys smithii*) mais parmi ces 14 espèces se trouvent les espèces les plus présentes en milieu perturbé tel qu'une bananeraie et 5 espèces présentent un intérêt plus particulier :

- *Pheidole jelskii*, espèce indigène et dominante dont les ouvrières sont, à plusieurs, à même de s'attaquer à un charançon adulte (observation personnelle, pour voir la vidéo c'est ici).
- *Camponotus sexguttatus*, espèce indigène dont le nid est situé dans les pseudotroncs de bananiers. De l'ADN de charançon a été retrouvé dans le contenu stomacal de cette espèce (Mollot et al., 2014).
- *Odontomachus ruginodis*, espèce indigène de grande taille dont une ouvrière peu à elle seule tuer un charançon (observation personnelle)
- *Solenopsis geminata*, espèce indigène, dominante et agressive. De l'ADN de charançon a été retrouvé dans le contenu stomacal de cette espèce (Mollot et al., 2014). Elle compte parmi les espèces les plus invasives au monde.
- *Paratrechina longicornis*, espèce invasive qui chasse en groupe de quelques ouvrières. Elle compte parmi les espèces les plus invasives au monde.

Les analyses de données de ce suivi de 3 ans n'ont révélé aucun lien statistique entre les fourmis et le charançon du bananier, uniquement des relations négatives entre les espèces de fourmis. En outre, la fouille des dépotoirs de *P. jelskii*, espèce écologiquement dominante dans l'essai, à la recherche de fragments de proies, a révélé que cette espèce consomme rarement du charançon, celui-ci représentant 0.5% des carcasses identifiées.

Si cette étude n'exclut pas complètement un rôle potentiel de fourmis dans la régulation du charançon adulte, elles montrent qu'il est probablement très faible. En outre, les dermaptères représentaient 1.5% des carcasses retrouvées, et il se pourrait donc que les fourmis aient par ailleurs un impact négatif au travers de la prédation intraguilde. Enfin, d'après les courbes de populations de charançons observés dans ces parcelles, qui suive une courbe logistique de type K, il semble qu'au moins un facteur puisse stabiliser les populations dans une bananeraie homogène (Figure 8). Mais celui-ci demeure inconnu...

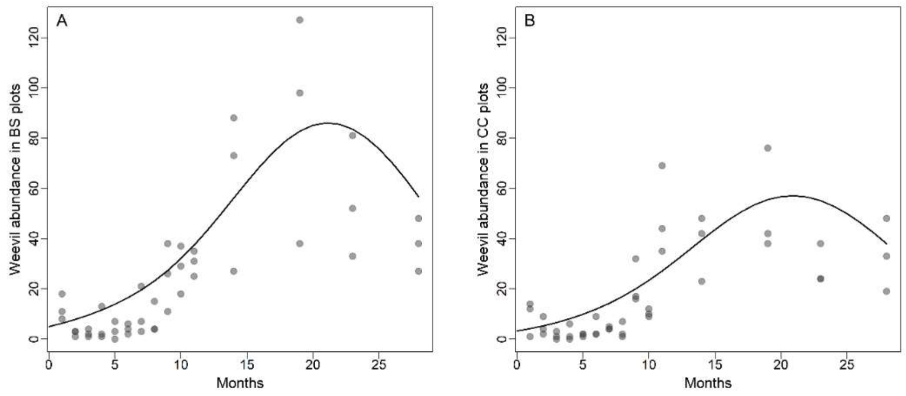

Figure 8. Dynamique de population de charançons dans les parcelles en sol nu (A) et enherbées (B) [ACL21].

Mais que fait la biodiversité ?

Nous avons vu plus haut des études en milieu homogène, c'est à des dires des monocultures de bananiers associée tout au plus à une autre espèce végétale, une plante de couverture.

Dans le cadre du contrôle biologique par conservation, l'hypothèse est que la diversification des cultures permet de réduire l'impact des ravageurs (i) en diluant la ressources, pour les ravageurs spécialisés comme notre ami *C. sordidus* et (ii) en augmentant l'abondance des ennemis naturels et donc les régulations naturelles. Des méta-analyses ont en effet montré qu'une plus grande richesse spécifique des plantes était associée à des effets positifs sur la régulation des ravageurs et/ou des dommages qu'ils causent (Dassou and Tixier, 2016; Letourneau et al., 2011). Mais d'autres études montraient, elles, un effet neutre ou négatif de la richesse spécifique des plantes sur la régulation des ravageurs (Letourneau et al., 2011; Poveda et al., 2008). Une critique de ces études peut être qu'elles se concentraient sur seulement un ou deux groupes trophiques : les ravageurs et leurs ennemis naturels déjà connus ou supposés. Soliveres et al. (2016) considèrent que la prise en compte d'un petit nombre de groupes trophiques menait à sous-estimer les services écosystémiques fournis par des niveaux élevés de richesse spécifique des plantes. Ainsi, dans le cadre de la thèse de Charlotte Poeydebat, nous avons usé d'une approche multitrophique, telle que décrite par Soliveres et al. (2016), pour estimer le rôle de la richesse spécifique des plantes sur la régulation du charançon du bananier et de ses dégâts (Poeydebat et al., 2017a) [ACL11].

Dans un gradient de diversité végétale au sein de parcelles au Costa Rica, allant de la monoculture à l'agroforesterie, nous avons analysé les relations entre la richesse des espèces végétales, l'abondance de cinq groupes trophiques d'arthropodes (détritivores, herbivores, omnivores autres que fourmis, fourmis omnivores et prédateurs) et la régulation de l'abondance et des dégâts de *C. sordidus*. Les effets sur les bananiers ont été mesurés sur 75 phytomètres dans 9 parcelles. Les hypothèses sous-jacentes étaient que i) la richesse en espèces végétales à l'échelle du champ a des effets positifs bottom-up (ascendants) qui augmentent l'abondance des ennemis naturels potentiels et ii) les omnivores autres que fourmis, les fourmis omnivores et les arthropodes prédateurs réduisent l'abondance des charançons du bananier et les dommages aux bulbes.

Nous avons ensuite utilisé des modèles mixtes d'équations structurelles (Lefcheck, 2016) pour analyser ce jeu de données et observer les liens trophiques entre les 5 différents groupes. Les résultats ont montré que la richesse spécifique des strates basses (< 1,5 m de haut) a eu un effet bottom-up positif sur l'abondance des proies herbivores, ce qui en retour augmentait l'abondance des omnivores autres que fourmis et des prédateurs. La couverture de litière a favorisé l'abondance de proies détritivores, qui en retour a favorisé les prédateurs et les fourmis omnivores (Figure 9). Ces deux derniers groupes trophiques étaient quant à eux négativement liés aux dommages causés par les charançons, suggérant que ceux-ci ont probablement consommés les œufs et/ou les larves de charançon (Figure 10)(Poeydebat, 2016).

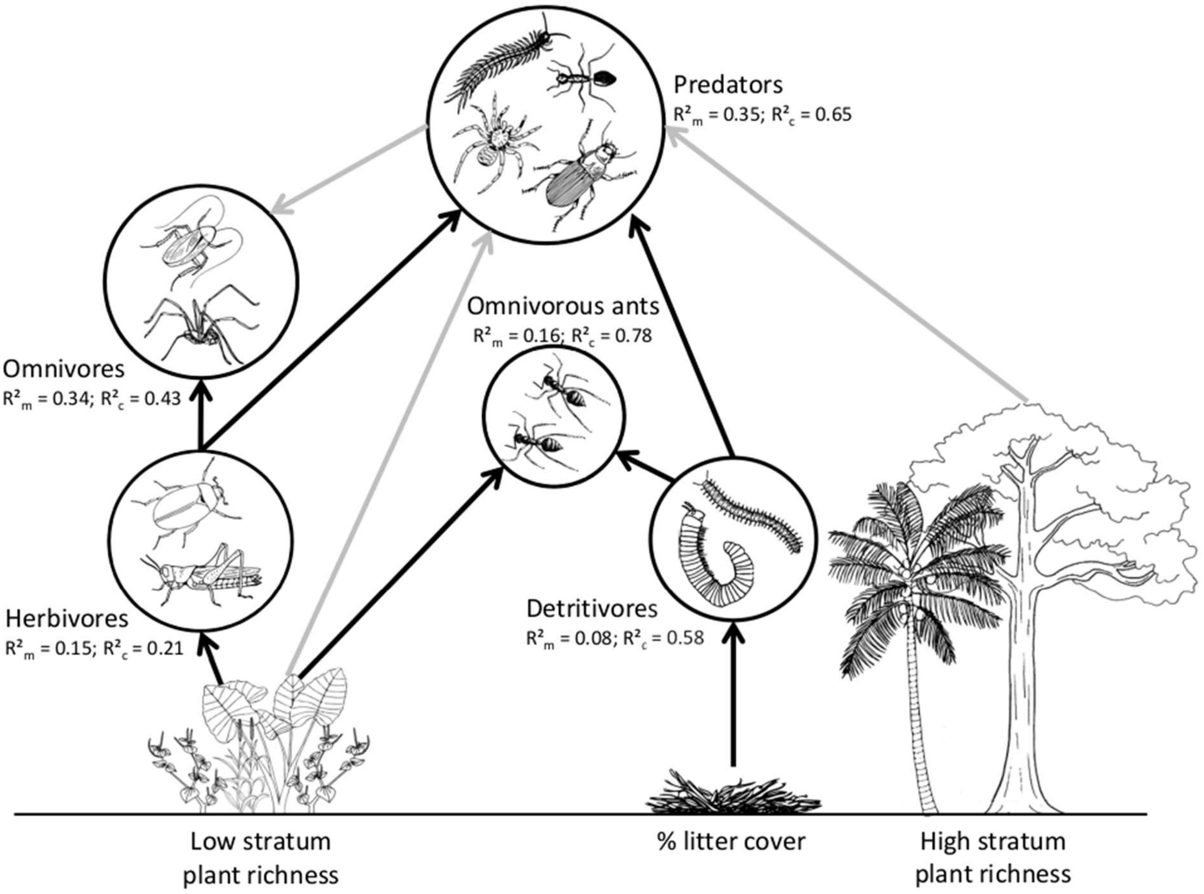

Figure 9. Modèle d'équation structurelle des relations entre les groupes trophiques d'arthropodes et des variables environnementales [ACL11]. Les valeurs marginales (m) et conditionnelles (c) du R² pour chaque variable de réponse sont indiquées.

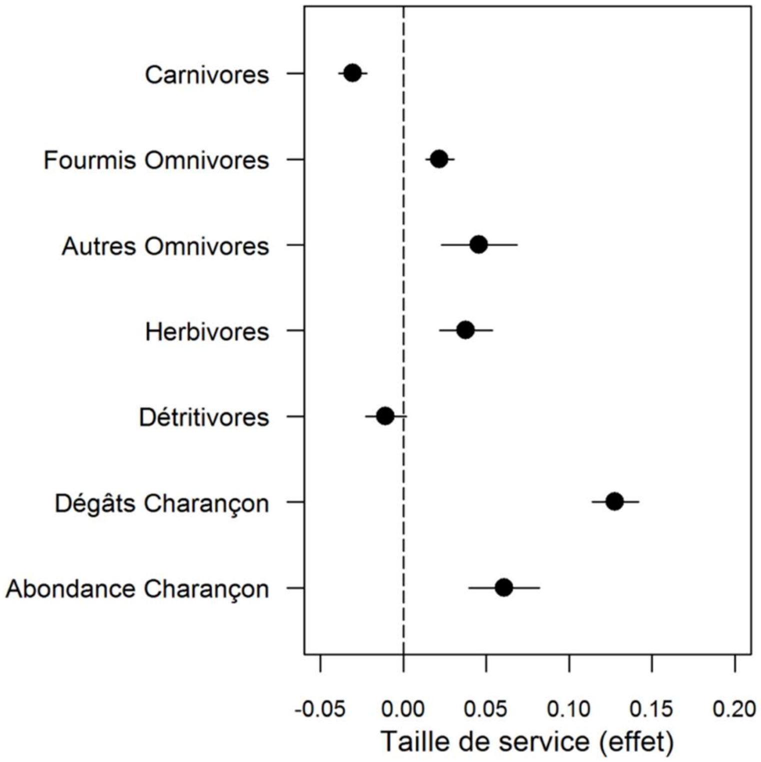

Figure 10. Taille de l'effet de la richesse spécifique totale en plantes sur le service écosystémique. Un effet positif sur le ravageur correspond à de la régulation. Un effet positif sur les différents groupes trophiques signifie une abondance plus élevée (Poeydebat, 2016).

D’après ces résultats, la richesse des plantes de la strate basse et le pourcentage de litière résultaient en un effet bottom-up positif sur les fourmis omnivores et les prédateurs (Figure 9), qui en retour avaient un effet top-down négatif sur les dégâts du charançon dans nos systèmes d’études au Costa Rica. Cela suggérait que la gestion des strates végétales peut être un levier de gestion des prédateurs du charançon, notamment les fourmis.

Nous avons évalué les effets de la densité de différentes strates (herbacée, arbustives, arborées) sur les communautés de fourmis fourrageant au sol dans 20 parcelles de plantains diversifiées au Cameroun (Dassou et al., 2017) [ACL13]. Nous avons montré que la densité des strates arbustives et arborées déterminait quelle espèce de fourmis dominerait la communauté de fourmis présentes (Figure 11) et donc que la gestion de ces strates serait un levier pour orienter les communautés de fourmis de sorte que les fourmis présentant un potentiel de régulation du charançon soient favorisées.

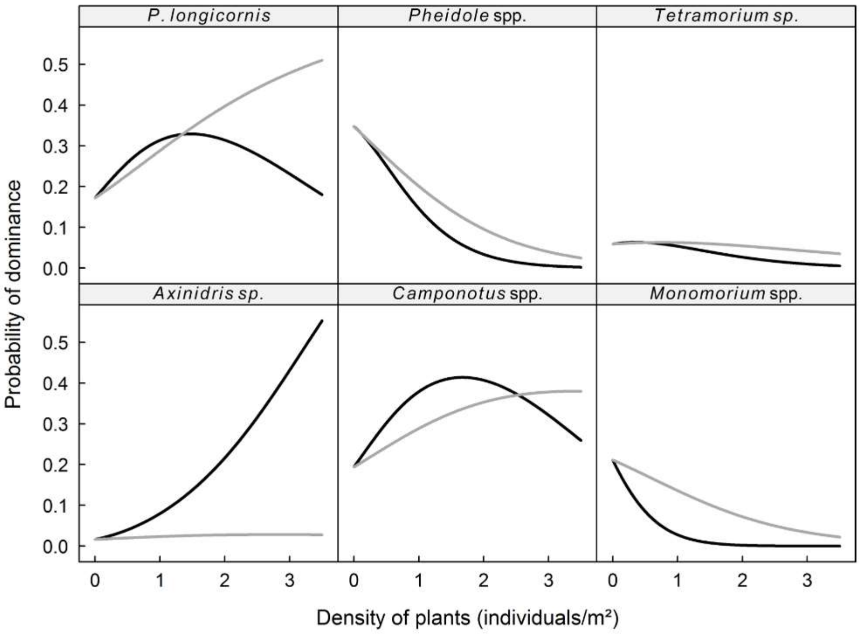

Figure 11. Probabilité prédite de dominance pour chaque taxon de fourmis. Courbes grises : réponse à la densité de plantation de strate intermédiaire ; Courbes noires : réponse à la densité végétale de strate haute [ACL13].

Il y a quelque chose de pourri au royaume de l'agroécologie

Faisons le bilan des travaux présentés jusqu'ici : on a vu, par des études corrélatives, que les fourmis étaient liées à une régulation des dégâts du charançon, ou bien qu'elles ne l'étaient pas. Evidemment, ces résultats proviennent de différents sites d'études où les espèces qui composent la communauté sont différentes. Par exemple, dans la thèse de Charlotte Poeydebat, nous avions montré un lien direct entre richesse spécifique de la strate basse et l'abondance des fourmis omnivores. Nous n'avons néanmoins pas trouvé d'effet de la diversité sur l'abondance des espèces de fourmis dans l'étude au Cameroun. Cette différence peut venir de différents facteurs comme le fait que la diversité végétale de la strate basse au Cameroun était de la diversité cultivée alors qu'au Cosa Rica, la diversité de la strate herbacée était spontanée. Une autre différence vient également de l'idiosyncrasie des agroécosystèmes étudiées : au Costa Rica, la diversité animale, notamment des fourmis, et végétale présente des niveaux bien plus élevés. Par exemple, dans l'étude du gradient de diversité végétale au Costa Rica, la communauté de fourmis étaient composées d'une soixantaine d'espèces alors que dans les autres études (Martinique, Cameroun), la diversité des fourmis avoisinait la quinzaine d'espèces. La méthode d'analyse est également à pointer : dans l'étude au Cameroun, les fourmis sont analysées au niveau spécifique ou générique alors qu'au Costa Rica elles étaient regroupées en groupe trophique. Dans l'étude en Martinique, c'est au niveau spécifique que les études ont été menés avec des hypothèses trophiques basées sur la littérature ou la fouille de dépotoir.

Sur ce dernier point, j'arguerai qu'en écologie, bien que des principes généraux existent et doivent émerger d'études spécifiques, il est plus pertinent de travailler au niveau taxonomique le plus précis (idéalement au niveau spécifique voir sub-spécifique) car les différences dans l'écologie et le comportement d'espèces apparentées peuvent être immenses.

Les travaux réalisés dans la thèse de Charlotte Poeydebat ont apporté des informations intéressantes sur le rôle de la diversité végétale dans le fonctionnement d'agroécosystèmes. L'approche multitrophique a permis de retracer des relactions fonctionnelles entre les différents groupes trophiques. Il faut noter que cette approche a représenté un investissement considérable dans les mesures de terrain et les déterminations d'espèces. Les résultats en Afrique ont permis de montrer que les communautés pouvaient être orientées par les strates végétales mises en place. Les travaux de Martinique ont mis en évidence un rôle potentiel des dermaptères dans la régulation du charançon.

Cependant, ces études sont corrélatives et elles ne constituent pas de preuves de cause à effet. Qu'il y ait moins de dégâts quand il y a plus de fourmis ou plus de dermaptères ne signifie pas que ce sont ces espèces qui régulent directement le charançon. Les études sur le contenu stomacal d'arthropodes avait fait ressortir 2 espèces de fourmis et 1 espèce de dermaptère qui présentaient de l'ADN de charançon : *Camponotus sexguttatus*, *Solenopsis geminata* et *Euborellia caraibea*. Mais cela non plus ne signifie pas que ces espèces mangent du charançon. En particulier, *C. sexguttatus* est une espèce omnivore, qui présente des comportements de charognard. Si elles se nourrissent de charançons, il peut s'agir de cadavres et leur rôle dans la régulation serait alors nul. Personnellement, je doute que cette espèce puisse s'attaquer à des adultes. Le charançon est robuste et cette fourmi est peu agressive, fourrageant en petits nombres d'ouvrières. J'ai à ce sujet une anecdote : j'ai fait quelques tests en proposant des charançons adultes à des *C. sexguttatus* d'un élevage. Elles ne les tuaient pas directement mais elles enterraient ces pauvres charançons sous des débris et déchets, ceux-ci finissaient par mourir et elles ne le mangeaient pas… Evidemment, un élevage n'est pas représentatif d'un comportement en milieu naturel et il faut noter qu'ici le charançon ne pouvait s'enfuir. Ceci étant dit, il faut par ailleurs noter que les fourmis de l'espèce *C. sexguttatus* ont pour habitude de faire leur nid au niveau des gaines foliaires à la base des pseudotroncs morts ou vivants des bananiers et elles fourragent au sol. Elles sont donc aux premières loges lorsqu'une femelle pond et représentent là un potentiel ennemi naturel des œufs de charançon. Après tout, nous n'avons pas trouvé de lien direct entre cette espèce et l'abondance du charançon dans l'étude en Martinique, mais je rappelle que cette espèce était plus présente dans les parcelles enherbées que dans les parcelles sols nus. Mais alors, elles auraient un impact plus faible que les dermaptères puisque les jeunes émergents sont proportionnellement plus présentes en parcelle enherbée.

Une étude réalisée dans mon unité a suggéré que la fourmi de feu tropicale *S. geminata* mangeait plus d'œufs de charançon dans des parcelles enherbées que dans des parcelles au sol nu (Mollot et al., 2012). Dans cette étude, il était utilisé des proies sentinelles : les œufs étaient déposés à un temps *t* et le nombre d'œufs restants à *t+1h* était comptabilisé. Cette étude avait pour avantage de mimer la ponte d'une femelle en insérant des œufs à la base du bananier, mais il est important de noter que les dépôts ont eu lieu le jour. En outre, la relation entre le taux de prédation et l'abondance de cette fourmi est encore une fois corrélative. A noter que même si dans cette étude les plantes de couverture appartiennent également au

Poacées, ils trouvent une relation positive entre la présence des plantes de couvertures et l'abondance-activité de *S. geminata*, ce que je n'ai pas observé sur le même site lors de mon suivi de 3 ans.

Bref, on a beau regrouper les pièces, on n'avance pas beaucoup sur le puzzle.

Bon on fait quoi alors maintenant ?

Comme je l'ai écrit plus haut, il m'apparait essentiel de bien connaître les espèces que l'on étudie et les interactions qu'elles entretiennent entre elles. On en revient aux questions initiales : qui est là ? qui fait quoi ? qui mange qui ? et combien ?

On peut bien sûr combiner différentes méthodes pour obtenir des faisceaux d'indices voire des preuves de prédation : suivi de population, contenu stomacal, metabarcoding, immunomarquage, dépotoir de fourmilières, proies sentinelles… L'analyse de contenu stomacaux marchent bien chez des animaux où le lien de prédation est évident, comme pour les poissons par exemple (Grey et al., 2002) mais devient plus compliqué chez d'autres animaux notamment les arthropodes, qui malheureusement n'ont pas la bonne idée, à l'inverse des hiboux, de nous simplifier la vie avec des pelotes de réjection. Le métabarcoding des contenus stomacaux est révélateur de beaucoup d'informations mais demande un investissement considérable en barcoding ou un besoin en une base de données de barcodes fiables, et le lien trophique, qualitatif, n'est pas prouvé (prédation secondaire, nécrophagie, …). Les méthodes d'immunomarquages développées par Hagler (2019a, 2019b) sont très intéressantes. Elles peuvent permettre non-seulement de prouver la prédation, mais également d'observer du cannibalisme, de la prédation intraguilde et de connaître le stade de vie attaqué (Hagler et al., 2020a, 2020b; Hagler and Mostafa, 2019). Cependant, la durée de vie du marquage (notamment après prédation) et le procédé de capture-recapture des proies et des prédateurs sont des contraintes à l'usage de cette méthode de marquage immunologique, laquelle est utilisable surtout chez les invertébrés, un aspect sur lequel on reviendra plus tard. La fouille de dépotoir de colonies de fourmis permet de récupérer des informations sur la prédation d'invertébrés ayant un exosquelette rigide. Une telle méthode, couplée à un marquage physique des proies pourraient permettre de mesurer des taux de prédations en milieu naturel de ravageurs par ces insectes sociaux. Les proies sentinelles, quant à elles, représentent une méthode permettant de mesurer la prédation d'invertébrés dans des conditions au champ (Lövei and Ferrante, 2017). Les proies peuvent être réelles ou artificielles en plasticine et représenter une fausse chenille, un faux papillon, une fausse grenouille, un faux œuf d'oiseau ou encore un faux serpent. Ces proies artificielles sont généralement, mais pas exclusivement, utilisées pour mesurer la prédation par les oiseaux grâce aux traces de bec que ceux-ci laissent sur la plasticine. Deux contraintes majeures aux études utilisant les proies sentinelles sont l'immobilité de la proie (si celle-ci est en réalité mobile) et le statut vivant ou non de la proie. En effet, une proie mobile et vivante doit être contrainte, souvent par l'usage de glue, pour différentier une prédation d'une simple fuite de la proie, mais cela rend le dispositif plus éloigné des conditions naturelles. Par ailleurs, Loveï et Ferrante (Lövei and Ferrante, 2017) ont trouvé que 20% des études analysées dans leur revue utilisaient des cadavres, rendant impossible la différentiation entre nécrophagie et vraie prédation. A noter par ailleurs, que l'offrande de proies réelles immobilisées risque, selon moi, d'apporter des informations de prédation par des espèces au comportement opportuniste.

Une façon d'améliorer la méthode de proies sentinelles est de la coupler à une surveillance vidéo. Grieshop et al. (2012) utilisèrent ce couplage proies sentinelles - surveillance vidéo pour étudier la prédation de ravageurs (la pyrale *Acrobasis vaccinii* et le scarabée japonais *Popillia japonica*) de la myrtille (*Vaccinium corymbosum*). Ils ont pu révéler le rôle majeur des fourmis, dont la durée de visite des sites des proies sentinelles était positivement corrélée à la mortalité des proies. De manière similaire, Zou et al. (2017) ont montré que la prédation de cicadelles *Nilaparvata lugen* vivantes et mobiles étaient le fait de la grenouille *Rana limnocharis*, le rôle de cette grenouille dans la régulation de ce ravageur étant jusqu'alors non-suspectée. Ils ont également montré l'importance du type de proies, car si la grenouille s'attaquait aux proies vivantes et mobiles, la sauterelle *Conocephalus longipennis* ne s'attaquait qu'aux cicadelles mortes tandis que les cicadelles vivantes et immobilisées étaient les proies de carabes. Grieshop et al. (2012) relèvent tout de même que si l'utilité de la surveillance vidéo est bien démontrée, il existe au moins deux limites importantes : la faible fenêtre d'échantillonnage de la caméra et le temps nécessaire à l'analyse d'image.

Dans les 3 prochains chapitres, je présenterai des aspects méthodologiques et techniques réalisés au cours de mes travaux sur l'étude des interactions dans les communautés animales et la régulation du charançon.

Weevil & images

Au cours de l'année 2018, j'ai ainsi commencé à m'intéresser à l'analyse d'image et la vision par ordinateur. La vision par ordinateur a grandement avancé dans la décennie 2010-2020 de par les progrès techniques notamment au niveau des cartes graphiques (GPU, Graphics Processing Unit) qui ont apporté l'essor des réseaux de neurones (LeCun et al., 2015). Si vous souhaitez plus d'information sur la vision par ordinateur et les réseaux de neurones, je vous invite à lire la thèse de Paul Tresson (Tresson, 2021).

Je me suis rapproché de William Puech (ICAR, LIRRM, CNRS-UM2) pour débuter un travail sur l'identification de fourmis et de charançon sur des images en couleur. Avec Régis Graptin, alors stagiaire de William Puech, nous avons d'abord adapté le modèle de classification Inception-V3 (Szegedy et al., 2016) à la reconnaissance de fourmis *Messor barbarus* sur des images (Figure 12).

Figure 12. La fourmi *Messor barbarus* (Crédit photos D. Carval, CIRAD).

En vision par ordinateur, la classification est la méthode d'intelligence artificielle qui permet de classer un objet (ici une fourmi) sur une image. Ces méthodes sont utilisées sur des images contenant un seul gros objet (Figure 13). Cependant, si nous voulons utiliser l'image et la vision par ordinateur pour étudier des interactions, il faudra que l'algorithme soit capable non seulement de classer les individus par espèces mais aussi de les localiser : c'est ce qu'on appelle la détection (Figure 14).

Figure 13. Exemples d'images utilisés pour la classification. Le résultat du modèle Inception étant : c'est une fourmi (en haut), ce n'est pas une fourmi (en bas).

Figure 14. Exemple d'images utilisés pour la détection. L'algorithme doit être à même de retrouver et d'identifier les différentes fourmis dans un environnement simple en premier lieu (gauche), puis plus complexe (droite).

C'est pourquoi nous avons ensuite utilisé une méthode de fenêtre glissante. Il s'agit de découper l'image en petites imagettes qui sont ensuite données au modèle de classification. A chaque imagette correspond une probabilité que celle-ci contiennent une fourmi *M. barbarus*. Sur la base de ces probabilités, on peut construire une carte de chaleur sur l'image initiale et détecter les régions de l'image où sont effectivement présentes des fourmis (Figure 15a). Pour compliquer la tâche, nous avons générer un jeu de données avec du "bruit" en disposant différent éléments naturels (écorce, feuilles, fleurs, cailloux), ce qui a permis aussi aux fourmis d’être dans différentes poses (Figure 15b).

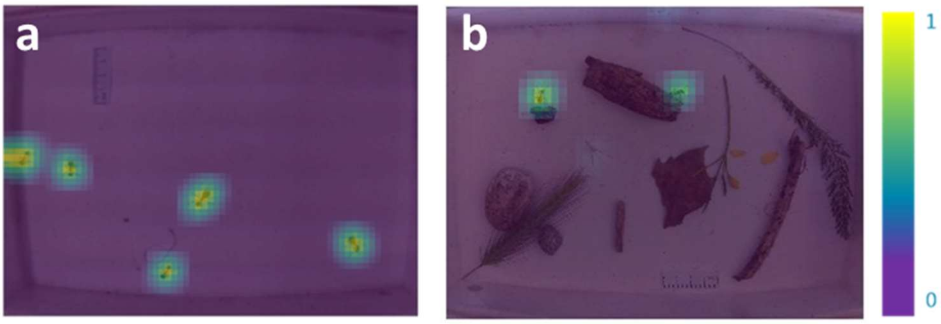

Figure 15. Détection de fourmis *M. barbarus* par la combinaison d'une fenêtre glissante, la classification avec Inception-V3 et les cartes de chaleurs. a : fond sans bruit. b : fond bruité.

Par la suite, avec ma collègue Leïla Bagny Beilhe (UMR PHIM, CIRAD), nous avons monté le projet PredaTV dans le but de faire une preuve de concept de l’utilisation des outils d’intelligence artificielle (IA) de la vision par ordinateur. Je me suis intéressé à l’utilisation de YoloV3 (Redmon et al., 2016), un réseau de neurones convolutif pour détecter, identifier et dénombrer des objets. Ce modèle de détection permet la détection et la classification simultanée d’objets avec une précision et une rapidité plus importante que notre méthode de classification combinée à une carte de chaleur.

En effectuant des prises de vues en laboratoire de *Messor barbarus* et de charançons du bananier, j’ai établi un jeu de données qui m’a servi à entraîner YoloV3. Les résultats sont alors prometteurs et nous décidons de passer à des essais de terrain (Figure 16). En effet, en laboratoire, il a été facile d’obtenir des résultats concluants car les objets (les fourmis et les charançons) sont relativement grands (~1 cm) et relativement peu nombreux. Si nous voulons étudier à partir d’images des communautés animales, notamment composées d’arthropodes et d’autres invertébrés, nous devons considérer le fait que nous aurons des animaux de tailles très différentes, parfois très petits, et en abondance variée, parfois importante.

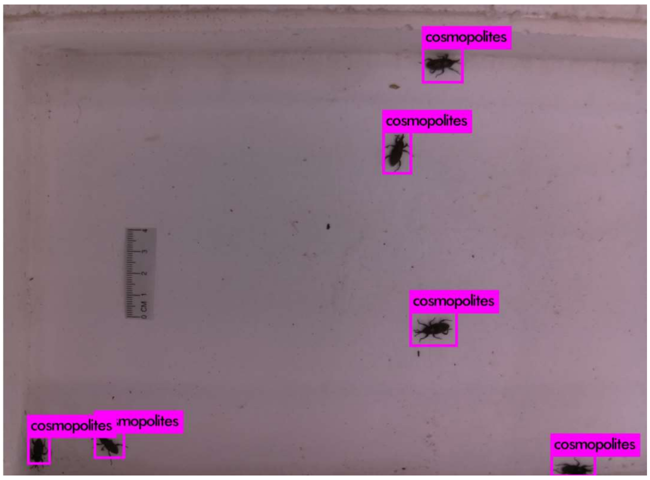

Figure 16. Détection par Yolo de charançon du bananier.

Au cours du projet PredaTV, je suis parti au Costa Rica pour réaliser des prises de vue *in situ* dans des systèmes agroforestiers. Le dispositif de prise de vue consistait en un appareil photo monté sur trépied et protégé de la pluie par un abri (Figure 17). Les prises de vue nocturne se réalisaient en time lapse avec flash pour conserver les informations liées aux couleurs. En effet, les canaux rouge, vert et bleu apporte des informations importantes lors de l'apprentissage par le réseau de neurones. Après plusieurs essais, le fond de prise de vue retenu était constitué d'une planche de contreplaqué sur laquelle était fixée une feuille de papier de dessin. Pour stimuler l'activité d'animaux sous notre objectif, nous avons placé des proies sentinelles : larves de charançon de la canne (*Metamasius sp.*), et des carcasses de charançons noirs de bananier morts. Les différentes espèces observées ont été déterminées au laboratoire, à l'espèce ou à la morpho-espèce et les photos ont été labellisées.

Figure 17. Dispositif au Costa Rica (protection contre la pluie). Fond sans bruit (sauf au bord car intégré à la litière).

Petits objets, gros problèmes

Notre jeu de données complexes est prêt. Mais ici l'utilisation de Yolo ne nous sera d'aucune aide. En effet, les modèles de détection tel que Yolo (Bochkovskiy et al., 2020; Redmon et al., 2016), Fast-RCNN (Girshick, 2015), RetinaNet (Lin et al., 2017), sont développés pour détecter des objets relativement grand et peu nombreux. Or nous avons de très petits objets et en grand nombre.

Les CNN utilisent des calculs matriciels et les informations contenues dans ces matrices correspondent aux pixels des images. Pour que votre GPU ne surchauffe pas et stoppe le programme, il ne faut pas que ces matrices soient trop grandes. Dans Yolo, les images sont redimensionnées à l'entrée du réseau de neurones, en général entre 256*256 soit 65 536 pixels et 640*640 soit 409 600 pixels. Ce redimensionnement crée une perte d'information. Celle-ci ne sera pas trop grande si vos objets sont constitués d'un très grand nombre de pixels initialement, mais dans le cas de petits objets constitués de peu de pixels, la perte d'information sera énorme et l'apprentissage ne pourra se faire.

Nos images originales sont en haute définition[1] (3000 x 4000 soit 12 000 000 pixels) et dans le meilleur des cas notre image passe en 640*640 dans Yolo, ce qui correspond à une diminution de la définition de 96.6%.

Par exemple, sur nos images originales, considérant les boîtes englobantes de la labélisation, les fourmis *Pheidole radoszkowskii* sont constituées d'environ de 5000 à 6000 pixels (Figure 18). Si on utilise l'image originale, le changement de définition en 640*640 à l'entrée du réseau de neurones réduirait ces fourmis à des objets d'environ 200 à 250 pixels et ne permettrait pas de reconnaissance (Figure 19).

Figure 18. Image type issue de l'expérimentation proie-sentinelle au Costa Rica.

Figure 19. Effet de la transformation de l'image à l'entrée du réseau. A gauche, la définition native, au centre une entrée en 640*640, à droite une entrée en 256*256. Les images correspondent aux régions entourées de vert sur la Figure 16. En haut, *Odontomachus bauri*. En bas, *Pheidole radoszkowskii* (major).

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[1] La définition d'une image matricielle correspond au nombre total de pixels qui la compose. Il ne faut pas confondre avec la résolution de l'image qui s'exprime en dpi (*dot per inch*), métrique utilisée lors des impressions de l'image numérique sur papier.

Dans notre jeu de données utilisé pour l’apprentissage, 4087 animaux appartenant à 23 classes étaient présents, avec une moyenne de 21,8 objets par image. La largeur moyenne de l'objet présenté est de 98,7 ± 64,5 pixels (2,4 % de la largeur de l'image) et la hauteur moyenne des objets présentés est de 98,1 ± 63,9 pixels (3,2 % de la hauteur de l'image). Nos images présentent alors de nombreux et petits objets. En comparaison, l'ensemble de données pour le Pascal Visual Object Classes Challenge (Everingham et al., 2010) présente une moyenne de 3,12 objets par image avec une largeur et une hauteur correspondant en moyenne respectivement 30,1 % et 38,8 % de la hauteur et la largeur de la hauteur de l’image.

La solution était à nouveau de passer par une méthode de fenêtre glissante. Nous avons développé un pipeline en langage Python qui permet de découper l’image originale en imagettes, avec un chevauchement des imagettes (Figure 18). Après découpage, les tranches contenant des objets comportent en moyenne 1,73 objets de largeur et hauteur moyennes de 21,8% et 21,9% respectivement, des chiffres très proches de ceux cités plus haut sur les données du Pascal Visual Object Classes Challenge. Ces imagettes sont envoyées ensuite au réseau de neurones pour la détection des individus. Puis l’image est reconstruite et les doublons de prédictions supprimées grâce à la mise en place d’un seuil calculant le ratio intersection/union des boîtes englobantes des détections (IoU, Intersection over Union) qui permet de garder uniquement la meilleure détection d’un même individu (Tresson et al., 2019) [ACL16].

Ce pipeline peut ainsi détecter les individus présents sur une images en les identifiant à l’espèce ou morpho-espèce, voire même en différentiant les castes de fourmis au sein d’une même espèce et de sortir des métriques écologiques d’intérêt (Figure 20). Par exemple, à partir du jeu de données élaboré au Costa Rica pour développer le pipeline, nous avons pu reconstruire un réseau d’interactions trophiques et non-trophiques (Figure 21a). Grâces aux métadonnées des images, il nous a même été possible de sortir des informations précises sur la dynamique de recrutement de fourmis (Figure 21b).

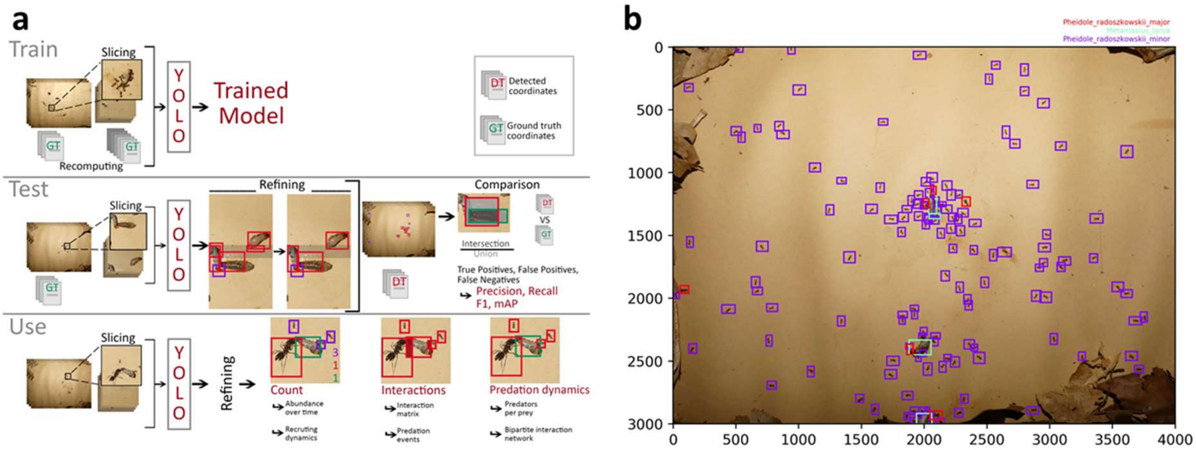

Figure 20. a: Description des différentes étapes du pipeline. b: Exemple de détections réalisées par le pipeline.

D’autres expérimentations de proies sentinelles ont été réalisées au Costa Rica. Dans le cas du charançon du bananier, les expérimentations et les images du Costa Rica nous ont apportés une information : aucune prédation de charançon adulte vivant n’a été observée (données non publiées), allant dans le sens des résultats obtenus en Martinique et publiés dans Carval et al. (2022) [ACL21]. Ces expérimentations ont été menées selon le même protocole d’obtention d’images que celui réalisé pour le développement du pipeline, mais nous avons rajouté une phéromone d’agrégation (Jayaraman et al., 1997) pour attirer les charançons de la parcelle sous l’objectif. Et ceux-ci n’ont pas été inquiétés par les fourmis. Sur une séquence d’images, on a pu observer par exemple un charançon adulte se déplaçant pendant plusieurs minutes sur le pseudotronc où sont cachées les larves. Il est alors attaqué par plusieurs ouvrières *Solenopsis geminata*, mais il ne semble pas affecté par leur tentative de piqûre ou de morsure. Quant aux *Camponotus atriceps* présentes, fourmis nocturnes de grandes tailles, elles ne semblent s’intéresser qu’aux cadavres de charançons, laissant le charançon vivant tranquille et les larves aux *S. geminata*. Ces dernières, ainsi que les fourmis *Pheidole radoszkowskii*, s’acharnent à extraire les larves de leurs cachettes. Si ce dispositif n’est pas parfait, les larves ne sont pas directement exposées (à l’inverse des prises de vue pour la méthodologie) mais cachées dans un trou dans un pseudotronc. Il y a donc une prédation réellement active des larves par la fourmi de feu ou par des *P. radoszkowskii*. La prédation des adultes par les fourmis semble donc rare et difficile pour certaines espèces même agressives et abondantes.

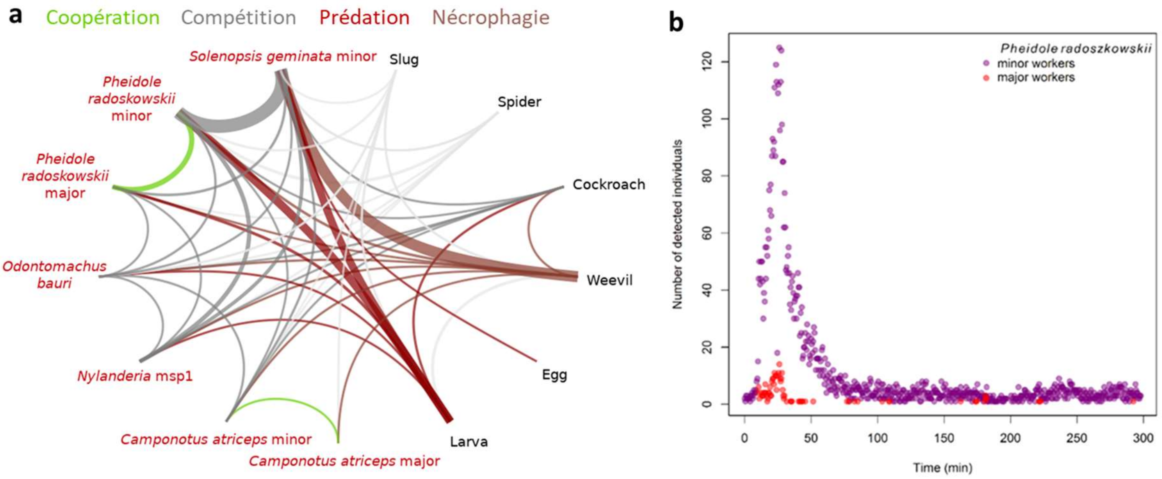

Figure 21. a: Interactions trophiques et non-trophiques révélées par l'analyse d'images. L'épaisseur du lien est proportionnelle au nombre d'interactions observées. b: Dynamique de recrutement de *P. radozskowskii* lors d'une expérience de proie sentinelle.

C’est rare que j’aie la classe

Cependant, si les résultats se sont avérés satisfaisants, riches d’informations, certains problèmes ont émergé. En particulier le problème des classes rares. Ainsi, dans le jeu de données des expérimentations du Costa Rica, les analyses ont bien fonctionné, différentiant 43 espèces et castes, sauf pour une nuit sur un site. Le taux de confusion entre 2 espèces (*S. geminata*) et une espèce appartenant au genre *Nylanderia*) était trop grand pour que l’analyse soit valable. L’explication de cette confusion est que ces *Nylanderia* ont été très peu présentes dans ces expérimentations et le pipeline n’a eu que très peu d’exemples pour apprendre à reconnaître cette espèce et à la différencier de *S. geminata*. Comment gérer ce problème de classe rare et comment s’assurer de la certitude dans l’identification ? En vision par ordinateur, le déséquilibre des classes est un problème souvent rencontré dans le monde animal et en biologie de manière général (Sampath et al., 2021).

Pendant la thèse de Paul Tresson, nous avons décidé de nous intéresser au problème. L’idée que j’ai suggérée était que (i) comme la vision par ordinateur utilise des indices visuels et (ii) qu’une *Solenopsis* et une *Nylanderia* sont toutes deux des fourmis, on pouvait s’inspirer de la classification phylogénétique, comme on le fait avec des clefs de détermination, et réaliser un pipeline de classification hiérarchique (Tresson et al., 2021a) [ACL19].

L’idée est la suivante : on demande au pipeline d’abord de détecter au niveau des super-classes[2] avec d’un côté les araignées, les fourmis, les cochenilles, etc. Puis, une fois les objets détectés et placés au bon niveau taxonomique (*e.g.* Formicidae), on va aller dans un classifieur entraîné à reconnaître les fourmis et rien que les fourmis (Figure 22). On a donc créé un jeu de données à la Réunion comprenant 22 espèces de différents genres ou famille. Et les résultats sont là : le pipeline hiérarchique augmente de 30% sa précision !

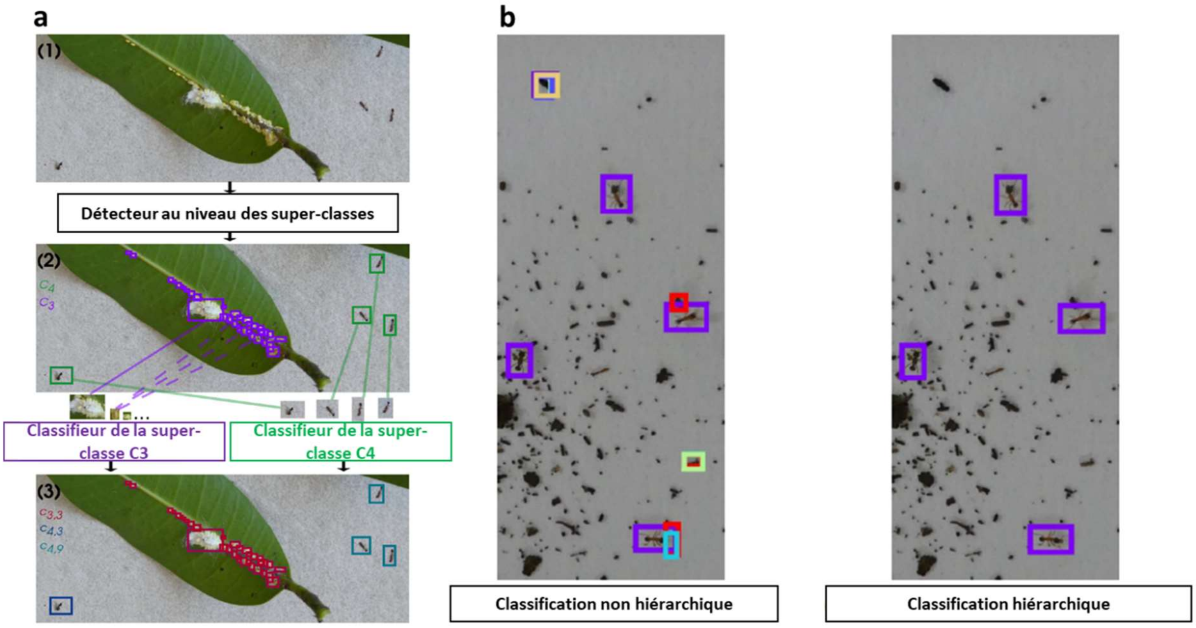

Figure 22. a: Illustration du fonctionnement du pipeline hiérarchique. b: Le pipeline hierarchique permet la suppression d'erreurs de classification.

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[2] J’utilise ici le vocabulaire de la vision par ordinateur et non celui de la biologie. Les *objets* présents sur une image sont les entités à détecter et elles appartiennent à une *classe*, par exemple la classe "voiture". Ces *objets* peuvent être regroupés à un niveau hiérarchique supérieur au sein d’une *super-classe*, par exemple la *super-classe* "véhicule".

Soyons adultes !

Bon c’est super tout ça, on va enfin pouvoir savoir qui mange notre charançon !

Cela n’est pas si simple… Et si on était sur une fausse piste depuis le départ ? Revoyons ce qui est connu sur la prédation du charançon. Au cours de la thèse de Paul Tresson, nous avons effectué une revue de la littérature sur le contrôle biologique du charançon, avec un focus sur le contrôle biologique par conservation (Tresson et al., 2021b) [ACL20]. Et on a retrouvé les mêmes doutes : il ne semble pas qu’on connaisse les animaux responsables de sa régulation… tout au moins responsable de la prédation des adultes. Selon moi, il y a un *biais arthropode* dans les études sur le contrôle biologique par les ennemis naturels. Beaucoup de chercheurs partent du postulat implicite, possiblement inconsciemment, que pour réguler un ravageur invertébré il faut trouver le bon ennemi naturel invertébré. Bien sûr il y a un grand nombre d’études sur la prédation par les oiseaux. Dans leur revue sur les proies sentinelles, Loveï & Ferrante (2017) relèvent que la moitié des articles qu’ils ont sélectionnés concerne la prédation par les oiseaux. D’ailleurs, une méta-analyse sur les services de biocontrôle rendus par les oiseaux (Díaz-Siefer et al., 2022) démontrent que l’exclusion d’oiseaux diminue l’abondance des ravageurs et des dommages, et augmente le rendement. Díaz-Siefer et al. (2022) considèrent également qu’il y a des paradigmes et une perception traditionnelle du contrôle biologique centré sur les parasitoïdes et les insectes prédateurs. Si les vertébrés les plus étudiés demeurent les oiseaux et les chauve-souris, d’autres études ont montré que les amphibiens (Wanger et al., 2011; Zou et al., 2017), les lézards (Dor et al., 2014) et les rongeurs peuvent contribuer à la régulation de ravageur (Tschumi et al., 2018).

Le charançon est un insecte que l’on peut considérer comme une espèce K-sélectionnée (Pianka, 1970) avec un long développement holométabole (environ 2 mois), une faible fécondité (1 à 2 œufs par semaine) et une grande longévité de l’imago (1 à 4 ans) (Gold et al., 2001). Il serait donc intéressant de cibler l’adulte pour réguler les populations.

Le stage de Chloé Tellier portait sur le développement d’un modèle multi-agents (langages C++ et Python) d’un agrosystème bananier. Ce modèle individu-centré simule la croissance de bananiers au sein d’une parcelle pouvant être infestée par des charançons. La modélisation des bananiers et des charançons est inspirée respectivement des travaux de Tixier et al. (2008) et de Vinatier et al. (2009), et utilise des paramètres dont les gammes de valeurs sont issues de la littérature lorsque ceux-ci étaient disponibles. La parcelle peut également contenir différents types de prédateurs du charançon. Ceux-ci différaient par (i) leur méthode de chasse (immobiles, à l’affut ; mobiles, au fourragement actif) et (ii) par le stade qu’ils attaquaient (œufs, larves ou adultes).

L’analyse du modèle (Figure 23) montre que dans les parcelles sans prédateur ou avec des prédateurs immobiles, la population de charançons n’est pas ou très peu régulée avec une très forte infestation des bananiers et des rendements plutôt faibles (entre 5 et 10 tonnes de matière sèche/ha/an). Toutes choses étant égales par ailleurs, dans les parcelles où des prédateurs mobiles sont introduits, la population de charançons est bien régulée avec une infestation des bananiers plus faible et des rendements meilleurs (entre 15 et 18 tonnes de matière sèche/ha/an).

Par ailleurs, à taux d’attaque similaire (probabilité d’attaque du charançon par le prédateur), les prédateurs des charançons adultes induisent une bien meilleure régulation des charançons que les prédateurs des autres stades. Ainsi, les résultats du modèle vont dans le sens que le stade cible pour une bonne régulation du charançon est le stade adulte et qu’une recherche des prédateurs de ce stade doit être priorisé

Dans la thèse de Paul Tresson, nous avons cherché à identifier les espèces responsables de la prédation des charançons adultes et des œufs à la Réunion en utilisant des expérimentations de proies-sentinelles couplées à de la vidéosurveillance et à une analyse d’image semi-automatisée.

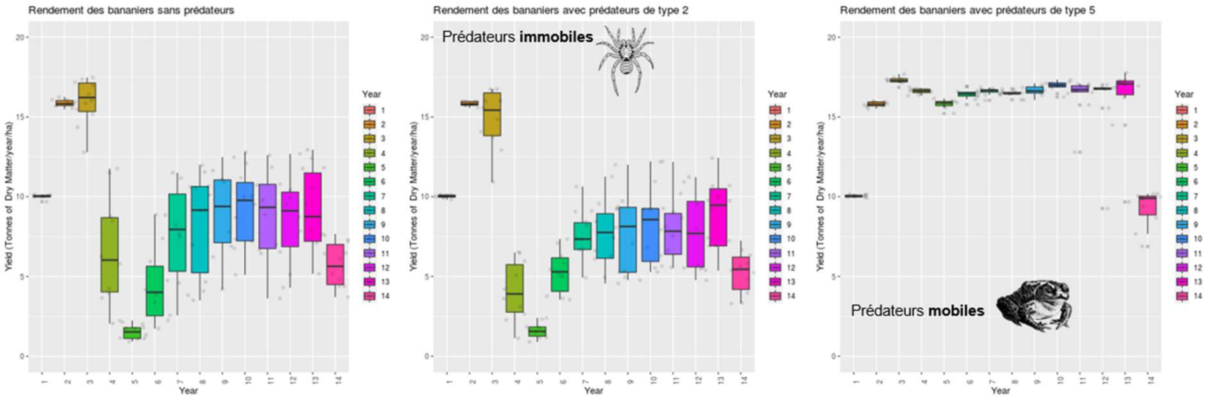

Figure 23. Sorties du modèle de simulation: les prédateurs de type mobile permettent une bonne régulation du charançon et le maintien d'un bon rendement.

Le meurtrier était…

Les expérimentations s’inspirent de celles réalisées au Costa Rica à la différence que les charançons adultes vivants étaient attachés au niveau des élytres à un fil de pêche leur permettant de se déplacer dans la zone de prise d’image tout en les empêchant de s’échapper. Un morceau de pseudotronc servait d’abri aux adultes pendant la journée. La zone échantillonnée par l’appareil photo était un peu plus grande (Figure 24).

Ces expérimentations de proies-sentinelles ont été réalisées dans 5 parcelles de producteurs de bananes, avec 5 sites de prises de vue par parcelles et répétées 5 fois. Les prises de vue consistaient en un time-lapse de 30 secondes de fréquence sur une durée de 24h. Au total 312 024 images ont été prises correspondant à 3000h d’observation.

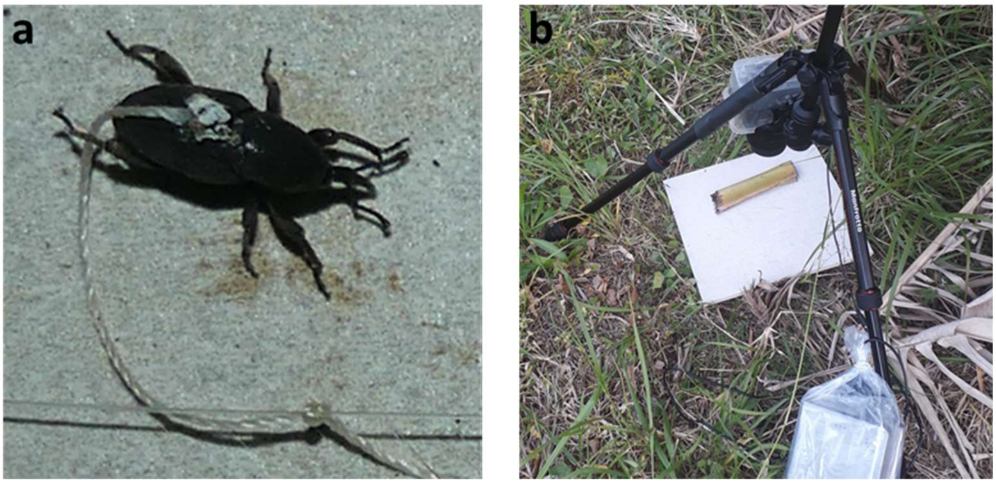

Figure 24. Dispositif expérimental à la Réunion. a: Le charançon est relié à un fil de nylon par un fil de pêche, ce qui lui permet de se déplacer. b: Appareil photographique relié à sa batterie externe.

La grande quantité d'images ne permettaient pas une analyse manuelle (ou alors elle aurait été extrêmement chronophage). Une méthode de sélection des images d'intérêts, c'est-à-dire où un évènement comme le passage d'un animal ou la prédation d'un charançon, a été établie. Cette méthode se base sur l'utilisation d'une moyenne glissante des valeurs de pixels des images. En comparant chaque image à la moyenne réalisée et en fixant un seuil de différence, on a pu extraire les images où des évènements particuliers survenaient (Figure 25).

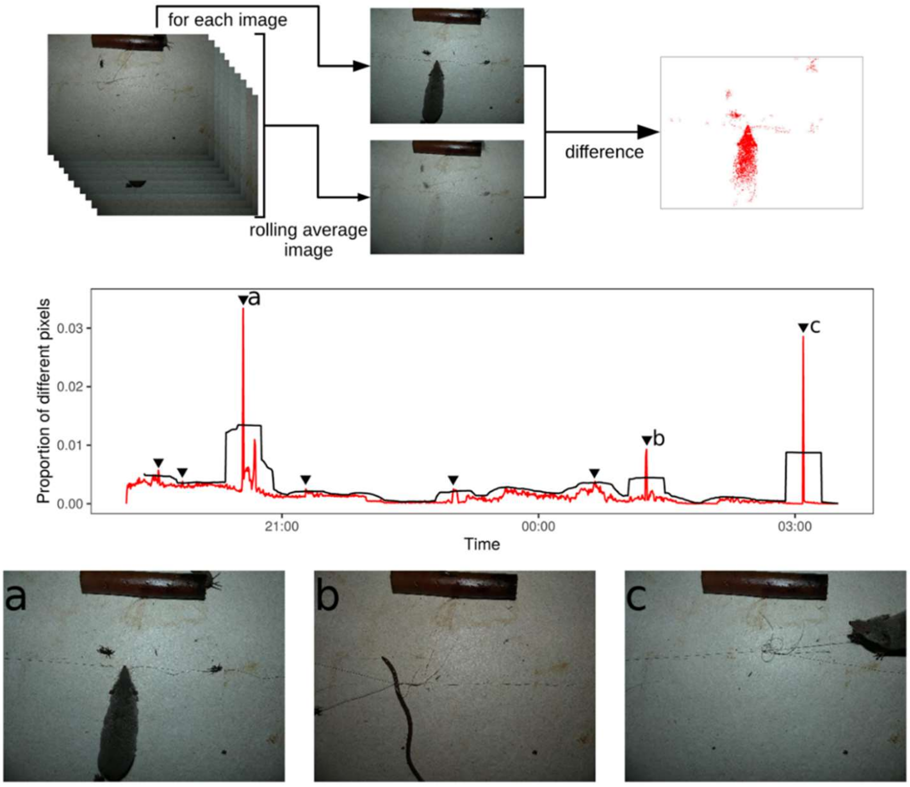

Figure 25. La méthode de la moyenne glissante permet de sélectionner les évènements d'intérêts. a: Une musaraigne musqué arrive un peu avant 21h. b: Un ver passe sous l'objectif vers 23h. c: Une musaraigne musquée mange un charançon vers 3h.

Grâce à cette analyse, on a pu obtenir les taux de prédations par parcelle étudiée (Figure 26b) et par prédateur. Dans cette étude, 32.8% des proies sentinelles (55) ont subi une prédation. Dans 67% des cas, la musaraigne musquée *Suncus murinus* en était responsable. Les autres prédateurs responsables des prédations étaient tous des vertébrés (Figure 27) : la souris *Mus musculus* (4 prédations), l'agame versicolor *Calotes versicolor* (4 prédations) et le crapaud guttural *Sclerophrys gutturalis* (1 prédation).

Autre information importante que nous avons pu récupérer est l'heure de la prédation. On voit notamment que la plus grande partie des prédations par la musaraigne se sont produites dans les premières heures de la nuit (Figure 26a), période d'activité la plus importante du charançon comme mentionné au début de ce chapitre (Figure 2). On peut aussi suggérer qu'il y a eu plus d'évènements de prédation en début de nuit parce que les charançons une fois mangés, et bien il n'y a tout simplement plus de charançon à manger… Ce potentiel biais pourrait être éviter en faisant débuter les expérimentations à différentes heures.

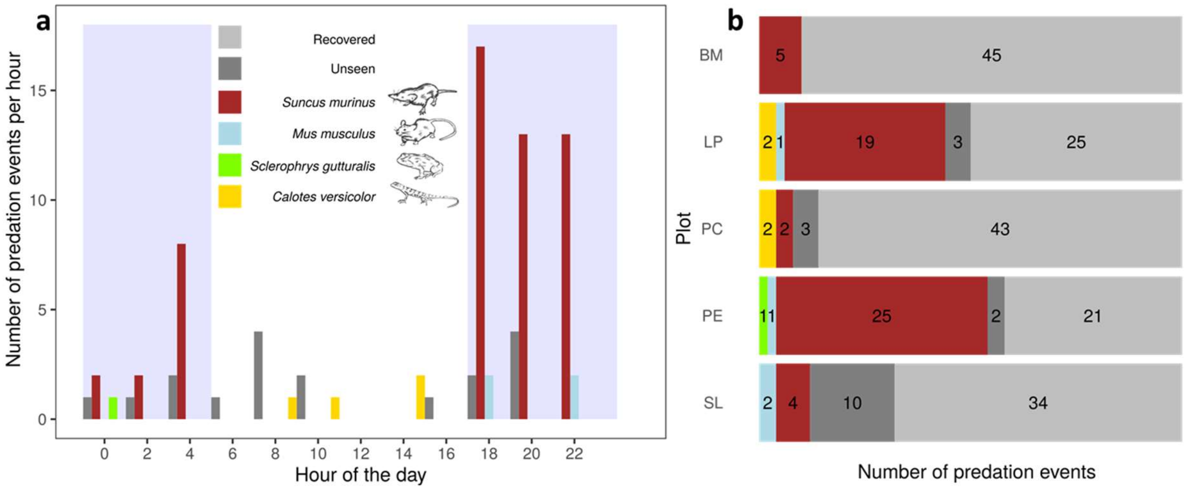

Figure 26. a: Distribution des évènements de prédation selon l'heure. b: Nombre total d'évènements de prédation par parcelle et par prédateur.

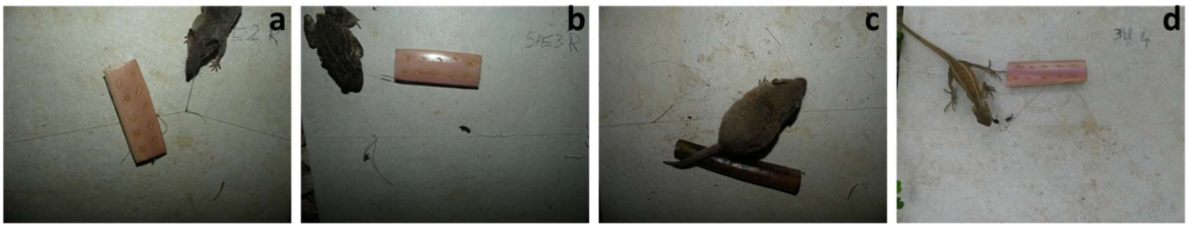

Figure 27. Evènements de prédation par: a. la musaraigne musquée *Suncus murinus*. b: le crapaud guttural *Sclerophrys gutturalis*. c: la souris *Mus musculus*. d: l'agame versicolor *Calotes versicolor*.

Des biais sont cependant à évoquer : (i) la présence d'un flash peut avoir attiré ou au contraire repoussé certains prédateurs nocturnes ; (ii) la présence d'un carreau au sol peut avoir attiré ou au contraire repoussé certains prédateurs nocturnes ; (iii) les prédations diurnes sont probablement des artefacts dû à une plus forte exposition du charançon, qui le jour se cache souvent sans doute mieux que sous un bout de pseudotronc au milieu d’une pièce de carrelage.

S’il n’y a rien d’exceptionnel à avoir observer une prédation par ces animaux dont on sait qu’ils sont insectivores, nous avons néanmoins prouvé un lien trophique, ce qui était notre objectif premier. Et cela montre l’importance de sortir du *biais arthropode* pour connaître les prédateurs du charançon adulte. Cette méthode nous a par ailleurs permis d’observer des évènements d’hyperprédation. La figure 28 illustre la suite d’évènement suivante : (i) une musaraigne attaque un charançon (prédation) puis s’en va ; (ii) une blatte vient se nourrir des restes du charançon (nécrophagie) ; (iii) la musaraigne, en supposant qu’il s’agisse du même individu, revient sur le site de ses méfaits et s’attaque à la blatte (hyperprédation, on verra pourquoi plus bas ce terme). Notre méthode permet ainsi de voir avec précision les liens trophiques au sein de la communauté animale du sol.

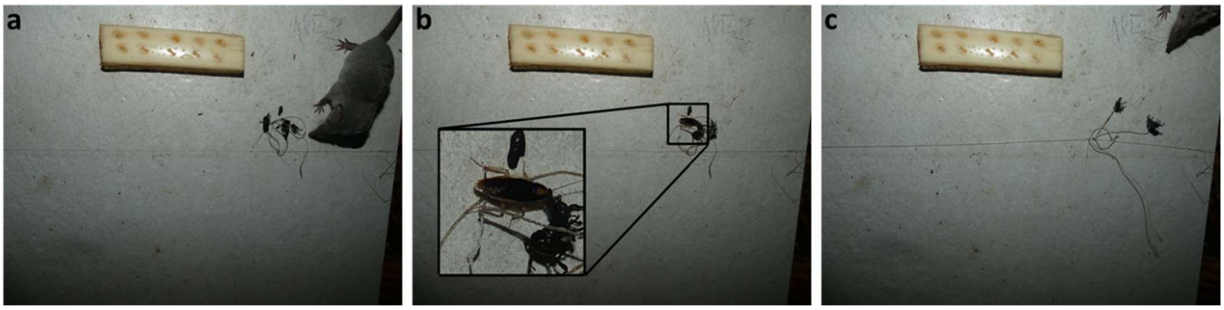

Figure 28. Hyperprédation d'une blatte par une musaraigne musquée. a: une musaraigne mange un charançon. b: une blatte vient se repaître des restes du charançon. c: une musaraigne vient de manger la blatte.

Je n’en crois pas mes œufs

Grâce à l’utilisation d’images et d’une méthode d’analyse semi-automatique, on a pu identifier des prédateurs vertébrés du charançon à la Réunion. L’autre stade potentiellement vulnérable étant le stade œuf nous avons aussi regardé qui venait les manger. Au cours de la même expérience, nous avons placé sous l’objectif, un tronçon de pseudotronc de bananier présentant 10 petites cavités où étaient insérer des œufs (de coccinelle pour des raisons logistiques, similaires en taille à ceux du charançon, Figure 29).

En découpant automatiquement nos images autour de la zone d’intérêt qu’est le pseudotronc, puis en utilisant la même méthode de fenêtre glissante, nous avons pu détecter les différents évènements se déroulant sous l’objectif (Figure 27).

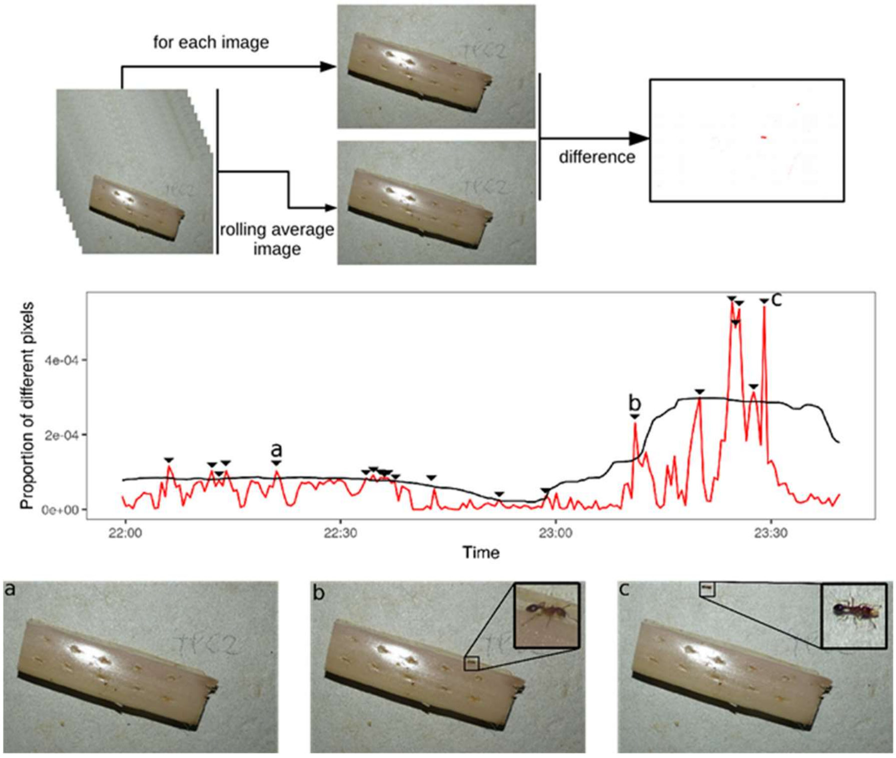

Figure 29. La méthode de la moyenne glissante permet de sélectionner les évènements d'intérêts. a: quelques collemboles sont détectés. b: une fourmi de l'espèce *Tetramorium bicarinatum* apparaît à 23h10. c: elle fourrage pendant 20 minutes avant de capturer un œuf.

Au-delà de l'identification de prédateurs des œufs (Figure 30), nous avons pu voir lesquels avaient un effet significatif sur le taux de prédation observé. Pour chaque espèce ou morpho-espèce nous avons enregistré son abondance et le nombre de contacts avec les œufs. Nous avons retrouvé une relation positive significative entre l'abondance des espèces/morpho-espèces et le nombre de contacts qu'elles ont avec les œufs. En reliant le nombre de contact que chaque espèce a eu avec les œufs et les taux de prédation observés, nous avons trouvé que non seulement les fourmis avaient un rôle significatif dans la prédation des œufs mais également les limaces et les blattes. Ces dernières, rappelez-vous, peuvent être les proies des musaraignes lors d'évènement d'hyperprédation.

Figure 30. Quelques scènes de prédation.

Mon projet

Préambule

Dans le chapitre précédent, j'ai présenté le déroulé de mes recherches passées autour du contrôle biologique du charançon et du contrôle biologique par conservation. Ces activités de recherche se concentraient sur une étude de processus biologiques ayant cours dans des agrosystèmes. Nous avons vu, par exemple, que le choix de l'approche méthodologique était un point crucial pour identifier des prédateurs et quantifier la prédation et la régulation. Nous avons également vu qu'identifier les prédateurs des différents stades de ce ravageur et quantifier l'effet de cette prédation sur la régulation du ravageur ne sont pas choses aisées. Les travaux présentés demeurent du champ de l'écologie appliquée à des systèmes agricoles. Même si dans certaines études menées, des mesures de rendement ont été réalisées, les questions centrales demeuraient *qui ?*, *quand ?* et *quelle intensité de régulation du ravageur ?*, avec comme objectif de rechercher un effet positif du contrôle biologique par conservation, notamment au travers de l'intensification écologique. Ainsi ces activités de recherche se situaient à un bas niveau de maturité technologique (Technology Readiness Level, TRL).

Dans le présent chapitre, je vais discuter de mes projets de recherches futurs qui se composeront d'une part d'activités se situant à des niveaux plus élevés de l'échelle TRL et d'autre part d'activités demeurant aux niveaux inférieurs de cette échelle. Si les thématiques centrales ne vont pas beaucoup évoluer et demeurer portées par des recherches sur l'intensification écologique, la régulation de bioagresseurs et la diversification des cultures, elles vont donc se situer à différents niveaux TRL et impliquer des approches variées. Dans les paragraphes qui suivent, je tente d'expliquer ces choix par une analyse brève et critique des travaux qui concernent mon domaine de compétences à l'échelle de la communauté scientifique.

Démarche du projet

Mon projet scientifique se découpera en 3 axes. Un premier axe où je poursuivrai mes recherches à l'échelle des processus biologiques au sein d'agrosystèmes et toujours en lien avec les interactions entre auxiliaires et bioagresseurs. Un second axe qui constitue un projet de recherche sur la diversification des systèmes de culture et l'agroforesterie à la Réunion avec une approche participative. Un troisième axe porté par le projet Sadur. Le détail que j'apporterai sur chaque axe reflète le degré de maturité de ces actions.

En premier lieu, je discuterai donc du projet de recherches en écologie comportementale, fortement axé sur les fourmis de feu tropicales *S. geminata*, et utilisant des méthodes issues des travaux de la thèse de Paul Tresson et des méthodes à développer. Cette partie reprend un projet de thèse qui débutera fin 2022 à la Réunion. Ce projet découle d'un mélange entre mes envies et intérêts de recherche et d'une demande d'acteurs locaux. En effet, depuis mon affectation en Martinique, j'ai développé un intérêt certain pour les fourmis et je souhaite donc m'orienter vers plus de recherches sur celles-ci, en particulier sur l'écologie comportementale, toujours dans l'aspect gestion des ravageurs et dans la dualité de profil de certaines espèces de fourmis qui sont à la fois ravageurs et auxiliaires. En outre le développement des technologies et de l'intelligence artificielle offre de nouvelles possibilités pour des études fines des interactions entre espèces. Ce projet de thèse provient également d'un besoin au niveau régional de gérer certaines espèces invasives de fourmis qui impactent négativement les cultures. Je vais ainsi m'orienter vers l'étude d'une autre culture, celle de l'ananas.

Arrête tes cochenilles !

A la Réunion comme dans d'autres zones de production, la culture de l'ananas est largement impactée par le complexe de virus du Wilt. Les cochenilles de l'espèce *Dysmoccocus brevipes* sont les principales cochenilles retrouvées sur ananas (Muller and Nibouche, 2016) et sont vectrices de ces virus (Sether et al., 1998). Pour limiter la propagation du complexe viral, il convient donc de lutter contre les cochenilles. Aujourd'hui, l'utilisation d'un insecticide (Spirotetramat) est la seule méthode de lutte existante. Cependant, d'autres agents interviennent dans ce complexe cochenilles-virus : les fourmis. Celles-ci entretiennent et protègent les cochenilles contre les prédateurs, tandis que ces dernières fournissent aux fourmis du miellat. Ce mutualisme complique grandement la régulation des cochenilles. En effet, les fourmis peuvent attaquer les prédateurs ou les empêcher (Offenberg, 2001) de se nourrir des cochenilles. De même, l'efficacité des parasitoïdes est diminuée par la présence de fourmis (Campos et al., 2006; Fanani et al., 2020; Feng et al., 2015; Tanga et al., 2015) et l'oviposition peut être jusqu'à 10 fois inférieure en leur présence (Fanani et al., 2020).

Il est considéré que l'agressivité des fourmis, et en conséquence le taux de prédation, est positivement corrélée au niveau de carbohydrates disponibles et consommés (Offenberg, 2001). Une augmentation de la quantité de carbohydrates disponibles favorise l'activité des ouvrières et l'agression de proies riches en protéines (Kay et al., 2010; Ness et al., 2009). La plupart des études montrent que la présence d'une ressource alternative de carbohydrates diminue la fréquentation des hémiptères par les fourmis (Carabalí-Banguero et al., 2013; Offenberg, 2001; Win et al., 2018). Quand certaines études ont montré que cette ressource alternative induit une prédation plus importante de pucerons (voir par exemple Offenberg, 2001), Win et al. (2018) n'ont pas observé de comportement d'agressivité ni de prédation de *Pheidole megacephala* envers *D. brevipes*. Similairement, Carabalí-Banguero et al. (2013) n'ont pas observé de prédation de *Solenopsis geminata* sur *D. brevipes*. Cependant, toutes ces études, qu'elles soient menées en laboratoire ou au champ, on été été réalisées sur des temps courts (16h à 28 jours), et celles menées en laboratoire n'ont pas considéré les effets des ressources alternatives sur la fitness des foumis, ni sur la croissance de leur colonie. Or ce mutualisme dépend des intérêts des deux espèces en interaction et il est nécessaire d'étudier les intérêts privés de chacune d'elles et le bien commun qu'elles s'apportent (Van Baalen and Jansen, 2001).

Par ailleurs, en milieu naturel, les plantes sont une source alternative de carbohydrates via les nectars floraux (NF) et les nectars extra-floraux (NEF). Des plantes produisant des NEF peuvent être utilisées dans une gestion intégrée des ravageurs (Jones et al., 2017). En effet, il a été démontré que le NEF attire et améliore les performances d'autres prédateurs (Koptur et al., 2015) et des parasitoïdes (Irvin et al., 2014; Irvin and Hoddle, 2015; Jamont et al., 2014). L'installation de plantes produisant des NEF dans les systèmes de cultures suit une stratégie de « attract-and-reward », qui a pour but d'attirer les ennemis naturels des herbivores (Simpson et al., 2011). Dans le cas du complexe fourmis-cochenilles sur ananas, l'installation de telles plantes pourraient possiblement permettre de: (i) diminuer la présence de fourmis sur ananas, amoindrir la protection de cochenilles et diminuer leur population ; (ii) rendre les fourmis plus agressives envers les ravageurs, et notamment les cochenilles (disruption du mutualisme) (iii) accroître la fitness de parasitoïdes et leur abondance sur ananas. De nombreuses espèces cultivées produisent du NEF (*e.g*. *Viscia sativa*, *Manihot esculenta, Vicia faba*) et leur association avec de l'ananas rentrerait dans une démarche d'agroécologie pour la protection des cultures.

Les fourmis pourraient également être impliquées dans la dispersion de *D. brevipes*. Certaines études montrent que *D. brevipes* peut coloniser des plants d'ananas grâce au transport par le vent (González-Hernández et al., 1999; Jahn and Beardsley, 2000), mais l'importance relative de ce mode de dispersion et du transport par les fourmis n'est pas connue.

Au travers d'exéprimentation au laboratoire, je m'atèlerai avec le futur doctorant, que j'encadrerai fin 2022, à répondre à 5 questions en vérifiant les hypothèses sous-jacentes (Box 1).

Les méthodes développées pour l'étude des interactions lors de la thèse de Paul Tresson seront utiles pour récolter les données en laboratoire mais également *in situ*. Avec William Puech, nous envisageons de poursuivre le développement méthodologique afin de pouvoir utiliser la vidéo pour suivre les individus et identifier le type d'interactions (ex : prédation, aggression, fuite, coopération). Le domaine de la vision par ordinateur, de par sa communauté active et sa culture de l'open-source, avance très vite. Ainsi, Romero-Ferrero et al. (2019). ont mis au point IdTracker.ai, un développement de Id.Tracker (Pérez-Escudero et al., 2014) utilisant les CNN et permettant de suivre des individus d'une même espèces (dont la fourmi *Diacamma indicum*) sans marquage. Depuis, d'autres algorhitme ou logiciel ont été développés (pour une revue, voir Panadeiro et al., 2021) et celui de Wu et al. (2020) est particulièrement intéressant car il permet le suivi d'individus non marqués en conditions simplifiées (laboratoire) mais aussi en extérieur avec un fond complexe (Figure 31).

Figure 31. Suivi de fourmis dans des scènes in situ grâce à la vision par ordinateur et les CNN. Extrait de Wu et al. 2020.

Box 1. Questions et hypothèses relative à la thèse "Interactions cochenilles-fourmis dans les systèmes de culture d'ananas à la Réunion"

Q1 : Quelles sont les espèces de fourmis les plus impliquées dans les interactions avec les cochenilles dans les sytèmes de culture d'ananas à la Réunion?

***H1 :** Les fourmis de l'espèce* Solenopsis geminata *sont les plus impliquées dans les interactions avec les cochenilles. Cela s'explique par leur dominance comportementale (agressivité) et écologique (numérique), par leur polydomie et leur polyginie qui leur confèrent un potentiel d'invasion d'une parcelle supérieure aux autres espèces. La fourmi à grosse tête (*Pheidole megacephala*) et la fourmi folle (*Paratrechina longicornis*) sont probablement les autres espèces impliquées dans les systèmes de culture d'ananas mais dans une moindre mesure.*

Q2 : Quel est l'effet de ressources alternatives sur la croissance et le développement de colonie ?

***H2 :** La croissance d'une colonie (fécondité, survie, polygynie) est dépendante des ressources : une colonie ayant accès à des ressources en carbohydrates plus importantes recherchera plus de sources protéiques et aura une croissance plus importante.*

Q3 : Quel est l'effet de ressources alternatives sur le taux de fréquentation des cochenilles par les fourmis pour récupérer le miellat ?

***H3 :** Une source alternative de carbohydrates va diminuer le taux de fréquentation des cochenilles. Une ressource plus importante en protéines va accroître le taux de fréquentation des cochenilles (en l'absence d'une source alternative de carbohydrate)*

Q4 : Quel est l'effet de ressources alternatives sur l'agressivité et le taux prédation des fourmis ?

***H4 :** Une source alternative de carbohydrates va accroître la prédation des cochenilles. Une source de protéine alternative va diminuer la prédation des cochenilles (en l'absence d'une source alternative de carbohydrate).*

Q5 : Quel est le rôle des fourmis dans la dispersion des cochenilles au sein d'une parcelle ?

***H5 :** Les fourmis ont un rôle actif dans la dispersion des colonies de cochenilles de par le transport de celles-ci d'une plante à une autre. Ceci est renforcée chez* S. geminata *par sa polygynie et sa polydomie.*

Ensemble, c'est tout

Si la compréhension des processus écologiques et des interactions au sein des communautés des agrosystèmes est essentielle, elle répond plus aux attentes des chercheurs concernés qu'à celles des acteurs du monde agricole. Kleijn et al. (2019) rapporte que, même si aux cours des dernières décennies les études scientifiques mettent en avant de plus en plus les avantages de l'intensification écologique et que les décideurs politiques soutiennent la mise en œuvre de pratiques favorisant la biodiversité au travers du financement de programme environnementaux, les agriculteurs [européens] voient en général très peu d'intérêt dans les pratiques agroécologiques. Ainsi, les agriculteurs [européens] tendent généralement à favoriser les pratiques qui interfèrent le moins avec les pratiques habituelles (Kleijn et al., 2019). Par exemple, ils préfèrent l'installation de haies ou d'arbres à la mise en place d'une plante de de couverture ou de bandes fleuris dans leur champ (Brédart et al., 2017). Le constat de Kleijn et al. (2019) est que les chercheurs tendent à se focaliser sur les processus induisant les services écosystémiques plutôt que sur les attentes des agriculteurs telle que la profitabilité. Bien sûr, des études montrent que l'intensification écologique induit en moyenne un rendement plus important (voir par exemple Jain et al., 2020). Mais seules quelques études ont démontré de manière convaincante que la biodiversité et les services écosystémiques rendus, tels que l'amélioration de la pollinisation ou la régulation des ravageurs produisent des avantages agronomiques ou économiques nets. Par exemple, Salazar-Díaz & Tixier (2019) ont montré que, dans des systèmes agroforestiers, si le revenu par plante de la plupart des cultures fruitières, de bois de chauffage et de bois d’œuvre augmentait avec le niveau de diversité de plantes, celui provenant des bananes et des cacaos diminuait. Sur l’ensemble des articles de la littérature montrant le bénéfice de l’intensification écologique sur la pollinisation ou sur la régulation de ravageurs qu’ils ont sélectionnées pour leur revue, Kleijn et al. (2019) relèvent que seules trois d’entre elles suggèrent que le bénéfice de rendement serait suffisant pour compenser le coût d’établir les éléments nécessaires à cette intensification (Morandin et al., 2016; Pywell et al., 2015; Tschumi et al., 2015). Un exemple de coût d’installation des bandes fleuries ou des haies peut être la perte d’une surface de la culture de rente. Ce coût est par ailleurs contexte dépendant et peut être prohibitif dans les zones à fortes contraintes agricoles où la valeur des terrains est élevée. Similairement, ces auteurs n’ont trouvé dans leur revue de la littérature uniquement deux études qui montraient que les bénéfices issus de l’augmentations de rendement dans le temps surpassaient les coûts pour l’agriculteur (Blaauw and Isaacs, 2014; Morandin et al., 2016).

Par ailleurs, les agriculteurs sont seul décideur de la gestion des zones cultivées et non cultivées de leur ferme. Leur décision de prendre ou non le risque d’appliquer une pratique d’intensification écologique, à la place de leurs pratiques habituelles, va nécessiter plus qu’une preuve de concept scientifique. Cela est exacerbé par le fait que, même si les études sur l’intensification écologique montrent en moyenne des avantages rendus par les services écosystémiques, il existe une forte variabilité et donc des incertitudes qui freinent l’adoption d’une pratique par les agriculteurs. De leur côté, les agriculteurs recherchent par eux-mêmes des innovations en testant des changements de pratiques (Hatt et al., 2018) et doivent être intégrés comme acteurs dans les programmes de recherche (MacMillan and Benton, 2014). Les innovations qu’engagent les agriculteurs peuvent être le fait d’initiatives personnelles ou d’une union de producteurs dans lesquelles l’échange d’information sur les pratiques est facilité. La science participative regroupant les différentes partie prenantes (agriculteurs, chercheurs, institutions, décideurs, citoyens) est une méthode inclusive qui permet de considérer les besoins et les contraintes de chaque acteur du système alimentaire[3]. Ce type d’approche permet d’établir un cahier des charges et de dresser des scénarios à tester auxquels les différents acteurs adhèrent dès le début du projet. Cependant, elle demande à chacun de sortir d’une zone de confort où les habitudes sont bien ancrées. Le chercheur doit élargir son domaine de recherche et s’approprier des méthodologies nouvelles, telles que le jeu sérieux (ComMod, 2005), qu’il doit transmettre au groupe de travail. C’est aussi dans ces réunions que le groupe de travail doit, dès le début du projet, définir les différents indicateurs qui permettront d’évaluer la qualité des scénarios testés. Le chercheur peut avoir comme indicateur un service écosystémique issu d’un processus biologique, alors que l’agriculteur voudra connaître l’impact de l’innovation sur sa marge brute et que le politique souhaitera connaître l’impact de l’innovation sur le développement de son territoire. Ainsi,

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[3] Voir le chapitre "Pourvu que Sadur !" pour une définition du système alimentaire.

l'accompagnement par la recherche dans l'approche participative doit être non-seulement transdisciplinaire pour l'étude des processus biologiques mais également intégrer les sciences économiques et sociales. Ces approches participatives sont importantes pour définir collectivement les projets de l'utilisation des terres, et ce plus particulièrement dans les zones subtropicales et tropicales où l'expansion de l'agriculture est aujourd'hui particulièrement forte (Laurance et al., 2014).

Je vais à présent discuter de conception et d'évaluation de systèmes diversifiés par une approche participative. Les connaissances et l'expertise, issues de mes travaux de recherche passés et de ceux de mes collègues sur les bioagresseurs de différentes cultures de fruits et légumes à la Réunion, peut permettre d'avancer vers la conception de systèmes diversifiés où l'intensification écologique répond aux attentes des agriculteurs. Je prévois de réaliser cela à travers la conception et l'évaluation de systèmes diversifiés de type agroforestier qui pourront servir de base à un transfert aux agriculteurs réunionnais tout en continuant une étude à l'échelle des processus biologiques.

Promenons-nous dans les bois

Comme expliqué plus haut, de nombreuses études sur l'intensification écologique et les services écosystémiques rendus ont été réalisées. Néanmoins l'applicabilité et l'adoptabilité des méthodes mais aussi la compréhension des processus nécessitent encore des recherches. En outre, l'idiosyncrasie propre aux agrosystèmes, que ce soit à l'échelle parcellaire, de l'exploitation ou paysagère, implique qu'il est difficile de généraliser les résultats obtenus dans les travaux de recherche agroécologiques.

A la Réunion la production locale couvre près de 75% des besoins en légumes frais et 65% des besoins en fruits frais (DAAF de la Réunion, 2020). Parmi ceux-ci, la tomate, l'ananas, la banane, les letchis et les mangues sont les principales cultures. Face à la pression de bioagresseurs, le recours aux pesticides et aux intrants demeure important et les cultures sont majoritairement de type monocultural. Des projets sont en cours pour concevoir des systèmes diversifiés en maraîchage, cultivés sans pesticides de synthèse (Systèmes de production Tropicaux 0 Pesticide de synthèse – ST0P, Ecophyto Dephy Expé) avec une évaluation, par mon collègue Joël Huat (Hortsys, CIRAD) sur le site expérimental du Cirad de Bassin Plat, des effets de la diversification sur les ravageurs mais aussi sur la viabilité économique de telles systèmes. Cette étude génèrera de nouvelles connaissances, lesquelles viendront s'ajouter au corpus de connaissances existant à la Réunion sur le service de régulation de différents bioagresseurs de ces cultures.

Dans mes perspectives de recherche, j'envisage de mettre en application ce corpus de connaissances dans un projet de conception et d'évaluation d'agrosystèmes diversifiés. En particulier, la demande locale en conception de système de type agroforestier devient plus prégnante (Eveno, 2021). Ce contexte offre une opportunité de coconstruire avec les acteurs locaux un projet répondant aux besoins des agriculteurs, des institutions et de la société civile pour le développement d'une agriculture réunionnaise durable. L'objectif étant à la fois de coconcevoir des agrosystèmes, d’en évaluer la valeur socio-économique et environnementale tout en continuant à analyser les processus biologiques présent dans ces systèmes.

Dans ce cadre, l’approche basée sur la théorie C-K (Concept-Knowledge) peut être utilisée (Hatchuel and Weil, 2003). Cette approche considère que la conception se compose de deux espaces distincts, celui des concepts C et celui des connaissances K, qui évoluent ensemble. L’espace des concepts contient des entités qui ne sont ni vraies ni fausses, tandis que l’espace des connaissances est un espace logique contenant des entités vraies ou fausses. Pour innover, il faut que des nouveaux concepts apparaissent dans l’espace C. Ces nouveaux concepts peuvent aboutir à d’autres concepts C ou à de la connaissance K selon une boucle d’interactions. Cette approche peut permettre d’améliorer la créativité autour d’innovations en faisant émerger des concepts qui peuvent être facilement expérimentés ou appliqués si l’espace des connaissances est déjà suffisant ou alors éclairer sur les expérimentations à mener pour acquérir les connaissances nécessaires à la réalisation du concept. Salembier et al. (2018) relie cette approche de conception innovante au domaine de l’agronomie en explorant les facteurs qui influencent les agronomes dans la conception de systèmes innovants (Figure 32). Ce type d’approche en agriculture a pu être utilisée en couplage avec le jeu sérieux et la modélisation d’accompagnement lors de la thèse de Pauline Della Rossa (Della Rossa, 2020; Della Rossa et al., 2022) dans le cas de la réduction de la pollution aux herbicides d’une rivière en Martinique. La modélisation d’accompagnement est une démarche d’appui à la gestion de ressources renouvelables issue du travail d’un collectif de chercheurs de ce domaine (ComMod, 2005; Étienne, 2013). Cette démarche repose sur un collectif de personnes, les parties prenantes, qui y participent activement. La démarche est notamment ponctuée par des temps forts collectifs qui sont le lieu d’échanges particuliers entre les parties prenantes. Lors du processus, les parties prenantes partagent leurs connaissances sur la problématique concernée mais doivent également s’engager dans la finalité du processus qui est de modifier le fonctionnement de système, de changer de paradigme. Au cours de ce processus, qui est généralement composé de boucles itératives, la modélisation permet d’appréhender la complexité de la problématique dans le monde réel en la simplifiant. Cela permet d’expliciter la problématique et de faire partager les points de vue des différentes parties prenantes sur le sujet. Cet apprentissage collectif permet de dresser des scénarios, de les tester ou encore de les modifier. La modélisation peut être le fait de jeux sérieux dans lesquels les acteurs jouent un rôle ou des simulations informatiques, généralement des modèles multi-agents (Grimm, 1999). Ces derniers sont d’un intérêt particulier car ils peuvent permettre au chercheur de voir comment des propriétés émergent au niveau du système à partir du comportement des individus (Grimm et al., 2006; Grimm and Railsback, 2006).

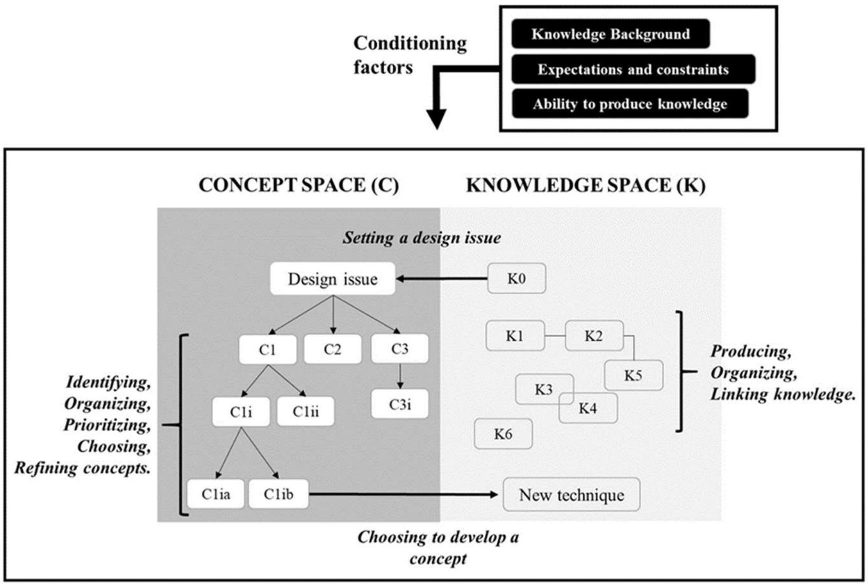

Figure 32. Représentation de la conception par l'approche C-K. Extrait de Salmenbier et al. 2018.

L'utilisation de ces approches permettraient ainsi de dégager un cahier des charges définissant les objectifs, les intérêts de chacune des parties prenantes, les indicateurs de réalisation des objectifs et le plan de mise en œuvre des actions.

Dans le cadre de projet de recherche-développement autour de l'agroforesterie à la Réunion, cette approche permettra de définir les types de systèmes étudiés. Quelles cultures sont à privilégier ? Sont-ce les cultures principales actuelles en horticultures et en maraîchage ? Quelles associations sont possibles ou envisageables sur la base des connaissances actuelles ? Quelles associations sont possibles ou envisageables sur la base des contraintes et envies des agriculteurs ? Faut-il créer des systèmes *de novo* (*e.g.* à partir de friches) ou modifier des systèmes de plantes pérennes existants ?

Les hypothèses sur les plus-values de tels systèmes sont également à établir. Un système agroforestier peut induire une meilleure stabilité de revenus pour l'agriculteur en étalant une production diversifiée sur l'année (Salazar-Díaz and Tixier, 2019). On peut également partir de l'hypothèse que l'utilisation de pesticides dans ces systèmes peut être réduite ou supprimée, par des effets de dilution ou d'une meilleure régulation des bioagresseurs comme tendent à le montrer les recherches passées. Les systèmes agroforestiers pourraient aussi être plus résilients ou résistants aux évènements extrêmes (cyclones, sécheresse) qui vont s'intensifier sous l'effet du changement climatique (Change, 2021). Les effets positifs sur la biodiversité peuvent également être une motivation des différentes parties prenantes. La prise en compte d'intérêt individuels et d'externalités comme le bien-être de l'agriculteur, le maintien de la diversité endémique ou de traditions, ou encore des retombées économiques extérieures à production (*e.g.* développement de l'agritourisme) sont également à considérer comme indicateurs.

J'aspire donc à mettre en œuvre un tel projet pour les années à venir dont la réalisation sera dépendante de ma capacité à rassembler un collectif de chercheurs, d'ingénieurs et de techniciens mais comprenant aussi les autres parties prenantes telles que les agriculteurs, les associations de producteurs, les opérateurs professionnels, les instituts techniques, les institutions et les décideurs politiques et à le porter en réponse aux appels à projets.

Dans ce projet embryonnaire, je maintiendrai des activités sur l'étude des processus en lien avec la régulation de bioagresseurs. En particulier, je projette de continuer à étudier le rôle des vertébrés et des invertébrés dans la régulation du charançon. Ces études porteront sur aussi sur l'effet d'éléments constitutifs de l'agrosystème dans la modulation de cette régulation. Par exemple, au travers de l'installation d'habitats favorables à certaines espèces, comme des haies, des mares ou des plantes à nectaires extra-floraux. Ou encore sur l'agencement spatial d'un couvert végétal à partir des pistes issues du modèle de Blanche Collard. Au niveau des bioagresseurs foliaires du bananier, les impacts sur la dynamique de la cercosporiose eumusae et du freckle seront analysés.

Plus globalement, avec le collectif qui sera engagé dans un tel projet, je travaillerais sur les bioagresseurs et auxiliaires d'autres cultures. J'ai déjà engagé un pas dans ce sens en intégrant l'encadrement de la thèse de Thibaut Nève (2022-2025), co-encadrée par Anaïs Chailleux (UR Hortsys, CIRAD), Joël Huat (UR Hortsys, CIRAD), Julien Haran (UMR CBGP, CIRAD) et dirigée par Marie-Stéphane Tixier (L'Institut Agro). Lors de cette thèse sur la biodiversité et amélioration de la régulation naturelle des arthropodes ravageurs, Thibaut cherchera à identifier les bioindicateurs les plus pertinents du niveau de la régulation naturelle. Il étudiera les réseaux trophiques en jeu dans des systèmes en rotation de cultures de solanacées, astéracées et cucurbitacées de la Réunion, en mobilisant des outils de métabarcoding et d'analyses d'images. Dans le cadre de ces recherches, je continuerai d'utiliser des méthodes basées sur l'analyse d'images prises *in situ* (camera trap, photographie time lapse, vidéo…) adaptant et développant des méthodes décrites dans ce mémoire.

Pour terminer, je vais discuter de l'approche 'de la fourche à la fourchette' du projet SADUR. Si dans cette partie, je reviendrai également sur la conception et l'évaluation d'agrosystèmes, il y sera plutôt question de sortir de la parcelle et de prendre la posture d'une vision d'ensemble, incluant les différents acteurs impliqués dans le système alimentaire de la Réunion.

Pourvu que Sadur !

Ces 3 dernières années, depuis mon affectation à la Réunion, mon implication dans l'axe 3 de mon unité de recherche (*Conception et évaluation de systèmes de cultures innovants et durables*) a largement crû. En débutant des activités d'essais variétaux de bananiers (pour plus de détails, voir *Annexe 1 ou ce que j'ai laissé de côté*) sur la Réunion, j'ai commencé à interagir étroitement avec mes collègues de l'UMR Qualisud, notamment au travers de questionnements sur la qualité post-récolte. Par la suite, les aspects filières et commercialisation ont commencé à être abordés avec Claire Cerdan, une collègue géographe de l'UMR Innovation, et avec des acteurs locaux de la filière fruits et légumes. De par l'arrivée récente de nouveaux collègues de l'UMR Qualisud, avec des compétences en transformation des produits, l'envie et l'intérêt de travailler en collaboration avec ces collègues et les différents acteurs locaux sur l'entièreté de la chaîne, depuis la production jusqu'au consommateur, a pris de l'importance. Cette volonté de relier le système alimentaire de la Réunion à nos activités de recherche a abouti au projet SADUR (Système Alimentaire Durable en milieu insulaire, Figure 33). Un système alimentaire comprend tous les éléments (ressources naturelles, personnes, intrants, processus, infrastructures, institutions, produits, etc.) et activités liées à la production, à la transformation, à la distribution, à la préparation et à la consommation des aliments et aux extrants de ces activités, y compris les impacts socio-économiques et environnementaux (Timmermans et al., 2014). Un système alimentaire durable est un système alimentaire qui assure la sécurité alimentaire et la nutrition pour tous de manière à ne pas compromettre les bases économiques, sociales et environnementales de la sécurité alimentaire et de la nutrition des générations futures (Loconto, 2020; Timmermans et al., 2014).

Dans ce projet que je coordonne avec ma collègue Layal Dahdouh, les objectifs finaux sont (i) de transférer et d'accompagner des innovations techniques et marchandes issues de nos activités de recherche et développement sur les interactions plantes-bioagresseurs en agroécologie, les itinéraires techniques de productions agroécologiques et sur la valorisation des ressources locales par conservation, transformation et stabilisation et (ii) évaluer les impacts économiques, environnementaux et nutritionnels de ces innovations.

Par ailleurs, les projets alimentaires territoriaux (les PATs), issus de la loi d'avenir pour l'agriculture, sont des initiatives collectives qui cherchent à répondre à une problématique locale de façon concrète aux visées sociales, économiques et environnementales. Les PATs peuvent être à différentes échelles spatiales, allant de la commune au territoire national.

Le nombre de PATS sont en large expansion au niveau national en général et à la Réunion en particulier, où l'on en dénombre aujourd'hui sept. Ces PATS réunionnais forment un contexte favorable à ce transfert et à cet accompagnement des innovations que nous visons à produire, que ce soit des nouvelles variétés de fruits ou légumes, de procédés de transformation pour des petites unités ou encore une pratique culturelle visant à réduire la pollution de bassins versants par des pesticides.

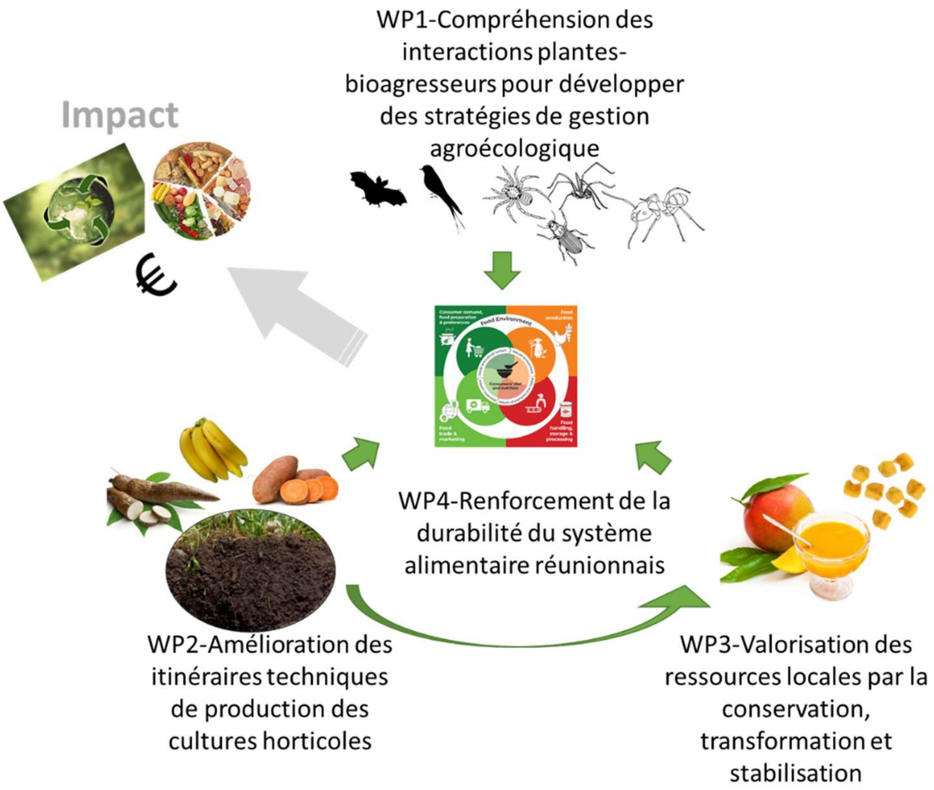

Figure 33. Les 4 Work Packages du projet Sadur.

Direction de recherches

Dans ces cours chapitres, je vais exposer brièvement ma vision de l'encadrement de doctorants puis de la recherche.

J'peux vraiment pas l'encadrer !

Encadrer un doctorant doit être un investissement pleinement réfléchi. En premier lieu, il faut que le sujet de thèse soit suffisamment abouti pour qu'il garantisse au doctorant un sujet réfléchi, réalisable et stimulant. Autrement dit les questions de recherche, les hypothèses et la méthodologie doivent être clairement établies et les moyens humains techniques, financiers et humains nécessaires doivent être prévus. Cependant, un déroulé de thèse n'est pas figé par le sujet initial et les recherches menées au cours de la thèse peuvent dévier de la trajectoire initialement prévue. Cela en raison des résultats obtenus au cours de la thèse mais aussi selon le doctorant et la façon dont il s'est approprié le sujet. Ces déviations relatives au doctorant lui-même dépendent de sa personnalité, de son affection particulière pour, ou son aversion envers, telle ou telle discipline, ses projets personnels et professionnels. Aussi, un début de thèse est un peu en soi un saut vers l'inconnu, tant pour le doctorant que pour ses encadrants. Il convient, selon moi, que le ou les encadrants joue à ce niveau un rôle de guide, d'accompagnateur, laissant le doctorant prendre un chemin de traverse quand sa pertinence nous semble convaincante, et à l'inverse empêcher le doctorant de se perdre dans les méandres du fleuve de la dispersion.

Si l'obtention de l'habilitation à diriger des recherches dépasse le fait d'avoir la possibilité de diriger pleinement une thèse, c'est tout de même ce sésame qui me motive en premier lieu. Des trois thèses que j'ai co-encadrées, j'ai pu retenir trois scénarios différents. La première thèse que j'ai co-encadrée était celle de Charlotte Poeydebat, avec Luc de Lapeyre comme co-encadrant et Philippe Tixier comme directeur de thèse. Outre tout ce que m'a apporté cette thèse en expérience de co-encadrement, j'ai le ressenti que l'influence partagée entre la doctorante et les 3 encadrants étaient harmonieuse. Harmonieuse dans le sens où la concertation sur les voies à prendre au cours du déroulé de la thèse était pleine et les décisions finales étaient issues de consensus. Dans la thèse de Blanche Collard, je fais le constat de deux différences notables. Premièrement, je n'étais à l'origine du sujet de thèse mais j'ai été invité par mes collègues Claire Lavigne et Thomas Delattre de l'UMR PSH (INRAE Avignon), que je remercie d'ailleurs pour cette aventure scientifique et humaine, à encadrer Blanche dans la partie concernant les agrosystèmes bananiers. Deuxièmement, et c'est là sans doute la différence majeure, je n'étais pas l'encadrant au quotidien. C'est deux différences résultent en une implication moins forte, et une donc une influence moins forte, dans la réalisation de la thèse. Ce constat est un ressenti et est peut-être faux. C'est aussi peut-être vrai et propre à moi, en quel cas je serai à blâmer. Enfin, dans la dernière thèse que j'ai encadré avec William Puech, que je remercie à nouveau d'avoir accepté de nous accompagner dans ce voyage "agronumérique", et Philippe Tixier, que je remercie d'être toujours là pour me soutenir, le scénario est encore différent. Etant à l'origine du projet de thèse, j'ai sans doute été plus sensibles aux déviations prises lors du déroulé de la thèse, déviations, qui, si dans la thèse de

Charlotte étaient des consensus, ont été pour moi ici plus des compromis. L'obtention de l'HDR est pour moi ainsi importante car elle me permettra de moins partager la barre avec d'autres encadrants et de tracer la route sur la carte doctorale vers les destinations établies avec le doctorant. Ceci étant dit, le co-encadrement de la thèse de Paul fut un réel plaisir, et je le crois, une réussite par et pour Paul !

Comme évoqué dans l'avant-propos du présent mémoire, l'encadrement d'une thèse doit répondre à trois objectifs. En premier lieu, et c'est une évidence, il est du devoir de l'encadrant de former le doctorant à l'approche scientifique de la recherche tout en laissant de laisser le doctorant exprimer sa créativité. Ceci inclut un transfert de connaissances, de méthodologie, d'éthique. Ce transfert vise bien sûr à développer non seulement les compétences du doctorant mais aussi son autonomie dans la démarche de chercheur. Le deuxième objectif que, selon mon opinion, se doit de réaliser l'encadrant est de remplir son rôle de facilitateur. L'encadrant doit pourvoir aux bonnes conditions de travail de son étudiant, que ce soit au niveau des moyens techniques, financiers et humains, ou en mettant en relation l'étudiant avec des collègues ou des partenaires quand la solution ne peut venir de lui-même. Pour cela, l'encadrant doit se comporter avec une certaine bienveillance envers son étudiant. Ces deux objectifs remplis, l'encadrant devrait atteindre le troisième, celui d'avoir donné l'envie de choisir notre merveilleux métier pour son avenir !

Plus on est de fous, moins y'a de riz

Ma façon de travailler a bien évoluer depuis mon intégration au Cirad. Au début de ma carrière, je travaillais de façon plutôt solitaire et cherchais à réaliser tout par moi-même, sans jamais déléguer. Ceci pouvait venir de mon expérience doctorale et postdoctorale au cours desquels j'ai été amené à travailler la plupart du temps seul, ce que je ne souhaitais pas cependant. Cela pouvait venir aussi de ma propre personnalité. Quoiqu'il en soit, j'ai par la suite été amené à travailler en collectif (de gré ou non), et y voir des points parfois négatifs mais souvent positifs. Coconstruire un projet de recherche, s'ouvrir aux disciplines des autres, manager un collectif, partager le professionnel et le personnel au quotidien avec l'ensemble du collectif de recherche, aider et se faire aider rend notre travail plus agréable, motivant, efficace et pertinent. Mais je garde néanmoins une part de travail personnel, sur les sujets de recherche que j'affectionne particulièrement, tel que la myrmécologie et la vision par ordinateur, deux domaines auxquels, pourtant, je ne consacre pas assez de temps.

De manière plus vaste, le collectif ce sont aussi les pairs et le travail de révision d'articles ou de projets. C'est une tâche de fond que chaque chercheur est amené à réaliser et qui est indispensable à la recherche scientifique dans ce monde où le fameux *publish or perish* a fait et fait tant de dégâts. Dans ce travail de révision, je suis un jour tombé sur un manuscrit pour lequel je suspectais, et le terme est faible, une fraude scientifique. Comme pour beaucoup de choses dans la vie, il est une chose d'entendre parler de fraude scientifique, il en est une autre d'en voir une de ses propres yeux. J'étais déjà attentif à cette problématique avant de recevoir ce manuscrit. Soit par l'entrefaite de sites web dont c'est l'objectif de détecter des recherchées publiées alors que frauduleuses. Soit par le fait que parfois, s'il n'y a pas fraude, je trouvais en lisant les annexes comprenant les données et les analyses statistiques, que ces dernières étaient, disons-le gentiment, globalement peu convaincantes et les conclusions des chercheurs largement exagérées. Et pourtant, cela n'empêche pas leur publication dans des revues de rang A et d'être par la suite citées par un nombre conséquent d'auteurs. Aussi aujourd'hui veille-je à rendre accessible les données, les analyses statistiques ou encore les codes publiés. Ceci par un souci de transparence mais aussi parce qu'il faut considérer que chacun d'entre nous peut commettre des erreurs involontaires. L'accès ouvert aux données et analyses permet à la communauté, scientifique ou non, d'être en mesure de vérifier les travaux publiés.

A titre d'anecdote, après avoir conseillé à l'éditeur de rejeter le manuscrit car je suspectais une fraude scientifique, j'ai reçu quelques semaines après une invitation à réviser un manuscrit pour un autre journal. Il s'est avéré que c'était le même manuscrit… Certains n'ont vraiment pas de chance !

C’est votre dernier mot ?

Et voilà, vous avez atteint la fin de ce mémoire. Je vous remercie de l’avoir lu, espérant que vous ayez trouvé cette lecture intéressante, agréable et un minimum instructif.

Vous pouvez maintenant fermer manuellement ou numériquement ce document, si vous comptez le relire, ou le jeter dans la corbeille, qu’elle soit réelle ou virtuelle…

Attendez un moment ! Avant cela, si le cœur vous en dit il y a une petite annexe à lire juste après...

Annexe 1 ou ce que j’ai laissé de côté

Pour la rédaction de cette HDR, j’ai fait le choix de présenter principalement mes recherches sur le contrôle biologique du charançon. Je vais dans cette annexe décrire brièvement d’autres activités de recherche passées et actuelles.

Et si on s’associait ?

Le modèle développé avec Charlotte Poeydebat (Poeydebat et al., 2016) [ACL7] utilisait une approche générique basée sur les processus qui prenait en compte les effets d’une plante associée au bananier et ceux de ravageurs foliaires et des racines (Figure 34). Outre la volonté de conceptualiser et théoriser la diversification des agroécosystèmes, un des objectifs était de quantifier les niveaux de services régulation de régulation des bioagresseurs que devrait fournir l’agroécosystème diversifié pour atteindre un niveau de rendement comparable à une monoculture.

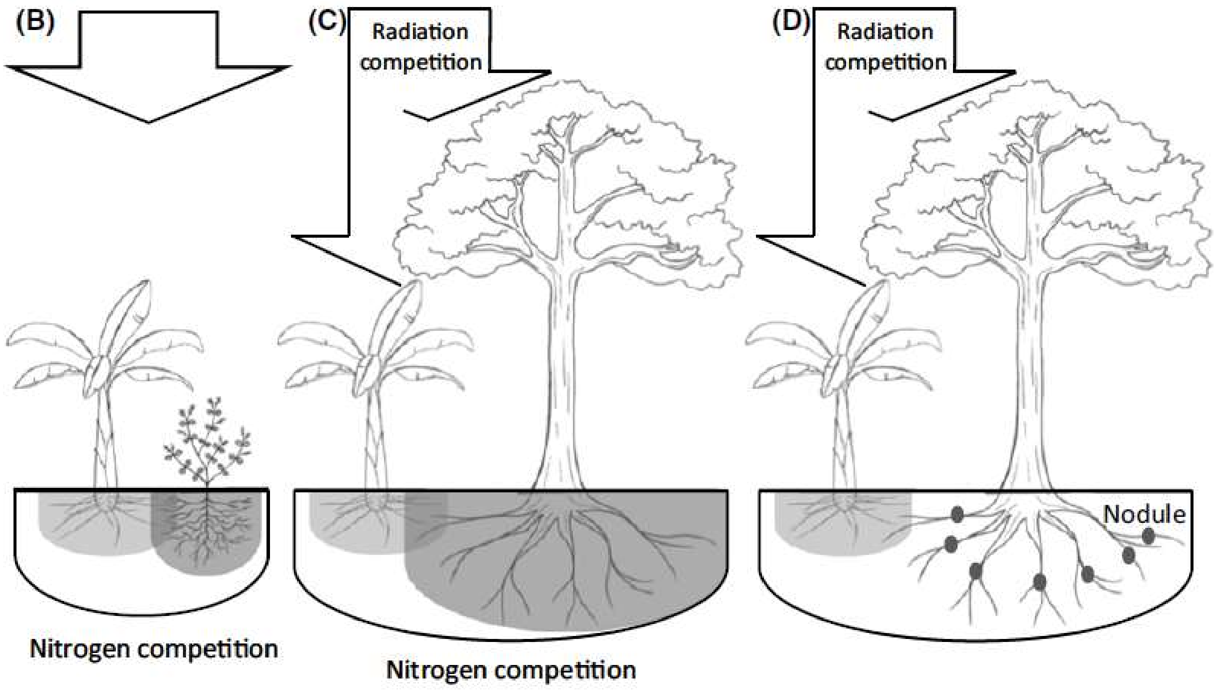

Figure 34. Les 3 types d'associations modélisées.

Les propriétés de la communauté en termes de partage des ressources (dans notre cas azote et lumière) et de régulation des bioagresseurs (racinaires et foliaires) déterminent respectivement les quantités de ressources disponibles pour la culture (ici le bananier) et de la fonctionnalité de ses organes. Elles déterminent donc conjointement la performance de la culture. La sensibilité de la culture (en termes de biomasse) aux dégâts des bioagresseurs dépend de la disponibilité des ressources. Dans des conditions de ressources élevées, la culture peut supporter des niveaux de dégâts des bioagresseurs plus importants en association qu’en peuplement monospécifique, notamment en lien avec le stress azoté que peut subir le bananier. Pour plus de détails sur les résultats obtenus, vous pouvez vous référez au manuscrit de thèse de Charlotte (Poeydebat, 2016), notamment la partie 3.2 de la discussion dont j'ai repris ci-dessus l'essentiel.

Comme disait Leeloo Wallace : "multi-pest !"

Dans la thèse de Charlotte Poeydebat, les travaux sur le gradient de diversité ne se résumaient pas à la régulation des charançons et aux réseaux trophiques d'invertébrés. L'effet du gradient de diversité sur les nématodes phytoparasites (Poeydebat et al., 2017b) [ACL12] et sur la cercosporiose noire du bananier (Poeydebat et al., 2018) [ACL14] ont également été étudiés afin d'avoir une vision "multi-pest" des systèmes. Les résultats obtenus pour la cercosporiose vont dans le même sens que ceux obtenus pour le charançon du bananier : la richesse végétale de la strate basse (<5m) favorise les régulations (Figure 35). Pour les nématodes, la richesse végétale totale n'a pas eu d'effet significatif sur les abondances des nématodes phytoparasites ni sur les dégâts de ces bioagresseurs. Cela est probablement lié au caractère généraliste des nématodes phytoparasites qui sont plus sensibles à l'identité des plantes (statut d'hôte) qu'à la richesse en général.

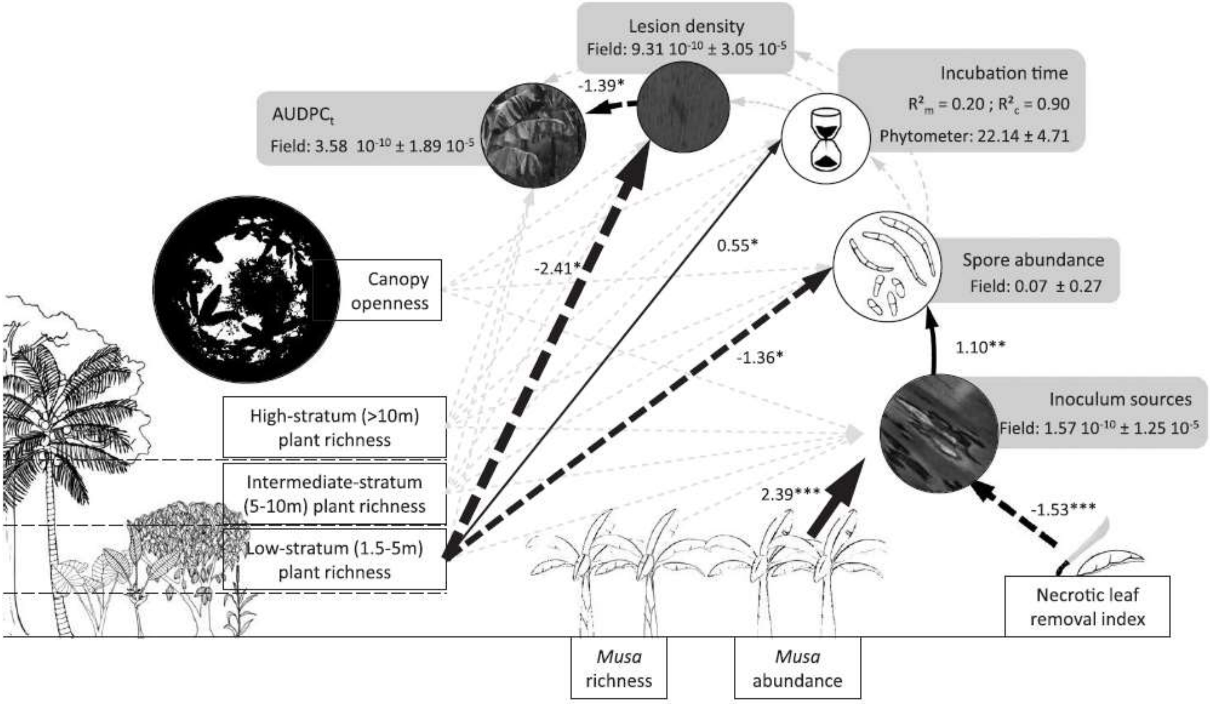

Figure 35. Modèle d'équation structurelle des relations entre les paramètres de la maladie des raies noires (BLSD) (boîtes grises) et les caractéristiques de la communauté végétale et les pratiques d'effeuillage (cases blanches bordées de noir).
Les flèches représentent les relations causales entre les variables. Les flèches pleines noires indiquent des relations positives et les flèches en pointillés noirs indiquent des relations négatives significatives. Les flèches en pointillés gris indiquent des relations non significatives (p-value >0.05). L'épaisseur des chemins est proportionnelle aux valeurs normalisées des coefficients de chemin. Les R^2m et R^2c (*i.e.* R^2 marginal et conditionnel) des sous-modèles sont fournis dans les cases de variables de réponse correspondantes. La valeur et l'écart-type associés à l'effet aléatoire (champ ou phytomètre) dans chaque sous-modèle sont fournis dans la case de la variable de réponse correspondante.

Et si on jouait à cache-cache ?

Dans la thèse de Blanche Collard, outre le modèle de mouvement de dermaptère dans les parcelles de bananiers, nous avons mené une étude de l'effet du couvert (sol nu, herbe, résidus) sur le déplacement d'*Euborellia caraibea* en milieu contrôlé à l'aide d'images vidéo. Dans cette partie de sa thèse, Blanche a travaillé sur le développant d'une méthode de suivi d'individus dans des environnements homogènes ou hétérogènes en conditions contrôlées (Collard et al., 2022, preprint). Le mouvement du dermaptère, et donc son comportement de fourragement, est susceptible d'être influencé par la couverture du sol. Cependant, l'analyse des mouvements à l'intérieur d'une parcelle agricole nécessite de collecter des images de haute définition à petite échelle spatiale, ce qui soulève des obstacles techniques. Lors de ces expériences, le dermaptère, marqué à l'aide d'un matériau réfléchissant (Figure 36), se déplaçait dans une arène comportant uniquement du sol nu ou bien des zones couvertes de résidus (Figure 37). Dans ce dernier environnement, le dermaptère disparaissait régulièrement et pour des durées variables sous les résidus, rendant difficile la reconstruction des trajectoires. Le fait que le dermaptère présente une activité nocturne ne facilite pas les choses. La méthode développée permet de surpasser ces contraintes et de reconstruire la trajectoire d'*E. caraibea* (Figure 38).

Figure 36. Un individu *Euborellia caraibea* avec son marquage réflecteur.

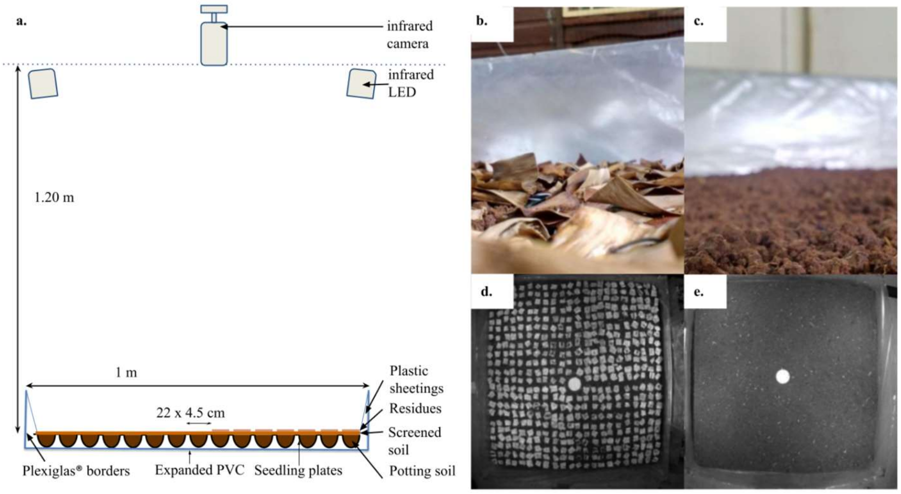

Figure 37. Détails du dispositif expérimental.

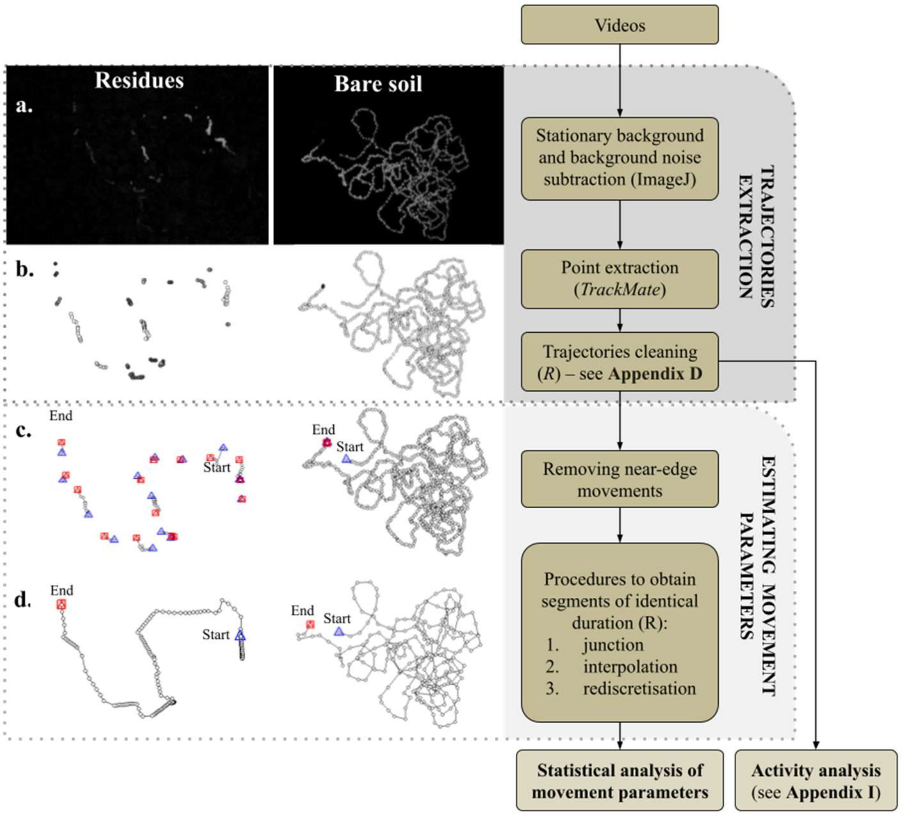

Figure 38. Descriptif de la méthodologie utilisée pour reconstruire les trajectoires des dermaptères.

Elles sont belles mes bananes ! Elles sont belles !

Depuis mon affectation il y a près de 3 ans à la Réunion, je ne suis plus seulement impliqué dans l'axe 1 de l'UR GECO mais également dans l'axe 3. Qu'est-ce que cela signifie ? Eh bien qu'auparavant je travaillais (quasi) uniquement sur la thématique "Dynamique des bioagresseurs et des communautés en conditions d'intensification écologique" et qu'aujourd'hui mon temps de travail est partagé avec une autre thématique intitulée "Conception et évaluation de systèmes de cultures innovants et durables".

Dans ce cadre, je mène des essais sur des nouvelles variétés de bananes à la Réunion. Ces évaluations sont d'ordre agronomiques, phytosanitaires mais aussi en lien avec la qualité post-récolte, la commercialisation et l'adoption de ces variétés. Un premier essai d'évaluation concerne six variétés (Figure 39) : deux variétés Cavendish comme témoins (MA13 et 902), 3 nouvelles variétés du Cirad (925, 931 et 938) et la Red Dacca.

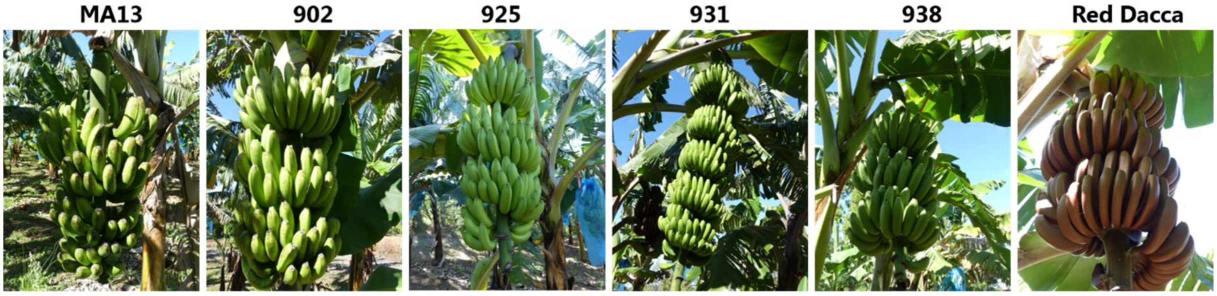

Figure 39. Les 6 variétés de bananes desserts en cours d'évaluation.

Les performances et le profil agronomiques sont évalués au travers du suivi de la croissance, des intervalles plantation-floraison-récolte, du poids et la configuration du régime (taille, nombre de mains et de doigts). Les variétés sont également évaluées selon leur comportement vis-à-vis de la cercosporiose eumusae (*Pseudocercospora eumusae*) et le freckle (*Phyllosticta cavendishii*), principaux bioagresseurs des bananiers à la Réunion.

Mais l'évaluation ne s'arrête pas au champ. Le comportement post-récolte doit aussi être évalué. Cela demande des expérimentations pour définir la qualité fonctionnelle et sensorielle des fruits. Je collabore donc étroitement avec mes collègues de l'UMR Qualisud (Christian Soria, Mathilde Hoarau et Mathieu Lechaudel) pour établir cette caractérisation variétale, et cela au travers du co-encadrement de stages dans le projet Sadur.

Ce travail s'effectue également au travers d'un réseau d'acteurs que j'ai construit et que je construis encore. Ce réseau intègre des agriculteurs, l'Armefhlor, les pépinières, les coopératives et l'association réunionnaise de fruits et légumes (ARIFEL) ou encore des magasins de fruits et légumes (*e.g.* Terra Coop), et vise à l'intégration d'autres acteurs comme les transformateurs. Il s'agit donc d'une approche qui intègre l'ensemble de la filière, filière qu'il est nécessaire de bien connaître. C'est pourquoi, je collabore avec Claire Cerdan, géographe (UMR Innovation, CIRAD) à travers le co-encadrement d'un stage visant à définir les acteurs de la filière en post-récolte (agriculteurs, bazardiers, marché forains, grandes et moyennes surfaces, transformateurs…) et à identifier les différentes pratiques relatives au murissage, à la conservation et à la mise en vente et à la transformation des bananes.

Ces évaluations variétales ont aussi une composante multisite, afin de caractériser leur comportement dans différentes situations pédoclimatiques mais aussi sociétales, avec des essais en Martinique et en Guadeloupe menés par mes collègues Frédéric Salmon (UMR AGAP, CIRAD) et Mathieu Lechaudel (UMR QUALISUD, CIRAD).

Dans le cadre de cette diversification variétale, j'évalue également la variété CARBAP-K74 au sein d'un système l'associant à de l'ananas sans usage de pesticides, avec mon collègue Adrien Négrier (UR GECO, CIRAD, Figure 40). Enfin, je travaille à la diversification de la culture de bananiers à la Réunion au travers de la recherche de variétés locales de bananiers et plantains pour la confection d'une collection.

Figure 40. Essais Bananas, associant la variété de bananier Carbap-K74 à de l'ananas Victoria dans un système sans pesticides.

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Annexe 2 – Tirés à part des principales publications

N.B. Les auteurs dont le nom est ci-dessous souligné sont les doctorants que j'ai co-encadrés.

Carval D., Resmond R., Dassou A. G., Cotté V., Achard R. & Tixier, Philippe. 2022. Influence of a cover crop on ants and dermapterans in banana plantations: consequences for the regulation of the banana weevil. *International Journal of Pest Management* (*online*) (A). https://doi.org/10.1080/09670874.2022.2029972. (A)

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Influence of a cover crop on ants and dermapterans in banana plantations: consequences for the regulation of the banana weevil

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ABSTRACT
The banana weevil *Cosmopolites sordidus* Germar is the most important pest of banana and plantain. In banana agroecosystems, cover cropping is a practice that prevents the use of herbicides and may provide natural habitats for generalist predators. Here, we assessed the effect of a cover crop, *Paspalum notatum* Flüggé on the ant community, dermapterans and *C. sordidus*. In investigating the dumps of *Pheidole jelskii* Mayr colonies, we found that most of carcasses belonged to other ant species (> 96%) and very few (< 1%) belonged to *C. sordidus*. In plots with banana plants and with and without a cover crop, the occurrences of almost all ant species were negatively correlated with each other, but the occurrence of ants was not correlated with weevil abundance. However, we found a negative relationship between the abundances of dermapterans and *C. sordidus*, both of which were negatively related to presence of the cover crop. These results indicate that dermapterans are probably the main biological control agents of *C. sordidus* and that cover cropping may increase *C. sordidus* regulation.

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1. Introduction

Banana ranks 14th in terms of crop production and is the second most produced fruit worldwide (FAO 2018). The banana weevil *Cosmopolites sordidus* Germar is the most important pest of banana and plantain (Gold et al. 2001, Okolle et al. 2009). Banana weevil females lay eggs in small cavities in the corm or lower pseudostem of banana plants (Cuillé 1951). The larvae bore galleries as they feed on the corm, which weakens the plant and causes yield losses as high as 100% when plants topple before harvest (Gold et al. 2001).

Integrated pest management strategies to reduce weevil infestation include fallow, crop rotation, clean planting material, trapping and pesticides (Budenberg et al. 1993; Beauhaire et al. 1995; Gold et al. 2001; Rhino et al. 2010; Duyck et al. 2011; Okolle et al. 2020). Application of chlordecone in the French West Indies during two decades led to major public health problems (Devault et al. 2018; Joachim et al. 2019). Therefore, alternatives to pesticides must be found to complete the actual integrated pest management strategies. The conservational biological control represents a sustainable way to contribute to pest management. As other parts of integrated pest management strategies (Kogan 1998), it can contribute to a reduction in pesticide use. The contribution of natural enemies to pest management was estimated as being more important than pesticides (Pimentel and Burgess 2014). The conservational biological control relies on the statement that diversity of natural enemies may be conserved or increased through maintaining natural habitats in agrosystems, and that, in return, natural enemies would contribute to pest regulation (Begg et al. 2017). Several studies have been conducted to look for natural enemies of *C. sordidus* (Tresson et al. 2021). Among the identified potential predators (see Tresson et al. 2021 for a review), dermapterans and ants seem to be of a particular interest in *C. sordidus* management (Koppenhöfer et al. 1992; Abera-Kalibata et al. 2006, 2007, 2008; Mollot et al. 2012; Carval et al. 2016; Tresson et al. 2019). Koppenhöfer et al. (1992) searched for potential predators of the banana weevil in Kenya and assessed their feeding capacity in laboratory experiments. They found that the earwig *Euborellia annulipes* Lucas (Dermaptera) was able to feed on egg and larval stages of the weevil. Abera-Kalibata et al. (2006)

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conducted field surveys for natural enemies of *C. sordidus* in the Indo-Malay region, from which the banana weevil is supposed to have originated (Waterhouse 1998). Among the detected predators, the histerid *Plaesius javanus* Erichson larvae and adults attacked larvae and pupae of *C. sordidus* in laboratory experiments. Abera-Kalibata et al. (2006) also reported the direct observation of individuals of the predaceous ant *Myopopone castanea* Smith preying upon *C. sordidus* larvae in crop residues. Elsewhere, sentinel experiments have shown that the tropical fire ant *Solenopsis geminata* Fabricius prey upon eggs of *C. sordidus* (Mollot et al. 2012; Tresson et al. 2019). Abera-Kalibata et al. (2008) demonstrated the ability of two ant species (*Odontomachus troglodytes* Santschi and one species of the *Pheidole* genus) to prey upon naturally layed eggs in banana corms. In French West Indies, studies have identified the earwig *Eurborellia caraibea* Hebard (Dermaptera) and the ant species *S. geminata* and *Camponotus sexguttatus* Fabricius as potential predators of the banana weevil (Mollot et al. 2014; Carval et al. 2016).

Among plant diversification practices, the addition of a cover crop represents the minimal increase of plant diversity in monocropping agrosystems. The first ecological service provided by cover crops is the replacement of herbicide treatment. Elsewhere, the cover crop may also increase the quantity of available resources (food and habitats) to alternative prey (Chailleux et al. 2014) and natural enemies, resulting in a modification of their diet (Duyck et al. 2011; Mollot et al. 2014). However, the modification of trophic networks induced by the addition of a natural habitat, such as a cover crop, does not systematically result in an increase of the regulation of a target pest (Tscharntke et al., 2016).

In the present study, we present a 3-year survey of an ant community, dermapterans, and *C. sordidus* in bare soil and cover cropped banana fields. We aim to (i) investigate on trophic relationships between the dominant ant species of the community and other ants, dermapterans and *C. sordidus* by analyzing colony dumps; (ii) assess the influence of the addition of a cover crop on the ant community, dermapterans and *C. sordidus*.

2. Materials and methods

2.1. Study site and experimental design

The experiment was conducted in Martinique (French West Indies) between July 2012 and April 2015 on an experimental farm in Rivière-Lézarde (14°39'45.04'N; 60°59'59.08'W) in an area initially free from weevil. Six plots were established, each with an area of 361 m^2 and with 49 banana plants (Cavendish Grande Naine cultivar). The banana plants were planted on 24 July 2012. The cover crop *Paspalum notatum* was planted in three of the six plots on 11 June 2012, while the other three plots were maintained with bare soil. The plots with the cover crop and with bare soil are hereafter referred to as CCP and BSP, respectively. On 30 of October 2012, 70 banana weevils (sex ratio 1:1) were added to each plot. Each month, banana plants were uniformly fertilized, the cover crop was cut back and weeds were controlled with herbicide (glyphosate) in BSP.

2.2. Sampling of banana weevils and earwigs

Banana weevil and dermapteran abundances were estimated with banana pseudostem traps (pieces of pseudostems 30 cm long cut in half lengthwise) from December 2012 to April 2015, first monthly until November 2013 then in January 2014, April 2014, June 2014, October 2014 and April 2015. At each sampling date, new pseudostem traps, were deposited at the bottom of each banana plant (49 traps per plot), and weevils and earwigs found in the traps 7 days later were counted (Koppenhöfer et al. 1992; Gold et al. 2001). Two species of dermapterans were retrieved: *Euborellia caraibea* and *E. annulata* Dohrn (Brindle 1971). However, earwigs were counted and released at field, and it was impossible to distinct the two species during this sampling.

2.3. Ant sampling

Ant abundances and occurrences were estimated from July 2012 to April 2015, first monthly until November 2013 then in January 2014, June 2014, October 2014 and April 2015. We placed 12 white ceramic tiles (30 × 30 cm) in each plot at each sampling date. In each subplot, we measured ant occurrence by using canned tuna-honey baits. One bait, which had a diameter of 4 cm was placed in the centre of each ceramic tile. Each tile was sampled 15 and 90 minutes after the baits were deployed. At each sampling time, we identified and estimated the number of individuals of different species present on the tile using the following six-point scale of scores: 1 = 1 ant, 2 = 2-5 ants, 3 = 6-10 ants, 4 = 11-20 ants, 5 = 21-49 ants and 6 ≥ 50 ants (Andersen 1997; Parr 2008; Baccaro et al. 2010). From abundance data, we obtained presence-absence data and we calculated the occurrence of each species among a plot at each sampling time of each sampling date. Samples of all species were collected and conserved in 70% alcohol then we performed identification to species. Sampling was performed between 7:00 and 11:00 in the morning.

2.4. Dominant analysis

We used the percentage of bait controlled as a measure of dominance (Bestelmeyer 2000; Baccaro et al. 2010). A bait was considered controlled by a species (i) if the number of individuals was > 20 and no other ant was present or (ii) if one species was at least twice as numerous as the second numerous taxa when several species were present, and the total number of individuals was > 20. Following Baccaro et al. (2010), an ant species was considered as a dominant species when (i) it occurred at a proportion of baits > 5%, (ii) it controlled a proportion of baits > 25% whenever it was present and (iii) it had a mean abundance score > 4. Conversely, an ant species was considered as a subdominant species when (i) it occurred at a proportion of baits > 5%, (ii) it controlled a proportion of baits > 20% whenever it was present and (iii) it had a mean abundance score > 2.5. All other species that did not meet all these criteria were considered as subordinate species.

2.5. Investigation of dumps of *P. jelskii* colonies

Since we identified the ant *P. jelskii* as the dominant species (Table 1), we searched the dumps of 27 colonies with the objectives to find out arthropod carcasses to identify competitive and trophic links in which *P. jelskii* is involved. Dumps were sampled using a Cordless Insect Vacuum (BioQuip® Products, Inc.Bioquip) and conserved in a plastic bag. Then, in laboratory, we looked for hard fragments of carcasses with focusing on identifiable fragments according to a collection of arthropod samples from the same field communities: we counted (i) the number of head capsules of each identifiable ant species, (ii) the number of left and right forceps of dermapterans and (iii) the number of cephalothorax, the number of left and right elytra and legs of weevils. We kept information on the number of dermapterans at the genus taxonomic level because we cannot identify to the species level on the basis of the forceps.

2.6. Statistical analysis

Based on the literature, the investigation of dumps of *P. jelskii* colonies and the population dynamics data, we defined a set of a priori hypotheses describing the relationships within the arthropod community, the effect of treatment (bare soil vs. cover crop) and the sampling time (months). We restricted this analysis to the occurrence of *P. jelskii*, the occurrence of the four ant species identified in the dumps of *P. jelskii* (*S. geminata*, *Paratrechina longicornis* Latreille, *C. sexguttatus*, *Odontomachus ruginodis* Smith) and to the abundance of *Euborellia* spp. and banana weevils, over the common sampling period (15 sampling dates). From these hypothetical links, we constituted a global path model composed of a set of 5 linear sub-models (Table 3). According to response variable distributions, we used binomial generalized models (GLM) for the occurrence of ant species and negative binomial GLM for the abundance of *Euborellia* spp. and *C. sordidus* (Zuur et al. 2009). To consider the influence of population dynamics and temporal autocorrelation, we added the sampling time to each statistical model, from linear to cubic polynomial of time. We then used structural equation modelling (SEM) (Grace 2006) with the piecewiseSEM R-package (Lefcheck 2016)

Table 1. Occurrence of dominant, subdominant, and subordinate ants at baits in all plots.

	Baits recorded (%)			Baits controlled (%)			Mean abundance score		
Species	All	BS	CC	All	BS	CC	All	BS	CC
Dominant	76.2	74.2	78.2	47.1	53.1	41.4	4.0	4.2	3.8
Pheidole jelskii									
Subdominant	21.0	23.3	18.7	33.0	37.1	27.9	3.1	3.2	2.9
Paratrechina longicornis									
Solenopsis geminata	15.9	15.9	15.8	22.3	25.3	19.2	2.8	2.9	2.7
Subordinate	55.2	52.8	57.5	13.9	11.5	16.1	2.8	2.6	3.1
Brachymyrmex patagonicus									
Camponotus sexguttatus	22.2	16.3	28.0	0.3	0.0	0.5	1.6	1.4	1.6
Cardiocondyla obscurior	16.6	18.4	14.9	0.6	0.4	0.9	1.6	1.6	1.5
Odontomachus ruginodis	10.9	11.2	10.6	0.9	0.6	1.2	1.5	1.4	1.5
Nylanderia guatemalemensis	9.3	10.0	8.7	1.4	0.0	3.1	1.7	1.7	1.8
Wasmannia auropunctata	5.7	3.6	7.7	9.4	9.3	9.4	2.4	2.2	2.5
Nylanderia fulva	4.3	4.2	4.4	2.3	1.6	3.0	2.0	1.9	2.0
Monomorium ebeninum	3.1	4.6	1.7	35.8	41.4	20.0	3.4	3.6	2.6
Pheidole vallifica	1.7	1.3	2.1	7.8	15.8	3.1	2.1	2.1	2.1
Tetramorium bicarinatum	1.6	0.2	3.0	18.8	0.0	20.0	2.6	1.3	2.7
Tapinoma melanocephalum	1.5	3.0	0	11.1	11.1	–	2.5	2.5	–

(All), in bare soil plots (BS) and in cover crop plots (CC).

to perform a confirmatory test of our global path model and identify the significant relationships. Shipley's tests of direct separation were used to test for missing paths, a Fisher's C statistic was then calculated from the p-values of those tests (Shipley 2009), and finally, we ran a chi-squared test on the C statistic. The global path model is considered to represent the data well when the p-value of this chi-squared test is greater than the significance threshold (Lefcheck 2016). All statistical analyses were performed with R 4.1.0 (R Core Team 2021) and with a significance threshold of 0.05.

3. Results

3.1. Dominant analysis

We recorded 14 species during bait samplings. We identified the ant *P. jelskii* as the dominant species since it had a high occurrence, controlled a large proportion of baits and had a high mean score abundance (Table 1). We identified the ant species *P. longicornis* and *S. geminata* as subdominant species because they had a high occurrence, controlled a moderate proportion of baits and had a moderate mean score abundance (Table 1). We identified all other species as subordinate species (Table 1).

3.2. Investigation of dumps of *P. jelskii*

We retrieved seven identifiable taxa from the 27 colonies (Table 2). The most frequently retrieved species was the ant *S. geminata*, followed by the ants *P. longicornis* and *C. sexguttatus*, the dermapterans of *Euborellia* spp., the ant *O. ruginodis* and the small banana weevil *Polytus mellerborgii* Boheman, and finally *C. sordidus* (Table 2). The highest number of retrieved individuals was associated to the ant *S. geminata* (64.5%), followed by the ant *P. longicornis* (20.8%), then the ant *C. sexguttatus* (10.4%). The numbers of retrieved individuals of other taxa were lower and *C. sordidus* counting for 0.5% of retrieved individuals (Table 2).

Table 2. Results from the investigation of dumps of 27 colonies of *P. jelskii*.

Species / Taxon	Percentage of *P. jelskii* colonies with carcasses	Number of individuals
Solenopsis geminata	89	1348
Paratrechina longicornis	63	434
Camponotus sexguttatus	85	217
Odontomachus ruginodis	44	22
Cosmopolites sordidus	30	10
Polytus mellerborgii	44	23
Euborellia spp.	48	31

3.3. Correlations between species and cover crop

Our global path model represented the data well (Fisher's C = 8.18, d.f. = 10, χ^2 test: p = 0.611), and 21 of the 34 links tested were significant. SEM results are presented in Table 4 and are summarized in the path diagram in Figure 1. The presence of the cover crop was positively related to the occurrence of *C. sexguttatus*, negatively related to the occurrence of *P. longicornis* and had no significant relationship with the occurrence of the remaining ant taxa. We found a negative relationship between the cover crop and the abundances of *C. sordidus* (Figure 2) and *Euborellia* spp. The occurrence of *P. jelskii* was negatively related to the occurrences of all the ant species except that of *O. ruginodis*. *P. longicornis* occurrence was negatively correlated with the occurrence of *S. geminata*. The occurrence of *S. geminata* was negatively related to that of *C. sexguttatus*. The abundance of the *Euborellia* spp. was negatively related to that of *C. sordidus*, while we found no significant relationship between the occurrence of ant taxa and *C. sordidus*. Finally, the time was correlated to all response variables (Table 4 and Figure 3).

4. Discussion

In the present study, we present a 3-year survey of an ant community, dermapterans and *C. sordidus* in bare soil and cover cropped banana fields. We aimed to (i) investigate on competitive and trophic relationships between the dominant ant species of the community and other ants, dermapterans and *C. sordidus* by analyzing colony dumps; (ii) assess the influence of the addition of a cover crop on the ant community, dermapterans and *C. sordidus*.

4.1. Colony dumps investigation

We found *P. jelskii* as being the dominant ant species of our community. By investigating dump of colonies of this species, we were able to access qualitative and quantitative information on its competitive and trophic relationships with other invertebrate species of the community. We found that the majority of identified carcasses belonged to other ant species (> 96%). Similarly, Retana et al. (1992) also found that ants represent respectively 71% and 43% of animal preys in *Pheidole pallidula* Nylander and *Tetramorium semilaeve* André, two omnivorous species. Although the search of dumps does not allow to differentiate between scavenging, predation or deadly combat in

Table 3. Set of GLMs constituting the global path model based on a priori hypotheses regarding the relationships between response variables and explanatory variables. Hypothesis are based on literature and raw data.

Response variable	Explanatory variable	Hypothesis	References
C. sordidus			
	P. jelskii *C. sexguttatus* *O. ruginodis* *Euborellia* spp.	Top-down control by predators	Mollot et al. 2014; Poeydebat et al., 2017
	P. notatum	No effect of the cover crop because of the oligotrophy of *C. sordidus*	Gold et al. 2001; Duyck et al. 2011
	Time Time^2	Population dynamics	Raw data (Figure 3)
C. sexguttatus			
	P. jelskii	Negative effect of intraguild predation by *P. jelskii*	Dumps of *P. jelskii* colonies
	P. notatum	Positive bottom-up effect of the cover crop	Duyck et al. 2011
	Time	Population dynamics	Raw data (Figure 3)
O. ruginodis			
	P. jelskii	Negative effect of intraguild predation by *P. jelskii*	Dumps of *P. jelskii* colonies
	P. notatum	Positive bottom-up effect of the cover crop	Duyck et al. 2011
	Time Time^2	Population dynamics	Raw data (Figure 3)
Euborellia spp.			
	P. jelskii	Negative effect of intraguild predation by *P. jelskii*	Dumps of *P. jelskii* colonies
	P. notatum	Positive bottom-up effect of the cover crop	Duyck et al. 2011
	Time Time^2 Time^3	Population dynamics	Raw data (Figure 3)
S. geminata			
	P. jelskii	Negative effect of intraguild predation by *P. jelskii*	Dumps of *P. jelskii* colonies
	P. longicornis	Competition	Wetterer et al. 1999
	P. notatum	Positive bottom-up effect of the cover crop	Duyck et al. 2011
P. longicornis			
	P. jelskii	Negative effect of intraguild predation by *P. jelskii*	Dumps of *P. jelskii* colonies
	P. notatum	Positive bottom-up effect of the cover crop	Duyck et al. 2011
	Time	Population dynamics	Raw data (Figure 3)
P. jelskii			
	P. notatum	Positive bottom-up effect of the cover crop	Duyck et al. 2011
	Time	Population dynamics	Raw data (Figure 3)

interspecific encounters, the high number of carcasses of *S. geminata*, *P. longicornis* and *C. sexguttatus* species suggests that direct intraguild predation by *P. jelskii* occurs on these three species. On the contrary, our results suggest low level of intraguild predation by *P. jelskii* on the *Euborellia* spp., which account for less than almost 1.5% of the identified carcasses. Similarly, the banana weevils, *C. sordidus* and *P. mellerborgii* account respectively for almost 0.5% and 1% of the identified carcasses, suggesting that *P. jelskii* ants play a marginal role in the regulation of adult weevils. Such investigation presents the advantage to bring diet information on a species while being non-lethal. In comparison, gut content assays of arthropod predator imply the trapping and killing of several individuals for post-mortem analysis (Mollot et al. 2014; Hagler 2019). Furthermore, we easily obtained both qualitative and quantitative assessment of prey consumption by a predator, while molecular gut content analysis provide only frequency as a proxy for quantitative evaluation of predation. However, both methods do not allow to discriminate between scavenging and true predation (Foltan et al. 2005; Juen and Traugott 2005). This problem can be circumvented by tagging arthropods and taking repeated samples from dumps. It is also worthy to note that when studying ant diet, molecular gut content analysis of foraging workers may not reveal real colony diet since animal preys may mainly be consumed by other life stages (Cassill and Tschinkel 1999). All being said, we argue that colony dump investigation may be a cost-efficient, non-lethal and complementary method to obtain information on trophic relationships occurring in a community of ants.

4.2. SEM and trophic relationships

4.2.1. Cover crop

In agroecology, it is hypothesized that biological control may be enhanced through bottom-up modification of the agrosystems. Here, we compared one-species plant plots to two-species plant plots. We found that this addition of a cover crop did not affect most of the omnivorous and predaceous ant occurrences. This may be partly explained by the fact that the experimental set-up may not be adequate for species that forage on large distances such as *S. geminata*, which may forage at least up to 20 m (Way and Heong 2009). However, we found

Table 4. Pathway coefficient estimates and p-values from the structural equation modelling.

Response variable	Explanatory variable	Estimate (±SE)	p value
C. sordidus	*P. jelskii*	−0.1307 (±0.5635)	0.8166
	S. geminata	−0.3932 (±0.6812)	0.5638
	P. longicornis	−0.0068 (±0.4938)	0.9890
	C. sexguttatus	0.0903 (±0.4938)	0.8522
	O. ruginodis	−0.7152 (±0.8448)	0.3972
	Euborellia spp.	−0.0147 (±0.0035)	<**0.0001**
	P. notatum	−0.4769 (±0.1775)	**0.0072**
	Time	0.2846 (±0.0528)	<**0.0001**
	Time^2	−0.0070 (±0.0016)	<**0.0001**
Euborellia spp.	*P. jelskii*	0.7612 (±0.6703)	0.2561
	P. notatum	−0.5443 (±0.2034)	**0.0075**
	Time	0.3518 (±0.1206)	**0.0035**
	Time^2	−0.0227 (±0.0101)	**0.0064**
	Time^3	0.0006 (±0.0002)	**0.0188**
O. ruginodis	*P. jelskii*	−0.3658 (±0.4550)	0.4214
	S. geminata	−1.2260 (±0.6448)	0.0573
	P. longicornis	−0.2548 (±0.4150)	0.5392
	P. notatum	0.1067 (±0.1432)	0.4562
	Time	0.4011 (±0.0493)	<**0.0001**
	Time^2	−0.0133 (±0.0016)	<**0.0001**
C. sexguttatus	*P. jelskii*	−1.0494 (±0.3608)	**0.0036**
	S. geminata	−1.7783 (±0.4828)	**0.0002**
	P. longicornis	−0.2703 (±0.3160)	0.3922
	P. notatum	0.8982 (±0.1103)	<**0.0001**
P. longicornis	*P. jelskii*	−2.5269 (±0.3254)	<**0.0001**
	P. notatum	−0.2249 (±0.1142)	**0.0490**
	Time	0.0831 (±0.0085)	<**0.0001**
S. geminata	*P. jelskii*	−2.4107 (±0.4634)	<**0.0001**
	P. longicornis	−1.3174 (±0.4634)	**0.0064**
	P. notatum	−0.0693 (±0.1263)	0.5830
	Time	−0.1255 (±0.0178)	<**0.0001**
P. jelskii	*P. notatum*	0.2056 (±0.1070)	0.0548
	Time	−0.0888 (±0.0065)	<**0.0001**

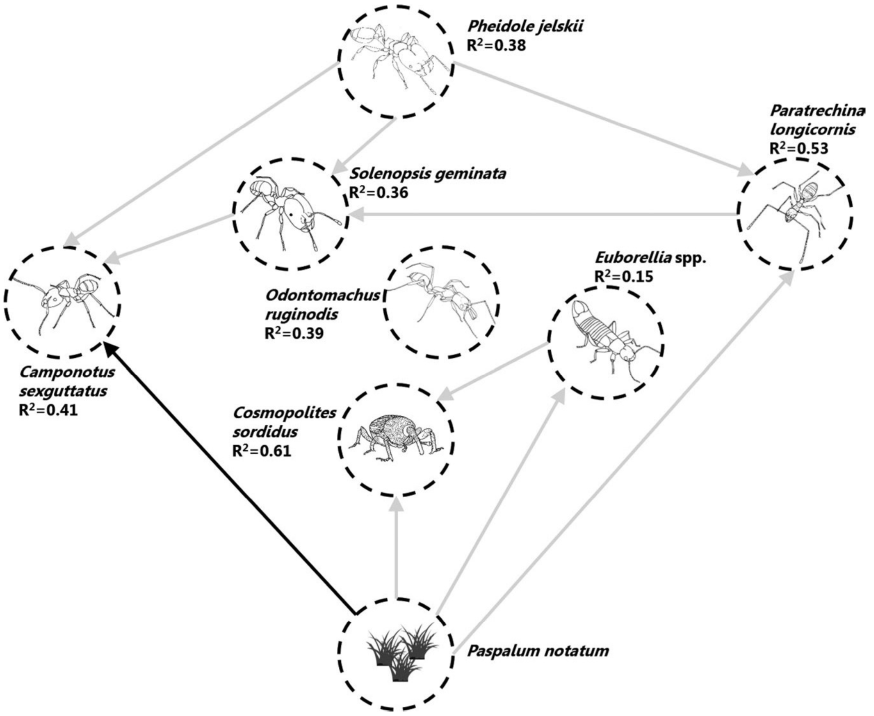

Figure 1. Structural equation model of exploring the relationships between the occurrence of the dominant ant *P. jelskii*, the subdominant ants *S. geminata* and *P. longicornis*, the subordinate ants *C. sexguttatus*, *O. ruginodis*, the abundance of *Euborellia* spp. and *C. sordidus*, and the cover crop *P. notatum*. Black and gray arrows represent significant ($p < 0.05$) positive and negative relationships, respectively. For clarity, the non-significant relationships between species and the relationships with the variable Time were not represent here (see Table 3).

that the carpenter ant *C. sexguttatus* occurrence is positively related to the presence of a cover crop. We observed that this subdominant species primarily nests in dead or living standing banana pseudostems, suggesting that the negative relationship with *P. jelskii* and *S. geminata* is due to

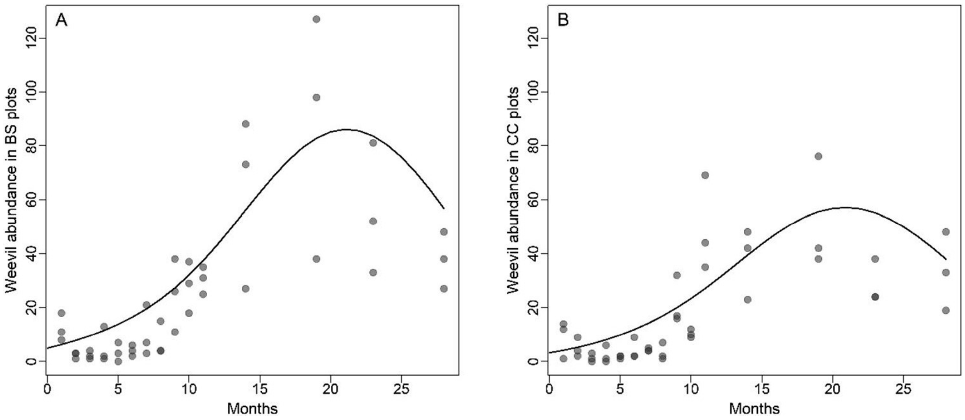

Figure 2. Weevil abundance in the bare soil (A) & cover crop plots (B). Curves are prediction from the fitted model.

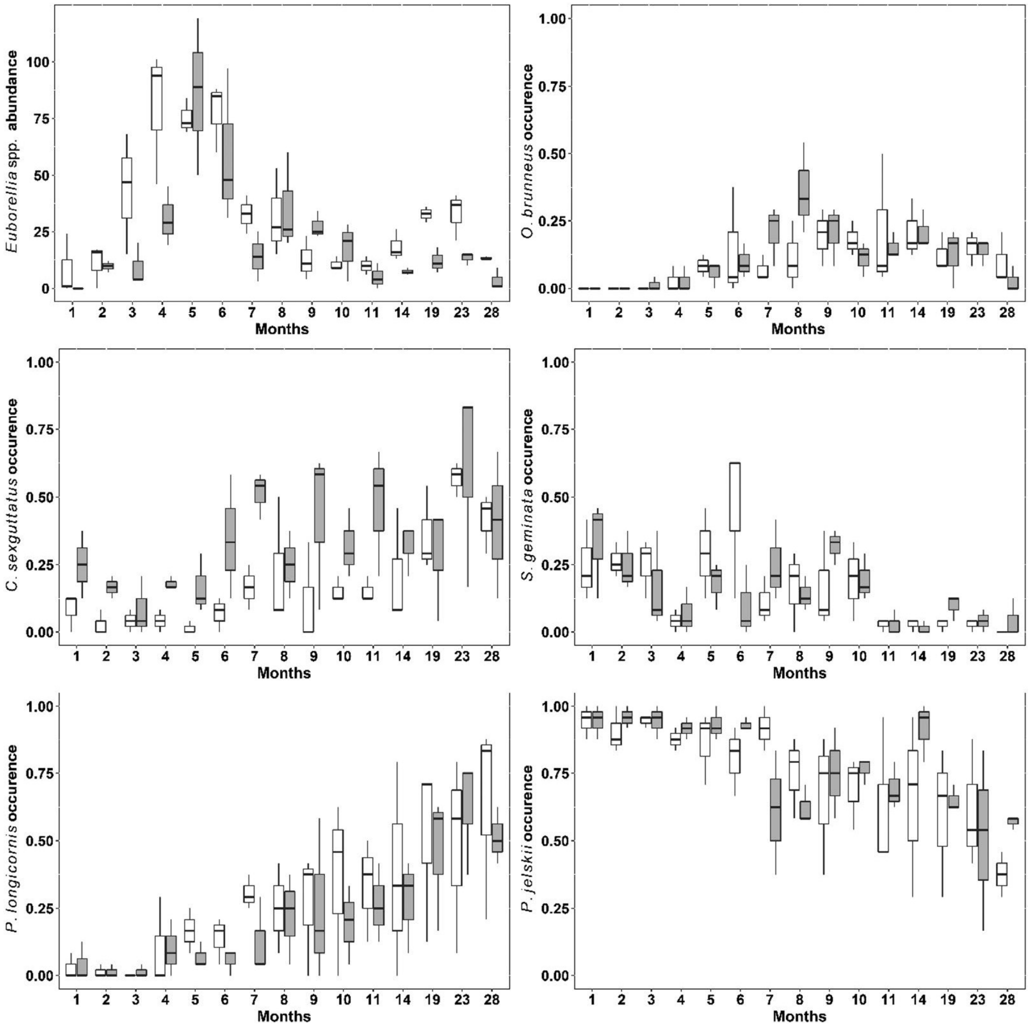

Figure 3. Abundances of *Euborellia* spp. and occurrences of the ants *O. ruginodis*, *C. sexguttatus*, *S. geminata* and *P. jelskii*. White boxes: Bare soil plots; Grey boxes: Cover crop plots. Note that scale of x-axis is not proportional.

competition in foraging since these two species are primarily ground-nesting species. *P. longicornis* was found to be scarce in the presence of other species (*P. megacephala*, *Wasmannia auropunctata* Roger) which, like *P. longicornis*, nest and compete with it at ground level (Way and Bolton 1997). However, *P. longicornis* may be a strong competitor in non-native area and may replace native ant fauna (Wetterer et al. 1999).

We expected a positive relationship between the abundance of dermapterans and the addition of a cover crop because cover crop can sustain dermapterans by attracting alternative prey that dermapterans can feed on. Furthermore, cover crop also supplies shading to arthropods thus providing a more suitable micro-climate than bare soil with less heat and more humidity, and a more suitable habitat for egg laying or larval development of dermapterans. However, we found a lower abundance of *Euborellia* spp. in cover crop plots than in bare soil crops. This may be due to a dilution effect affecting the sampling. Using an individual-based model of earwig-like foraging behaviour, Collard et al. (2018) have shown that the time spent by a generalist predator in the vicinity of banana plants decreases as the proportion of an alternative favourable habitat increases. In our case, the proportion of alternative habitat is maximal in cover crop plots. Since pseudostem traps were deposited at the bottom of banana plants, such dilution effect may have induced bias in the sampling by underestimating dermapterans abundance in cover crop plots.

4.2.2. Invertebrate community interactions

The results found by the SEM of the 3-years survey are consistent with the findings of the investigation of *P. jelskii* colony dumps. First, we found negative relationships between *P. jelskii* and the three ant species which were the most represented in the dumps of colonies. This suggests that the identified carcasses from dumps is a good quantitative representation of the intensity of competition and aggressive behaviour of *P. jelskii* towards its main competitors. Therefore, we argue that the retrieved carcasses are issued from direct attack or predation of this species on the others and that this aggressive behaviour explains partially the pattern of species occurrence during the survey, leading to the conclusion that interference competition is in our study case the main driver of community assemblage. The investigation of dumps of *S. geminata*, *P. longicornis* and *C. sexguttatus* colonies could have provided more information on the relationships between these species. For instance, we found that *C. sexguttatus* occurrence was negatively associated to *S. geminata* occurrence. This may be the result of interference competition and/or predation of *S. geminata* on *C. sexguttatus*, or due to exploitation competition. According to our results, none of the ant species seems to play a major role in the regulation of the banana weevil. Indeed, we found no significant relationships between *P. jelskii* occurrence and *C. sordidus* abundance, which is consistent with the very low number of carcasses retrieved from dumps. These results lead us to conclude that, even if *P. jelskii* is able to prey upon the banana weevils, this species probably plays a marginal role in the regulation of adult weevils and probably also on egg and larval stages of the weevils. *Solenopsis geminata* has been previously reported as a potential effective agent of pest regulation (Jaffe et al. 1990, Sirjusingh et al. 1992, Way and Heong 2009, Bailly Maître et al. 2012) in general and in the case of *C. sordidus* in particular (Mollot et al. 2012, 2014) but our 3-year monitoring led to a contradicting conclusion. Previous studies on the predation of *C. sordidus* by *S. geminata* were conducted to search for a trophic link between this ant species and the pest through prey-sentinel experiments with *C. sordidus* eggs as prey items (Mollot et al. 2012) or through molecular gut content analysis (Mollot et al. 2012, 2014). While these studies showed that predation on *C. sordidus* by *S. geminata* is possible, ours shows that such predation events are probably too scarce and opportunistic to lead to an efficient regulation of the population of *C. sordidus* in banana agrosystems. The same reasoning holds for *C. sexguttatus* since it was previously identified as a potential predator of *C. sordidus* (Mollot et al. 2014) but we failed to found relationship between its occurrence and the abundance of *C. sordidus*.

However, these results alone do not allow to conclude that these species have no role on the *C. sordidus* regulation, only that it is probably weak. Exclusion experiments should be performed to assess quantitatively the impact of ants on the dynamics of *C. sordidus* populations. Contrary to ants, the dermapterans seem to play a role in the *C. sordidus* regulation. Indeed, we found a negative relationship between the abundance of *Euborellia* spp. and the abundance of the banana weevils. Previous studies have reported dermapterans as potential predators of *C. sordidus* (Koppenhöfer et al. 1992; Mollot et al. 2014; Carval et al. 2016).

Identifying predators that prey upon a pest and quantifying such relationships is a primary importance in conservational biological control. However, studying trophic interactions in invertebrate communities in nature is difficult because of the smallness of organisms, their possible cryptic and nocturnal behaviour such as *C. sordidus*. Through a 3-year survey, we found that the dermapterans of the genus *Euborellia* could play a role in the *C. sordidus* regulation while ant species encountered in these communities would not have any impact on *C. sordidus* population. Further studies should be carried out in different banana growing regions, through the combined use of the different methods available today: population monitoring, DNA analysis of stomach contents and faeces, analysis of dumps of ant colonies and image capture and analysis through deep learning. Such studies should also consider vertebrates as potential agents of biocontrol of *C. sordidus* (Tresson et al. 2021).

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No potential conflict of interest was reported by the authors.

Data availability statement

Data and R analysis script are available on the Cirad dataverse at https://doi.org/10.18167/DVN1/CMYEVA.

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Hierarchical Classification of Very Small Objects: Application to the Detection of Arthropod Species

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ABSTRACT Automated image analysis and deep learning tools such as object detection models are being used increasingly by biologists. However, biological datasets often have constraints that are challenging for the use of deep learning. Classes are often imbalanced, similar, or too few for robust learning. In this paper we present a robust method relying on hierarchical classification to perform very small object detection. We illustrate our results on a custom dataset featuring 22 classes of arthropods used to study biodiversity. This dataset shows several constraints that are frequent when using deep learning on biological data with a high class imbalance, some classes learned on only a few training examples and a high similarity between classes. We propose to first perform detection at a super-class level, before performing a detailed classification at a class level. We compare the obtained results with our proposed method to a global detector, trained without hierarchical classification. Our method succeeds in obtaining a mAP of 75 %, while the global detector only achieves a mAP of 48 %. Moreover, our method shows high precision even on classes with the less train examples. Confusions between classes with our method are fewer and are of a lesser impact. We are able achieve a more robust object classification with the use of our proposed method. This method can also enable better control on the model's output which can be particularly valuable when handling ecological, biological or medical data for example.

INDEX TERMS Very small object detection, deep learning, robustness, biodiversity, taxonomy.

I. INTRODUCTION

Recently, there has been a wide adoption of deep learning techniques in various fields of study. For example, deep learning has recently been taken up by the medical and biological sector, biological and used in ecological research [1]–[3]. For several cases however, deep learning methods still have a lot of limitations and constraints that hinder their proper usage. Datasets may be limited, classes imbalanced or similar and the labelling task too heavy to build a robust model.

While such constraints maybe overcome with transfer learning or data augmentation for image classification, these methods might not be sufficient when dealing with object detection. As detectors tend to have a larger number of parameters than classifiers, they also require more training data to achieve satisfactory performances. This makes reliable object detection and classification a major challenge when working with a custom dataset [4]. Numerous cases work with imbalanced datasets *e.g.* in medical research, the number of sane examples can outnumber the diseased ones, in particular for very rare diseases. An unsufficiently robust deep learning model could generate false positives, if this is not taken into account [5].

The availability of a large enough dataset to ensure the robustness of the predictions remains a barrier to the use of deep learning with niche tasks. The training of a detector, with only a few training examples is known as ''low-shot object detection'' or ''few-example object detection''. Several methods have recently been developed. Multi-modal labelling, *i.e.* referring to objects with several classes is commonly

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used. Dong *et al.* propose a method relying on multi-modal labellisation and different learning paces depending on class difficulty [6]. Low-Shot Transfer Detector on the other hand relies on transfer learning [7]. Another method is to rely on distant metric learning [8]. Adding to the constraint of few examples, in many practical cases, objects featured in a dataset may be similar, requiring fine classification tasks, which may be challenging for a deep learning model, particularly when trained on imbalanced data. Furthermore, many cases in biology or medicine need control over the predictions of a model to avoid false negatives or false positives [2]. In such situations, the control and robustness of a prediction model over precise classes are more important than efficiency or inference time on general datasets.

In this paper, we propose a method to detect and hierarchically classify very small objects on large input images. We illustrate the usefulness of our method working on a custom dataset showing typical constraints that could be encountered when working on a fine detection task: limited training examples, class imbalance and fine classification.

The main contributions and key-points of our proposed paper can be summarized as follows:

- We propose a robust method of hierarchical classification when performing very small object detection.
- A pre-processing step is applied to perform a super-class detection of very small objects within large images.
- The detection and classification steps are independent, allowing us to work with sparse datasets.

In our context, the aim of this work is to robustly detect several species to latter study the interactions between them. Knowing these interactions is crucial for several purposes, such as resilient pest control. Our application highlights several constraints of the application of deep learning in real world situations with custom dataset.

The rest of this paper is organized as follows. First of all, Section II reports current state-of-the-art methods on hierarchical classification when detecting objects. Section III describes with details the proposed method. Experimental results are provided in Section IV. Finally, the conclusion is drawn and future work is proposed in Section V.

II. RELATED WORK

In this section we describe several related work concerning low-shot object detection, then hierarchical classification, small object detection and finally, applications in ecology.

A. LOW-SHOT OBJECT DETECTION

Low-shot object detection, *i.e.* the training of a detector with only a few examples per class is a recent but active research field. In this area, several methods have been developed [6]–[8]. A commonly used method is to refer to objects with several classes (multi-modal labelling) which is the approach we selected. Otherwise, Dong *et al.* propose a method communicating between model training and sample selection [6]. Then, using this method the most challenging yet reliable training samples are selected. This approach can be combined with multi-modal learning and varying learning paces, given the difficulty of the classes.

Chen *et al.* rely on transfer learning with a Low-Shot Transfer Detector [7]. While transfer learning might be prone to overfitting with only a few training examples, they address this challenge. The authors propose to combine SSD [9] and Faster RCNN [10] architecture, separating bounding box regression and object classification.

Another method is to rely on distant metric learning [8]. The extraction of low dimensional representations enables the learning of more generic features such as class only features. The losses are designed in an embedding space so that different categories are not only distinct, but that similar categories are close as well.

B. HIERARCHICAL CLASSIFICATION

Hierarchical classification has been used in deep learning for the handling of large datasets with numerous classes [11]–[13]. For classification tasks, Katole *et al.* achieved 3.2 % error rate on the ImageNet 10K dataset [11] that features over 10,000 classes using hierarchical classification [12]. Hierarchical classification was also used for detection tasks on ImageNet. For instance, Redmon *et al.* achieved a mAP of 76.8 % on over 9000 classes [13].

C. SMALL OBJECT DETECTION

Small objects are defined by the MS COCO (Microsoft Common Objects in Context) dataset as objects occupying areas under 32×32 *pixels* [14]. This is a challenging problem in computer vision and several methods can be used to address it [15]. One solution is to slice the large input image and perform detection on slices separately before merging all results. This method can be used for satellite imagery analysis [16] or insect detection for example [17].

D. APPLICATIONS IN ECOLOGY

Hierarchical classification is useful for small datasets requiring precise classification, typically for a use in biology [18], medicine [19] or ecology [20], [21]. Indeed, hierarchical classification enables to better control the error rates of the classifier [22]. For species identification, particularly, this approach has been used following the taxonomy of different species. While hierarchical classification has already been developed for species classification, it has to our knowledge not been carried out for fine detection tasks.

III. PROPOSED METHOD

In this section, we develop our proposed method for hierarchical classification of very small objects. An overview of our method is presented in Fig. 1. Objects detected on the input images belong to N super-classes C_i, with $1 \leq i \leq N$. Each super-class C_i contains k_i classes c_{ij}, with $1 \leq j \leq k_i$.

During the training step, a detector is trained with objects that have been labeled at the super-class level. The areas of these objects are then cropped from the original images and

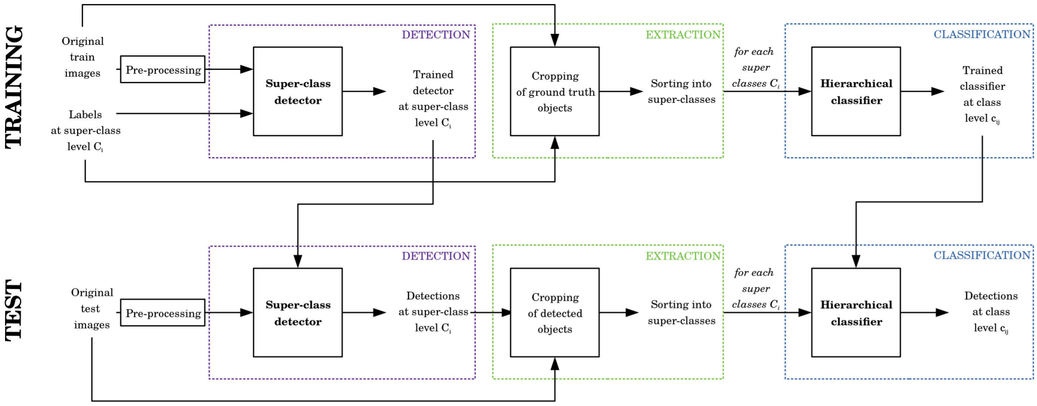


FIGURE 1. **Overview of our proposed hierarchical classification method.**

for each super-class C_i, a classifier is specifically trained to identify the objects within the super-class into c_{ij} classes.

During the testing step, objects are first detected at super-class level. Detected objects are then cropped and classified with the corresponding classifier.

The super-class detection part of the process is detailed in Section III-A, the hierarchical classification in Section III-B and the evaluation metrics used to assess the performances our method are described in Section III-C.

A. OBJECT DETECTION

With large input images, detection might require a pre-processing phase. For this step we propose to apply an approach based on the method proposed by Tresson *et al.* [17]. The pre-processing step is summarized in Algorithm 1. Original images are split into small slices for the input of a deep learning model. Slicing is performed with an overlap O in order to reduce the risk of an object being cut between two neighboring slices. Coordinates of the objects are recomputed within the referential of the slices and empty slices showing background only are discarded. The detector is then trained on the sliced dataset. Likewise, during testing, original images are sliced with the same parameters as during the training. Detections of slices belonging to the same original image are then merged together and refined to suppress potential false positives due to overlap. This pre-processing phase allows the detection of very small objects within very large input images. Detection is performed with objects identified at a super-class level.

B. OBJECT HIERARCHICAL CLASSIFICATION

For each super-class, a classifier is trained independently on cropped ground truth objects. The model is then able to classify objects into the k_i classes c_{ij} within this super-class as illustrated in Fig. 1. During the test step, the detected objects are cropped according to their coordinates obtained in the coordinate system of the entire original image. Cropped objects are then identified with the classifier model corresponding to their detected super-class.

Algorithm 1 Image and Label Pre-Processing

```
input  : Original image of size $n_W \times n_H$ pixels ($I_{orig}$),
         Original labels ($c_{ij}, x_i, y_i, w_i, h_i$),
         Slice of size $n_{slice} \times n_{slice}$ pixels,
         Overlap $O$
output : Sliced image, and recomputed labels
         ($c_{ij}, x'_i, y'_i, w'_i, h'_i$)
$I_{orig} \leftarrow$ slice($n_{slice}, O$)
for every slice do
    if $x_i, y_i$ within slice or 50 % of the object on the
    slice or 40 % of the slice covered by object then
        recompute label
    else
        Discard
```

C. EVALUATION METRICS

To assess detection performances, the model predictions on the test dataset are compared with ground truth labels. The *IoU* (Intersection over Union) is used to compare bounding boxes. Detections are accepted as True Positive (TP) if $IoU > 0.5$ and if the detected class is correct. Otherwise, the detection is counted as FP. As well, duplicates are counted as False Positive (FP). If a ground truth object is missed, it is counted as FN. Performances are assessed with precision, recall and F1-score:

$$precision = \frac{TP}{TP + FP}, \tag{1}$$

$$recall = \frac{TP}{TP + FN}, \tag{2}$$

$$F1 = 2 \times \frac{precision \times recall}{precision + recall}. \tag{3}$$

For each class, the Average Precision (AP) is computed as the area under the precision-recall curve. AP is used to compare performances between classes.

The mAP is favored as this indicator reacts strongly to performance loss on a class, regardless of the number of objects within the class. This is a good indicator of the performances

TABLE 1. Classes and corresponding Super-classes.

Super-classes	Train/Test examples	Classes	Train/Test examples
C_1 Arachnida	1048/252	$c_{1,1}$ *Isometrus maculatus*	109/23
		$c_{1,2}$ *Lycosidae* msp. 1	464/117
		$c_{1,3}$ *Lycosidae* msp. 2	237/52
		$c_{1,4}$ *Salitcidae* msp. 1	145/39
		$c_{1,5}$ *Salitcidae* msp. 2	93/21
C_2 Coccinellidae	722/147	$c_{2,1}$ *Cheilomenes sulphurea*	127/25
		$c_{2,2}$ *Exochomus laeviusculus*	386/74
		$c_{2,3}$ *Psyllobora variegata*	209/48
C_3 Coccoidea	8779/2929	$c_{3,1}$ *Ceroplastes sinensis*	132/24
		$c_{3,2}$ *Dysmicoccus brevipes*	394/147
		$c_{3,3}$ *Icerya seychellarum*	8253/2758
C_4 Formicidae	13400/3219	$c_{4,1}$ *Brachymyrmex aphidicola*	189/37
		$c_{4,2}$ *Cyphomyrmex rimosus*	1114/290
		$c_{4,3}$ *Paratrechina longicornis*	560/129
		$c_{4,4}$ *Pheidole megacephala* major	3076/878
		$c_{4,5}$ *Pheidole megacephala* minor	1814/461
		$c_{4,6}$ *Solenopsis geminata* minor	2982/620
		$c_{4,7}$ *Tapinoma melanocephalum*	1176/286
		$c_{4,8}$ *Technomyrmex albipes*	2197/428
		$c_{4,9}$ *Tetramorium bicarinatum*	292/90
C_5 Myriapoda	3018/862	$c_{5,1}$ *Pachybolidae* msp.	2545/774
		$c_{5,2}$ *Paradoxosomatidae* msp.	473/88

of rare classes. However, the F1-score however still provides information on the overall detection performances of a model.

We compare the performances obtained with our proposed method with the performances obtained with a global detector trained directly across all n classes without hierarchical classification.

IV. EXPERIMENTAL RESULTS AND DISCUSSION

In this section, the different results obtained with our hierarchical classification method for very small objects are discussed. First we describe the dataset we built in Section IV-A and the deep learning models and parameters used in Section IV-B. In Section IV-C our method is applied to a large image from the test dataset and presented in detail. Section IV-D gives overall performance analysis of our method and compares the results with a global classification.

A. DATASET

For our experiments we have developed a custom dataset featuring various insects on large input images ($3,000 \times 4,000$ *pixels*). This dataset shows typical constraints when performing object detection in biology.

Indeed, as illustrated in Fig. 2, some arthropods featured in this dataset are easily distinguishable, while other classes are visually very close one to another. For instance, *Pachybolidae* msp. ($c_{5,1}$) (Fig. 2.a) is easily distinguishable. On the other hand, ant species such as *Technomyrmex albipes* ($c_{4,8}$) (Fig. 2.b), *Solenopsis geminata* minor ($c_{4,6}$) (Fig. 2.c), *Pheidole megacephala* major ($c_{4,4}$) (Fig. 2.d) or *Pheidole megacephala* minor ($c_{4,5}$) (Fig. 2.e) are very similar. While pictures were taken in controlled conditions, dirt and branches were added to the background to add noise and additional complexity for the deep learning models.

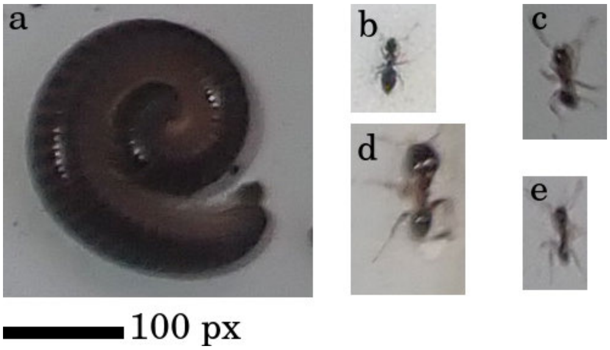


FIGURE 2. Examples of objects found in our custom dataset: a) *Pachybolidae* msp. ($c_{5,1}$), b) *Technomyrmex albipes* ($c_{4,8}$), c) *Solenopsis geminata* ($c_{4,6}$), d) *Pheidole megacephala* major ($c_{4,4}$), e) *Pheidole megacephala* minor ($c_{4,5}$).

A total of 4,102 images are used as a training dataset and 955 as a test dataset. After pre-processing, the actual training dataset for the detector is 27,160 slices and the test dataset is comprised of 7,000 slices.

The dataset features 26,967 objects belonging to the 5 super-classes (C_1 to C_5) and 22 classes in total (see Table 1). Classes are imbalanced as some species are more frequent than others, between and within super-classes. For instance, there are 16 times more *Pheidole megacephala* major ($c_{4,5}$) training examples as *Brachymyrmex australis* ($c_{4,1}$) and 62 times more *Icerya sechellarum* ($c_{3,3}$) as *Ceroplasted sinensis* ($c_{3,1}$). The most frequent class is *Icerya sechellarum* ($c_{3,3}$) which shows 8,253 training examples, whereas Salticidae msp. 2 ($c_{1,5}$) features only 93 training examples.

The objects featured on the dataset are very small with an average width of 102.54 *pixels* and an average height of 81.9 *pixels*, derived from images of $3,000 \times 4,000$ *pixels*, hence the utility of the pre-processing step.

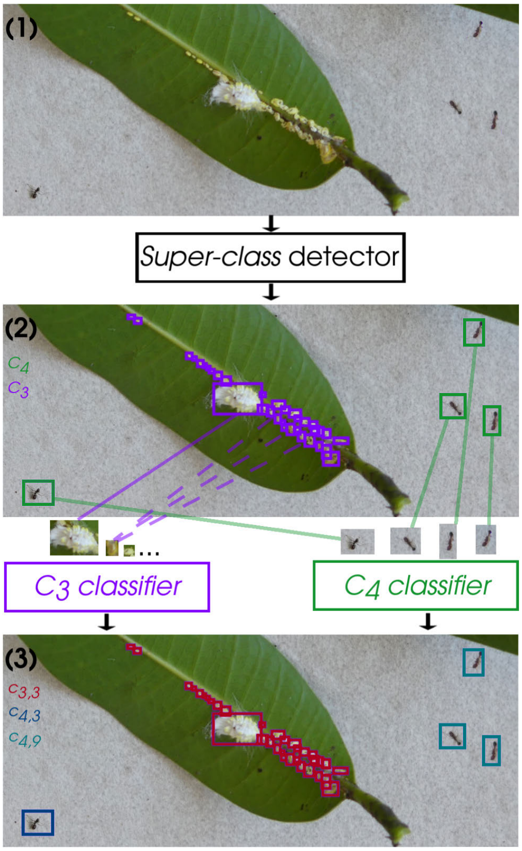


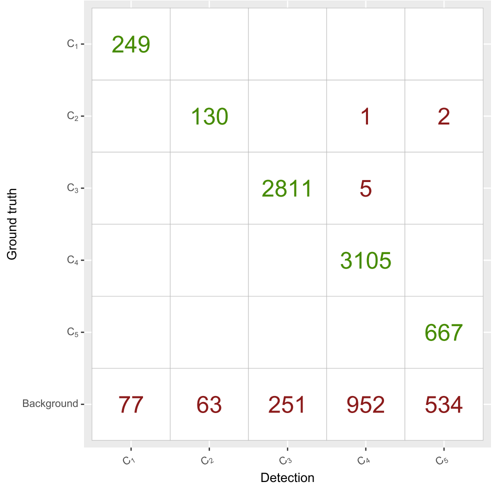
FIGURE 3. **A full example illustrating the two main steps of our hierarchical classification method: 1) A part of an original image of our dataset. 2) Super-class detection: Objects of super-classes C_3 and C_4 are detected. 3) Obtained hierarchical classification: Objects of classes $c_{3,3}$, $c_{4,3}$ and $c_{4,9}$ are classified.**

TABLE 2. **Overall performances of our hierarchical classification method compared to a global classification.**

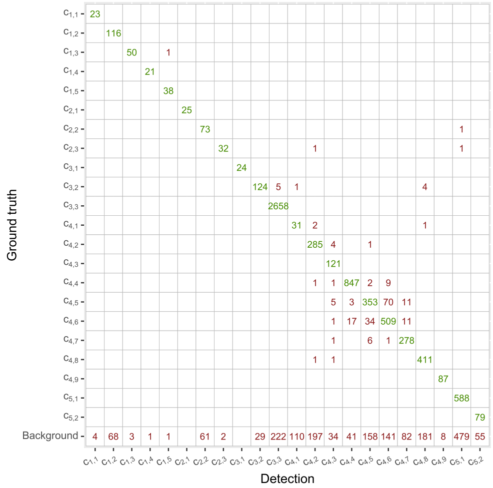
Metric	Global classification	Hierarchical classification	Gain
Precision	0.46	**0.77**	0.31
Recall	**0.92**	0.89	-0.03
F1-score	0.61	**0.83**	0.22

B. PARAMETER DESCRIPTION

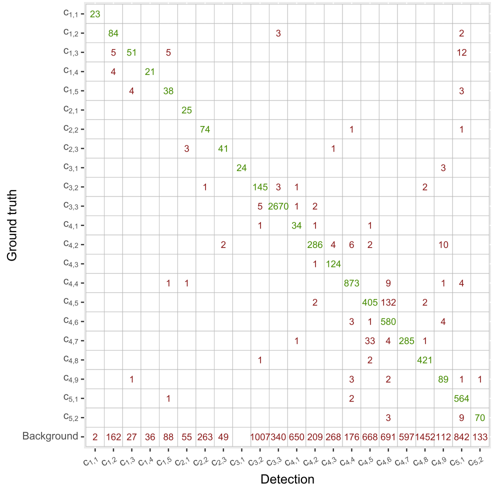
Several networks were trained to obtain our experimental results. For our method, a detector over the five super-classes presented in Table 1 (Arachnida, Coccinellidae, Coccoidea, Formicidae and Myriapoda) and specific classifiers for each super-class. A global detector over the 22 classes was trained as a comparison. All networks states were chosen to maximise mAP on test dataset. We use YOLOv3 [23] as a super-class detector. Squeezenet [24] was chosen as a classifier after a benchmark for this task. YOLOv3 features 106 fully convolutional layers. The model was trained for 39 epochs for our super-class detector (66 epochs for the global detector as a comparison) with a batch size of 4 and a learning rate of 0.001, using Adam as an optimizer. Squeezenet features 11 layers and was trained for each class. All training cycles lasted between 20 and 30 epochs with a batch size of 8 and a learning rate of 0.001, using SGD as an optimizer.



(a) Super-class detection for our hierarchical classification



(b) Hierarchical classification



(c) Comparison with a global classification

FIGURE 4. **Confusion matrices obtained from our proposed approach: a) At the super-class detection step; b) After our proposed hierarchical classification; c) Comparison with a global classification.**

TABLE 3. Detection and classification performances for the different Classes and Super-classes.

Super-classes	Super-class detection AP	Classes	Global classification AP	Hierarchical classification AP	Gain
C_1 Arachnida	0.66	$c_{1,1}$ *Isometrus maculatus*	**0.98**	0.93	-0.05
		$c_{1,2}$ Lycosidae msp. 1	0.24	**0.72**	0.48
		$c_{1,3}$ Lycosidae msp. 2	0.84	**0.93**	0.09
		$c_{1,4}$ Salitcidae msp. 1	0.44	**0.96**	0.52
		$c_{1,5}$ Salitcidae msp. 2	0.31	**0.96**	0.65
C_2 Coccinellidae	0.59	$c_{2,1}$ *Cheilomenes sulphurea*	0.32	**1.00**	0.68
		$c_{2,2}$ *Exochomus laeviusculus*	0.22	**0.54**	0.32
		$c_{2,3}$ *Psyllobora variegata*	0.41	**0.65**	0.24
C_3 Coccoidea	0.84	$c_{3,1}$ *Ceroplastes sinensis*	**1.00**	**1.00**	0.00
		$c_{3,2}$ *Dysmicoccus brevipes*	0.18	**0.73**	0.55
		$c_{3,3}$ *Icerya seychellarum*	**0.89**	**0.89**	0.00
C_4 Formicidae	0.80	$c_{4,1}$ *Brachymyrmex aphidicola*	0.04	**0.21**	0.17
		$c_{4,2}$ *Cyphomyrmex rimosus*	**0.77**	0.70	-0.07
		$c_{4,3}$ *Paratrechina longicornis*	0.36	**0.77**	0.41
		$c_{4,4}$ *Pheidole megacephala* major	0.87	**0.94**	0.07
		$c_{4,5}$ *Pheidole megacephala* minor	0.38	**0.63**	0.25
		$c_{4,6}$ *Solenopsis geminata* minor	0.39	**0.66**	0.27
		$c_{4,7}$ *Tapinoma melanocephalum*	0.45	**0.75**	0.30
		$c_{4,8}$ *Technomyrmex albipes*	0.22	**0.67**	0.45
		$c_{4,9}$ *Tetramorium bicarinatum*	0.51	**0.89**	0.38
C_5 Myriapoda	0.45	$c_{5,1}$ Pachybolidae msp. 1	0.36	**0.44**	0.08
		$c_{5,2}$ Paradoxosomatidae msp. 1	0.29	**0.59**	0.30
mAP	0.67		0.48	**0.75**	0.27

C. A FULL EXAMPLE

A full example of the processing for our proposed hierarchical classification method is detailed in Fig. 3. The image on Fig. 3.1 is a detail of 980 × 400 *pixels* from an image of our test dataset. When fed to the super-class detector, scale insects (C_3 Cocooidae) and ants (C_4 Formicidae) are detected. The objects are then cropped given their coordinates and these cropped images are fed in to their respective classifiers for hierarchical classification into the *I. seychellarum* ($c_{3,3}$), *P. longicornis* ($c_{4,3}$) and *T. bicarinatum* ($c_{4,9}$) classes.

D. PERFORMANCE ANALYSIS

The overall performance of our method compared to a global detector trained on all classes is available in Table 2. First considering only the detection task, our method achieves an overall precision of 0.77, a recall of 0.89, meaning a F1-score of 0.83. However, global detection and classification achieves a precision of 0.46 and a recall of 0.92. This leads to an overall F1-score of 0.61 (see Table 2). So, when considering the detection task only, hierarchical classification leads to better results with a gain of 0.22 on the F1-score, thanks to the super-class detector having better generalised than a global detector.

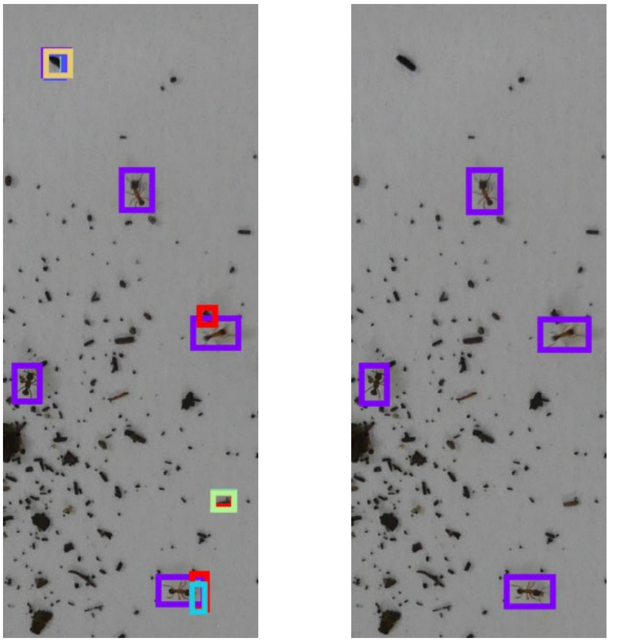
As shown in Table 3, global classification achieves a mAP of 0.48 with strong disparities among classes. Indeed, some classes such as *I. maculatus* ($c_{3,3}$), *C. sinensis* ($c_{3,1}$) and *P. megacephala* ($c_{4,4}$) show very good AP, whereas others, such as *B. australis* ($c_{4,1}$) or *T. albipes* ($c_{4,8}$) show very poor AP. With our proposed hierarchical classification, we achieve a far greater mAP of 0.75. Furthermore, disparities between classes are lower. These performance differences are particularly noticeable for classes with less training examples. Indeed, the average AP of the global classifier on classes with less than 500 training examples ($c_{2,1}$ *Cheilomenes sulphurea* or $c_{3,2}$ *Dysmicoccus brevipes* for instance) is of 0.44, whereas it is of 0.77, with our hierarchical classification.

Fig. 4 illustrates the confusion matrices obtained from our proposed approach, just after the super-class detection step, Fig. 4.a, and at the end of our hierarchical classification, Fig. 4.b. As illustrated in Fig. 4, although our proposed method shows less confusions between classes compared to a global classification, as illustrated in Fig. 4.c (197 confusions against 315 for the global detector), this alone does not explain the difference in precision between the two methods. Indeed, the vast majority of the false positives generated by the global detector are detections of non-existent objects in the background (7,981 out of the total 8,296 false positives) noted in red in the last row of the confusion matrices in Fig. 4. The better performances of our proposed method comes from a more robust detection than from a finer classification.

An example illustrating this difference is presented in Fig. 5. We can see in Fig. 5a that several false positives have been detected. On the contrary, with our approach, illustrated in Fig 5b, all the false positives have been removed, whilst keeping all true positives.

Furthermore, we observe on Figure 4 that most of the confusions by our hierarchical approach are within the same super-class (mostly ants from other ants). These confusions are arguably of a lesser impact than confusions between objects of different super-classes (ants for spiders, for example).

It should be noted from these results that the image resolution could be decreased for the detection step with minimal degradation to the results obtained. However, the specialized classifiers should always work on the best resolution images.



(a) Global classification (b) Hierarchical classification

FIGURE 5. Comparison of obtained results between our proposed hierarchical classification and a global classification on an image detail. Our method generates less false positives with noised backgrounds.

This would further reduce the inference time with minimal impact on performance. Regarding the inference time, with the parameters described in Section IV-B and the hardware used (GPU: Nvidia GeForce GTX 1080, 32 GB RAM), the inference time for the detection with YOLOv3 [23] is about 20 *ms* per slice (*i.e.*, 140 *ms* on average, per entire original image) and the inference time per object for classification is about 20 *ms*, including the cropping step.

V. CONCLUSION

In this paper, we described a hierarchical classifier which is a robust method to achieve small object detection and fine classification. We demonstrate the utility of our method on a custom dataset showing classical constraints that may limit the use of deep learning, such as class imbalance, few examples, similar or noisy objects. This method could be very valuable to researchers still encountering issues while working with deep learning on custom datasets.

The robustness and reliability of our proposed method could be further improved by adding specific confidence thresholds for the different classes and super-classes (see Villon *et al.* [22]).

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APPLICATION

Methods in Ecology and Evolution BRITISH ECOLOGICAL SOCIETY

CORIGAN: Assessing multiple species and interactions within images

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Abstract

1. Images are resourceful data for ecologists and can provide a more complete information than other methods to study biodiversity and the interactions between species. Automated image analysis however often relies on extensive datasets, not implementable by small research teams. We are here proposing an object detection method that allows the analysis of high-resolution images containing many animals interacting in a small dataset.
2. We developed an image analysis pipeline named 'CORIGAN' to extract the characteristics of animal communities. CORIGAN is based on the YOLOv3 model as the core of object detection. To illustrate potential applications, we use images collected during a sentinel prey experiment.
3. Our pipeline can be used to detect, count and study the physical interactions between various animals. On our example dataset, the model reaches 86.6% precision and 88.9% recall at the species level or even at the caste level for ants. The training set required fewer than 10 hr of labelling. Based on the pipeline output, it was possible to build the trophic and non-trophic interactions network describing the studied community.
4. CORIGAN relies on generic properties of the detected animals and can be used for a wide range of studies and supports. Here, we study invertebrates on high-resolution images, but the same processing can be transferred for the study of larger animals on satellite or aircraft images.

KEYWORDS
animal detection, Convolutional Neural Network, image processing, interaction study, on-field image, sentinel prey study, trophic networks

1 | INTRODUCTION

Understanding the functioning of ecosystems depends on accurate information on biodiversity, species behaviour, trophic and non-trophic interactions and other ecosystem properties. Such information can be very useful for biodiversity conservation, invasive species monitoring and biological pest control (Reid et al., 2005).

However, classical methods used to sample biodiversity or to identify the behaviours of species are often either time-consuming, information-poor, or expensive. Depending on the studied species and objectives of the studies, these methods include direct observation, the use of trap cameras, Barber traps, sentinel prey, or satellite images for instance. Among these methods, camera observations have several advantages and present few biases.

For the study of arthropods with sentinel preys, Grieshop et al. (2012) demonstrate the usefulness of the collected data and mentioned as only limits of this techniques the small sampling window of a camera and the time investment needed for image analysis. In fact, ecologists and biologists are therefore increasingly using automated methods to analyse images (Pimm et al., 2015).

To date, one of the most developed applications of computer vision in ecology is the identification of species (Wäldchen, Mäder, & Cooper, 2018; Weinstein, 2018). In comparison with species identification, the counting of objects and the describing of animal behaviours and interactions are less developed applications of computer vision in ecology (Weinstein, 2018). Furthermore, the existing methods to identify, count, or describe animals are often designed for specific uses and rely on extensive datasets and citizen science initiatives (Norouzzadeh et al., 2018; Willi et al., 2018).

In this manuscript, we describe the CORIGAN pipeline that uses object detection to identify and locate numerous small objects in high-resolution images and uses these detections to compute information about species interactions. We illustrate how CORIGAN can be applied on a small custom dataset of images of invertebrate communities from a sentinel prey experiment in a tropical agrosystem.

2 | MATERIALS AND METHODS

2.1 | Overview

2.1.1 | Image and detection processing

We use the YOLOv3 Convolutional Neural Network (CNN) (Redmon & Farhadi, 2018) as core of our image-processing pipeline. This model outputs the bounding box coordinates of the objects it recognizes on an input image. As this model is best fit for small images featuring large objects, we have developed an image-processing pipeline inspired from satellite images analysis methods (Van Etten, 2018) to be able to work with high-resolution images featuring numerous small objects. The image-processing is summarized in Figure 1 and details on image labelling, processing and CNN training are presented in Supplementary Material S1. Images are first sliced into $n_{\text{slices}} \times n_{\text{slices}}$ pixel slices with a given *overlap* to reduce the risk of an object being cut in non-identifiable parts.

For model training, ground truth labels of the train dataset are recomputed within each slice referential with P_{object} and P_{slice} parameters to handle how small and large labels will be recomputed. The CNN is then trained on this new dataset. Here, we have performed data augmentation as Redmon and Farhadi (2018) and payed particular attention to overfitting, given the size of our example dataset.

For model testing, detection is performed on slices using trained model weights and a separate test dataset. These detections are then merged back together within the referential of the original image. The overlap of the slicing may generate duplicates and a refining of the detections with *Overlap Threshold* (*OT*) and *Confidence Threshold* (*CT*) parameters is performed to suppress duplicates. Refined detections are then compared with ground truth to assess the performances of the model. Detected and ground truth bounding boxes are compared using Intersection over Union (IoU), which is the ratio between the area of intersection and the area of union of two bounding boxes. An IoU of 1 indicates that the detected box and ground truth box overlap perfectly. Detections are accepted as True Positive (TP) if $IoU > 0.5$ and if the detected class is correct. Otherwise, the detection is considered as False Positives (FP). As well, duplicates are considered as FP. If a ground truth object is missed, it is considered as False Negative (FN). Overall performances are assessed with precision, recall and F1-score.

$$\text{precision} = \frac{\text{TP}}{\text{TP} + \text{FP}}$$

$$\text{recall} = \frac{\text{TP}}{\text{TP} + \text{FN}}$$

$$F1 = \frac{2 \times \text{precision} \times \text{recall}}{\text{precision} + \text{recall}}$$

For each class, the average precision (AP) is computed as the area under the precision–recall curve. AP is used to compare performances between classes.

Once the model shows acceptable performances and the best processing parameters determined, the pipeline can be used to study interactions between animals.

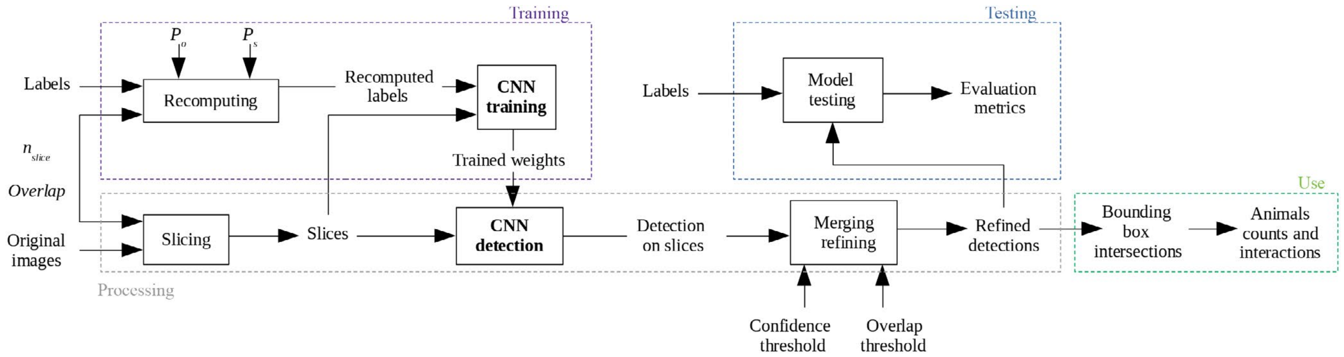

FIGURE 1 Overview of the proposed method

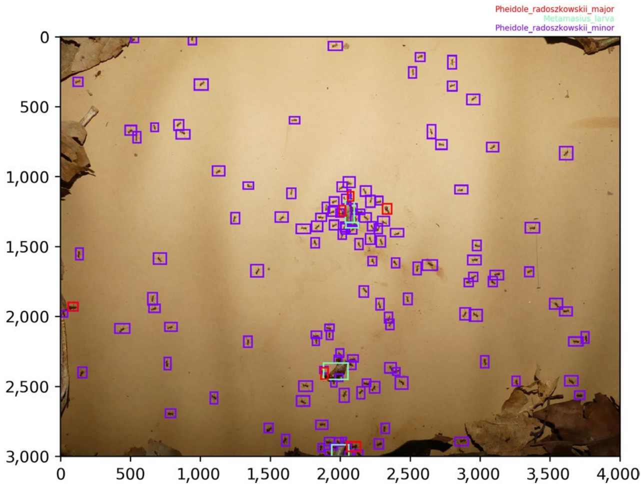

FIGURE 2 Output of the pipeline for an image of the test dataset. Values on x and y axes are pixel coordinates

2.1.2 | Interactions

Since we observe animals on a 2D surface, we can thus use the intersection of bounding boxes to detect physical interactions between two individuals. There may be intersections of bounding boxes without real physical contact but the intersection of bounding boxes ensures that animals are within very close range to each other. We chose to consider this as a physical interaction, as this means that at least one of the participants of the interaction is willing to engage physical contact with the other.

To provide further nuances, interactions may be characterized depending on the known or observed behaviour of a species towards another. In our example, interactions between predators and prey are labelled as *predation* if the prey is alive and *scavenging* if the prey is already dead at the beginning of the experiment. Interactions between two predators of different species are labelled as *competition*, whereas interactions between two predators of the same social species are labelled as *cooperation*. Finally, animals whose behaviour towards others were not clearly identified are labelled as *undefined*. Moreover, the number of individuals of a predator species interacting with a prey on an image is counted, providing information about the predator unit investment needed for the capture of a prey during a predation event. All results are exported in CSV dataframes. R scripts are provided for analysis and production of graphics.

2.2 | Example dataset

To illustrate how CORIGAN can assess multiple species and interactions within images, we have conducted sentinel prey experiments, using eggs and dead or alive adults of *Cosmopolites sordidus* and larvae of *Metamasius* sp. as prey under the camera.

Detailed protocol is presented in Supplementary Material S2. These experiments have produced 1,240 images of 3,000 x 4,000 pixels and we have used 95 images as training dataset, 95 different images as test dataset and 1,191 to study invertebrate interactions. Training and test dataset feature 4,087 invertebrates belonging to 24 classes: these include 21 species and morphospecies; three ant species are further labelled to caste level (minor or major workers). For the sake of clarity, results are here presented with these classes summarized into seven super classes (ant, cockroach, weevil, spider, larva, egg, slug) but see Table 1 in Supplementary Material S3 for complete results on all classes. An output example for a test image of this dataset is shown in Figure 2.

3 | RESULTS

3.1 | Network performance

Given our dataset, we choose n_{slice} = 416 pixels and an *overlap* of 0.2. Each original image then generates 108 slices. Labels are kept for $P_{\text{object}} = 0.4$ and $P_{\text{image}} = 0.5$. We chose an *OT* of 0.4. and *a CT* of 0.2. Details on the choice of values of these parameters are provided in Supplementary Material S1.

Given our hardware (detailed in Supplementary Material S1), training on 95 images (corresponding to 10,260 slices) required about 24 hr. Tests on 93 original images (meaning 10,044 slices) required <5 min. The presented state of the network shows maximal test performance and a test loss to training loss ratio of 1.01.

The model had a precision of 86.6%, a recall of 88.9%, and an F1-score of 87.8% on detailed classes. If classes are summarized into super classes, precision, recall and F1 increased to 89.6%, 91.2% and 90.4% respectively. AP for the different super classes are shown on Table 1.

TABLE 1 Average precision (AP) per super classes. This underlines a limitation of the use of deep learning with small datasets, as class imbalance can lead to poor performances on rare classes. See Table 1 in Supplementary Material S3 for detailed results on all classes

Super classes	Classes	Training examples	Test examples	AP (± *SD*)
Ant	10	1,467	1,395	0.84 ± 0.29
Cockroach	3	35	31	0.18 ± 0.15
Egg	1	89	85	0.85 ± 0.00
Larva	1	296	294	0.94 ± 0.00
Slug	2	16	14	0.63 ± 0.55
Spider	6	18	14	0.64 ± 0.50
Weevil	1	173	167	0.90 ± 0.00

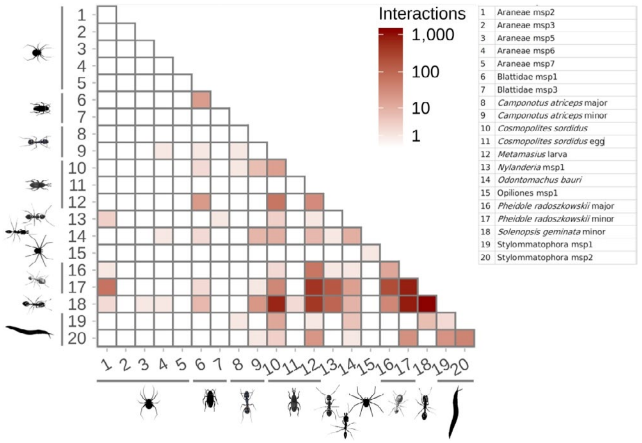

FIGURE 3 Interaction matrix showing interactions on our example dataset

3.2 | Interaction analysis

All interactions between animals are displayed on Figure 3. Such a matrix can be used to show the importance of intraspecific interactions. For instance, our example shows numerous intraspecific interactions for the ants *Pheidole radozkowskii* and *Solenopsis geminata*. Interspecific interactions can be shown as an interaction network and qualified given the participants of the interaction (Figure 4).

The number of predators interacting with a prey on an image is shown on Table 2. For example, smaller ants (*e.g. P. radoszkowskii*, *S. geminata*) need to invest more individuals for the capture of one prey than larger ants (*e.g. Odontomachus bauri*).

4 | DISCUSSION

4.1 | Time investment to apply the method

For our example, labelling (train and test datasets) took 12 hr of human work. This time can as well be reduced with the use of active learning methods (Qiu, Wu, Ding, Xu, & Feng, 2016). Using our method, with accurate knowledge of the imaged species, a dataset achieving 90% precision requires less than a day of work and is applicable by small research teams working on custom datasets.

4.2 | Interaction and predation definition

In this research, we assessed interactions between two individuals as the overlapping of bounding boxes. A source of error while studying interactions is the confusion between species of similar size and

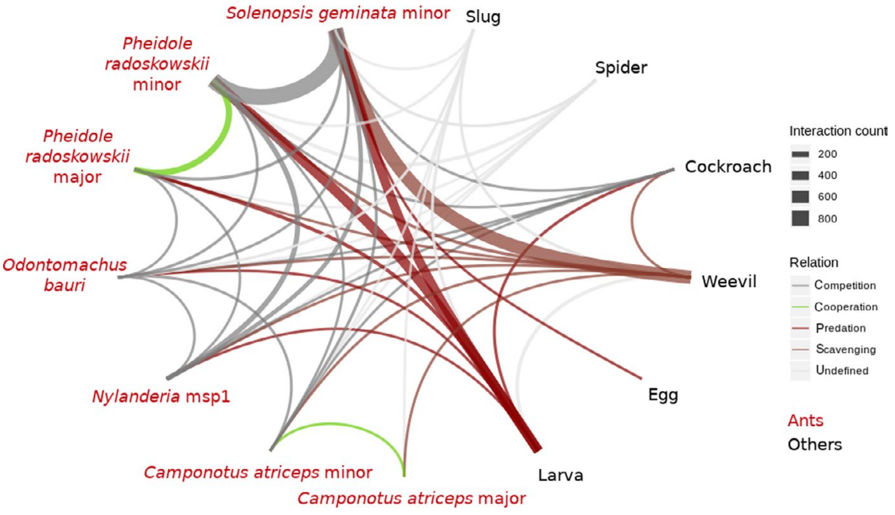

FIGURE 4 Trophic and non-trophic interaction network between species of the observed community

TABLE 2 Mean (± *SD*) numbers of predators surrounding an individual sentinel prey (± standard variation) as detected by automated image analysis. The values in parentheses (*n*) are the number of predation events recorded between the two species. msp = morphospecies, and Na indicates that the predator was never detected interacting with the prey

Predator	*Metamasius* larva (*n*)	*Cosmopolites sordidus* carcass (*n*)	*Cosmopolites* egg (*n*)
Blattidae msp1	1.05 ± 0.22 (19)	1.00 ± 0.00 (2)	Na
Camponotus atriceps minor	Na	1.00 ± 0.00 (6)	Na
Camponotus atriceps major	Na	1.00 ± 0.00 (1)	Na
Nylanderia msp1	1.00 ± 0.00 (1)	1.00 ± 0.00 (3)	Na
Odontomachus bauri	1.16 ± 0.37 (6)	1.00 ± 0.00 (10)	Na
Pheidole radoszowskii minor	3.03 ± 2.25 (153)	1.03 ± 0.16 (35)	Na
Pheidole radoszowskii major	1.37 ± 0.61 (45)	1.00 ± 0.00 (2)	Na
Solenopsis geminata minor	3.47 ± 2.05 (120)	1.94 ± 0.46 (347)	1.00 ± 0.00 (2)

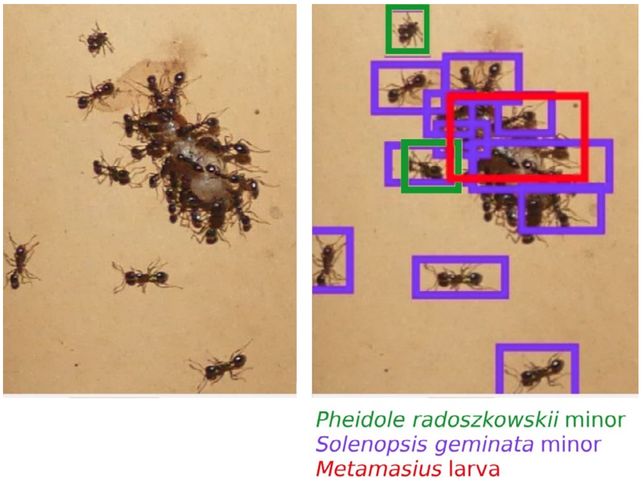

FIGURE 5 Example of complex situation leading to misclassifications, FP and FN. Some minor worker of *Solenopsis geminata* were confused with minor worker of *Pheidole radoszkowskii*, another species of the Myrmicinae subfamily and of similar size

general morphology. The high number of interactions between *P. radoszkowskii* and *S. geminata*, for example, was an artefact mostly due to confusion between the two classes. In images displaying an *S. geminata* attack on *Metamasius* larvae, 1,050 of 9,436 *S. geminata* were also incorrectly detected as *P. radoszkowskii*, resulting in the generation of false positives. These confusions mostly occur in complex, crowded scenes, which are difficult to assess even for a human observer (see Figure 5).

4.3 | Robustness of the method

One problem facing deep-learning methods, especially with small datasets, is overfitting. Here, despite the limited amount of training data, our model was not overfitted, as indicated by the test loss to training loss ratio and the test performances. Our model is robust partly as a consequence of the slicing of the original image. With the slicing of original images, the model does not learn directly from the original images but from the slices after pre-processing (with our example parameters, this means a 108 times larger dataset). Furthermore, a vast majority of the slices show background that provides various details and shapes at a precise level (branches, soil particles, etc.) that could have been confounded with invertebrates. These details are learned by the model and reduce possible confusion. This effect could be associated with hard negative mining, which has been a successful strategy to improve neural network performance (e.g. Ogier Du Terrail & Jurie, 2017; Sun, Wu, & Hoi, 2018). Data augmentation is also important for ensuring robustness (Goodfellow, Bengio, & Courville, 2016), particularly with small datasets. Performances and robustness of the model depend on the dataset but the use of high-resolution images and slicing ensures a relative robustness even for small datasets.

4.4 | Further improvements

To reduce the risk of false positives and false negatives (especially when dealing with unknown species), hierarchical classification approaches could be developed. These methods are a known technique to improve model generalization and have been shown to be relevant in handling biological data (Colonna, Gama, & Nakamura, 2018; Redmon & Farhadi, 2016).

In our example dataset, images were taken with short time steps and are not independent, leading to a possible bias in the frequency of interactions. This bias could be overcome by the tracking of individuals over multiple images (e.g. see Romerro-Ferrero, Bergomi, Hinz, Heras, & Polavieja, 2019).

DATA AVAILABILITY STATEMENT

Code is available on Github https://github.com/PTresson/Corigan/tree/v1.0 or on Zenodo https://zenodo.org/record/3357305. Data available from the Dryad Digital Repository https://doi.org/10.5281/zenodo.3357305 (PTresson, 2019). Training and testing datasets are available online on Dryad Digital Repository https://doi.org/10.5061/dryad.t03b7b8 (Tresson et al., 2019).

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AUTHORS' CONTRIBUTIONS

Pa.T., D.C., Ph.T. and W.P. conceived of research idea. Pa.T. implemented and evaluated the methods and led the writing of the manuscript. D.C. and S.R. conducted the field study. D.C., C.P. and Pa.T. contributed to the labelling task. L.B.B. initiated the project. All authors contributed critically to the drafts and gave final approval for publication.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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Plant richness enhances banana weevil regulation in a tropical agroecosystem by affecting a multitrophic food web

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ABSTRACT

Field-scale plant diversification of agroecosystems is a promising way to enhance ecological pest regulation. Existing studies, however, have provided inconsistent results and have generally focused on only a few trophic groups or a few levels of plant diversification. Using field data from banana agroecosystems and structural equation modelling, we assessed (i) the effects of plant species richness (two height strata) and soil cover (% of living plant cover and% of litter cover) on a multitrophic arthropod food web, (ii) the links among five trophic groups of arthropods (detritivores, herbivores, non-ant omnivores, omnivorous ants, and predators) and (iii) the effect of natural enemies on the abundance and the damage of the banana weevil, *Cosmopolites sordidus*. Plant species richness of low strata (< 1.5 m high) had a positive bottom-up effect on herbivore prey abundance, which in turn enhanced the abundance of non-ant omnivores and of predators. Litter cover promoted the abundance of detritivore prey, which in turn enhanced predators and omnivorous ants. The latter two trophic groups were negatively related to weevil damage and probably reduced damage by consuming weevil eggs and larvae. Finally, on the basis of our results, we suggest how the plant community and soil cover within the field could be managed to enhance ecological regulation of the banana weevil.

1. Introduction

Field-scale plant diversification of agroecosystems has been proposed as a promising means of restoring ecological pest regulation and of reducing environmental and health problems resulting from pesticide applications (Gurr et al., 2003; Malezieux et al., 2009; Ratnadass et al., 2012). Several recent reviews have concluded that plant species richness has a generally positive effect on the regulation of herbivorous pest abundance or damage (Dassou et al., 2015; Letourneau et al., 2011). Some studies, however, have reported that plant species richness may have neutral or negative effects on the regulation of herbivores (Letourneau et al., 2011; Poveda et al., 2008). A limitation of many studies on this topic is that they focus on the abundance and/or richness of only one or two trophic groups (for instance, herbivorous pests and their natural enemies) even though changes in ecosystem services very likely result from changes in the abundance and richness of many interacting trophic groups (Soliveres et al., 2016). The latter authors showed that the consideration of only a small number of trophic groups has caused researchers to greatly underestimate the importance of ecosystem services provided by higher levels of plant richness. Here, using a multitrophic approach as described by Soliveres et al. (2016), we assessed the effect of field-scale plant species richness on the regulation of the abundance and the damage of an oligophagous pest of banana, *Cosmopolites sordidus* (Germar) (Coleoptera: Curculionidae).

The banana weevil, *Cosmopolites sordidus*, is the most important insect pest of bananas and plantains (Cuillé, 1950; Gold et al., 2001), which together are the second most important global fruit crop and the fourth most important global food commodity (after rice, wheat, and maize) in terms of production (Echezona et al., 2011). *Cosmopolites sordidus* is a narrowly oligophagous pest, attacking wild and cultivated clones of *Musa* and *Ensete* (Gold et al., 2001). Free-living adult weevils are nocturnal and disperse by walking, usually for short distances (Carval et al., 2015; Gold et al., 2001; Vinatier et al., 2010). Females lay eggs near the soil surface in the corm or at the base of the pseudostem of banana plants. The larvae bore galleries in the corm to feed (Cuillé, 1950; Koppenhöfer, 1993b), causing severe damage to the crop (Gold et al., 2001). Previous studies reported the potential for the control of the abundance or damage of *C. sordidus* by natural enemies (Abera-Kalibata et al., 2008; Carval et al., 2016; Dassou et al., 2015; Koppenhöfer et al., 1992; Mollot et al., 2012). Some of these studies

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have indicated that the regulation of *C. sordidus* could be affected by plant species richness possibly via effects on the arthropod community (Carval et al., 2016; Dassou et al., 2015; Mollot et al., 2012). However, it is difficult to draw general conclusions on the effect of plant richness on banana weevil regulation from these studies because (i) they did not consider a gradient of plant species richness and/or (ii) they only considered one species or group of species at a single trophic level of the arthropod food web. Here, we analysed the relationships between plant species richness, the abundance of five arthropod trophic groups (detritivores, herbivores, non-ant omnivores, omnivorous ants, and predators) and the regulation of *C. sordidus* abundance and damage. We hypothesised that i) field-scale plant species richness has positive bottom-up effects that increase the abundance of potential natural enemies and that ii) non-ant omnivores, omnivorous ants, and predatory arthropods reduce the abundance of adult banana weevils and the corm damage. To test these hypotheses, we collected data from banana agroecosystems covering a gradient of plant species richness. We then used structural equation modelling and generalised mixed-effects models to investigate i) the links between plant species richness in two height strata and the abundance of arthropod trophic groups and ii) the effects of plant species richness on the regulation of banana weevil abundance and damage.

2. Materials and methods

2.1. Study sites and design

We conducted a field study in the Reserve of Talamanca (9 °00′ – 9 °50′ N, 82 °35′ – 83 °05′ W) in Costa Rica. In this area, banana agroecosystems mainly consist of diversified agroforestry, but also include systems ranging up to intensive monoculture. The different types of agroecosystems differ in terms of plant community structure and composition (*Musa* genotypes and non-crop plant species). Agroforestry systems are generally long-established, they may contain several cultivars of plantains and bananas, and can include remnant forest trees, cultivated trees (e.g., cocoa), medicinal plants, ground crops (e.g., taro, cassava), and weeds (Somarriba and Harvey, 2003). The mean annual temperature and air relative humidity measured at several points within our sampling area during the study were 24.8 ± 0.3 °C and 91 ± 4.2%, respectively. The mean annual rainfall is about 3500 mm in this tropical-humid region (Deheuvels et al., 2012).

We monitored a network of 75 twenty-meters diameter circular plots distributed in 9 heterogeneous banana-based farmers' fields. Fields and plot locations were selected *a priori* to cover a wide range of plant species richness situations (Table 1). We installed one *in vitro*-propagated banana plant (*Musa* AAA, Cavendish subgroup, Grande Naine cultivar) in the center of each plot as a phytometer (Fig. 1). The phytometers are standardized plants (genetically similar) initially free of weevils and experimentally transplanted in contrasted situations to assess responses to environmental variables (Dietrich et al., 2013). Each phytometer was placed 1.5 m distant from an existing banana plant. Within one field, adjacent phytometers were at least 20 m apart so that two adjacent plots never overlapped. The study began in July 2014 and ended in January 2016. There was no chemical control or pheromone trapping of weevils in any of the fields.

In each plot, we evaluated plant species richness below and above 1.5 m high, the abundance of various trophic groups of the ground-dwelling arthropod food web, the abundance of adult banana weevils, and the damage caused by the weevils to the phytometer corm.

2.2. Plot-scale plant community

Plant species richness is commonly used as an indicator of ecosystem biodiversity (Dassou et al., 2015; Letourneau et al., 2011). Within each plot, we subdivided the plant community into a low stratum (plant height at top of the crown < 1.5 m) and a high stratum (plant height at top of the crown ≥1.5 m) to account for differential effects related to differences in plant traits such as height, growth rate, or lifespan. Plant species richness of the high-stratum was calculated as the number of plant species present in the plot after identification of each plant to species level. We evaluated the species richness of plants smaller than 1.5 m high along four transects of 10 m, going from the phytometer to the border of the plot and oriented toward the four cardinal points (Fig. 1). Plant species richness of the low stratum was obtained by averaging the four species richness values. Plants were identified using recent literature on the plants of Costa Rica (Gargiullo et al., 2008) and/or according to local, traditional knowledge (Cook et al., 2014). When a species was not identifiable, a morphospecies was assigned to the individual on the basis of morphological specificities, to allow for richness calculation. *Musa* genotype richness was assessed separately because of the particular role of this plant family in the life cycle of *C. sordidus* (Gold et al., 2001). Ultimately, we evaluated the percentage of living-plant soil cover and litter soil cover (including crop and other plant residues) within the plot as proxies for living and dead plant biomass, respectively.

2.3. Multiple trophic groups of ground-dwelling arthropods

Ground-dwelling arthropods were sampled using pitfall traps (Cosmotrack®, Calliope) containing water with a few drops of detergent (commercial dish cleaner) to weaken water surface tension. One trap was buried 50 cm away from each phytometer, and the trapped arthropods were retrieved 2 days later. Ants were identified to species using keys (Baccaro et al., 2015; Bolton, 1994; Bolton, 2000; Dash, 2011; Feitosa et al., 2008; Fernández, 2007; Jiménez et al., 2007; LaPolla and Fisher, 2014; Longino and Fernández, 2007; Mackay and Mackay, 2010; Pacheco and Mackay, 2013; Wild, 2005; Wilson, 2003). Other arthropods were identified to family (Delvare and Aberlenc, 1989), but a morphospecies was attributed to each individual based on morphological specificities, allowing further calculation of richness (Barratt et al., 2003). Each individual was assigned to one of the following trophic groups according to its species or family: detritivores,

Table 1
Total, low-stratum and high-stratum plant species richness (mean number of species ± standard-deviation of the plots), number of phytometers (or plots), *Musa* genotype richness and *Musa* density per hectare of the nine banana fields selected.

Field	Total plant species richness (± sd)	Low-stratum plant species richness (± sd)	High-stratum plant species richness (± sd)	Number of phytometers (± sd)	*Musa* genotype richness	*Musa* density per ha (± sd)
1	8 ± 2	7 ± 1	1 ± 1	8	1	2898 ± 287
2	10 ± 4	7 ± 4	3 ± 1	5	6	1982 ± 304
3	11 ± 4	7 ± 3	4 ± 2	14	2	505 ± 202
4	15 ± 3	12 ± 2	3 ± 1	5	2	2166 ± 287
5	15 ± 4	8 ± 2	7 ± 4	8	10	1477 ± 496
6	17 ± 9	13 ± 6	5 ± 3	10	8	994 ± 602
7	19 ± 3	17 ± 2	2 ± 2	10	3	857 ± 328
8	21 ± 6	13 ± 4	8 ± 3	8	5	677 ± 304
9	25 ± 2	17 ± 3	8 ± 2	8	7	912 ± 340

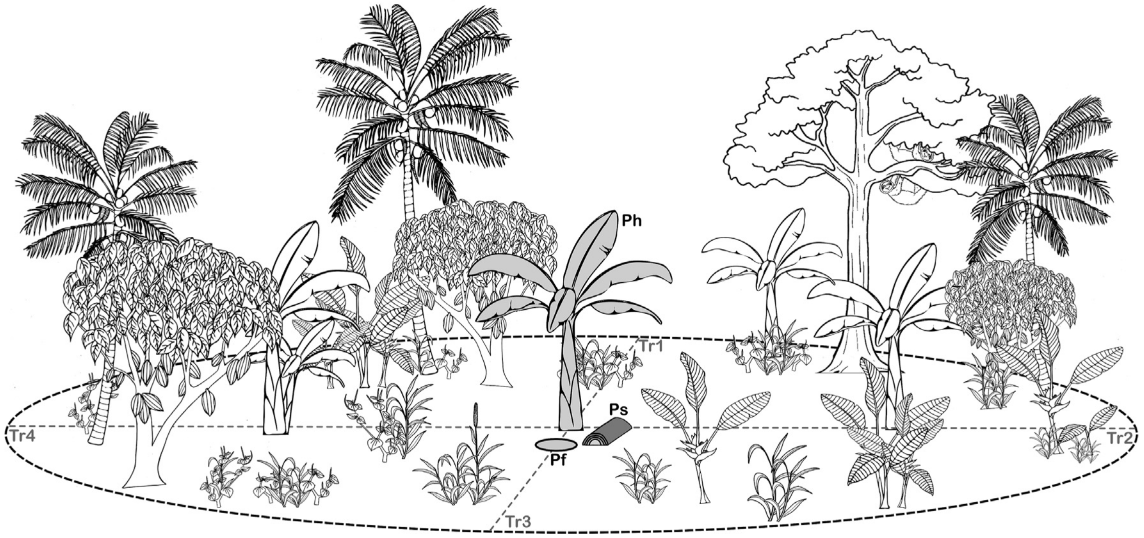

Fig. 1. Plot configuration. The phytometer (Ph) is placed in the center of the 20-meters diameter circular plot (dark dashed line). Gray dashed lines represent the four transects (Tr1, Tr2, Tr3, Tr4) used to assess low stratum plant species richness. Pseudostem (Ps) and pitfall traps (Pf), used for weevil and arthropod sampling respectively, are represented.

herbivores, non-ant omnivores, omnivorous ants, and predators. Pitfall sampling was performed twice in April 2015. For analyses, the abundances of each group at both sampling events were summed to obtain a single estimate for each arthropod group.

2.4. Banana weevil abundance and damage

The abundance of adult banana weevils was assessed using 30 cm-long pieces of banana pseudostem (*Musa* AAA, Gros Michel subgroup, Gros Michel cultivar) that were cut in half longitudinally and used as attractive traps (Gold et al., 2001). Pseudostem traps were first kept under controlled conditions outside the fields for one week, during which time they decomposed and thereby became more attractive to the weevil (Mestre and Rhino, 1997). One pseudostem trap was placed at the base of each phytometer where it was left for one week. The traps were surveyed six times every 2 days in April 2015, and each time the adult weevils present on the trap were counted. For analysis, the six counts were summed to obtain a single estimation of adult weevil abundance per phytometer.

At the end of the study, each phytometer was unearthed, and corm damage was assessed by stripping the entire circumference of the corm. The percentage of the corm circumference with weevil galleries was used as a corm damage score (0–100 scale; modified from Vilardebo (1973)). This method has been proved to be representative of the true level of corm damage (Dassou et al., 2015). Because of accidental cutting of phytometers by farm workers before the end of the study, only 56 of the 75 phytometers were evaluated for damage.

2.5. Data analysis

On the basis of the literature, we identified the *a priori* most probable hypotheses for the causal links among the variables describing the plant community and the abundances of the trophic groups of the food web of ground-dwelling arthropods. From these hypothetical links among the variables, we constituted a global path model composed of a set of 5 linear sub-models (Table 2). According to response variable distributions, all sub-models were Poisson general linear mixed models (GLMMs). To address the non-independence of sampling between fields, we added field identity as a random intercept effect in all sub-models (Zuur et al., 2009). We used structural equation modelling (SEM) (Grace, 2006) to realise a confirmatory test of our global path model and identify the significant relationships. Because the application of traditional SEM is restricted to normally distributed data, we used the *piecewiseSEM* R-package (Lefcheck, 2016), which generalises the method to a larger range of distribution families. In the piecewise SEM approach, Shipley's tests of direct separation are used to test for missing paths and a Fisher's C statistic is calculated from the p-values of those tests (Shipley, 2009). The confirmatory test of the global path model consists in running a chi-squared test on the C statistic. According to the piecewise SEM method described in Lefcheck (2016), the global path model is considered to represent the data well when the p-value of this chi-squared test is greater than the significance threshold. In addition, the *piecewiseSEM* package provides a coefficient for each path and two types of R^2 (the marginal R^2_m, which is the variance explained by fixed effects, and the conditional R^2_c, which is the variance explained by both fixed and random effects) as indicators of the goodness-of-fit of each sub-model (Nakagawa and Schielzeth, 2013).

We used Poisson GLMMs to assess i) the effect of each group of predatory arthropods (non-ant omnivores, omnivorous ants, and predators) and the effect of *Musa* abundance and richness on the abundance of adult weevils, and ii) the potential effects of the abundance of adult weevils and the abundance of each group of predatory arthropods on weevil corm damage score. We included field identity as a random intercept effect (Zuur et al., 2009) to account for uncontrolled field-scale effects. In each case, we selected the best model by removing non-significant fixed-effect parameters in a backward-stepwise process using likelihood ratio tests (LRTs) (Bolker et al., 2009). Following Nakagawa and Schielzeth (2013), we used R^2 as an absolute value for the goodness-of-fit of the models. We tested for potential correlation between total plant species richness and *Musa* abundance using linear regression.

All GLMMs were estimated using the 'lme4' package (Bates et al., 2011), in which the maximum likelihood of parameters is approximated by the Laplace method (Bolker et al., 2009). All statistical analyses were performed with R 3.3.1 (R Development Core Team, 2016) and with a significance threshold of 0.05.

3. Results

3.1. Plot-scale plant community

Plant richness in the plots ranged from 2.5 to 22.5 species in the low stratum and from 0 to 16 species in the high stratum. Total plant richness ranged from 4.5 to 32.25 species. *Musa* abundance and total plant species richness were negatively but weakly correlated ($R^2 = 0.10$; p-value < 0.001). In decreasing order of frequency, the

Table 2
Set of GLMMs constituting the global path model based on *a priori* hypotheses regarding the relationships between response variables (trophic group abundances) and explanatory variables (environmental variables). D: Detritivore abundance; H: Herbivore abundance; OA: Omnivorous ant abundance; O: Non-ant omnivore abundance; P: Predator abundance; LSR: Low-stratum plant richness; HSR: High-stratum plant richness; LC: % of litter cover; PC: % of living-plant cover.

Response variable	Explanatory variables	Hypothesized mechanisms	References
D	$LSR^1 + HSR^1 + LC^1$	^{1}Positive bottom-up effect of plant richness and% of litter cover	Landis et al. (2000), Birkhofer et al. (2008)
H	$LSR^2 + HSR^2 + PC^2$	^{2}Positive bottom-up effect of plant richness and% living-plant cover	Landis et al. (2000), Birkhofer et al. (2008)
OA	$H^3 + D^3 + LSR^4 + HSR^4 + PC^4 + P^5$	^{3}Positive bottom-up effect of prey abundance	Landis et al. (2000), Zehnder et al. (2007)
		^{4}Positive bottom-up effects (trophic and non-trophic) of plant richness and% of living-plant cover	Landis et al. (2000)
		^{5}Intraguild predation by predators	Gagnon et al. (2011)
O	$H^6 + D^6 + LSR^7 + HSR^7 + PC^7 + P^8$	^{6}Positive bottom-up effect (trophic and non-trophic) of plant richness and% of living-plant cover	Landis et al. (2000)
		^{7}Positive bottom-up effect of prey abundance	Landis et al. (2000), Zehnder et al. (2007)
		^{8}Intraguild predation by or competition with predators and omnivorous ants	Gagnon et al. (2011)
P	$H^9 + D^9 + LSR^{10} + HSR^{10} + PC^{10}$	^{9}Positive bottom-up effect of prey abundance	Landis et al. (2000), Zehnder et al. 2007
		^{10}Positive bottom-up effect of plant richness and% of living-plant cover	Landis et al. (2000), Birkhofer et al. (2008)

Musa genotypes present in the study plots were Gros Michel, Cavendish, Plantain, Quadrado, Lacatan, Fressinette, Chopo Colorado, Chopo Blanco, and Cocori.

3.2. Effects of plant species richness and soil cover on multitrophic food web of ground-dwelling arthropods

Our global path model represented the data well (Fisher's C = 21.17, d.f. = 14, χ^2 test p = 0.097), and 10 of the 23 links tested were significant. SEM results, including pathway coefficients and significance levels, are presented in Table 3. The significant causal relationship between trophic group abundances and environmental variables are summarised in the path diagram in Fig. 2. The arthropod orders found in the plots are listed in Table 4.

Table 3
Pathway coefficient estimates and p values from the structural equation modelling. D: Detritivore abundance; H: Herbivore abundance; P: Predator abundance; LSR: Low-stratum plant richness; HSR: High-stratum plant richness; LC: % of litter cover; PC: % of living-plant cover.

Response variable	Explanatory variable	Estimate (± SE)	p value
Detritivores	LSR	0.012 (± 0.020)	0.5565
	HSR	−0.007 (± 0.026)	0.7866
	LC	1.024 (± 0.342)	**0.0027**
Herbivores	LSR	0.054 (± 0.025)	**0.0297**
	HSR	−0.045 (± 0.032)	0.1695
	PC	0.051 (± 0.462)	0.9123
Omnivorous ants	H	−0.001 (± 0.018)	0.9587
	D	0.028 (± 0.009)	**0.0038**
	LSR	0.045 (± 0.0153)	**0.0031**
	HSR	0.010 (± 0.017)	0.5368
	PC	−0.371 (± 0.219)	0.0901
	P	−0.015 (± 0.008)	0.0705
Non-ant omnivores	H	0.178 (± 0.056)	**0.0014**
	D	−0.074 (± 0.053)	0.1644
	LSR	0.083 (± 0.043)	0.0517
	HSR	−0.019 (± 0.038)	0.6253
	PC	0.289 (± 0.832)	0.7288
	P	−0.103 (± 0.042)	**0.0147**
Predators	H	0.045 (± 0.020)	**0.0262**
	D	0.027 (± 0.010)	**0.0087**
	LSR	−0.046 (± 0.016)	**0.0054**
	HSR	−0.047 (± 0.020)	**0.0201**
	PC	0.436 (± 0.238)	0.0668

Values in bold are statistically significant at an alpha level of 0.05.

3.3. Biological control of the banana weevil by natural enemies

Adult weevil abundance was positively related to the abundance of *Musa* (χ^2(df = 1) = 4.56, p = 0.033) but was not related to *Musa* genotype richness (χ^2(df = 1) = 0.27, p = 0.604), the abundance of omnivorous ants (χ^2(df = 1) = 1.07, p = 0.299), the abundance of non-ant omnivores (χ^2(df = 1) = 1.06, p = 0.304), or the abundance of predators (χ^2(df = 1) = 1.18, p = 0.277). The marginal and conditional R^2 values (including the random intercept effect) of the selected model were 0.12 and 0.61, respectively.

The corm damage score was negatively related to the abundance of omnivorous ants (χ^2(df = 1) = 329.20, p < 0.001) and to the abundance of predators (χ^2(df = 1) = 139.01, p < 0.001) (Fig. 3). However, it was not related to the abundance of adult weevils (χ^2(df = 1) = 0.53, p = 0.465) or to the abundance of non-ant omnivores (χ^2(df = 1) = 1.20, p = 0.272). The selected model explained a large percentage of the variance with a marginal R^2 of 0.59 and a conditional R^2 of 0.97.

4. Discussion

4.1. Effect of plant species richness and soil cover on multitrophic food web of ground-dwelling arthropods

We found that the food web of ground-dwelling arthropods was shaped by both a detritivory and an herbivory bottom-up cascade that propagated up to the predaceous trophic levels and affected the abundance of the potential natural enemies of the banana weevil. In the case of the herbivory pathway, the low-stratum plant species richness had a positive bottom-up effect on the abundances of herbivores and of omnivorous ants but had no direct effect on the abundance of omnivores, although a substantial portion of the diet of opilions, which represented 83% of this group, includes fruits and other plant materials (Halaj and Cady, 2000; Schaus et al., 2013). Omnivorous ants combine predation, scavenging, and consumption of plant-based resources to meet their nutritional requirements. Plant-based resources used by ants are various and mostly consist of honeydew (from association with trophobionts), extra-floral nectaries, and seeds (Bluthgen and Feldhaar, 2010). The importance of plant-based resources in the diet of omnivorous ants

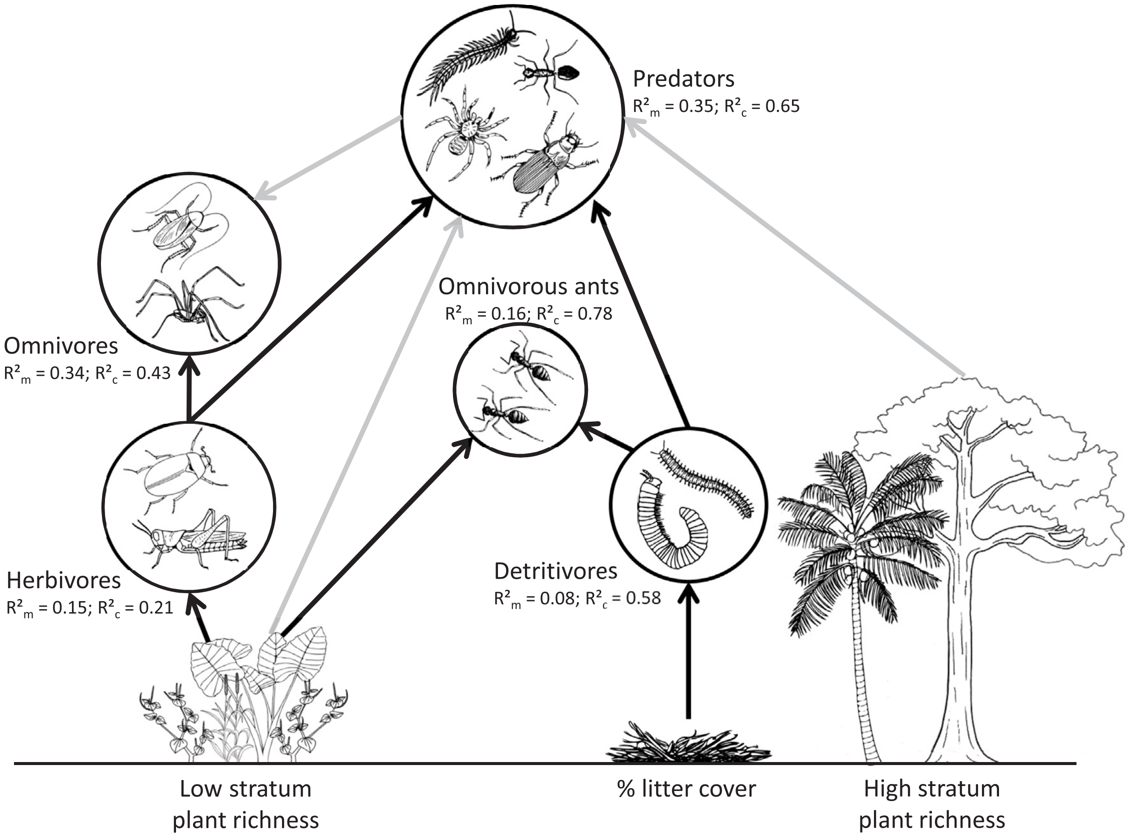

Fig. 2. Structural equation model of a multitrophic ground-dwelling arthropod food web. Structural equation model of the relationships among ground-dwelling arthropod trophic groups, low-stratum and high-stratum plant species richness, % of living plant cover, and % of litter cover. Black and grey arrows represent significant ($p < 0.05$) positive and negative relationships, respectively. The % of living-plant cover had no effect on any trophic group and is not shown. Non-significant relationships ($p > 0.05$) are not shown. Marginal (m) and conditional (c) R^2 values for each response variable are indicated.

Table 4
List and total abundance of arthropod orders of each trophic group sampled during the field study.

Trophic group	Class	Order	Individuals
Detritivores	Insecta	Collembole	201
		Coleoptera	26
	Diplopoda	Polydesmida	63
		Spirobolida	8
		Julida	7
		Stemmiulida	3
	Malacostraca	Isopoda	42
Herbivores	Insecta	Orthoptera	77
		Hemiptera	66
		Coleoptera	36
		Homoptera	15
		Hymenoptera	3
		Lepidoptera	2
		Thysanoptera	1
Omnivores	Insecta	Hymenoptera (ants)	904
		Blattodae	10
	Arachnida	Opiliones	49
Predators	Insecta	Hymenoptera (ants)	331
		Coleoptera	92
		Hemiptera	19
		Dermaptera	4
		Mantodae	1
	Arachnida	Araneae	309
		Scorpiones	1
	Chilopoda	Lithobiomorpha	2

is consistent with our finding that plant richness had a positive effect on the abundance of omnivorous ants.

We found no effect of the percentage of living-plant cover, which served as a proxy for plant biomass, on any trophic group. This is consistent with Scherber et al. (2010), who found that herbivore and omnivore abundances were positively related with plant richness but not with plant biomass. Because the percentage of living-plant cover was not associated with arthropod abundances, we infer that the effect of plant richness on arthropod groups was more likely due to niche

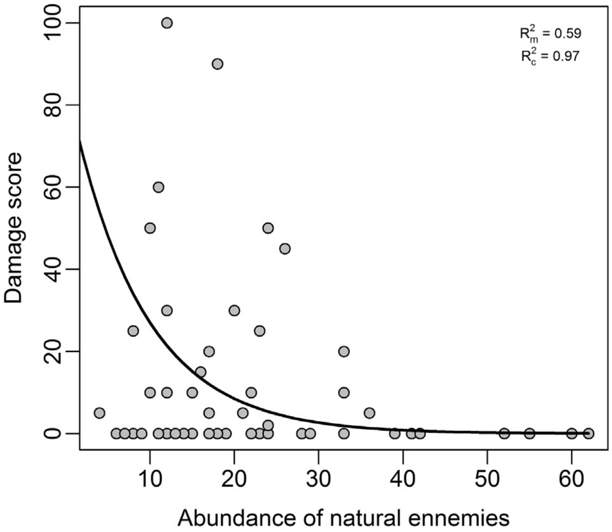

Fig. 3. Weevil damage *vs.* natural enemies' abundance. Relationship between damage by *C. sordidus* and the abundance of natural enemies (i.e. the sum of the abundance of omnivorous ants and predators, which were found to be both negatively correlated to the damage score). Circles: observed data; Line: relationship predicted by a Poisson GLMM.

diversity and complementarity rather than to resource abundance. In addition, the abundance of detritivores increased with the percentage of litter cover, likely because of increases in the availability of food and shelter.

Surprisingly, our study detected a negative effect of high- and low-strata plant richness on the abundance of predators. Malumbres-Olarte et al. (2013) found that the response to tussock cover differed among ground-active spider families and even among species within the Lycosidae family, which was the most represented spider family in our study. Such inconsistent responses to plant characteristics among spiders, which represented 42% of the predator group, suggest that the global negative effect of plant richness on predators in the current study may have masked the positive response of the abundance of certain spider species. However, pitfall trapping reflects relative arthropod activities, which depend on population density and activity (Curtis, 1980), rather than absolute abundances. Therefore, the global negative effect of plant richness on predators that we observed may also be explained by trapping bias. Higher plant species richness is expected to increase the structural complexity of vegetation, which may reduce the capacity or the need for predators to move to find shelter, mates, or food. Reduced movement may reduce trapping probability and lead to an underestimation of predator abundance. By manipulating the vegetation structure, Birkhofer et al. (2008) demonstrated that increasing vegetation complexity led to a decrease in the activity and abundance of ground-active spiders in a winter wheat field.

We found a positive, indirect bottom-up effect of the low strata plant richness on the abundance of omnivores and predators through the increase in the availability of alternative herbivore prey. In addition, predators seemed to benefit substantially from the detritivory pathway in that their abundance was positively related to the abundance of detritivores. A previous study showed that spiders, which were the second most abundant taxa within the predator group of the current study, can feed on both herbivory and detritivory pathways (Oelbermann et al., 2008).

Among the predaceous ants, which represented 45% of the predator group, 66% were *Ectatomma ruidum*. These large ants feed on herbivores, detritivores, and omnivores (Ibarra-Nunez et al., 2001) and are able to attack opilions and other large preys. This suggests that the negative effect of predator abundance on non-ant omnivore abundance was driven by intraguild predation of opilions by *Ectatomma ruidum*, especially given that those two taxa accounted for large proportions of their respective groups.

Our results support the hypothesis that the positive effects of vegetation on higher trophic levels are primarily driven by additional alternative prey rather than by structural complexity and highlight the potential role of plant-based resources on natural enemies, especially on omnivorous ants (Landis et al., 2000; Wackers et al., 2007) .

4.2. Plant richness and the biological control of the banana weevil by natural enemies

Our results show that plant species richness is associated with a reduction of weevil abundance and corm damage (see Fig. 2 in Poeydebat et al. (submitted)), suggesting that the regulation of this pest might be enhanced by field-scale agroecosystem plant diversification. Such diversification may reduce pest abundance (Letourneau et al., 2011; Scherber et al., 2010; Symondson et al., 2002) through top-down effects associated with herbivore prey amplification and higher enemy abundance (Dassou et al., 2016; Letourneau et al., 2011; Poveda et al., 2008). However, we did not find a relationship between the abundance of *C. sordidus* adults and any potential natural enemy, i.e., we did not find evidence of top-down control of adults. In *C. sordidus*, the adult is cryptic and nocturnal and has a hard cuticle that may deter attack by predators (Koppenhöfer et al., 1992). Abera-Kalibata et al. (2006) searched for co-evolved natural enemies in the native region of *C. sordidus* but failed to find natural enemies that attacked adults. Adult suppression associated with plant species richness may rely on other predators or pathogens. Consistent with the resource concentration hypothesis (Root, 1973), the abundance of *C. sordidus*, which is an oligophagous pest, decreased with the abundance of *Musa*. The negative relationship between plant species richness and *Musa* abundance in our study corroborates the role of host plant dilution in the regulation of weevil abundance.

Nevertheless, our results suggest that plant species richness enhance weevil corm damage regulation by promoting herbivorous and detritivorous preys and natural enemies that feed on immature stages of *C. sordidus*. Indeed, one may consider the damage score as a proxy for the incidence of immature stages (Carval et al., 2016). Researchers have reported that generalist predators consume banana weevil eggs and larvae (Abera-Kalibata et al., 2006; Koppenhöfer, 1993a; Koppenhöfer et al., 1992; Mollot et al., 2012) and that ants consume the eggs of various pest species (Way and Khoo, 1992).

In our study, the abundance of predators had a negative effect on the abundance of non-ant omnivores, which is likely a result of intraguild predation. Although intraguild predation may reduce predation on pests, this risk is thought to be relatively low (Chailleux et al., 2014; Rosenheim, 2007). In the current study, intraguild predation did not disrupt biological control because non-ant omnivores did not contribute to the control of weevil damage.

Because susceptibility to weevil attack varies among *Musa* cultivars (Kiggundu et al., 2007; Ortiz et al., 1995), we would have expected to detect positive (or negative) effects of *Musa* richness on weevil abundance if the cultivars were more susceptible (or more resistant) than the phytometer. In our study, the absence of an effect of *Musa* richness on the abundance of adult weevils may have resulted from a low variability in the susceptibility to the pest among the cultivars or from the balancing effect of a combination of more susceptible and more resistant cultivars compared to the phytometer.

Consistent with previous studies (Gold et al., 2001; Vilardebo, 1973), we found no relationship between weevil abundance and damage. This can be explained by the gap between the dispersal ability and lifespan of adults and immature stages and/or by the difference between the cumulative nature of the corm damage score, which integrates larval damage over time, and the punctual assessment of adult abundance.

5. Conclusions

Our results are consistent with the idea that pest regulation in agroecosystems can be enhanced through field-scale plant diversification. More specifically, our results suggest how the plant community and soil cover affect banana weevil regulation in banana and plantain agroecosystems. Omnivorous ants and predatory arthropods (including predaceous ants) were the groups likely responsible for the control of *C. sordidus* damage through eggs or larvae predation. The predator group contained different sub-groups of arthropods but was dominated by spiders, ants, and coleopterans. Plant species richness did not directly promote predator abundance, but indirectly, by supporting increases in omnivorous and herbivorous preys. Predators were also found to feed on detritivores, whose abundance was positively related to the percentage of litter cover. Ground-dwelling spiders and carabids prefer open habitat patches for movement and foraging (Birkhofer et al., 2008) but are also dependant on prey from plant diversified patches and litter patches. Omnivorous ants fed on detritivores and on plant-based resources, whose abundances positively depended on soil litter cover and plant richness, respectively. Additionally, bare soil has been shown to promote predation by ants (Jaffe et al., 1990). Finally, because the percentage of living-plant cover had no effect on any trophic group, we infer that plant richness rather than abundance is important for biological pest control. Thus, we suggest that future research should be conducted to evaluate the following three management strategies. First, the crop field should consist of a matrix that includes (i) plant-diversified patches that promote the abundance and diversity of alternative herbivore preys and plant-based resources; (ii) crop and noncrop litter patches to promote the abundance of alternative detritivore prey; and (iii) bare soil patches to promote predator and omnivore foraging. Second, the plant species within the plant-diversified patches should be carefully selected because (i) plants that produce extrafloral nectaries can enhance biological control (Rezende et al., 2014), and (ii) some plant species may be hosts of other polyphagous pests of the crop (Zehnder et al., 2007) including plant-parasitic nematodes (Queneherve et al., 2006). Third, according to our results and to the resource concentration hypothesis (Root, 1973), farmers should reduce the planting density of the major cash crop(s) whenever it is economically viable and could compensate for the loss in production by planting other food crops or cash crops. Finally, the local fragmentation of habitats recommended here could be achieved with mixed systems that included annual, semi-perennial, and perennial crops.

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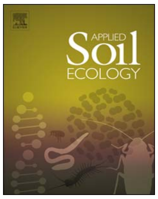

Does plant richness alter multitrophic soil food web and promote plant-parasitic nematode regulation in banana agroecosystems?

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ABSTRACT

Agroecosystem plant diversification at the field scale has been shown to enhance ecological pest regulation. We explored the effects of plant community composition and soil properties on the soil nematode community, with a particular interest in the regulation of banana plant-parasitic nematodes (PPN). We monitored banana phytometers (Cavendish Grande Naine cultivar) in 85 plots distributed along a plant richness gradient. Plant community composition, soil properties, abundance of bacterivorous, fungivorous and proportion of predaceous soil free-living nematodes, and abundance and damage of PPN (*Radopholus similis*, *Pratylenchus coffeae*, *Helicotylenchus multicinctus*, and *Meloidogyne* spp.) in phytometer roots were measured. We used structural equation modeling to investigate ecological processes leading to PPN regulation. Low-stratum plant species richness, but not high-stratum, was positively related to microbivore nematode abundances, supposedly because it promoted qualitative diversity of organic inputs and micro-climatic effects supporting more soil microorganisms. *Musa* genotype and low-stratum plant species richness induced associational susceptibility because of differential susceptibility of *Musa* genotypes to PPN and because of polyphagia of PPN spreading outside the *Musa* family, respectively. We found no regulation of PPN by predaceous nematodes, probably because food web complexity prevented trophic cascades from propagating. Ultimately, fungivorous nematode abundance was negatively related to PPN abundance, suggesting apparent competition or increased regulation by antagonistic fungi. Our results suggest that, when facing generalist pests, cropped plant communities should be diversified to promote pest regulation but must be carefully assembled to limit pest susceptibility heterogeneity among crop genotypes and to exclude alternative host plant species.

1. Introduction

According to the “resource concentration hypothesis” (Root, 1973), monocultures are prone to pest and disease infestation. Since the 1990’s, agroecosystem plant diversification is increasingly considered a promising way to restore positive interactions among plants and promote ecological pest regulation (Altieri, 1999; Malézieux et al., 2009; Tscharntke et al., 2012; Leakey, 2014; Isbell, 2015). Meta-analyses have shown that field-scale agroecosystem plant diversification might be associated with regulation of diverse pests (Quijas et al., 2010; Letourneau et al., 2011; Boudreau, 2013; Dassou and Tixier, 2016), including plant-parasitic nematodes (PPN). In some cases, however, plant diversification may favor pests (Schroth et al., 2000; Norris and Kogan, 2005) leading to increased damage (Quijas et al., 2010; Letourneau et al., 2011).

Plant diversification can have positive, negative or neutral effect on PPN abundance in agroecosystems (Boudreau, 2013). Several studies have demonstrated that the effect of primary resource diversification on the soil food web depends on the identity of the plants and is more likely attributable to the complementarity in resource quality than to an increase in total resource quantity (Wardle et al., 2003; de Deyn et al., 2004; Djigal et al., 2012). In these studies, authors compared the soil food webs before and after an artificial change in vegetation during short experiments (from 8 to 28 months). Therefore, they rather assessed the effect of perturbations on nematode communities than the influence of plant diversity or richness on these communities in perennial cropping systems. *A fortiori*, nematodes belong to the below-ground compartment of ecosystems, which presents inertia in responding to changes in the plant community (Korthals et al., 2001;

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Eisenhauer et al., 2010; Wardle and Jonsson, 2014). Because of their direct dependence on plant resources, PPN are more responsive to changes in vegetation than nematodes belonging to other trophic groups (Korthals et al., 2001). Short-term studies may therefore observe transitive community states rather than the final consequence of plant diversification on the soil food webs and ultimately on PPN regulation.

Banana-based agroecosystems provide a good model to study the effect of plant community diversity on the soil food web and the regulation of PPN since bananas are grown as semi-perennial or perennial crop under wide ranges of plant community structure and composition. Among the most damaging pests in banana agroecosystems are the PPN (Gowen et al., 2005) which reduce yields by disrupting soil resource uptake and by causing banana plants to topple (Quénéhervé, 2008). Banana roots are attacked by various PPN species presenting different parasitic modes (Gowen et al., 2005; Quénéhervé, 2008). The main banana PPN are the migratory and strict endoparasites *Radopholus similis* and *Pratylenchus coffeae* which perform their entire cycle within the central cylinder of the roots (Gowen et al., 2005), the migratory semi-endoparasite *Helicotylenchus multicinctus* which is confined to the cortical cells of the roots (Orion et al., 1999), and the sedentary endoparasite *Meloidogyne* genus, in which females form root galls before releasing juveniles in the soil. In export banana production, nematicides have been widely used to control PPN resulting in 5–267% yield increases (Quénéhervé, 2008). However, nematicides represent a threat to beneficial nematodes (Timper, 2014), human health and the environment (Matthews, 2006), and their efficiency may decrease with repeated application (Moens et al., 2004). In French West Indies, nematicides have led to water, soil and reef pollutions (Bocquené and Franco, 2005; Cabidoche et al., 2009) with consequences on human health and ecosystem functioning. To control PPN more sustainably, growers may adopt cultural practices to interrupt PPN population growth such as fallow or rotation with non-host crops and clean material replanting (Quénéhervé, 1993). Unfortunately, these practices did not lead to economic and environmental benefits in all farm contexts (Blazy et al., 2009). Elsewhere, cultural practices relying on biodiversity, i.e. mixed crops or cultivars, the introduction of antagonistic or trap plants or the use of resistant cultivars, have emerged in subsistence agriculture where farmers cannot afford nematicides (Bridge, 1996). Such field-scale spatial diversification practices have been reported to enhance PPN regulation for several crops but rarely for bananas.

In banana agroecosystems, the mixture of banana genotypes is likely to affect PPN abundances, as banana genotypes are more or less susceptible to PPN (Quénéhervé et al., 2009, 2011). The addition of cover crops has been showed to affect the abundance of multiple nematode trophic groups (Djigal et al., 2012). Moreover, the composition of the plant community may determine the quality and quantity of organic matter and interfere with the composition of the soil community (detritivore micro-organisms and nematodes) and affect PPN regulation (Tabarant et al., 2011). Trophic links may be involved in the regulation of PPN (Khan and Kim, 2007; Holtkamp et al., 2008). Recent studies using molecular gut analysis confirmed that predaceous nematodes were feeding on PPN, especially when in contact with the rhizosphere, (Cabos et al., 2013; Wang et al., 2015). However, the efficacy of predaceous nematodes as biological control agent may depend on their abundance relatively to that of PPN, the length of their life cycle, their sensitivity to soil perturbations and their degree of specialization (Neher, 2010). Antagonistic fungi trapping or feeding on PPN are also expected to play a role in PPN regulation (Siddiqui and Mahmood, 1996; Dong and Zhang, 2006; Mendoza and Sikora, 2009).

In this study, we monitored multitrophic soil food webs including free-living and plant-parasitic nematodes in a gradient of plant species richness in farmers' banana fields established for more than two years. We used structural equation modelling to test for and understand the effects of plant richness (crop and non-crop) and soil properties on the soil food web, and ultimately on banana PPN regulation.

2. Methods

2.1. Study regions

We conducted a field study in the Lamentin Plain in the center of Martinique, French West Indies (14°28′–14°40′ N, 60°54′–61°05′ W) and in the Talamanca Reserve (9°00′–9°50′ N, 82°35′–83°05′ W) in south-eastern Costa Rica. These two tropical, humid regions have similar pedo-climatic conditions and cover complementary ranges of agroecosystem plant diversity, ranging from intensive monoculture to highly diversified agroforestry. In the Lamentin Plain, bananas and plantains are mainly grown as a monoculture on bare soil or with a cover crop; fields eventually include spontaneous cover or marginal crops or trees (e.g., citrus trees, coconut trees, sugar cane). In the Talamanca Reserve, banana agroecosystems mainly consist of agroforestry systems varying in terms of plant community structure and composition, but including monocultures. Agroforestry systems may contain a mix of cultivars and include remnant forest trees, cultivated trees (e.g., cacao trees), medicinal plants, ground crops (e.g. taro, cassava) and weeds. The mean annual temperature measured within our sampling zone during the study was 26.7 ± 0.4 °C in Martinique and 24.8 ± 0.3 °C in Costa Rica. The mean annual rainfall ranges from 1500 to 2500 mm from south to north on the Lamentin Plain (Duyck et al., 2012) and is about 3500 mm in the Talamanca Reserve (Deheuvels et al., 2012). Soils are alluvial soils or Ferrisols (Colmet-Daage and Lagache, 1965; Winowiecki, 2008).

2.2. Phytometers

We monitored a network of 85 twenty-meters diameter circular plots (29 plots in Martinique and 56 plots in Costa Rica) distributed in 9 heterogeneous banana-based farmers' fields. All fields were established for at least 2 years at the beginning of the experiment. Fields and plot locations were selected *a priori* to cover a wide range of plant species richness situations. We installed one *in vitro*-propagated banana plant (*Musa* AAA, Cavendish subgroup, Grande Naine cultivar) in the center of each plot as a phytometer (**Fig. S1** in Supplementary material). The phytometers are standardized plants (genetically similar) initially free of nematodes and experimentally transplanted in contrasted situations to assess responses to environmental variables (Dietrich et al., 2013). Each phytometer was placed 1.5 m distant from an existing banana plant. Within one field, adjacent phytometers were at least 20 m apart so that two adjacent plots never overlapped. The study began in July 2014 and ended in January 2016. No chemical control of nematodes or soil perturbation occurred in any of the fields during the study. In each plot, we evaluated the abiotic properties of the soil, plant richness, *Musa* abundance and richness, abundance of free-living nematodes in the soil according to trophic group, PPN abundance in the phytometer roots and damage caused to the phytometer roots.

2.3. Plant community

Plant species richness is commonly used as an indicator of ecosystem plant biodiversity (Letourneau et al., 2011; Soliveres et al., 2016). Within each plot, we subdivided the plant community into a low stratum (plant height at top of the crown < 1.5 m) and a high stratum (plant height at top of the crown ≥1.5 m) to account for differential effects related to differences in plant traits such as root depth and growth dynamics. Plant species richness of the high stratum was calculated as the number of plant species present in the plot after identification of each plant to species level. We evaluated the species richness of plants smaller than 1.5 m high along four transects of 10 m, going from the phytometer to the border of the plot and oriented toward the four cardinal points (**Fig. S1**). For each transect, we counted the number of plant species encountered along the transect within a 20-cm wide strip. Plant species richness of the low stratum was obtained by

Table 1

Summary of the sub-models composing the overall structural equation model. LSPR: low-stratum plant species richness; HSPR: high-stratum plant species richness; SH: soil humidity; SOM: soil organic matter (%); SCN: soil C:N ratio; MA: *Musa* abundance; MR: *Musa* richness; BN: abundance of bacterivorous nematodes; FN: abundance of fungivorous nematodes; PN: proportion of predaceous nematodes; Rsim: abundance of *Radopholus similis*; Pcof: abundance of *Pratylenchus coffeae*; Hmul: abundance of *Helicotylenchus multicinctus*; Melo: abundance of *Meloidogyne* spp.; RD: root damage.

SEM sub-models

Response variable	Explanatory variables
BN	LSPR[1] + HSPR[1] + SH[2] + SOM[3] + SCN[4]
FN	LSPR[1] + HSPR[1] + SH[2] + SOM[3] + SCN[4]
PN	LSPR[1] + HSPR[1] + SH[2] + SOM[3] + SCN[4]
Rsim	LSPR[5] + HSPR[5] + MA[6] + MR[7] + BN[8] + FN[8] + PN[9]
Pcof	LSPR[5] + HSPR[5] + MA[6] + MR[7] + BN[8] + FN[8] + PN[9]
Hmul	LSPR[5] + HSPR[5] + MA[6] + MR[7] + BN[8] + FN[8] + PN[9]
Melo	LSPR[5] + HSPR[5] + MA[6] + MR[7] + BN[8] + FN[8] + PN[9]
RD	Rsim[10] + Pcof[10] + Hmul[10] + Melo[10]

SEM *a priori* hypotheses	References
[1]Plant species richness affects the composition of the soil food web through effects on the quantity and the quality of basal resources and on soil properties.	Eisenhauer et al. (2010), Djigal et al. (2012) and Lange et al. (2014, 2015)
[2]Soil humidity affects the activity of soil organisms.	Schnürer et al. (1986)
[3]Soil organic matter content affects the activity of soil saprophytic microorganisms and the texture of the soil.	Bongers and Bongers (1998), van der Putten et al. (2006) and Tabarant et al. (2011)
[4]Soil C:N ratio determines the relative abundances of bacterivorous and fungivorous soil free-living nematodes.	Ferris and Matute (2003)
[5]Plant richness affects the abundance of banana plant-parasitic nematodes through effects on the quantity and quality of hosts.	Duyck et al. (2009)
[6]Host abundance (or density) determines pest abundance by dilution effect.	Root (1973)
[7]Host genotype richness affects the level of pest inoculum and the abundance of pest observed on the phytometer.	Barbosa et al. (2009) and Quénéhervé et al. (2009, 2011)
[8]The abundances of free-living bacterivorous and fungivorous nematodes are proxies for the abundances of soil bacteria and fungi, respectively; Antagonistic bacteria or fungi (pathogen or predator) particpates in banana PPN regulation.	Ferris et al. (2001), Neher (2001), Siddiqui and Mahmood (1996), Dong and Zhang (2006) and Mendoza and Sikora (2009)
[9]Predaceous free-living nematodes feed on banana PPN.	Khan and Kim (2007), Holtkamp et al. (2008) and Cabos et al. (2013)
[10]PPN cause root damage.	Gowen et al. (2005) and Quénéhervé (2008)

averaging the four species richness values. Plants were identified using recent literature (Gargiullo et al., 2008; Rohwer, 2012) and/or according to expert, local and traditional knowledge (Cook et al., 2014). When a species was not identifiable, a morphospecies was assigned to the individual on the basis of morphological specificities, to allow for richness calculation. *Musa* genotype richness was assessed separately because of the particular role of this plant family in the life cycle of banana PPN (Gowen et al., 2005). We tested for potential correlation between total plant richness (sum of low- and high-stratum plant species richness) and *Musa* abundance, and between total plant species richness and nematode community SI and MI using linear regression.

2.4. Soil properties and free-living nematodes

Soil samples were collected in September 2015 in Martinique and in August 2015 in Costa Rica. For each plot, six soil samples were taken within an area of 50-cm radius around the phytometer (**Fig. S1** in Supplementary material) and from 0 to 30 cm depth, and then mixed to form one composite sample per plot. Composite soil samples were divided in two subsamples; one 50-g subsample was used for soil analyses, and another 300-g subsample was used to assess the abundance of three trophic groups of free-living nematodes. Soil humidity, soil organic matter content and soil C:N ratio were analyzed by the Laboratory of Soil Analyses US 49, CIRAD (France). Soil free-living nematodes were extracted from the composite soil subsamples by elutriation (Seinhorst, 1962) and then the extracted material was passed through modified Baermann funnels (Whitehead and Hemming, 1965). Nematodes were subsequently fixed, identified to family or genus, and counted. According to their taxa, nematodes were assigned to one of the following trophic groups: bacterivorous, fungivorous or predaceous (omnivorous and strictly carnivorous), and the abundance of each trophic group was assessed. For further analysis, we calculated the proportion of predaceous nematodes in the soil nematode community as this metric was expected to better relate to soil suppressiveness, i.e. PPN regulation (Sánchez-Moreno and Ferris, 2007). Free-living nematodes were also classified into five c-p (colonizer-persister) groups in order to calculate the maturity index (MI) (Bongers, 1990) and the structure index (SI) (Ferris et al., 2001) of the community. MI and SI range from 1 to 5 and from 0 to 100 and increase with environmental stability and food web complexity, respectively. Since free-living fungivorous and bacterivorous nematodes have been proven to be good proxies for soil fungi and bacteria, respectively (Ferris et al., 2001; Neher, 2001), we did not measured directly the abundance of soil fungi and bacteria.

2.5. PPN abundance and damage assessment

After flowering (or at the end of the experiment for phytometers that did not flower), phytometer root samples were taken between 5 and 30 cm depth near the corm. The roots were longitudinally cut in two parts, and damage was evaluated by a single observer on a 0 (no damage) to 5 (complete damage) scale (Bridge et al., 1993). Damage assessment accounted for both the cortex and the central cylinder. The same root samples were used to assess the abundance of the four main PPN taxa: *R. similis*, *P. coffeae*, *H. multicinctus*, and *Meloidogyne* spp. Nematodes were extracted from banana roots following Araya-Vargas (2002). They were identified to species level and counted with a ×50 stereomicroscope.

2.6. Structural equation modelling

On the basis of the literature, we identified *a priori* probable hypotheses for the causal links among the variables describing the plant community, the properties of the soil, the abundances of the trophic groups of free-living nematodes, the abundances of the banana PPN taxa and the root damage. From these hypothetical links among

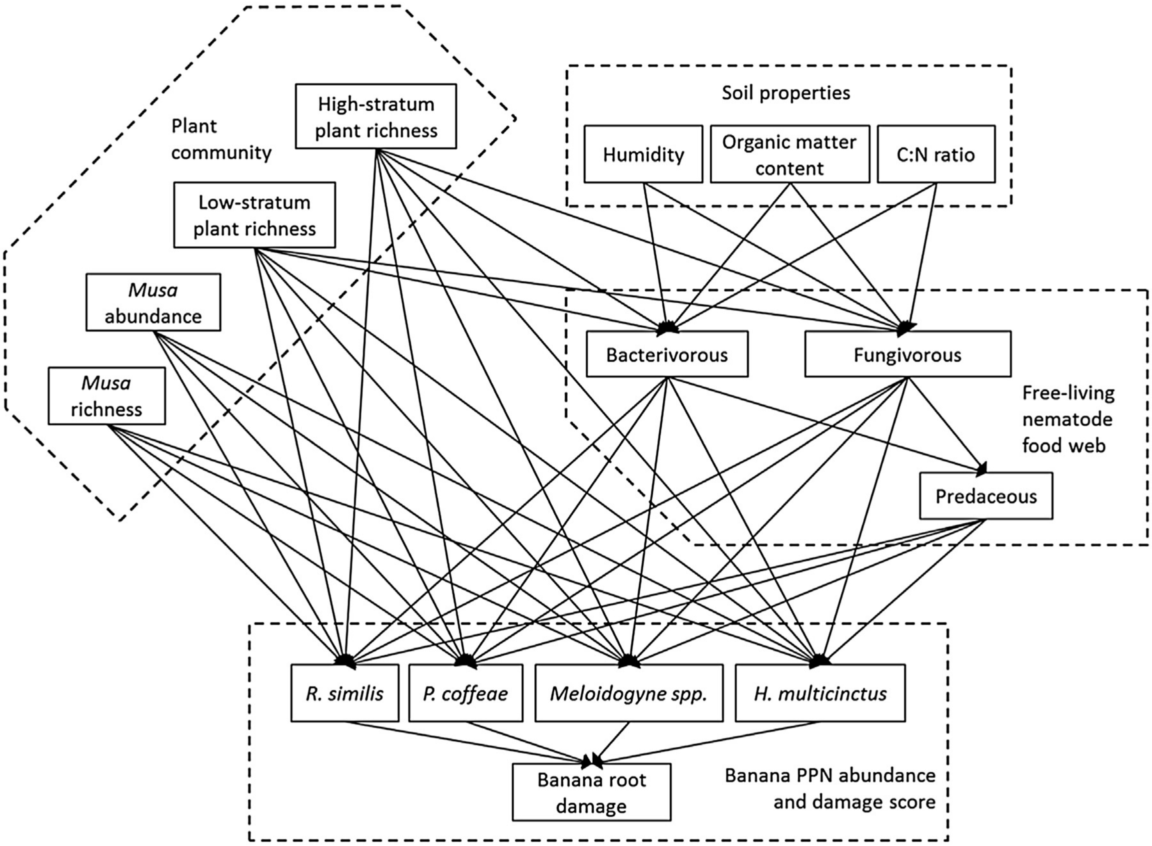

Fig. 1. Structural equation model. Path diagram of the overall structural equation model to be tested describing the links among plant community composition descriptors, soil properties, soil free-living nematode abundances or proportion and plant-parasitic nematode abundance and damage. Arrows represent tested relationships among variables. Dashed frames symbolize the different compartments.

the variables, we constituted a global path model composed of a set of 8 linear sub-models (Table 1, Fig. 1). According to response variable distributions, and following Bolker et al. (2009), we corrected the standard errors of all sub-models using quasi-Poisson generalized linear mixed models (GLMM) for each sub-model, except for the proportion of nematode predators for which we used a quasi-binomial linear mixed model. To address the non-independence of sampling between fields, we added field identity as a random intercept effect in all sub-models (Zuur et al., 2009). We used structural equation modelling (SEM) (Grace, 2006) to realise a confirmatory test of our global path model and identify the significant relationships. Because the application of traditional SEM is restricted to normally distributed data, we used the *piecewiseSEM* R-package (Lefcheck, 2016), which generalises the method to a larger range of distribution families. In the piecewise SEM approach, Shipley's tests of direct separation are used to test for missing paths and a Fisher's C statistic is calculated from the p-values of those tests (Shipley, 2009). The confirmatory test of the global path model consists in running a chi-squared test on the C statistic. The global path model is considered to represent the data well when the p-value of this chi-squared test is superior to the significance threshold. In addition, the *piecewiseSEM* package provides a coefficient for each path.

All statistical analyses were performed with R 3.2.3 (R Development Core Team, 2015) and with an alpha level of 0.05.

3. Results

Plots covered a wide range of plant species richness levels: plant richness ranged from 0.5 to 22.5 species in the low stratum, from 0 to 16 species in the high stratum, and from 0.5 to 32.25 when considering the sum of both strata. The list and abundances of *Musa* genotypes encountered in the plots during the experiment is presented in Table 2. Mean values of soil properties, plant community characteristics and nematode abundance, proportion or damage score are provided in Table 3. The complete list of soil nematode families or genus encountered in the experimental plots is provided in **Table S1** in Supplementary materials, along with mean abundances per 100 g of dry soil and standard-deviations. Most plots contained soil nematode communities with high SI values (Fig. 2**a**) and MI values comprised between 2 and 4 (Fig. 2**b**), indicating that the phytometers were located in moderately to little disturbed environments where food webs were mostly complex. Structure Index ($p < 0.0001$) and MI ($p = 0.0369$) were positively related to total plant species richness (Fig. 2**a & b**). We found that *Musa* abundance and total plant species richness were negatively correlated (**Fig. S2** in Supplementary material; $p < 0.001$; $R^2 = 0.24$).

Our structural equation model represented the data well (Fisher's

Table 2
Total abundance of *Musa* genotypes encountered in the plots in each study region.

Study region	*Musa* genotype (group)	Nb. of plants
Talamanca Reserve, Costa Rica	Gros Michel (AAA)	1138
	Cavendish (AAA)	747
	Plantain (AAB)	606
	Quadrado (ABB)	197
	Lacatan (AAA)	76
	Fressinette (AA)	39
	Chopo Colorado (AAA)	27
	Chopo Blanco (AAA)	21
	Cocori	12
Lamentin Plain, Martinique	Cavendish (AAA)	2526
	Plantain (AAB)	363
	Figue pomme (AAB)	37
	Fressinette (AA)	5

Table 3
Mean and standard-deviation (sd) of the variables related to vegetation, soil, free-living nematodes and plant-parasitic nematodes measured in the plots.

Variable group	Variable	Unit	Mean (± sd)
Vegetation[a]	*Musa* genotype richness	number of genotypes in the plot	2 ± 1
	Musa abundance	number of plants in the plot	45 ± 27
	Low-stratum plant richness (< 1.5 m)	number of species in the plot	10 ± 6
	High-stratum plant richness (> 1.5 m)	number of species in the plot	3 ± 3
Soil[b]	Soil organic matter	%	3.64 ± 1.51
	Soil C:N ratio		8.54 ± 1.30
	Soil humidity	%	33.61 ± 5.40
Soil free-living nematodes[b]	Fungivores	nb. of individuals per 100 g of dry soil	79 ± 76
	Bacterivores	nb. of individuals per 100 g of dry soil	98 ± 103
	Predators	nb. of individuals per 100 g of dry soil	36 ± 49
		% of individuals among the total abundance of soil free-living nematodes	5.96 ± 5.77
Banana plant-parasitic nematodes[c]	*Radopholus similis*	nb. of individuals per 100 g of roots	2959 ± 5627
	Helicotylenchus multicinctus	nb. of individuals per 100 g of roots	5332 ± 9279
	Pratylenchus coffeae	nb. of individuals per 100 g of roots	872 ± 1914
	Meloidogyne spp	nb. of individuals per 100 g of roots	510 ± 1100
	Banana root damages	score (1 to 5 scale)	0.63 ± 0.65

test $p = 0.819$) and 13 of the 44 relationships tested were significant (Fig. 3, **Table S2**). Soil humidity ($p = 0.0130$) and low-stratum plant species richness ($p = 0.0331$) were positively correlated with the abundance of bacterivorous nematodes while soil organic matter was negatively correlated with the abundance of bacterivorous nematodes ($p = 0.0209$). The abundance of fungivorous nematodes was positively correlated with low-stratum plant species richness ($p < 0.0001$; Fig. 4**a**). The abundance of fungivorous nematodes had a significant and positive effect on the proportion of predaceous nematodes in the soil free-living nematode community ($p = 0.0001$; Fig. 4**b**) whereas the abundance of bacterivorous nematodes had no effect on the proportion of predaceous nematodes ($p = 0.4430$). Elsewhere, the abundance of bacterivorous nematodes was positively correlated with the abundance of *Meloidogyne* spp. in the roots of the phytometers ($p = 0.0008$). The abundance of fungivorous nematodes was negatively correlated with the abundance of *H. multicinctus* ($p = 0.0270$; Fig. 4**c**) and positively with *P. coffeae* abundance ($p = 0.0117$). Low-stratum plant species richness was positively correlated with the abundance of *R. similis* ($p = 0.0260$).

Musa abundance did not significantly affect the abundance of any of the four banana PPN taxa ($p = 0.3151$, 0.3013, 0.7417, 0.1130 for *R. similis*, *H. multicinctus*, *P. coffeae* and *Meloidogyne* spp., respectively). However, *Musa* genotype richness had direct, significant and positive bottom-up effect on the abundances of *R. similis* ($p = 0.0137$) and *P. coffeae* ($p = 0.0225$) but not on *H. multicinctus* and *Meloidogyne* spp. ($p = 0.7296$ and 0.3124, respectively). Phytometer root damage was significantly and positively related to the abundances of *R. similis* and *H. multicinctus* ($p = 0.0001$ and $p = 0.0348$, respectively; Fig. 5) but was not related to the abundance of *P. coffeae* and of *Meloidogyne* spp. ($p = 0.2890$ and 0.3845, respectively).

4. Discussion

4.1. Effects of plant community and soil properties on the free-living nematodes

Low-stratum plant species richness had a positive effect on the abundance of free-living fungivorous and bacterivorous nematodes, likely to be mediated by soil saprophytic fungi and bacteria through a bottom-up trophic cascade. Plant species richness was shown to have a positive effect on microbial biomass and activity in semi-natural grasslands mostly due to qualitatively more diverse carbon inputs (plant litter and root exudates) (Eisenhauer et al., 2010; Lange et al., 2015). Lange et al. (2014) showed that higher plant richness was associated with higher leaf area index which provided more favorable microclimatic conditions for microbial activity.

Interestingly, we found no effect of high-stratum plant species richness on the free-living nematode community, what suggests that low-stratum plants played a more important role in organic matter quality and soil functioning of the upper layers than high-stratum plants. High-stratum plants (> 1.5 m height) were mostly perennial species, having deep root systems, unlikely to favor interactions of the roots (decomposing biomass and root exudates) with microorganisms that we sampled in the top soil layer. The effect of high-strata trees is maybe more likely to be reflected by tree identity. It has been showed that tree identity can determine organic matter quality through leaf litter and rhizodeposits and subsequently affect the soil food web (Cesarz et al., 2013). Our contrasted results among plant height strata differed from Zhao et al. (2014) who showed that both overstory and understory vegetation could affect soil microorganism and nematode diversity as a result of bottom-up effects and soil microclimate alteration.

We found no effect of the quality of the soil organic matter, i.e. soil C:N ratio, on fungivorous and bacterivorous nematodes. The low variability of the C:N ratio among our plots (see Table 3) may have dampened the observation of any effect. Otherwise, we found a negative relationship between soil organic matter content and the abundance of bacterivorous nematodes. Generally, organic amendments induce an enrichment effect having opposite consequences, i.e., a fast and temporary stimulation of bacterial decomposer activity (Bongers and Bongers, 1998; van der Putten et al., 2006). The pulses of organic matter from amendments in the latter studies were probably responsible for perturbations that interfered with successional processes (Korthals et al., 2001; van der Putten et al., 2006). In our study, the nematode community was not subject to perturbation by an experimental treatment and roots and litter from the established plant community provided constant input of organic matter. Our results support the diversity-stability hypothesis, stating that more diverse systems have greater resistance to external forces such as nutrient perturbations (Balvanera et al., 2006), and bring a new and more generic perspective on the effect of plant diversification on soil communities of agroecosystems. An alternative explanation of the negative relation that we found between the soil organic matter and bacterivorous nematodes is that other predators (such as tardigrades, rotifers, protozoa or microarthopods) may cause a diversion of the carbon cascade (Ferris et al., 2012) by feeding on bacteria or preying on bacterivorous nematodes.

The effect of low-stratum plant species richness on soil decomposers and microbivore nematodes positively cascaded to the upper trophic level (predaceous nematodes) through the fungal pathway only. These

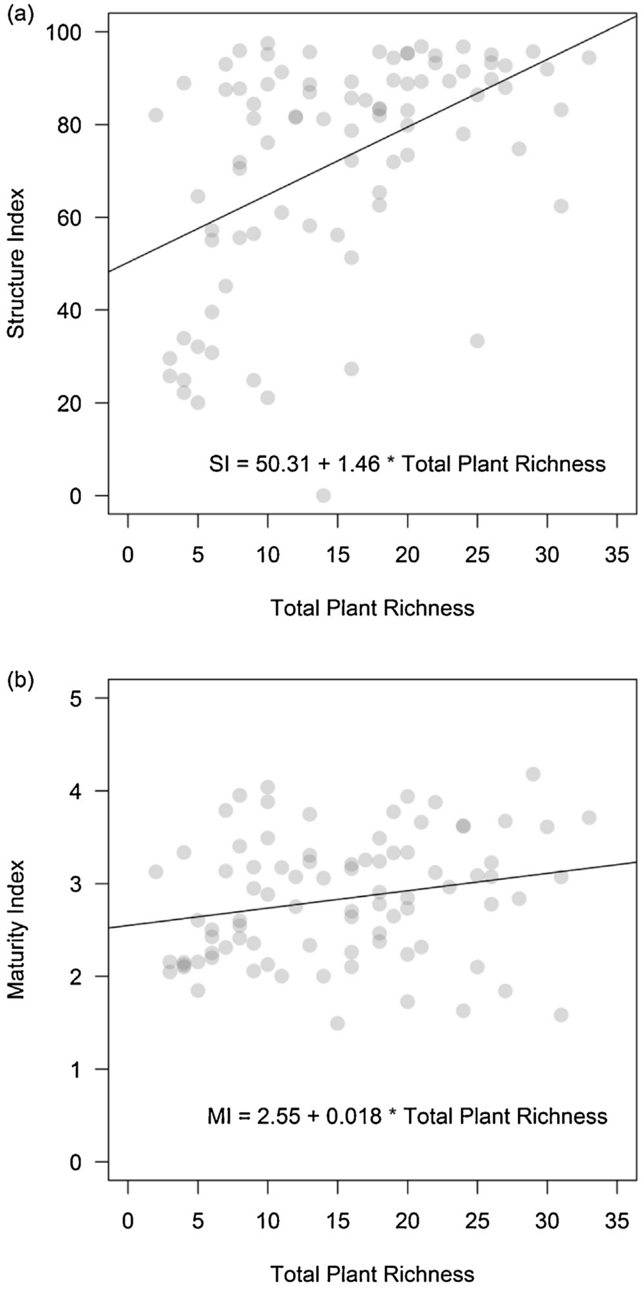

Fig. 2. Nematode community indices. Relationships between total plant species richness and (a) structure (SI) and (b) maturity (MI) indices of the soil nematode community. Total plant richness corresponds to the sum of high- and low-stratum plant species richness. Each point represents the data from one plot.

results are in accordance with those of Tabarant et al. (2011) which showed that PPN regulation after organic amendments were related to an increase of the abundance of fungivorous and of the proportion of carnivorous nematodes.

4.2. Regulation of PPN abundance

4.2.1. Associational susceptibility

A great amount of literature confirms that increasing biodiversity improves resistance of ecosystems to pests (Balvanera et al., 2006; Letourneau et al., 2011). In contrast, we found that plant species richness directly promoted PPN abundance in the phytometer roots. Indeed, our data showed that the number of *Musa* genotypes was associated with an increase of the abundances of *R. similis* and *P. coffeae* and that the abundance of *R. similis* was additionally promoted by low-stratum plant species richness. This outcome is known as “associational susceptibility” and refers to the decrease of pest regulation with biodiversity (Tahvanainen and Root, 1972). The observed associational susceptibility supports the hypothesis that the inclusion of more susceptible genotypes within a population of more resistant or tolerant genotypes will increase the exposure and infestation of the latter genotypes to the pest (Barbosa et al., 2009). It is also consistent with results from Quénéhervé et al. (2011), who demonstrated that the susceptibility of *Musa* to PPN varied among genotypes and that the abundance of PPN was driven by the most susceptible host when multiple genotypes were growing together. Very similarly, Castagneyrol et al. (2012) found that the genetic diversity in oak stands increased the susceptibility to an herbivore pest of genotypes more resistant in pure stands. The positive effect of low-stratum richness on abundance of PPN was likely explained by the polyphagia of PPN whose host ranges include various plant species from various plant families outside the Musaceae (Quénéhervé et al., 2006). Polyphagia allowed pests to diversify their diet and to increase their fitness in diversified plant communities (Bernays et al., 1994; Karban et al., 2010). Along with other studies (Jactel and Brockerhoff, 2007; Castagneyrol et al., 2012), these results support the hypothesis that plant diversity is more likely to confer associational resistance against specialist pests than against generalist ones.

Unexpectedly, PPN abundances did not depend on the abundance of *Musa* in the community. In our experiment, lower *Musa* abundance was associated with higher total plant species richness. We hypothesized that the dilution effect of diversity expected to increase with plant diversity was dampened by the polyphagia of the banana PPN. More explicitly, PPN abundances could have increased or remained high regardless of *Musa* abundance because of the presence of alternative hosts compensating for *Musa* suppression replaced the roots of *Musa* individuals.

4.2.2. Predation

Although the cascading effect of plant species richness on free-living nematodes resulted in higher predaceous nematode proportion, our results did not support the hypothesis of PPN regulation by predation. Contrastingly, Djigal et al. (2012) showed that in response to the addition of a cover crop banana predaceous nematode abundance increased while PPN abundances decreased. However, these observations reflected a response to a shift from bare soil to monospecific cover, what greatly differs from our gradient-based study. In addition, the food webs in our study were composed of long and complex trophic chains as indicated by the high SI values. Such complexity along with the presence of abundant alternative preys (fungivorous and bacterivorous nematodes) may have limited predation of PPN by predaceous nematodes (Polis and Strong, 1996; Ferris et al., 2001).

4.2.3. Non-trophic interactions with free-living nematodes

The abundance of bacterivorous nematodes, which was favored by low soil organic matter content and high soil humidity, had a positive effect on the abundance of *Meloidogyne* spp. This result is in opposition with previous studies in which addition of organic matter reduced the damage caused by these PPN (Akhtar and Alam, 1993) because of the toxicity of organic acids, the increased numbers of antagonistic fungi or bacteria, or changes in soil texture (Dong and Zhang, 2006). Although *Meloidogyne* spp. finally did not contribute to root damage, further investigations are required to explain this result.

We found that the abundance of fungivorous nematodes had opposite effects on the abundances of *P. coffeae* and *H. multicinctus*. We hypothesise that the negative relationship between fungivorous nematodes and *H. multicinctus* may be explained i) by apparent competition between those two co-located preys that share common predators, and ii) by the effect of antagonistic soil fungi on PPN, as the abundance of fungivorous nematodes was a proxy for fungi abundance.

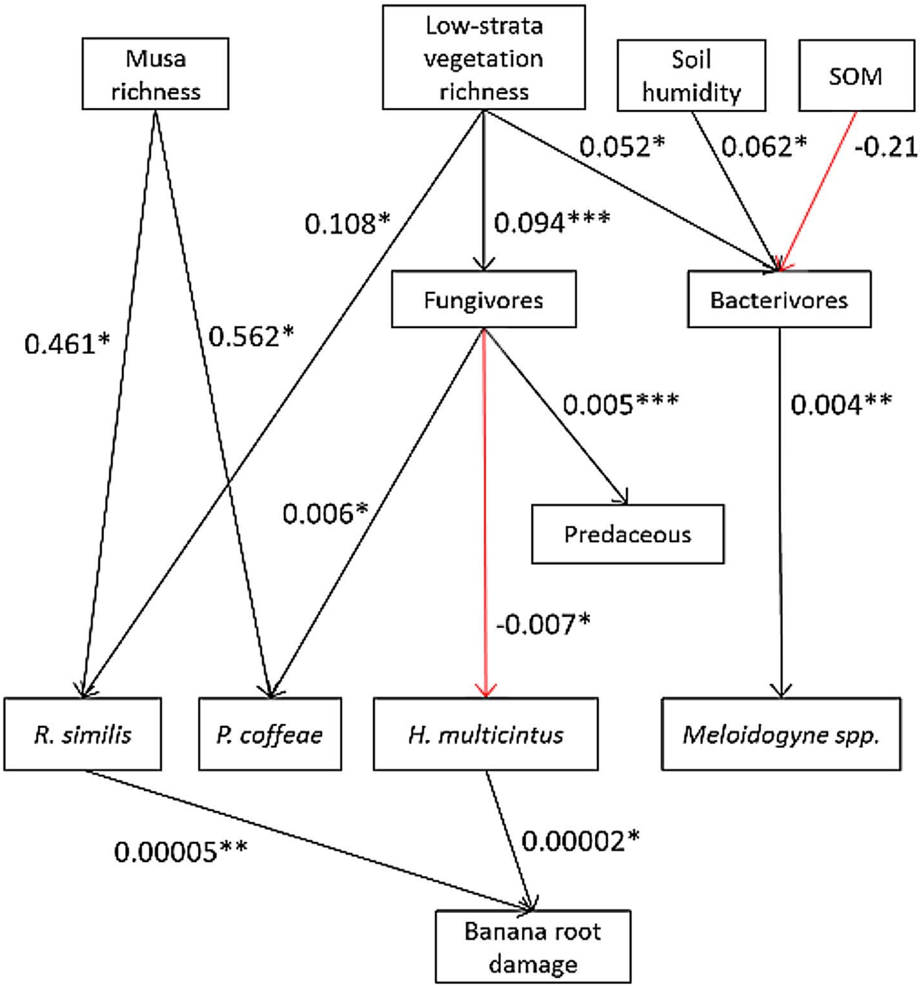

Fig. 3. Validated structural equation model. Validated structural equation model off the relationships between plant community composition descriptors, soil properties, soil free-living nematode abundances or proportion and plant-parasitic nematode abundance and damage. Black and red arrows represent significant ($p < 0.05$) positive and negative paths, respectively. Unstandardized path coefficients are indicated adjacent to the corresponding arrows. Stars symbolized the level of significance of the paths. Non-significant paths ($P > 0.05$) are not shown (see Table S1 in supplementary saterial). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

The second hypothesis possibly involved antagonistic fungi i) sharing the same host and competing for resources (photosynthesis products) and infection sites on host roots, ii) modifying root suitability or the microbial community of the rhizosphere, iii) eliciting plant defense mechanisms (Azcon-Aguilar and Barea, 1996) or iv) being involved in fungal predation or parasitism (Dong and Zhang, 2006). Since competition for root resources has been demonstrated between *H. multicintus* and endoparasitic nematodes (Tixier et al., 2008), the increase of *P.*

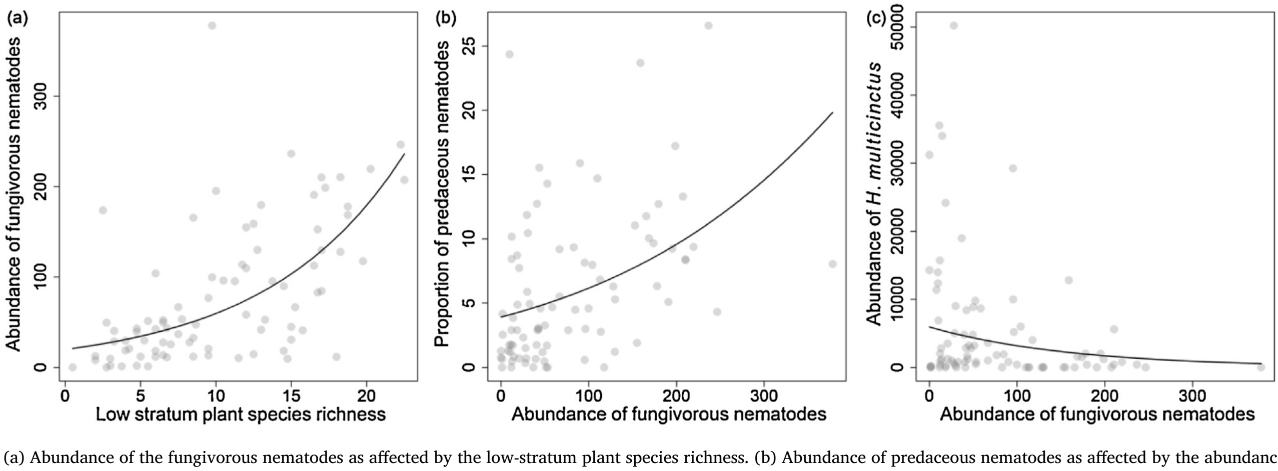

Fig. 4. (a) Abundance of the fungivorous nematodes as affected by the low-stratum plant species richness. (b) Abundance of predaceous nematodes as affected by the abundance of the fungivorous nematodes. (c) Abundance of *H. multicinctus* as affected by the abundance of the fungivorous nematodes. Points: observed data; Lines: relationship predicted by the SEM sub-models.

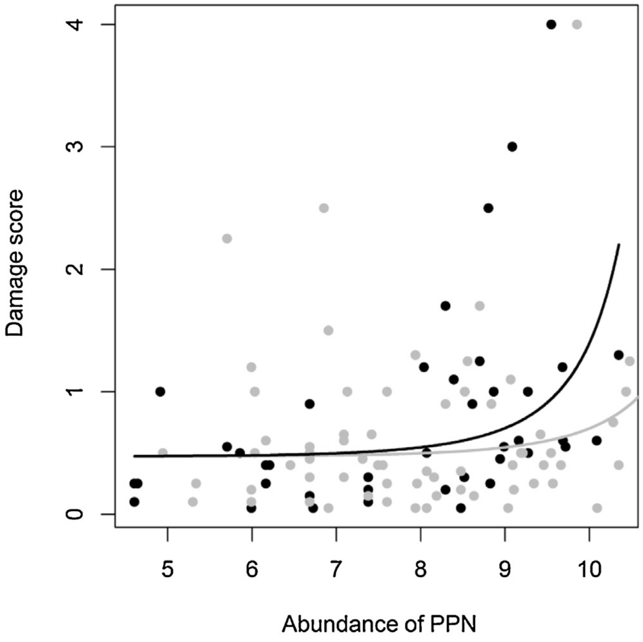

Fig. 5. Phytometer root damage score as affected by the abundance of *R. similis* (black) and by the abundance of *H. multicinctus* (grey). Points: observed data; Lines: relationship predicted by the SEM sub-models.

coffeae with fungivore abundance may be an indirect consequence of the decreased abundance of *H. multicinctus.*

4.2.4. *Differences among PPN responses*

The four PPN taxa exhibited different regulation pathways: *R. similis* was only affected by plant community effects, *Meloidogyne* spp. and *H. multicinctus* were only affected by non-trophic interactions with soil free-living nematodes, and *P. coffeae* was affected by both types of effect.

Differences in response of PPN taxa to soil properties and free-living nematode abundances (or proportion) was supposedly related to differences in PPN life history traits. *Radopholus similis* and *P. coffeae* are migratory endoparasites that can complete their entire cycle in the central cylinder of the root (Gowen et al., 2005) limiting their exposure to soil and soil organisms as long as the root they live in provides sufficient food. Although the *Meloidogyne* spp. spend part of their life cycle within the roots of their host, the J2 juveniles that hatch from the eggs must move through soil to find a new host root (Karsen and Moens, 2006). *Helicotylenchus multicinctus* is a semi-endoparasitic nematode that is confined to the outer cells of the root cortex and more exposed to the soil compartment (Orion et al., 1999). Recent advances suggested that microbial biological control efficacy varied among PPN species, with more encouraging results for ectoparasitic or semi-endoparasitic species than for migratory endoparasitic species (Gowen et al., 2005; van der Putten et al., 2006). Our results confirmed a lower level of interaction of strictly endoparasitic species such as *R. similis* and *P. coffeae* with the soil compartment.

The four PPN taxa had contrasting responses to plant diversification, probably also explained by biological differences. *Radopholus similis* was particularly responsive to the composition of the plant community probably because of its low ability to survive in the soil in absence of host plants (Chabrier et al., 2010), while the absence of plant community effects on *Meloidogyne* spp. and *H. multicinctus* could be explained by their stronger interaction with the soil compartment.

4.3. *PPN damage*

Radopholus similis and *P. coffeae* are the first and second most damaging banana PPN, respectively (Gowen et al., 2005; Quénéhervé, 2008). As expected, *R. similis* was significantly responsible for banana root damage. However, *P. coffeae* had no significant effect on damage. Instead, *H. multicinctus* was found to significantly cause root damage. In the roots of the phytometers, we found either a majority of *H. multicinctus*, a majority of *R. similis* or low abundance of both species (**Fig. S3** in Supplementary material). This pattern suggests the existence of a competitive exclusion between both species and reveals that damage is generally not additive. In agreement with our results, *Meloidogyne* spp. have been reported to cause no or little damage even when abundant (Chabrier et al., 2002).

4.4. *Conclusion*

In our study, plant diversity was most of the time the outcome of both farmers' management and spontaneous colonization of the field. We showed that uncontrolled increase of plant richness could lead to associational susceptibility of *Musa* crops to PPN. Associational susceptibility is probably one of the reasons explaining the non-negligible occurrence of negative relationships between plant diversity and pest regulation (Quijas et al., 2010; Letourneau et al., 2011) and could constitute a major limitation in developing plant-diversified schemes in agriculture. Nevertheless, our results provide insights into sustainable plant community management for the regulation of PPN abundance and damage. When facing generalist pests, cropped plant communities can be diversified but must be carefully assembled to limit pest susceptibility heterogeneity among crop genotypes and to exclude alternative host plant species. Moreover, diversification of the low-stratum plant community is required to stimulate the substantial effects of free-living nematodes on PPN regulation. The literature provides a substantial amount of studies in which the role of environmental factors in PPN regulation is ‘artificially’ tested by the use of experimental treatments. However, such studies are likely to provide information on processes of recovery from perturbations caused by experimental treatments and generally compare a limited number of treatments. We suggest further studies should make greater use of gradient of plant richness or diversity existing in farmers' fields. Such gradient allows comparing states of diversity and could provide better comprehension of ecological processes implied in crop pest regulations.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.apsoil.2017.04.017.

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ORIGINAL RESEARCH

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Balancing competition for resources with multiple pest regulation in diversified agroecosystems: a process-based approach to reconcile diversification and productivity

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Abstract

Agroecosystem plant diversification can enhance pest biological regulation and is a promising alternative to pesticide application. However, the costs of competition for resources between plants may exceed the benefits gained by pest regulation. To disentangle the interactions between pest regulation and competition, we developed a generic process-based approach that accounts for the effects of an associated plant and leaf and root pests on biomass production. We considered three crop–plant associations that differ in competition profiles, and we simulated biomass production under wide ranges of both pest regulation rates and resources' availability. We analyzed outputs to quantify the pest regulation service level that would be required to attain monoculture yield and other production goals. Results showed that pest regulation requirements were highly dependent on the profile of resource interception of the associated plant and on resources' availability. Pest regulation and the magnitude of competition between plants interacted in determining the balance between nitrogen and radiation uptake by the crop. Our findings suggest that productivity of diversified agroecosystems relative to monoculture should be optimized by assembling plants whose characteristics balance crops' resource acquisition. The theoretical insights from our study draw generic rules for vegetation assemblage to optimize trade-offs between pest regulation and production. Our findings and approach may have implications in understanding, theorizing and implementing agroecosystem diversification. By its generic and adaptable structure, our approach should be useful for studying the effects of diversification in many agroecosystems.

KEYWORDS
crop model, injury profile, plant trait, resource balance, vegetation assemblage, yield losses

1 | INTRODUCTION

According to the resource concentration hypothesis (Root, 1973), intensive cropping systems, in which crops are cultivated at high densities in large fields, are prone to pest infestation. In such systems, crop protection and yield rely on pesticides that can threaten biodiversity and human health (Aktar, Sengupta, & Chowdhury, 2009; Tilman, Cassman, Matson, Naylor, & Polasky, 2002). To be more sustainable, but still efficient in limiting yield losses, pest management should be based on a systemic approach that accounts for multiple pests and that combines biopesticides, biological control agents, pheromones, ecological engineering of plant biodiversity, and cultural practices (Birch, Begg, & Squire, 2011; Lewis, Van Lenteren, Phatak, & Tumlinson Iii, 1997). In this sense, agroecosystem plant diversification is increasingly considered a promising way to restore ecosystem functions, including ecological pest regulation (Altieri, 1999; Gurr, Wratten, & Luna, 2003; Leakey, 2014; Malézieux et al., 2009; Tscharntke et al., 2012).

Plant diversification alters the properties of agroecosystems in terms of both resource partitioning (Malézieux et al., 2009) and pest regulation (Letourneau et al., 2011). On the one hand, field-scale diversification often results in yield losses (Letourneau et al., 2011; Quijas, Schmid, & Balvanera, 2010) because of competition for resources between the crop and associated plants. The magnitude of this competition depends on the availability of resources and on the functional and architectural complementarity of plant traits involved in resource capture (Brooker et al., 2015; Roscher et al., 2012; Zuppinger-Dingley et al., 2014). On the other hand, plant diversification may interfere with pest regulation by affecting life cycles and dispersion of populations of pests and agents of biological control and their interactions through modifications of (1) the microclimate; (2) the diversity and concentration of resources; (3) the diversity and fragmentation of habitats; and (4) the chemical environment (Altieri & Letourneau, 1982; Norris & Kogan, 2005; Ratnadass, Fernandes, Avelino, & Habib, 2012; Schroth, Krauss, Gasparotto, & Duarte, 2000; Trenbath, 1993). Agroecosystem plant diversification at the field scale has apparently enhanced ecological pest regulation in many cases and for diverse pests (Letourneau et al., 2011; Quijas et al., 2010). In some situations, however, plant diversification can favor pests (Norris & Kogan, 2005; Schroth et al., 2000) and can reduce pest regulation and increase pest damage (Letourneau et al., 2011; Quijas et al., 2010).

Because most pests damage crop organs involved in resource acquisition, pest regulation, and resource partitioning strongly interact to determine crop growth and yield. Consequently, the increased ecological pest regulation gained from plant diversification may be outweighed by a stronger competition for resources. To optimize crop biomass production when introducing associated plants in an agroecosystem, yield losses induced by competition for resources between the crop and associated plants should be compensated by yield gains resulting from higher pest regulation.

Insights into the effects of plant diversification on production, pest regulation, and other ecosystem services have been obtained by combining experimental studies with statistical models (Bradford et al., 2014; Poveda, Martínez, Kersch-Becker, Bonilla, & Tscharntke, 2012) and by meta-analyses (Iverson et al., 2014; Letourneau et al., 2011). Unlike process-based approaches, these methods allow little extrapolation, prediction, or clarification of the underlying processes. Schipanski et al. (2014) assessed various ecosystem services using process-based modeling but were forced to use semiquantitative estimates of pest regulation, based on the literature and expert knowledge, because of a lack of an appropriate simulation tool. Although process-based models have been used to assess the effect of pest management strategies on pest dynamics and crop performance, authors have not included plant diversification as a strategy and thus ignored the potential effects of plant competition (Grechi et al., 2012; Lô-Pelzer et al., 2010). Other authors designed models simulating the effect of plant diversity on crop production through competition without including pests (Brisson, Bussière, Ozier-Lafontaine, Tournebize, & Sinoquet, 2004; Munier-Jolain, Guyot, & Colbach, 2013; Schipanski et al., 2014; Shili-Touzi, De Tourdonnet, Launay, & Dore, 2010). To our knowledge, no process-based model has been specifically developed to disentangle the interactions between competition for resources and pest regulation at crop scale in a general plant diversification perspective.

In this study, we present a process-based agroecosystem modeling approach that combines a validated crop growth model with the impact of an associated plant and two pest types on crop's resource uptake. We simulate three archetypal scenarios involving associated plants with different profiles of resource interception under wide ranges of resources' availability. We quantified pest regulation rates required to compensate for yield losses due to competition, compared to monoculture yield and a range of production goals, depending on the profile of resource interception of the associated plant and resources' availability. We analyzed model outputs to gain theoretical and generic knowledge about crop–plant–pest interactions in diversified agroecosystems.

2 | METHODS

2.1 | Process-based approach

From previous parametrized and calibrated modeling works (Ripoche, Achard, Laurens, & Tixier, 2012; Tixier, Malézieux, Dorel, & Wery, 2008), we developed a simplified model structure for the simulation of diversified agroecosystems that combine a crop model with profiles of pest injury and profiles of resource interception by an associated plant (Fig. 1). This model simulated crop biomass on a weekly time step. Three crop phenological stages were distinguished and successively triggered according to heat-unit accumulation thresholds. Biomass was allocated to the different parts of the crop according to the stage. Vegetative (leaves, roots, and pseudostem) and reproductive (fruit bunch) biomass were expressed as kg plant^{-1} year^{-1}. The global incident radiation (GRad), intercepted by the crop was proportional to the crop's leaf area index and was converted into biomass according to a radiation-use efficiency coefficient. The mineral nitrogen content of the soil (Nsoil), depended on the initial stock value and on a constant nitrogen mineralization rate (Nmin), and reflected overall soil fertility. Crop nitrogen uptake was deducted from Nsoil at each time step *t*. The amount of nitrogen available to the crop (Ncrop), was proportional to Nsoil but was also determined by the ratio between the actual root biomass at *t* and the potential root biomass that can be attained under optimal growth conditions. When Ncrop was below 38 kg N/ha, the crop was considered to suffer from nitrogen stress whose intensity

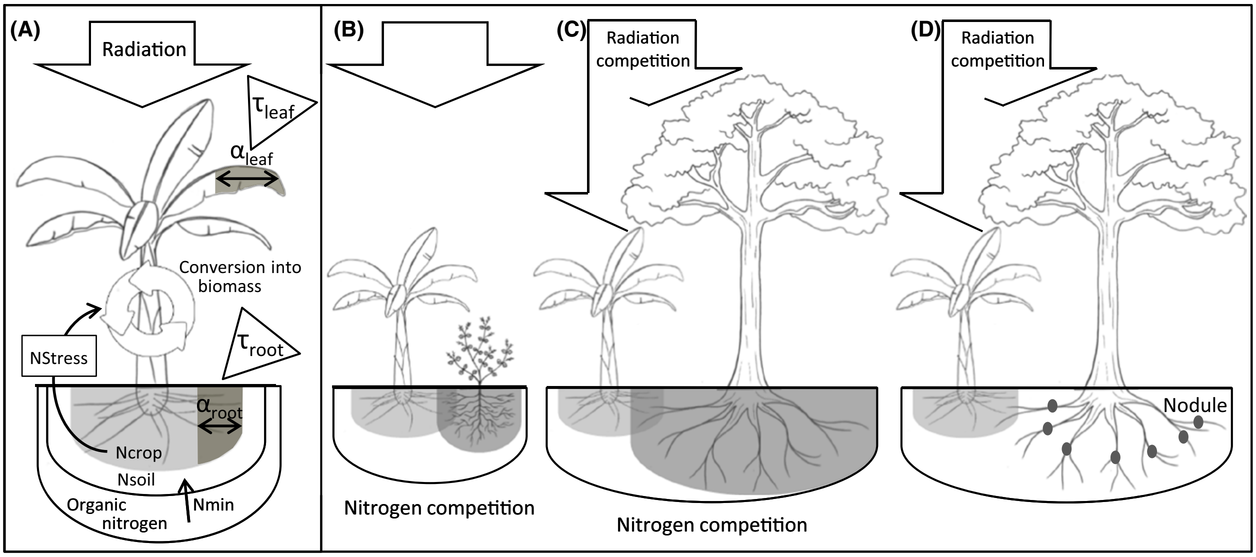

FIGURE 1 Schematic diagram of the modeling framework (A) and of the scenarios of diversification (B–D). (A) In the crop model, leaf area index and root biomass are damaged by pests following α_{leaf} and α_{root} rates, respectively. Leaf and root damages are regulated according to τ_{leaf} and τ_{root} rates, respectively. Organic nitrogen is mineralized at Nmin rate and added to the stock of soil mineral nitrogen. The part of Nsoil accessible to the crop, Ncrop, depends on the functional root biomass. When Ncrop fall below a threshold, crop growth is affected by nitrogen stress, NStress. Three plants were associated with the crop for simulation: (B) a ground plant competing for nitrogen only, (C) a nonleguminous tree competing for nitrogen and radiation (D), and a leguminous tree competing for radiation only

increased with Ncrop decrease (Ripoche et al., 2012). This stress affected crop growth by reducing heat-unit accumulation and biomass production. Water was considered to be nonlimiting for crop growth.

Additionally to crop growth simulation, our model accounted for the effects of pests and an associated plant on crop growth. Pests were classified into root and leaf pest types, and each type was characterized by the proportion of organ damaged at each time step, α_{root} and $\alpha_{leaf,}$ respectively. Pest damage rates were constant across simulations and throughout the crop cycle. Damages reduced functional biomass and thus the crop's ability to use nitrogen and radiation resources. Pest regulation rates, τ_{root} and τ_{leaf}, respectively, for root and leaf pests, that were constant throughout the crop cycle, were applied to pest damage rates to reduce pest damages. At each simulation time step, crop biomass production was penalized by the proportion of crop organs destroyed by the pests depending of the final damage rates resulting from the product between pest damage and regulation rates. The banana tree was considered to develop in an intermediary height stratum, while the associated plant was standing either below or above the crop. The relative height of the crop and the associated plant were constant throughout the crop cycle. We assumed that the associated plant had a constant biomass and was characterized by its light radiation interception coefficient, $\beta_{radiation}$, and its nitrogen demand, $\beta_{nitrogen}$. $\beta_{radiation}$ values depended on the height of the plant relative to that of the crop, and $\beta_{nitrogen}$ values depended on the plant's ability to fix atmospheric nitrogen; both coefficients were constant throughout the crop cycle. At each time step *t*, nitrogen uptake by the associated plant was deducted from Ncrop.

Details and R code of the framework are provided in Appendix 1 in Supporting Information.

2.2 | Application to virtual scenarios of banana agroecosystem diversification

The framework presented above may be used for any crop for which a parametrized and validated growth simulation model is available. Here, we used a banana agroecosystem as the model system because: (1) previous modeling work provided us with a calibrated banana crop model (Ripoche et al., 2012; Tixier et al., 2008); (2) banana plants have an intermediate position in the canopy, which is essential for studying interspecific competition for light radiation; and (3) the wet tropical conditions under which bananas are grown allowed us to assume that weather was constant and to avoid needing climatic data. To illustrate the relationship between production and pest regulation in diversified agroecosystems, we simulated three virtual scenarios of diversification in which the banana crop was associated with a plant with one of three resource interception profiles: (1) a ground plant (GP) standing below the crop and competing for nitrogen only (Fig. 1B); (2) a tree (T) standing above the crop and competing for radiation and soil nitrogen (Fig. 1C); and (3) a nitrogen-fixing tree (NFT), competing only for radiation (Fig. 1D). The coefficients of resource interception describing the profile of the associated plant in terms of competition were set arbitrarily to represent the different scenarios. Parameters from the crop model were calibrated from previous works (Table 1). Air temperature was set to be representative of tropical conditions and assumed to be constant. Nmin and GRad varied to represent the ranges of nitrogen and radiation availability likely to be encountered in fields.

The model was deliberately based on a series of assumptions, that is, no water limitation, constant weather, constant associated plant biomass and resource interception, constant relative heights of crop and associated plant, constant pest damage and regulation rates. This approach aimed at limiting the number of varying parameters and variables to provide simpler and clearer interpretations of modeling outputs while staying representative of real conditions, such as perennial systems or systems with regenerating GP cover under tropical conditions.

2.3 | Quantifying pest regulation service that would compensate for competition in diversified agroecosystems

From a general point of view, our objective was to simulate crop yield under a set of growth situations determined by resources' availability, resources' interception by an associated plant, and leaf and root pest damage (both resulting from the product of pest damage rate and pest regulation rate). We simulated all the possible combinations of variable values, as in a sensitivity analysis design, and then studied the combination of input and output variables to explore the relationship between yields, competition for resources and pest regulation.

More precisely, we first propose a generic procedure to quantify the minimal pest regulation effort (MPRE) required to compensate for yield losses in plant-diversified agroecosystems, as depending on resource competition and availability. The reference scenario against which the yield (bunch weight) and pest regulation rates of the diversification scenarios were compared was a banana monoculture in which pest regulation rates τ_{rootRef} and τ_{leafRef} were set at 0.2. The yield of this reference scenario, Y_{ref}, was simulated along a gradient of Nmin, while radiation was set at a median level. Crop yield of each

TABLE 1 Values and references for calibration of model parameters

Parameter	Value	Description	References for calibration
STFini (degree days)	1,400	Thermal time sum from planting to flowering initiation	
STFlo (degree days)	400	Thermal time sum from flowering initiation to flowering	
STFH (degree days)	900	Thermal time sum from flowering to harvest	Tixier (2004)
T_0 (°C)	14	Basal temperature for development	Tixier (2004)
Ea	0.95	Photosynthetically active radiation	
Ec	0.48	Photosynthetically active radiation intercepted	Ripoche et al. (2012)
Eb	0.018	Conversion efficiency	
K	0.7	Crop coefficient	Nyombi et al. (2009)
FWC	0.75	Fruit/bunch water content	
seneBF	0.017	Rate of leaf senescence before flowering	Ripoche et al. (2012)
seneAF	0.025	Rate of leaf senescence after flowering	Ripoche et al. (2012)
SLA (m^2/kg dry leaf)	7.4	Specific leaf area (leaf surface by biomass unit)	Ripoche et al. (2012)
LFpcent (%)	0.34	Percent of assimilates allocated to leaf during vegetative growth	Ripoche et al. (2012)
S (m^2)	5.3	Ground surface of the banana tree	Ripoche et al. (2012)
Rootmax[a] (kg)	1.75	Potential root biomass	
RTpcent	0.22	Percent of vegetative biomass allocated to the roots	Tixier (2004)
TNcrop (% N)	0.008	Banana tissue nitrogen content	
Nthreshold (kg N/ha)	38	Soil nitrogen content threshold below which stress can occur	Ripoche et al. (2012)
α_{leaf}	0.08	Leaf necrosis rate induced by pest	
τ_{leaf}[b]	0–1	Regulation rate of leaf pest damage	
α_{root}	0.05	Root necrosis rate induced by pest	
τ_{root}[b]	0–1	Regulation rate of root pest damage	
$\beta_{\text{radiation}}$[c] (%)	15	Percent of radiation intercepted by the associated plant when shading	
β_{nitrogen}[c] (kg N ha^{-1} $week^{-1}$)	2	Nitrogen demand of the associated plant when nonleguminous	
GRad[b] (MJ m^{-2} day^{-1})	9–15	Daily global radiation	
Temp (°C)	25	Air temperature	
Nmin[b] (kg N ha^{-1} $week^{-1}$)	0–6	Soil nitrogen mineralization rate	
Nsoil (Kg N/ha)	100	Initial stock of soil nitrogen	

[a] Rootmax value was obtained by simulating crop growth under potential growth conditions.

[b] The numbers in the "value" column correspond to the extreme values of the range used in the study.

[c] Parameters corresponding to resource interception by the associated plant. Indicated values correspond to cases where the associated plant competes with the crop for the resource. When the associated plant does not compete for a resource, the corresponding parameter is set to 0.

diversification scenario (bunch weight) was also simulated along the Nmin gradient with a median radiation level and for all combinations of values of τ_{root} and τ_{leaf} ranging from 0 when regulation was nil to 1 when regulation was complete. For a diversification scenario and resource level, we selected the combinations of τ_{leaf} and τ_{root} values that allowed crop yield to be greater or equal to Y_{ref}. In such situations, pest regulation rates induced yield gains that fully compensated for the yield losses due to competition. We calculated the Euclidean distance D between each selected combination and the combination of pest regulation rates of the reference scenario (Fig. 2A). We considered the minimal D value, D_{min}, to be the MPRE required to compensate for yield losses due to competition (Fig. 2B). Δ_{root}, the difference between $\tau_{rootRef}$ and τ_{root}, and Δ_{leaf}, the difference between $\tau_{leafRef}$ and τ_{leaf}, represented the root and leaf pest regulation efforts corresponding to the MPRE, respectively. We repeated this procedure along a gradient of light radiation, GRad.

2.4 | Sensitivity of crop yield to pest regulation in diversified agroecosystems

To broaden our analysis, we determined a series of production goals ranging from 0 to 45 kg bunch weight plant^{-1} year^{-1} and we explored the sensitivity of the yield to pest regulation under three contrasted levels of resource availability (low, intermediate, and high) and for each scenario of diversification. For each diversification scenario and resource level, we plotted one isocline per production goal corresponding to pairs of root and leaf pest regulation rates that allowed the attainment of the production goal. The procedure was reproduced for radiation and nitrogen resources.

3 | RESULTS

3.1 | Quantifying pest regulation service that would compensate for competition in diversified agroecosystems

Figure 3A shows the MPRE needed to attain Y_{ref} as a function of Nmin for three diversification scenarios involving associated plants with different profiles of resource interception: a GP, a tree (T), and a leguminous tree (NFT). For GP and T scenarios, Y_{ref} was impossible to achieve for the lowest Nmin values, and the overall MPRE decreased as Nmin increased. For low Nmin values, this decrease was related to the strong decrease of root pest regulation effort, which exceeded the increase in leaf pest regulation effort (Fig. 3B, C). For higher Nmin values, regulation efforts of both pests decreased. Inversely, for the NFT scenario, MPRE increased along the Nmin gradient, which was entirely related to the increase in leaf pest regulation effort (Fig. 3D), whereas root pest regulation effort decreased. MPRE was minimal for NFT at low-to-intermediate Nmin values but was minimal for GP at higher Nmin values. MPRE was always positive but the root pest regulation was negative for the highest Nmin values in GP and NFT.

Minimal pest regulation effort (MPRE) increased with incident radiation, GRad, in all diversification scenarios (Fig. 3E). It was always lower for NFT than for the other two scenarios. From low-to-intermediate GRad values, MPRE increased slightly in T and NFT and even more slightly in GP due to an increase in leaf pest regulation effort. Above intermediate GRad values, MPRE increased more in T and GP. This abrupt increase was related to increased root pest regulation effort, whereas leaf pest regulation effort decreased (Fig. 3F, G). Although MPRE had the same pattern in GP and T, it was lower in GP than in T. For the highest range of GRad values, Y_{ref} was not attainable in GP and T even with complete pest regulation (Fig. 3E). In NFT, MPRE increased constantly along the entire radiation gradient. In this scenario, the increase of MPRE mainly resulted from increased leaf pest regulation effort (Fig. 3H). Pest regulation efforts were always positive.

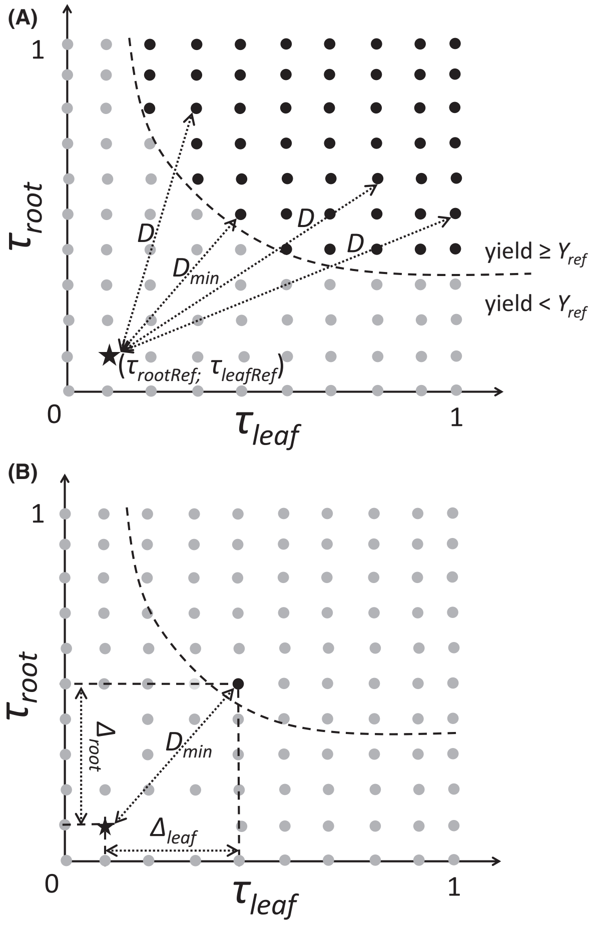

FIGURE 2 Calculation of the minimal pest regulation effort (MPRE) needed to attain the monoculture yield, Y_{ref}. The procedure was repeated for each diversification scenario in each resource context. In each case, the yield of the diversification scenario and Y_{ref} against which it was compared were resulting from the same resource context. (A) Black dots represented all the combinations of leaf and root pest regulations rates, τ_{leaf} and τ_{root}, respectively, enabling the attainment of or exceeding of Y_{ref}. The black star corresponded to the leaf and root pest regulation rates applied to the monoculture scenario, $\tau_{leafRef}$ and $\tau_{rootRef}$, respectively. Euclidean distances D between each black dot and the black star were calculated. (B) The minimal D value, D_{min}, was considered to be the MPRE. Δ_{leaf} and Δ_{root} are the values of leaf and root pest regulation efforts required to attain Y_{ref} corresponding to D_{min}

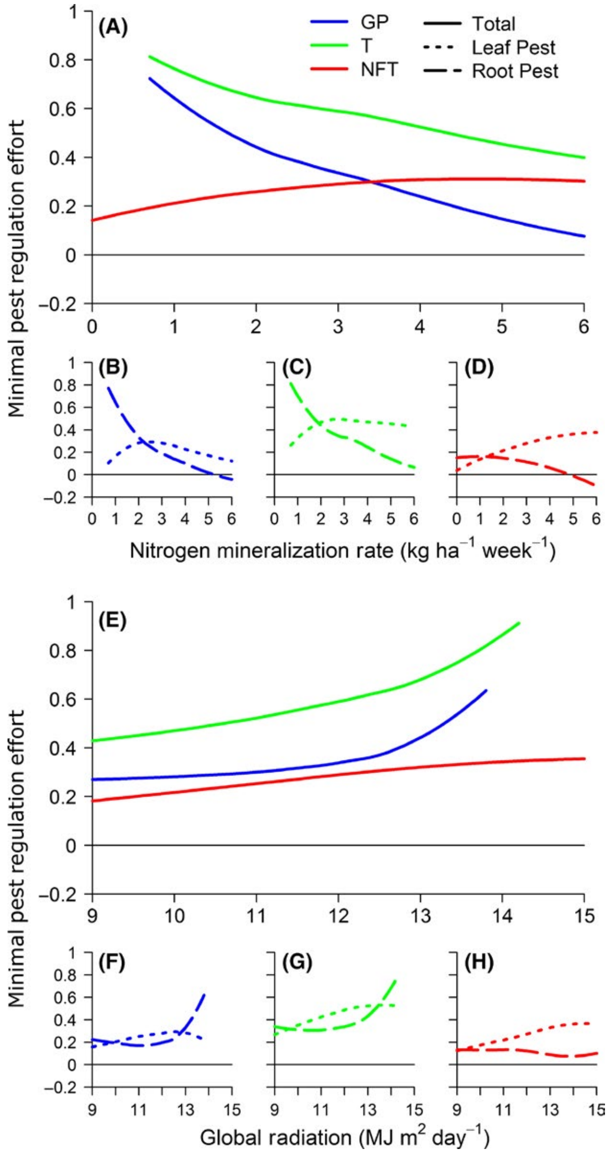

FIGURE 3 Minimal pest regulation effort (MPRE) needed to compensate for yield losses due to competition. MPRE is computed for three diversification scenarios: when a ground plant (GP), a tree (T), or a nitrogen-fixing tree (NFT) is introduced as an associated plant, and along a gradient of nitrogen mineralization rate (Nmin) (A) and a gradient of radiation (E). The regulation effort required for leaf pest and root pest is plotted using dotted lines and dashed lines, respectively, for the three diversification scenarios and for the Nmin gradient (B–D) and the radiation gradient (F–H)

3.2 | Sensitivity of crop yield to pest regulation in diversified agroecosystems

In a given context, different combinations of pest regulation rates may lead to the same production goal (Fig. 4A, B). In most cases, it was impossible to simultaneously minimize regulation rates for leaf and root pests. Negative slopes of isoclines indicated that if one pest regulation rate decreased, the production goal could be maintained by an increase in the other pest regulation rate. The steepness of the slope of the production isoclines demonstrated the relative importance of leaf and root pest regulation and the relative sensitivity of yield to both rates. Steeper slopes suggested that the yield was more sensitive to regulation of leaf pests than root pests. The distance between the production isoclines provided insight on the sensitivity of the yield to overall pest regulation.

In all scenarios, the steepness of the isoclines increased with Nmin, indicating a reinforcement of the relatively higher sensitivity of yield to leaf pest regulation as nitrogen availability increased (Fig. 4A). Under a low Nmin for GP and T and under an intermediate Nmin for GP only, isoclines were concave for the highest attainable production goals, indicating that above a given leaf pest regulation rate, high production goals were maintained because of a joint increase in both pest regulation rates. For all scenarios, the highest production goal attainable increased with the Nmin. With low and intermediate Nmins, the highest production goals were attained in NFT. With a high Nmin, the highest production goals were attained in GP. GP and T performed similarly in terms of highest attainable production goal across Nmins, but pest regulation rates were always higher in the T scenario for a given production goal under a given Nmin.

Because the steepness of the isoclines was constant and almost equal to −1, crop yield was constantly and equally sensitive to root and leaf pest regulation in GP and T regardless of radiation level. In NFT, isoclines steepness was always higher than in the other scenarios and slightly increased with radiation level suggesting that the higher sensitivity of yield to leaf pest regulation was reinforced as radiation availability increased (Fig. 4B). Under a high radiation level in GP and T and under an intermediate radiation level in GP only, the isoclines of the highest production goals were concave, indicating that above a given leaf pest regulation rate, production goals were maintained because of a joint increase in both pest regulation rates. Generally, the overall pest regulation required to attain a given production goal decreased as the radiation level increased. For a given level of radiation, the pest regulation rates corresponding to a given production goal were always highest in T. GP and T performed almost identically in terms of the pest regulation rates required to attain the highest production goals, and NFT always allowed the attainment of higher production goals than the two other scenarios.

4 | DISCUSSION

The combination of very low fertility and a nonleguminous associated plant may lead to early and strong nitrogen stress because of additive effects of nitrogen deficiency and competition. In such situations, the crop never attains the monoculture yield even with complete pest regulation. With low fertility, however, an associated leguminous tree leads to relatively high crop yields for relatively low pest regulation rates. Consistent with the concept of niche differentiation (MacArthur & Levins, 1967), the drastically lower root pest regulation rate required with a leguminous tree indicated that complementarity in profiles of nitrogen capture between the associated plant and the crop results in reduced competition for nitrogen. This phenomenon has been reported in many

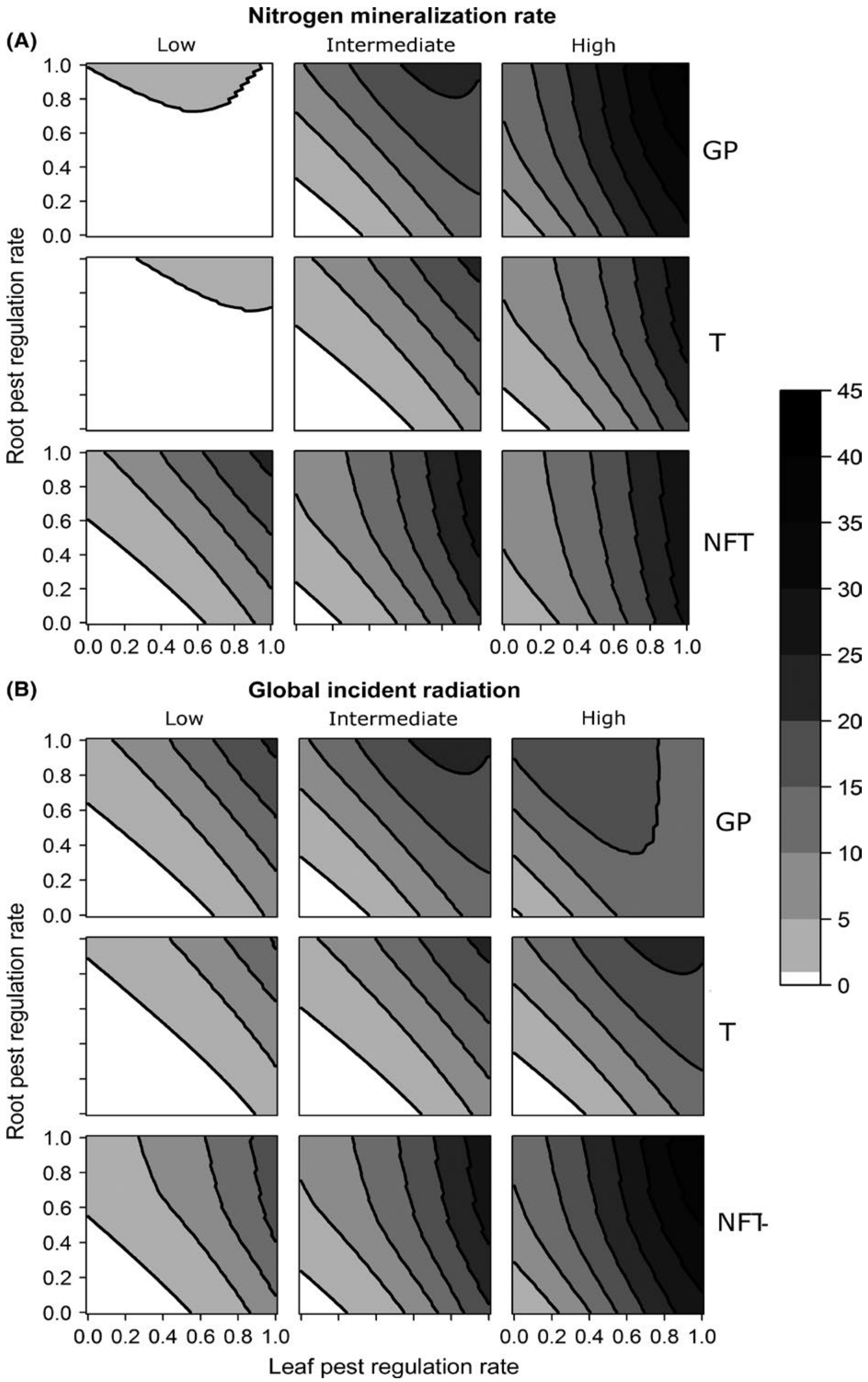

FIGURE 4 Isoclines of leaf and root pest regulation rates to attain production goals in associations. Pest regulation rates allow compensating for yield losses due to the association of the crop with plant having different profile of competition for resources: a ground plant (GP), a tree (T), or a nitrogen-fixing tree (NFT). They are reported for low, intermediate, and high nitrogen mineralization rates (Nmins) combined to intermediate radiation level (A) and for low, intermediate, and high radiation levels combined to intermediate Nmin (B). The scale on the right describes production goals expressed in kg plant^{-1} year^{-1}

intercropping systems involving legumes (Brooker et al., 2015). In addition to complementary nitrogen use, trees may induce facilitation in nitrogen-poor environments by improving radiation regulation and the nutrient status of the understory crop (Isaac, Ulzen-Appiah, Timmer, & Quashie-Sam, 2007). Facilitation based on a reduction in resource disparity has been confirmed to enhance resource use efficiency and crop performance (Garcia-Barros & Ong, 2004). In nitrogen-poor environments, complementarity or facilitation between plants may limit the need for pest regulation service provision. As fertility improves, however, the effect of competition for nitrogen on yield decreases, and the advantage of a leguminous versus a nonleguminous associated plant declines. When fertility is high, high leaf pest regulation or nonshading conditions are required to boost radiation conversion in order to support the high crop growth potential provided by nitrogen. These results confirm the prediction that, in agroforests, the benefit of soil fertility improvement through mulch, or avoided competition in the case of the leguminous tree, is greater with low than with high fertility where the negative effects of shading dominate (van Noordwijk, 1996).

Regardless of the profile of resource interception of the associated plant, the increase in radiation availability results in a counterintuitive requirement for higher pest regulation. With a leguminous tree where only radiation conversion limits growth, pest regulation increases slightly and is exclusively related to leaf pest regulation. With a nonleguminous associated plant, there is a threshold in the balance between both resources that induces a shift in pest regulation requirements. Below this threshold, although the root pest regulation effort also contributes importantly to overall pest regulation requirements, the increase in pest regulation is related to leaf pest in order to limit the nitrogen stress reinforcement induced by growing radiation conversion. Above the threshold, the increase in radiation reverses the balance between resources and induces a drastic demand for root pest regulation. The leguminous tree minimizes pest regulation requirements regardless of the level of radiation because shading limits radiation conversion and because competition for nitrogen is absent. In the other scenarios, the benefit of higher radiation conversion allowed by higher radiation availability is outweighed by its negative effect on crop growth because of increased nitrogen stress due to higher crop nitrogen demand. This result confirms the findings of Isaac et al. (2007), who suggested that the benefits of radiation reduction could be canceled when the shading tree competes for soil resources.

Given a particular level of resource availability and a particular associated plant profile, various combinations of the regulation rate of the two pests can lead to the attainment of targeted production goals. In most cases, the regulation of one pest may compensate for damage from the other. It means that, generally, the productivity of diversified agroecosystems can be optimized through vegetation characteristics providing either a strong control of one of the two pests or a medium control of both pests. However, when nitrogen availability is poor relative to radiation and when the production goal is high, both pest regulation rates are positively correlated and no longer compensate for each other. Instead, increased leaf pest regulation improves crop radiation conversion to the point where nitrogen may become limiting and this amplification of the disparity in resource supplies combined to a high production goal leads to an increase of the need for root pest regulation. Although our interest is in ecological pest regulation, these results may already be of particular importance to limit superfluous costs and pollution related to chemical or mechanical pest regulation. When nitrogen is nonlimiting, the range in pest regulation rates that allowed the attainment of a given production goal is high and narrow for the leaf pest while it could range from 0 to 1 for the root pest. This indicates that, when nitrogen is less limiting than radiation, crop yield is more sensitive to leaf pest than to root pest regulation and that radiation conversion limitation prevails in yield losses. Moreover, in such conditions, high levels of leaf pest regulation but reduced levels of root pest regulation are required to attain yield equivalent to the monoculture. In contrast, when nitrogen is the most-limiting factor, yield losses are compensated for by a high root pest regulation rate along with a low leaf pest regulation rate that also contributes in reducing crop demand for nitrogen and therefore nitrogen stress. Consequently, the relative sensitivity of crop yield to leaf or root pest regulation depends on the magnitude and direction of resource imbalance. Depending on resource conditions, improving yield of diversified agroecosystems will be easier by increasing regulation rate of one of the two pests preferentially.

Pest regulation requirements were highly dependent on the profile of resource interception of the plant and resources' availability. We showed that pest regulation and the magnitude of competition between plants interact in determining the balance between nitrogen and radiation uptake by the crop. Incorporating resource gradients in our study allowed us to detect and quantify the strong dependency of crop–plant–pest interactions on resource balance. Our findings suggest that productivity of diversified agroecosystems relative to monocultures should be optimized by assembling plants whose characteristics balance crop resource acquisition. This conclusion is consistent with Schroth et al. (2000), who suggested that diversified agroecosystems should be designed to reduce the disparity in resource supply and crop stress. Similar to growth stimulation that favors the organ that captures the most-limiting resource (Bloom, Chapin, & Mooney, 1985), we found that pest regulation was most beneficial when it protected the organ that captures the most-limiting resource. Under some resource conditions, however, pest regulation should not only consist of reducing damage to organs involved in most-limiting resource acquisition but also in leaving damage to organs involved in nonlimiting resource acquisition.

Explicit simulation process-based models were recently used to assess the effect of diversity on the stability and productivity of forests (Morin, Fahse, de Mazancourt, Scherer-Lorenzen, & Bugmann, 2014) and to assess the effect of outbreak severity on tree biomass while considering various pest damage pathways (Dietze & Matthes, 2014). The theoretical knowledge from our study demonstrates the value of such process-based integrative tools and contributes to a process-based understanding of the general relationship between ecosystem diversity and function. Turnbull, Levine, Loreau, and Hector (2013) and related studies have focused on within-trophic level interactions to explain the effect of diversity on ecosystem functioning, with an emphasis on coexistence and productivity in plant communities. They demonstrated that the difference in productivity between a mixture and equivalent monocultures, the "net biodiversity effect," results from selection and complementarity effects (Loreau & Hector, 2001) that depend on fitness and niche interspecific differences, respectively (Turnbull et al., 2013). Although we provide a more static representation of the plant community (we assumed a stable community and no fitness difference between the crop and the associated plant), our framework was nevertheless able to reproduce community-level interactions. For instance, the impossibility of achieving the yield of the monoculture when introducing an associated plant in some circumstances in our study reflects competitive exclusion. Most importantly, our results show that pest regulation may mitigate the effect of competition for resources between plants on crop yield, particularly in resource-limited environments. We suggest that the role of indirect plant–plant interactions involving multiple trophic levels or abiotic factors, such as pest regulation, should be integrated into frameworks that attempt to explain ecological community outcomes.

Our simple, process-based approach relied on the hybridization of a validated crop model with functional profiles of pests and associated plants. Functional profiles of plants have been shown to accurately describe resource partitioning and aboveground biomass production in complex agroecosystems (Collalti et al., 2014; Damour, Dorel, Quoc, Meynard, & Risède, 2014; Roscher et al., 2012). We also used pest functional groups depending on the crop organ affected, as has been successfully performed by previous authors (Dietze & Matthes, 2014; Willocquet et al., 2002). Because of its hybrid structure, our model embraces the complexity of diversified agroecosystems and bridges the gap between process-based and functional-trait approaches. In addition, the functional traits used to describe competition between plants may also be involved in pest regulation. For instance, height, which is useful to characterize radiation competition in a plant community (Kunstler et al., 2016), is related to the ability of plants to control pests (Damour et al., 2014; Schroth et al., 2000). Our approach could easily be adapted into a model including explicit ecological pest regulation pathways relying on vegetation characteristics. More generally, although our study focuses on archetypal situations, the generic and adaptable structure of our model should make it useful for application to a wide range of agroecosystems involving a wide range of pests.

In conclusion, our study provides generic rules for vegetation assemblages that may contribute to the implementation of agroecosystem diversification. It promotes the development of integrative approaches and tools to elucidate the complex interactions between plants, pests, and resources ruling the outcome of diversified agroecosystems. Moreover, our findings suggest that ecological theory concerning plant communities should be expanded to include indirect interactions between plants that may interfere with resource use and fitness of plant species, such as those involving pest regulations. Ultimately, the knowledge and approach presented here may be of valuable support to develop policies or diversified cropping system designs promoting multiple ecosystem services.

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CONFLICT OF INTEREST

None declared.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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ORIGINAL RESEARCH

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Dominance in a ground-dwelling ant community of banana agroecosystem

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Abstract

In tropical ecosystems, ants represent a substantial portion of the animal biomass and contribute to various ecosystem services, including pest regulation and pollination. Dominant ant species are known to determine the structure of ant communities by interfering in the foraging of other ant species. Using bait and pitfall trapping experiments, we performed a pattern analysis at a fine spatial scale of an ant community in a very simplified and homogeneous agroecosystem, that is, a single-crop banana field in Martinique (French West Indies). We found that the community structure was driven by three dominant species (*Solenopsis geminata*, *Nylanderia guatemalensis*, and *Monomorium ebeninum*) and two subdominant species (*Pheidole fallax* and *Brachymyrmex patagonicus*). Our results showed that dominant and subdominant species generally maintained numerical dominance at baits across time, although *S. geminata*, *M. ebeninum*, and *B. patagonicus* displayed better abilities to maintain dominance than *P. fallax* and *N. guatemalensis*. Almost all interspecific correlations between species abundances, except those between *B. patagonicus* and *N. guatemalensis*, were symmetrically negative, suggesting that interference competition prevails in this ground-dwelling ant community. However, we observed variations in the diurnal and nocturnal foraging activity and in the daily occurrence at baits, which may mitigate the effect of interference competition through the induction of spatial and temporal niche partitioning. This may explain the coexistence of dominant, subdominant, and subordinate species in this very simplified agroecosystem, limited in habitat structure and diversity.

KEYWORDS

pattern analysis, ant, dominance, interference competition, community, coexistence

1 | INTRODUCTION

Ants are ubiquitous, diverse, and abundant and are therefore key components of ecosystems. In tropical ecosystems, ants may represent a substantial portion of the animal biomass (Hölldobler & Wilson, 1990) and may help provide various ecosystem services, including pest regulation and pollination (Perfecto & Vandermeer, 2006; Philpott & Armbrecht, 2006). Hence, an important objective in the study of agroecology is to understand the factors affecting the structure of local ant communities.

The diversity and abundance of ant species and consequently the diversity of ant community structures may be explained by both physiological factors and ecological factors (Philpott & Armbrecht, 2006). The ecological factors can be further divided into habitat-related factors (e.g., nesting sites, microhabitats, food availability, and food diversity) and ecological interactions (e.g., interspecific competition and foraging interference). Habitat-related factors strongly influence ant communities through environmental filtering (Wiescher, Pearce-Duvet, & Feener, 2012), and coexistence of ants in heterogeneous environments has been extensively documented (Dassou, Carval, Depigny, Fansi, & Tixier, 2015; House, Burwell, Brown, & Walters, 2012; Murnen, Gonthier, & Philpott, 2013; Perfecto & Vandermeer, 1996; Vasconcelos, Leite, Vilhena, Lima, & Magnusson, 2008). However, intra- and interspecific interactions also play an important role in the structuring of ant communities (Fellers, 1987, 1989). This may be particularly true in homogeneous environments such as agroecosystems.

Intra- and interspecific competition can be divided into two types: interference competition, which includes all direct interactions involving aggressive encounters between ants (Fellers, 1987; Kenne et al., 2005), and exploitative competition, when the consumption of a limiting resource by one species reduces the availability of that resource for another species (Fellers, 1987; Kenne et al., 2005). Researchers have hypothesized that the coexistence of ants results from a trade-off between traits linked to interference competition and those linked to exploitative competition. For example, Fellers (1987) hypothesized that there is a trade-off between bait discovery and bait dominance, that is, those ant species adept at finding resources have poor interference competitive abilities while those species adept at dominating a resource have good interference competitive abilities but poor resource discovery abilities. However, this trade-off seems to be the exception rather than the rule (Castracani, Spotti, Grasso, Fanfani, & Mori, 2014; Parr & Gibb, 2012), and positive correlations between discovery and dominance have been reported (Parr & Gibb, 2012).

Interspecific interactions may determine which species are members of particular ant communities. In tropical ant communities, apart from the major arboreal and terrestrial guilds that have specialized foraging habitats, some species forage both in tree canopies and on the ground and may therefore compete (Bluthgen & Feldhaar, 2010). Ant species differ in competitive ability because of differences in foraging activity, colony size, or body size (Hölldobler & Wilson, 1990). In particular, dominant ants can alter the structure of ant communities by interfering in the foraging activity of other ant species (Savolainen & Vepsalainen, 1988). Dominant ants often have mutualistic associations with nonant herbivores that provide honeydew as a sugar source in exchange for protection against predators (Bluthgen, Stork, & Fiedler, 2004). Such mutualisms enable ants to build large colonies with many nests (Richard, Fabre, & Dejean, 2001). Dominant ants achieve superiority because of their aggressiveness, numerical dominance, superior interference behavior, and superior ability to participate in exploitative competition (Parr & Gibb, 2010); such ants are frequently found in disturbed habitats including intensive agroecosystems (King & Tschinkel, 2006). The spatiotemporal dynamics of such dominant ants greatly affect ant community structure (Zakharov, 2002).

In the humid tropics, bananas (*Musa* AAA genome) are mostly grown on bare soil and as a single crop. These semi-perennial agroecosystems contain regularly spaced banana plants and are extremely simple and homogeneous and, therefore, are well suited for studying ant community structure. In the current study, we performed a pattern analysis at a fine spatial scale and provided information on temporal and spatial dynamics of ants foraging in a single-crop banana agroecosystem: (i) We assessed the diurnal and nocturnal foraging activity of these species; (ii) determined which species are dominant, subdominant, and subordinate; (iii) assessed how numerical dominance at an impermanent resource (i.e., a bait) evolved through time; and (iv) assessed how abundance of species, at baits and in the neighborhood of the baits, were correlated.

2 | MATERIALS AND METHODS

2.1 | Fields, plots, and subplots

We conducted our study in an experimental banana field (Lamentin, Petit Morne, West French Indies, 14°37′25.1″N, 60°58′07.3″W, 3 m a.s.l) during the dry season (from 23 of April to 19 of June) of 2012. The sampling area or plot was 44 m long and 20 m wide. The banana crop (Cavendish Grande Naine) was in its first cycle when the data were collected to ensure homogeneity across the plot. The age of the banana plantation was 8 months. The climate at the study site is humid tropical with a mean (± *SE*) monthly temperature of 26.5 ± 0.3°C and a mean monthly rainfall of 174.6 ± 21.2 mm. Within the main plot, we defined 60 regularly spaced subplots (14.7 m^2 each; Figure 1).

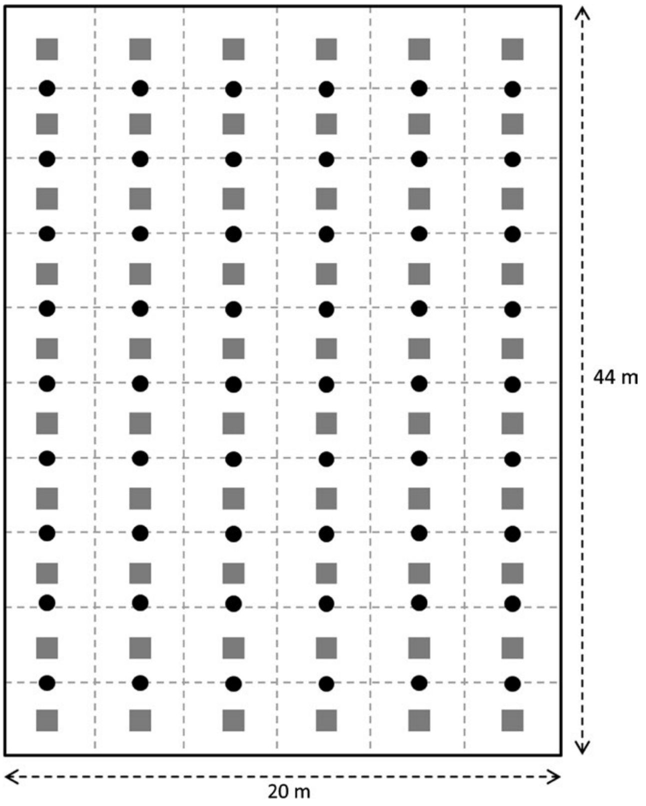

FIGURE 1 Schema of the experimental design. Gray squares: ceramic tile with baits; black circles: pitfall traps. Subplots correspond to areas delimited by dashed lines

2.2 | Ant sampling: day and night pitfall trapping

To assess the general foraging activity of the ant community, we carried out diurnal and nocturnal pitfall trapping. Pitfall traps were situated between each subplot, with a total of 54 pitfall traps (Figure 1). Pitfall traps contained 50 ml of water with a drop of dishwashing liquid. Pitfall traps were deployed at nightfall at 6:00 p.m., and the trapped ants were collected at 6:00 a.m. and conserved in 70% alcohol for identification. Next, pitfall traps were washed with water and refilled. Trapped ants were then collected at 6.00 p.m. and conserved in 70% alcohol for identification. This sampling method was replicated three times. For day and night period, we calculated the proportion of pitfall traps where the species were recorded as well as their mean abundance per pitfall trap. Next, we used Kruskal–Wallis tests to analyze the day–night variation in foraging activity.

2.3 | Ant sampling: baiting

One 30 × 30 cm white ceramic tile was placed at the center of each subplot, such that the tiles were regularly spaced across the main plot. In each subplot, we measured ant abundance using canned tuna–honey baits. One bait, which had a diameter of 4 cm, was placed in the center of each ceramic tile on the 23 of April 2012, which we called hereafter date 1. Each subplot was sampled 30, 90, and 180 min (sampling times 1, 2, and 3, respectively) after the baits were deployed. At each sampling time, we identified and counted the individuals of different species present on the tile. The ants were also recorded according to a six-point abundance scale (following Andersen, 1997; Baccaro, Ketelhut, & De Morais, 2010; Parr, Sinclair, Andersen, Gaston, & Chown, 2005). We used the percentage of bait controlled as a measure of dominance (following Bestelmeyer, 2000; Baccaro et al., 2010) rather than strict bait monopolization (Andersen, 1992). Baits were considered controlled by a species (i) if the number of individuals is >20 and no other ant was present (monopolization) or (ii) if one species was at least twice as numerous as the second numerous taxon when several species were present and the total number of individuals was >20). Samples of all species were collected and conserved in 70% alcohol, then we performed identification to genus according to the Bolton key (Bolton, 1994), and all ants were sent to J. Delabie (Laboratory of Myrmecology, UESC/CEPLAC, Brazil), who identified the ants to species. Sampling was performed between 8:00 and 11:00 in the morning and between 2:00 and 5:00 in the afternoon and repeated the 12 of May 2012, the 31 of May 2012, and the 19 of June 2012, which we called, respectively, hereafter dates 2, 3, and 4. For each species, we used Kruskal–Wallis tests to analyze the daily variation (morning vs. afternoon) in abundances.

2.4 | Dominant analysis

Following Baccaro et al. (2010), we used a combination of numerical and behavioral criteria of dominance to determine dominant, subdominant, and subordinate ants. An ant species was considered as a dominant species when (i) it occurred at a large proportion of baits; (ii) it controlled a large proportion of baits whenever it was present; and (iii) it had a high mean abundance score (Andersen, 1992; Baccaro et al., 2010; Parr, 2008). The dominant (respectively, subdominant) species were classified as those that were recorded in >10% of all baits, controlled >25% (respectively, >10%) of baits where they occurred, and with a mean abundance score (calculated by dividing the sum of the abundance scores for the species at all baits by the number of baits at which the species was present) of >3 (respectively, >2.5). All other species that did not meet all these criteria were considered as subordinate species.

2.5 | Statistical analysis

2.5.1 | Data mining and probability matrices of transition

We first performed a principal component analysis and a hierarchical cluster analysis, based on Ward's method (Ward, 1963), to classify the observations at baits according to their similarities in species distribution and abundance. We thus obtained a hierarchical classification of observations for each replicate tile at one sampling time. Once the partition of observations into groups on the basis of the Ward's minimum variance agglomerative clustering was obtained, we used that partition as the initial value for K-means partitioning (Murtagh & Legendre, 2014). This procedure was used to identify the type of "momentary" communities that we observed at baits and to established transition matrices. Moreover, the type of "momentary" community (which we called hereafter a group) observed at sampling time 1 are likely to be indicative of the colonies that was spatially close to the subplot (see below in *Subplot scale dynamics and correlations between ant species abundances*).

Once groups of observations were identified, we named these groups according to the numerically dominant species of each group. We next used the Markov chain approach to define the probability (in the form of probability matrices) that a numerically dominant species will maintain its numerical dominance on the resource or lose it to the benefit of another dominant or subdominant species from sampling time 1 to sampling time 2 and from sampling time 2 to sampling time 3. We then used 10,000 Markov chain simulations to obtain probabilities that each species will maintain numerical dominance from sampling time 1 to sampling time 3. Probability matrices of transition were obtained using the "markovchain" R-package (Spedicato, 2015).

2.5.2 | Autocorrelation

It is important to consider autocorrelation in studies of species interactions (Dormann et al., 2007), and the omission of spatial autocorrelation in analyses may lead to false conclusions (Kuehn, 2007). For the abundance of each of the identified dominant and subdominant species, we tested the spatial autocorrelation using the C index of Geary (1954). Low values of this index indicate that two locations are positively correlated, that is, that they are more likely to resemble each other. High values of this index indicate the absence of correlation between two locations. The C index of Geary was calculated for the abundance of each dominant and subdominant species for each replicate tile at each sampling time and for distances d ranging from 2.5 to 6.0 m. The effects of distance on the Geary C values were assessed with linear models (LMs) that took the form of $C = \alpha + \beta_1 d + \beta_2 d^2 + \varepsilon$ where α was the model intercept, β were regression coefficients, and ε was the normally distributed error term.

2.5.3 | Subplot scale dynamics and correlations between ant species abundances

We used Poisson generalized mixed-effect models (GLMMs) to assess correlations between abundances of dominant and subdominant species, which may reflect the outcome of species interactions at baits. Following Zuur, Ieno, Saveliev, and Smith (2009), we first tested for collinearity (i.e., correlation) between covariates using the variance inflation factor (VIF) method. Once the set of explanatory variables (fixed effects) was determined, we tested the random effect structure. Here, for each species i, we defined as the fixed effect, the local abundances of species j (i.e., abundances in subplots), the mean abundances of conspecifics of i and of species j in the neighborhood (i.e., abundances in the surrounding subplots situate at a distance defined for each species by the spatial autocorrelation analysis) of the considered subplot, and the sampling time.

Humidity, temperature, and other factors may cause the abundance of a species to be similar between subplots at the same sampling time on one date. To consider the nonindependence between data from subplots at the same sampling time on one date, we introduced this latter variable as a random intercept effect. Moreover, the ants observed at the sampling time 1 are likely to be indicative of the community that was spatially close to the subplot and the data from the three sampling times at a specific subplot are likely to be correlated. Therefore, to consider the nonindependence between sampling times at a same subplot, we introduced the group at sampling time 1, obtained by the data mining procedure, for each subplot as a random slope effect on sampling time. Following Zuur et al. (2009), we tested random effect structures by comparing nested GLMMs comprising all fixed effects. We used Akaike information criteria (AIC) and likelihood ratio tests (LRTs) to select the best random effect structure of the model for each ant species (Bolker et al., 2009).

After using the GLMMs to determine the best random structure for each species, we selected the best model by removing nonsignificant fixed-effect parameters in a backwards-stepwise process using LRTs. The selection procedure was continued until a model was found in which all effects were significant (Zuur et al., 2009).

All LMs and GLMMs were estimated using the "glmer" function in the "lme4" package (Bates, Maechler, & Bolker, 2012), in which the maximum likelihood of parameters is approximated by the Laplace method (Bolker et al., 2009). All statistical analyses were performed with R 2.15.0 (R Development Core Team, 2014) and with an alpha level of 0.05.

3 | RESULTS

3.1 | Diurnal and nocturnal foraging activity

A total of 6,229 ants belonging to 11 species were collected with pitfall traps. Among the 11 species trapped in pitfall traps, we found only two specimens of *Tetramorium bicarinatum* (Nylander), which species was not included in the analysis. *Solenopsis geminata*, *Nylanderia guatemalensis*, *Monomorium ebeninum*, *Pheidole fallax*, and *Cardiocondyla obscurior* were the most frequently recorded species, while *Wasmannia auropunctata*, *Odontomachus brunneus*, *Camponotus sexguttatus*, and *Paratrechina longicornis* occurred at low frequency (Table 1). *P. fallax* was largely the most frequently trapped species but also the most abundant trapped species in pitfall traps (Table 1). The foraging

TABLE 1 Occurrence of dominant, subdominant, and subordinate ants at pitfall traps

	Recorded pitfall traps (%)		Mean abundance (95% CI)	
	Day	Night	Day	Night
Dominant				
Solenopsis geminata (Fabricius)	29.63	15.43	0.69 (0.46–0.91)	0.21 (0.12–0.30)
Nylanderia guatemalensis (Forel)	12.35	33.95	0.14 (0.08–0.21)	0.56 (0.38–0.73)
Monomorium ebeninum Forel	22.84	8.02	0.62 (0.40–0.85)	0.13 (0.05–0.21)
Subdominant				
Pheidole fallax Mayr	96.91	87.65	23.21 (20.14–26.28)	5.68 (4.44–6.91)
Brachymyrmex patagonicus Mayr	67.90	38.27	3.13 (2.64–3.61)	1.11 (0.87–1.35)
Subordinate				
Cardiocondyla obscurior Wheeler	81.48	48.77	1.96 (1.60–2.32)	0.58 (0.44–0.72)
Wasmannia auropunctata (Roger)	2.47	3.70	0.02 (0.00–0.05)	0.04 (0.01–0.07)
Odontomachus brunneus (Patton)	5.56	5.56	0.06 (0.02–0.09)	0.06 (0.02–0.10)
Camponotus sexguttatus (Fabricius)	3.70	4.32	0.05 (0.01–0.09)	0.04 (0.01–0.07)
Paratrechina longicornis (Latreille)	7.41	2.47	0.09 (0.04–0.14)	0.07 (−0.03 to 0.17)

activity (the percentage of recorded pitfall traps and the mean abundance) of *S. geminata*, *M. ebeninum*, *P. fallax*, *Brachymyrmex patagonicus*, *C. obscurior*, and *P. longicornis* was greater during the day than at night, while *N. guatemalensis* was more active at night than during the day (Table 2). The foraging activity of *W. auropunctata*, *O. brunneus*, and *C. sexguttatus* was similar during the day and at night (Table 2). Maps of spatial distribution of species are provided in the Appendix (Figure A1).

3.2 | Dominant, subdominant, and subordinate species

A total of 10 species were recorded during bait experiments. These species were the same as recorded in pitfall traps with the exception of *T. bicarinatum*, which was never recorded at baits. At baits, the presence of all species was in relatively high proportion, ranging from 10% to 77% (Table 3). *S. geminata*, *N. guatemalensis*, and *M. ebeninum* were identified as dominant species because they controlled a large proportion of baits at which they were present and have a high mean score abundance (Table 3). *P. fallax* and *B. patagonicus* were identified as subdominant species because they controlled a moderate proportion of baits at which they were present and have a moderate mean score abundance (Table 3). All other species were identified as subordinate species (Table 3). Maps of spatial distribution of species are provided in the Appendix (Figure A2).

The abundance of *S. geminata*, *M. ebeninum* was greater in the afternoon than in the morning, while the abundance *N. guatemalensis* was greater in the morning than in the afternoon (Table 4). We found no difference between the abundances at baits in the morning and in the afternoon for *P. fallax* and *B. patagonicus* (Table 4).

TABLE 2 Comparisons of the diurnal and nocturnal foraging activity of the dominant, subdominant, and subordinate species (Kruskal–Wallis tests)

	Recorded pitfall traps			Mean abundance		
	Day vs. night			Day vs. night		
	χ^2	*df*	*p*	χ^2	*df*	*p*
Dominant						
Solenopsis geminata	9.3	1	**.002**	11.1	1	**<.001**
Nylanderia guatemalensis	21.2	1	**<.001**	22.6	1	**<.001**
Monomorium ebeninum	13.6	1	**<.001**	14.8	1	**<.001**
Subdominant						
Pheidole fallax	9.7	1	**.002**	119.7	1	**<.001**
Brachymyrmex patagonicus	38.0	1	**<.001**	57.3	1	**<.001**
Subordinate						
Cardiocondyla obscurior	28.5	1	**<.001**	42.2	1	**<.001**
Wasmannia auropunctata	0.4	1	.521	0.4	1	.521
Odontomachus brunneus	0.0	1	1.000	0.0	1	.989
Camponotus sexguttatus	0.8	1	.777	0.1	1	.796
Paratrechina longicornis	4.2	1	**.040**	4.1	1	**.041**

TABLE 3 Occurrence of dominant, subdominant, and subordinate ants at baits

	Recorded baits (%)	Controlled baits (%)	Mean abundance score
Dominant			
Solenopsis geminata	20.65	43.50	4.12
Nylanderia guatemalensis	75.74	32.12	3.26
Monomorium ebeninum	25.37	28.48	3.23
Subdominant			
Pheidole fallax	70.00	20.10	2.87
Brachymyrmex patagonicus	77.04	14.90	2.74
Subordinate			
Cardiocondyla obscurior	66.02	2.94	2.07
Wasmannia auropunctata	10.09	3.67	1.93
Odontomachus brunneus	26.48	0	1.86
Camponotus sexguttatus	34.44	1.88	1.59
Paratrechina longicornis	11.48	0	1.38

TABLE 4 Comparisons of the abundances in the morning and in the afternoon of dominant, subdominant, and subordinate ants at baits (Kruskal–Wallis tests)

	Mean abundance (95% CI)				
	Morning	**Afternoon**	**χ^2**	***df***	***p***
Dominant					
Solenopsis geminata	4.49 (3.37–5.60)	6.85 (5.49–8.20)	6.2	1	**.013**
Nylanderia guatemalensis	11.92 (10.86–12.97)	9.71 (8.65–10.78)	19.1		**<.001**
Monomorium ebeninum	3.20 (2.31–4.09)	6.02 (4.75–7.30)	6.9	1	**.009**
Subdominant					
Pheidole fallax	8.81 (7.55–10.07)	8.05 (6.82–9.29)	2.6	1	.105
Brachymyrmex patagonicus	7.62 (6.52–8.71)	10.67 (9.23–12.11)	0.7	1	.416
Subordinate					
Cardiocondyla obscurior	2.23 (1.98–2.49)	2.27 (2.00–2.55)	0.4	1	.544
Wasmannia auropunctata	0.43 (0.27–0.58)	0.49 (0.26–0.73)	1.1	1	.285
Odontomachus brunneus	0.93 (0.77–1.09)	0.60 (0.46–0.74)	19.9		**<.001**
Camponotus sexguttatus	0.78 (0.64–0.93)	0.99 (0.74–1.24)	0.1	1	.807
Paratrechina longicornis	0.12 (0.09–0.16)	0.32 (0.19–0.45)	5.1	1	**.024**

3.3 | Probability of transition matrices

Based on hierarchical classification and clustering methods, only the three dominant and the two subdominant species contributed to the community structure at the subplot scale. We characterized seven typical groups corresponding to different community structures at the subplot scale (Table A1). Five of the groups were numerically dominated by one species, that is, groups 1–5 were numerically dominated by *S. geminata*, *M. ebeninum*, *P. fallax*, *N. guatalamensis*, and *B. patagonicus*, respectively. Group 6 was numerically co-dominated by *N. guatalamensis* and *B. patagonicus*, and group 7 was not numerically dominated by any species. The probability that a species maintained numerical dominance of a resource between sampling times 1 and 2 was high for *S. geminata*, *M. ebeninum*, *B. patagonicus*, and *N. guatalamensis* + *B. patagonicus* (Table 5, Figure 2a); these probabilities were lower for *P. fallax* and *N. guatemalensis* (Table 5, Figure 2a). The probability that a species maintained numerical dominance of a subplot resource between sampling times 2 and 3 was again high for the *B. patagonicus* group (Table 5, Figure 2b), and Markov chain simulations indicated that the probability of this group (group 5) maintaining numerical dominance between sampling times 1 and 3 was 0.6 (Table 5). For each species, most of the subplots where numerical dominance was not maintained were taken over by group 7, that is, the group that lacked a numerically dominant species (Figure 2a,b). This was particularly true for *P. fallax* and *N. guatemalensis*, two species that displayed low probabilities of maintaining numerical dominance on subplots (Figure 2a,b). We also observed that subplots categorized as group 7 (which lacked a numerically dominant species) tended to stay in the group 7 at the following sampling time (Figure 2a,b).

TABLE 5 The probability that a species maintained dominance of a subplot resource between sampling times as determined by Markov chain simulations (10,000 iterations per group). *Sol*, *Solenopsis*; *Mon*, *M. ebeninum*; *Phe*, *P. fallax*; *Nyl*, *N. guatemalensis*; *Bra*, *B. patagonicus*; *BraNyl*, codominance *B. patagonicus*/*N. guatemalensis*; *ND*, no dominant species

Sampling times	Probability for the indicated dominant species						
	Sol	***Mon***	***Phe***	***Nyl***	***Bra***	***BraNyl***	***ND***
1–2	0.78	0.70	0.53	0.32	0.79	0.82	0.72
2–3	0.40	0.57	0.33	0.47	0.76	0.46	0.57
1–3	0.32	0.40	0.18	0.16	0.60	0.38	0.40

3.4 | Autocorrelation

For the abundance of each species, we found a positive spatial autocorrelation among neighboring subplots that were separated by as much as 6.0 m, and that values for Geary's *C* (according to LMs) were positively associated with distance (Figure 3) and we considered spatial autocorrelation distances of 3 m for *P. fallax*, 4 m for *M. ebeninum* and *S. geminata*, and 5 m for *N. guatemalensis* and *B. patagonicus*. For analyses in the next section, we used these spatial autocorrelation distances to calculate the abundance of each species present in the neighborhood of *P. fallax* and *M. ebeninum*, *S. geminata* and *N. guatemalensis*, and *B. patagonicus*.

3.5 | Subplot scale dynamics and correlations between ant species abundances

Statistical analyses of the relationships between the abundance of each ant taxon (interspecific interactions) are provided in the supporting information (Tables A2-A6), and the results are summarized in

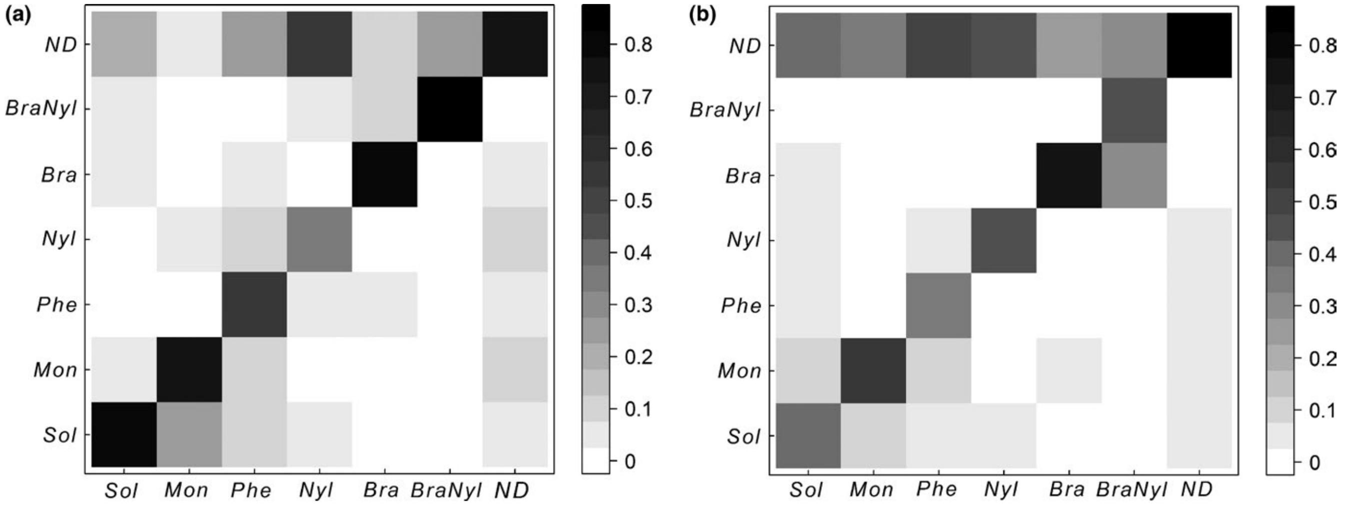

FIGURE 2 Probability of transition matrices. These figures display the probability that a numerically dominant species (listed on *X*-axis) will maintain its numerical dominance on the resource or lose it to the benefit of another dominant or subdominant species (listed on *Y*-axis) from: (a) sampling time 1 to sampling time 2; (b) sampling time 2 to sampling time 3. In (a) and (b), the diagonal indicates the probability that a species maintains dominance on the resource between sampling times. *Sol*, *S. geminata*; *Mon*, *M. ebeninum*; *Phe*, *P. fallax*; *Nyl*, *N. guatemalensis*; *Bra*, *B. patagonicus*; *BraNyl*, codominance *B. patagonicus/N. guatemalensis*; *ND*, no dominant species

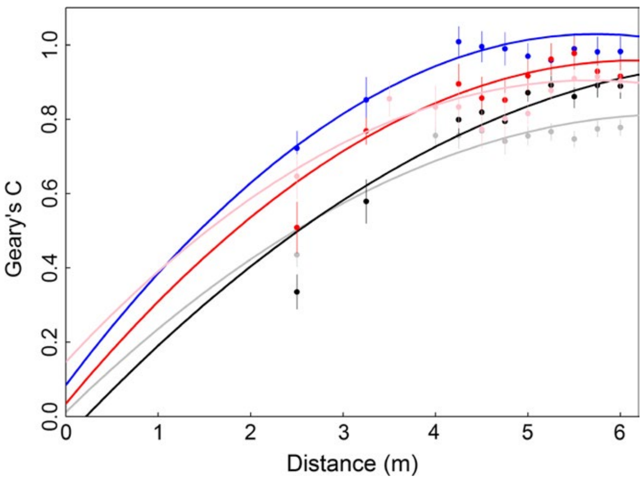

FIGURE 3 Mean values for Geary's C as affected by distance between two subplots. Points correspond to raw data, and curves are fitted from linear regression models. Gray: *N. guatemalensis* (r^2 = 0.83); black: *B. patagonicus* (r^2 = 0.94); blue: *P. fallax* (r^2 = 0.78); red: *S. geminata* (r^2 = 0.83); pink: *M. ebeninum* (r^2 = 0.38)

Figure 4a,b. Among the 15 pairwise local (within subplots) interspecific correlations, 14 were symmetrically negative (−/−), and one was symmetrically positive (+/+). The abundance of *S. geminata* was negatively correlated with the local abundances of other ant species (Figure 4a) but was positively correlated with the abundances of conspecifics and other ant species in its neighborhood (Table A2, Figure 4b). The abundance of *M. ebeninum* was negatively correlated with the local abundances of other ant species (Figure 4a) and with the abundances of conspecifics and other ant species in its neighborhood, except that *N. guatemalensis* abundance in the neighborhood was not correlated with *M. ebeninum* abundance (Table A3, Figure 4b). The abundance of *P. fallax* was negatively correlated with the local abundances of other ant species (Figure 4a); the abundance of *P. fallax* was also negatively correlated with the abundance of *S. geminata* in its neighborhood and was positively correlated with the abundances of *N. guatemalensis* and *B. patagonicus* in its neighborhood (Figure 4b). The abundance of *P. fallax* conspecifics and *M. ebeninum* in the neighborhood was not correlated with the abundance of *P. fallax* (Table A4, Figure 4b). The abundance of *N. guatemalensis* was negatively correlated with the local abundances of other ant species except that it was positively correlated with *B. patagonicus* abundance (Table A6, Figure 4A). The abundance of *B. patagonicus* was negatively correlated with the local abundances of other ant species except that it was positively correlated with *N. guatemalensis* abundance (Table A5, Figure 4a). The abundance of *B. patagonicus* was positively correlated with the abundances of conspecifics in its neighborhood and negatively correlated with the abundances of *S. geminata* or *N. guatemalensis* in its neighborhood (Table A5, Figure 4b). No correlation was detected between the abundance of *B. patagonicus* and the abundances of *P. fallax* or *M. ebeninum* (Table A5, Figure 4b). The abundance of *N. guatemalensis* was positively correlated with the abundances of conspecifics and *P. fallax* in its neighborhood, while the abundances of other ant species in its neighborhood were not correlated with its local abundance (Table A6, Figure 4b). The random effect of date on intercept and the random slope effect of dominant group significantly improved the GLMMs for all model species of abundance (Tables A2-A6).

4 | DISCUSSION

We performed bait and pitfall trapping experiments in a very simplified and homogeneous agroecosystem for studying ant community structure. Doing so minimized the effects of habitat-related factors

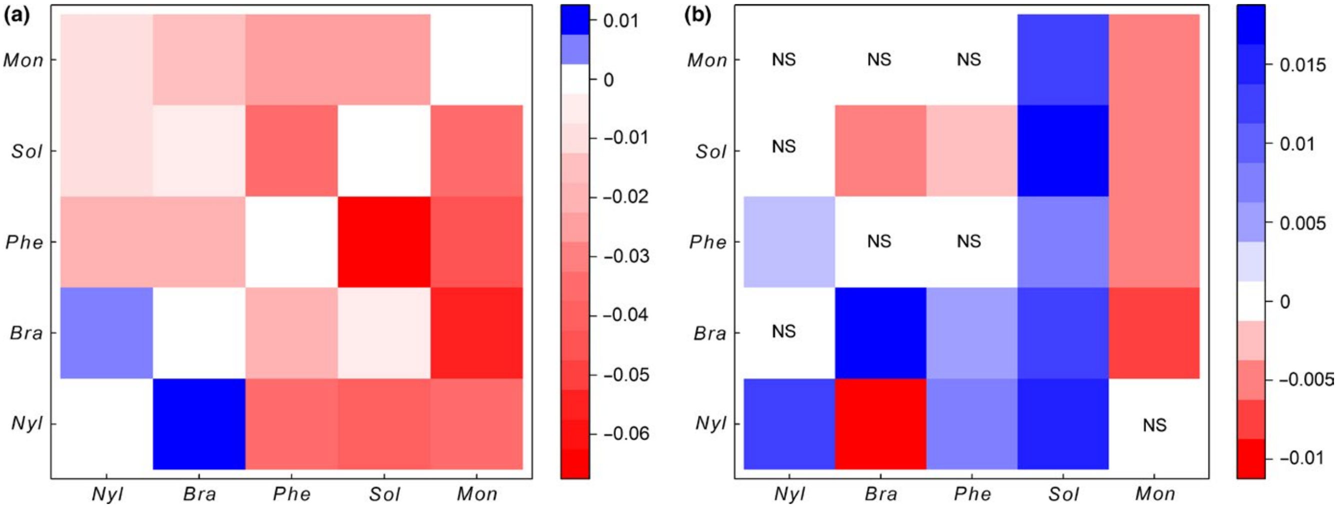

FIGURE 4 Estimates of correlations between ant species abundances. (a) Estimated effects of the abundance of a species (listed on *Y*-axis) in subplots on the abundance of a species (listed on the *X*-axis) in the same subplots. (b) Estimated effects of the abundance of a species (listed on the *Y*-axis) in neighboring subplots on the abundance of a species (listed on the *X*-axis) in subplots. *Sol*, *S. geminata*; *Mon*, *M. ebeninum*; *Phe*, *P. fallax*; *Nyl*, *N. guatemalensis*; *Bra*, *B. patagonicus*

that can affect community structure. The pattern analysis provided information on temporal and spatial dynamics of dominant, subdominant, and subordinate ants foraging in a single-crop banana agroecosystem.

We found that the community of ground-dwelling ants was dominated by *Solenopsis geminata*, *Monomorium ebeninum*, *Nylanderia guatemalensis*, *Pheidole fallax*, and *Brachymyrmex patagonicus*. Our results showed that species generally maintained numerical dominance of a subplot (bait) throughout each 180-min sampling date. *Solenopsis geminata* displayed a high probability of maintaining numerical dominance, although the probability decreased greatly with sampling time, that is, with resource consumption. This species actively recruits to food sources and is very aggressive toward competitors (Trager, 1991). When *S. geminata* did not maintain numerical dominance, it was usually not to the benefit of a particular species. A similar pattern of maintaining numerical dominance was observed for *M. ebeninum*, which is consistent with Hanson and Gauld (1995), who reported that this species behaves like *Solenopsis* in the field. However, when *M. ebeninum* did not maintain numerical dominance, it was mostly to the benefit of *S. geminata*, suggesting that the two species may have similar ecological niches. This is consistent with the similarity that we observed in their diurnal and nocturnal foraging activity and with the daily variation of occurrence at baits. *Brachymyrmex patagonicus* displayed high probabilities of maintaining numerical dominance at baits, and the decrease in its probability of maintaining numerical dominance over time was lower for this species than for the other species in our study. MacGown, Hill, and Deyrup (2007) reported that *Brachymyrmex* spp. in general and *B. patagonicus* in particular have the ability to coexist with a variety of other dominant species. These authors also suggest that *B. patagonicus* may be protected by potent chemicals. *N. guatemalensis* displayed the lowest probability of maintaining numerical dominance at baits. This is consistent with LaPolla, Brady, and Shattuck (2011), who described *Nylanderia* spp. as efficient foragers that rapidly find and recruit to resources but that rarely can defend the resources against other ants that arrive later. *P. fallax* displayed low probabilities of maintaining numerical dominance at baits. Perfecto and Vandermeer (2011) found that *Pheidole subarmata* tends to lose dominance at baits against *S. geminata*. In our study, *P. fallax* was apparently kept low at baits not only by *S. geminata*, which is a strong interference competitor (Perfecto & Vandermeer, 2011), but also by all of the other dominant and subdominant ant species. *Nylanderia* spp. are known to be good exploitation competitors (LaPolla et al., 2011), but our results suggest that, depending on the context and the competitors that they face, *Nylanderia* ants may also be interference competitors.

However, the patterns we observed may also depend, at least in part, on other factors such as daily variation in foraging activity because of thermal constraints. Thermal constraints have been shown to disrupt hierarchies in ant communities (Bestelmeyer, 2000; Cerdá, Retana, & Cros, 1997). We found that two of the three dominant species (*M. ebeninum* and *S. geminata*) were more abundant at baits in the afternoon than in the morning while the other one (*N. guatemalensis*) displayed the opposite trends. Moreover, the foraging activity of two former species was higher the day than at night, while it was the opposite for *N. guatemalensis*. The subdominant ants (*P. fallax* and *B. patagonicus*) had greater foraging activity during the day, with no difference in abundance at baits between the afternoon and the morning, while being the two most abundant species at night. Overall, the variation in foraging activities may explain the coexistence of dominant, subdominant, and subordinates species in this agroecosystem limited in habitat structure and diversity because of the induction of temporal niche partitioning (Albrecht & Gotelli, 2001; Cerdá, Retana, & Manzaneda, 1998).

All of the coefficients of local (i.e., at baits) interspecific correlations, with the exception of one pairwise correlation, were symmetrically negative, suggesting that interference competition prevails in this community of ground-dwelling ants. The coefficients of local interactions, however, were symmetrically positive between *B. patagonicus* and *N. guatemalensis*. Thus, competitive exclusion at an ephemeral food source does not occur between these two species of Formicinae, which seem to tolerate each other.

The positive correlation between the local abundance and neighborhood abundance of a considered species may reflect the absence of intraspecific competition between colonies. Indeed, *S. geminata* is known to be, at least temporarily, polygynous (Trager, 1991). Some *Nylanderia* spp. may also be polygynous (Arcila, Ulloa-Chacon, & Gomez, 2002), and MacGown et al. (2007) reported that *B. patagonicus* colonies may be situated very close to each other, displaying considerable mutual tolerance. McGlynn (2010) demonstrated that polygyny increases in response to the density of ant competition. The positive correlation between the local abundance of an ant species with the neighborhood abundance of another species may reflect an overlap in spatial distribution, which seems to be the usual pattern in tropical ant communities (Soares & Schoereder 2001). This should be particularly true in homogeneous agroecosystems where food and nesting resources display very few variations. Here, we found positive correlations between the local abundance of *P. fallax* and the neighborhood abundance of *N. guatemelensis*, and between the local abundance of *N. guatemelensis* and the neighborhood abundance of *P. fallax*. Similar spatial associations have been reported between unidentified species in the genus *Pheidole* and *Paratrechina* (Chong, Hoffmann, & Thomson, 2011), the latter genus having been recently separated into the genera *Paratrechina* and *Nylanderia* (LaPolla, Brady, & Shattuck, 2010). This positive spatial association, despite the competitive interference found between these two species at baits, could result from the dissimilarity between their temporal foraging activity. Indeed, our data support this hypothesis as *P. fallax* foraging activity is greater during the day while the foraging activity of *N. guatemalensis* greater at night. This should lead to the temporal sharing of resources. The positive spatial association could also result from a similarity in foraging behavior. We found the lowest probabilities of maintaining dominance in these two species, both of which are good exploitative competitors that rapidly discover resources (Itzkowitz & Haley, 1983; LaPolla et al., 2011), had a similar probability to losing dominance at baits to the benefit of the other. This should lead to the spatial sharing of resources at such fine spatial scale. We also found a positive correlation between the local abundance of *P. fallax* and the neighborhood abundance of *B. patagonicus*, whose local abundance was not correlated with the neighborhood abundance of *P. fallax*. Because *B. patagonicus* was highly numerically dominant at baits and had a high probability of maintaining its numerical dominance at baits, it is not surprising that the presence of the *P. fallax* in the neighborhood did not apparently affect *B. patagonicus*.

To our knowledge, this is the first study reporting information on ant community in a banana crop agrosystem in Martinique. In summary, we found that three dominant and two subdominant species structure the ant community in a very simplified banana agrosystem. All these species generally maintain numerical dominance at a "momentary" resource and that interference competition probably prevails in this ground-dwelling community. However, temporal and spatial niche partitioning may also explain, at least partly, the observed pattern. Moreover, the presence of invasive species, such as the fire ant *S. geminata*, the rover ant *B. patagonicus*, the little fire ant *W. auropunctata*, and the crazy ant *P. longicornis*, might greatly affect ecological processes and ecosystems (Lach & Hooper-Bui, 2010). Thus, we cannot extent our results to other ecosystems and consider that further studies in very simplified agrosystems should be carried out to better assess the relative contribution of these ecological processes in the structuring of ant communities.

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APPENDIX

TABLE A1 The mean composition of the seven typical groups of ants that differed in community structure in subplots of a banana field. The values indicate the mean (SE) number of individuals per subplot and sampling time of each species per group. The emboldened values indicate the dominant species in each group. Groups 1–5 had one dominant species; group 6 had two dominant species; and group 7 had no dominant species

Species	Group 1	Group 2	Group 3	Group 4	Group 5	Group 6	Group 7
Nylanderia guatemalensis	3.72 (0.66)	5.41 (0.84)	4.19 (0.51)	**34.91 (1.10)**	6.06 (0.90)	**25.09 (2.14)**	9.42 (0.39)
Brachymyrmex patagonicus	6.57 (1.21)	2.47 (0.31)	2.58 (0.48)	5.82 (0.92)	**46.06 (0.82)**	**46.36 (1.22)**	4.45 (0.28)
Pheidole fallax	2.83 (0.46)	3.16 (0.64)	**44.14 (0.84)**	2.70 (0.39)	2.44 (0.61)	3.42 (1.52)	4.28 (0.30)
Solenopsis geminata	**46.79 (0.77)**	1.76 (0.88)	0.38 (0.31)	1.42 (0.13)	0.68 (0.72)	0.06 (0.06)	1.41 (0.22)
Monomorium ebeninum	2.5 (0.65)	**48.0 (0.60)**	0.98 (0.24)	0.20 (0.06)	0.04 (0.03)	0.0 (0.0)	1.37 (0.22)

TABLE A2 Selection of the model explaining the local abundance of *Solenopsis geminata*. Results of likelihood ratio tests are also shown for the significance of retaining fixed and random effects in the model. Fixed or random effects were kept in the selected model if the *p*-value was ≤.05

Model	*df*	Δ*df*	AIC	ΔAIC	Log-likelihood	χ^2	*p*-value
Selected	13		8,072.8		−4,023.4		
Fixed effects							
Sampling time	12	1	8,242.7	169.9	−4,109.3	171.8	<.0001
Local abundance of							
Pheidole fallax	12	1	9,986.4	1,913.6	−4,981.2	1,915.6	<.0001
Monomorium ebeninum	12	1	8,647.9	575.1	−4,282.1	517.3	<.0001
Brachymyrmex patagonicus	12	1	8,086.1	13.3	−4,031	15.3	<.0001
Nylanderia guatemalensis	12	1	8,511.8	439	−4,243.9	441.0	<.0001
Neighboring abundance of							
P. fallax	12	1	8,079.9	7.1	−4,027.9	9.1	.003
Solenopsis geminata	12	1	8,239.5	166.7	−4,107.8	168.7	<.0001
B. patagonicus	12	1	8,116.8	44	−4,046.4	46.0	<.0001
M. ebeninum	12	1	8,152.7	79.9	−4,064.4	81.9	<.0001
N. guatemalensis	12	1	8,128.6	55.8	−4,052.3	57.8	<.0001
Random effects							
Date	12	1	8,160	87.2	−4,068	89.2	<.0001
Dominant group	12	1	19,108.9	11,036.1	−9,542.5	11,038	<.0001

TABLE A3 Selection of the model explaining the local abundance of *Monomorium ebeninum*. Results of likelihood ratio tests are also shown for the significance of retaining fixed and random effects in the model. Fixed or random effects were kept in the selected model if the *p*-value was ≤.05

Model	*df*	Δ*df*	AIC	ΔAIC	Log-likelihood	χ^2	*p*-value
Selected	12		8,970.8		−4,473.4		
Fixed effects							
Sampling time	11	1	9,005.8	35	−4,491.9	37.0	<.0001
Local abundance of							
Pheidole fallax	11	1	9,971.1	1,000.3	−4,974.6	1,002.3	<.0001
Solenopsis geminata	11	1	10,028.3	1,057.5	−5,003.1	1,059.5	<.0001
Brachymyrmex patagonicus	11	1	9,460.3	489.5	−4,719.2	491.5	<.0001
Nylanderia guatemalensis	11	1	9,320	349.2	−4,649	351.2	<.0001
Neighboring abundance of							
P. fallax	11	1	8,976.8	6	−4,477.4	8.0	.005
S. geminata	11	1	8,975.9	5.1	−4,476.9	7.1	.008
B. patagonicus	11	1	8,976	5.2	−4,477	7.2	.007
Monomorium ebeninum	11	1	8,981.5	10.7	−4,479.8	12.7	.0004
N. guatemalensis	–	–	–	–	–	–	.09
Random effects							
Date	11	1	9,017.3	46.5	−4,497.6	48.5	<.0001
Dominant group	11	1	16,169.8	7,199	−8,073.9	7,200.9	<.0001

TABLE A4 Selection of the model explaining the local abundance of *Pheidole fallax*. Results of likelihood ratio tests are also shown for the significance of retaining fixed and random effects in the model. Fixed or random effects were kept in the selected model if the *p*-value was ≤.05

Model	*df*	Δ*df*	AIC	ΔAIC	Log-likelihood	χ^2	*p*-value
Selected	11		12,215		−6,096.7		
Fixed effects							
Sampling time	10	1	12,264	49	−6,122.3	51.2	<.0001
Local abundance of							
Solenopsis geminata	10	1	13,574	1,359	−6,777	1,360.6	<.0001
Monomorium ebeninum	10	1	12,670	455	−6,324.7	456.2	<.0001
Brachymyrmex patagonicus	10	1	12,517	302	−6,248.3	303.2	<.0001
Nylanderia guatemalensis	10	1	13,195	980	−6,587.4	981.4	<.0001
Neighboring abundance of							
Pheidole fallax	–	–	–	–	–	–	.079
S. geminata	10	1	12,218	3	−6,098.8	4.2	.039
B. patagonicus	10	1	12,229	14	−6,104.6	15.8	<.0001
M. ebeninum	–	–	–	–	–	–	.525
N. guatemalensis	10	1	12,233	18	−6,106.7	20.1	<.0001
Random effects							
Date	10	1	12,298	83	−6,138.9	84.4	<.0001
Dominant group	10	1	16,391	4,176	−8,185.6	4,177.8	<.0001

TABLE A5 Selection of the model explaining the local abundance of *Brachymyrmex patagonicus*. Results of likelihood ratio tests are also shown for the significance of retaining fixed and random effects in the model. Fixed or random effects were kept in the selected model if the *p*-value was ≤.05

Model	*df*	Δ*df*	AIC	ΔAIC	Log-likelihood	χ^2	*p*-value
Selected	11		10,714		−5,346.2		
Fixed effects							
Sampling time	10	1	10,793	79	−5,386.4	80.3	<.0001
Local abundance of							
Pheidole fallax	10	1	11,069	355	−5,524.3	356.2	<.0001
Solenopsis geminata	10	1	10,742	28	−5,361.1	29.6	<.0001
Monomorium ebeninum	10	1	10,775	61	−5,377.1	62.1	<.0001
Nylanderia guatemalensis	10	1	10,734	20	−5,357.2	21.9	<.0001
Neighboring abundance of							
P. fallax	–	–	–	–	–	–	.15
S. geminata	10	1	10,802	88	−5,391.2	89.9	<.0001
Brachymyrmex patagonicus	10	1	10,950	236	−5,465.2	237.8	<.0001
M. ebeninum	–	–	–	–	–	–	.34
N. guatemalensis	10	1	10,723	9	−5,351.5	10.5	.09
Random effects							
Date	10	1	11,510	796	−5,745	797.5	<.0001
Dominant group	10	1	16,429	5,715	−8,204.3	5,716.2	<.0001

TABLE A6 Selection of the model explaining the local abundance of *Nylanderia guatemalensis*. Results of likelihood ratio tests are also shown for the significance of retaining fixed and random effects in the model. Fixed or random effects were kept in the selected model if the *p*-value was ≤.05

Model	*df*	Δ*df*	AIC	ΔAIC	Log-likelihood	χ^2	*p*-value
Selected	10		10,277		−5,128.3		
Fixed effects							
Sampling time	9	1	10,300	23	−5,141.2	25.9	<.0001
Local abundance of							
Pheidole fallax	9	1	10,815	538	−5,398.5	540.4	<.0001
Solenopsis geminata	9	1	10,422	145	−5,201.9	147.3	<.0001
Monomorium ebeninum	9	1	10,371	94	−5,176.7	96.8	<.0001
Brachymyrmex patagonicus	9	1	10,310	33	−5,145.8	35.0	<.0001
Neighboring abundance of							
P. fallax	9	1	10,295	18	−5,138.5	20.4	<.0001
S. geminata	–	–	–	–	–	–	.16
B. patagonicus	–	–	–	–	–	–	.50
M. ebeninum	–	–	–	–	–	–	.71
Nylanderia guatemalensis	9	1	10,468	191	−5,225.1	193.58	<.0001
Random effects							
Date	9	1	11,941	1,664	−5,961.5	1,666.5	<.0001
Dominant group	9	1	12,332	2,055	−6,157	2,057.4	<.0001

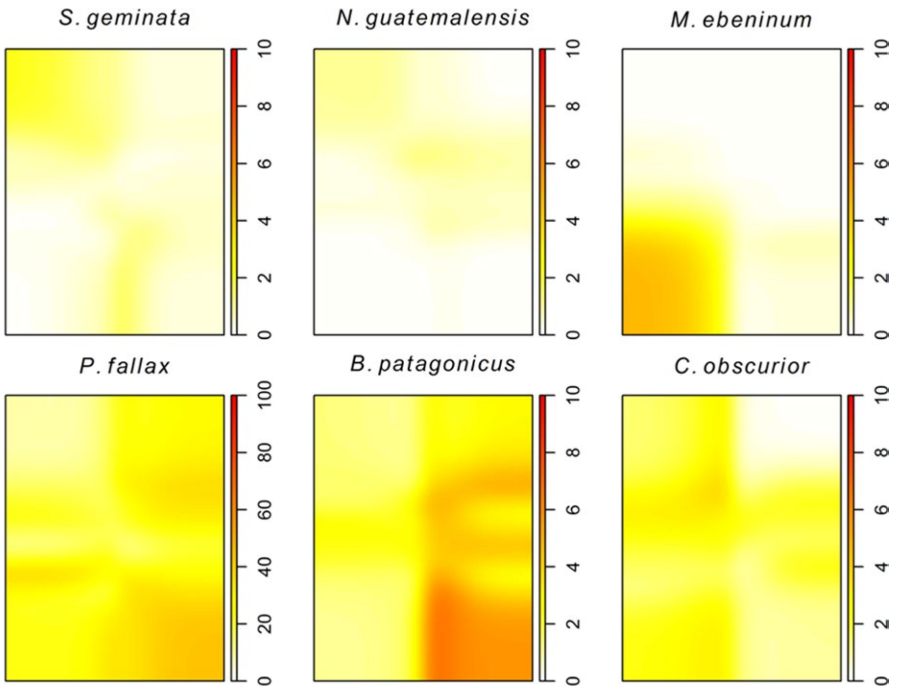

FIGURE A1 Spatial distribution of the dominant and subdominant ant species and of *Cardiocondyla obscurior* based on abundances recorded in pitfall traps

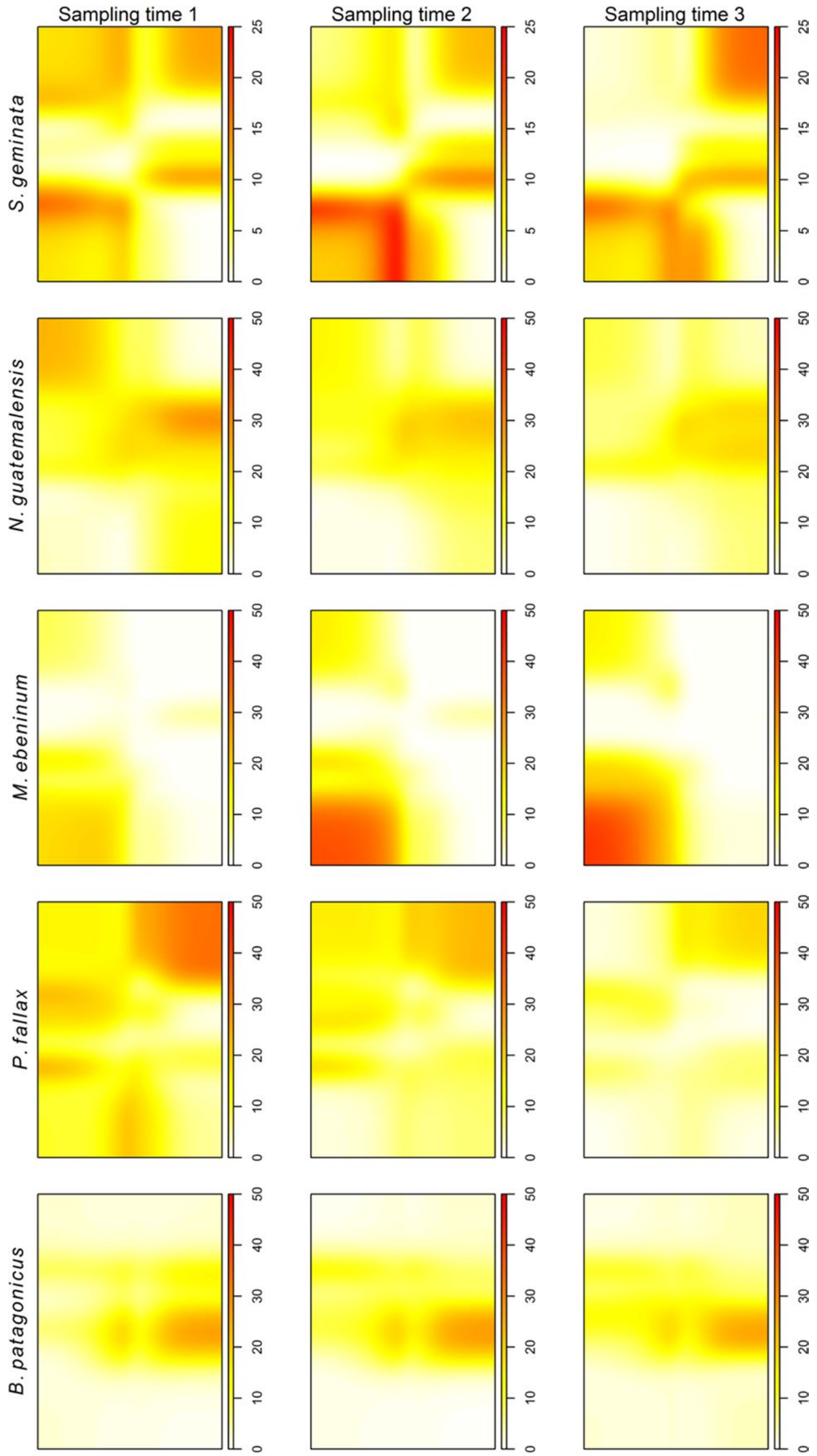

FIGURE A2 Spatial distribution of the dominant and subdominant ant species based on abundances recorded at baits

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A UNIFIED MODEL FOR THE COEVOLUTION OF RESISTANCE, TOLERANCE, AND VIRULENCE

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We present a general host–parasite model that unifies previous theory by investigating the coevolution of virulence, resistance, and tolerance, with respect to multiple physiological, epidemiological, and environmental parameters. Four sets of new predictions emerge. First, compared to virulence coevolving with resistance or tolerance, three-trait coevolution promotes more virulence and less tolerance, and broadens conditions under which pure defenses evolve. Second, the cost and efficiency of virulence and the epidemiological rates are the key factors of virulence coevolving with resistance and tolerance. Maximum virulence evolves for intermediate infection rate, at which coevolved levels of resistance and tolerance are both high. The influence of host and parasite background mortalities is strong on the evolution of defenses and weak on the coevolution of virulence. Third, evolutionary correlations between defenses can switch sign along single-parameter gradients. The evolutionary trade-off between resistance and tolerance may coevolve with virulence that either increases or decreases monotonically, depending on the underlying parameter gradient. Fourth, despite global attractiveness and stability of coevolutionary equilibria, not-so-rare and not-so-small mutations can beget large variation in virulence and defenses around equilibrium, in the form of transient "evolutionary spikes." Implications for evolutionary management of infections are discussed and directions for future research are outlined.

KEY WORDS: **Adaptive dynamics, host defense, infection, parasitism, pathogen, trade-offs.**

Host–parasite interactions pervade living systems, and understanding how parasite virulence and host defense evolve is a matter of major fundamental and applied interest across biological, agricultural, and health sciences (Woolhouse et al. 2002). This had led the development of a large body of mathematical theory, yet thus far most of the theory has focused on the evolution of a single species, and models that examine parasite virulence and host defense as continuous characters that coevolve remain relatively few (e.g., Hochberg and van Baalen 1998; van Baalen 1998; Gandon et al. 2002; Koella and Boete 2003; Restif and Koella 2004; Bonds 2006; Best et al. 2009; see also Dieckmann et al. 2002 for an overview).

In long-lasting, often specialized and in some cases obligate pairwise interactions, it is expected, however, that as one species evolves, selective pressures on the other change (e.g., Thompson 1994). Selection on parasite virulence involves a trade-off between within-host reproduction (replication resulting from exploitation of the host) and within-host survival (as affected by exploitation-induced host mortality) mediated at between-host level by transmission success (Anderson and May 1979; Frank 1996; Alizon et al. 2009). In response, there are basically two ways for the host to defend itself: with resistance, the host fights the parasite to prevent or limit exploitation; with tolerance, the host fights the "disease" to prevent or limit the adverse effect of exploitation. Resistance implies that the host invests resources into mechanisms (avoidance, control, recovery) that cause a reduction in the fitness of the parasite; tolerance implies that the host invests resources to limit its own fitness reduction by reducing the damage that the parasite causes (Clarke 1986; Barker 1993; Boots 2008). The significance of tolerance as a plant defense against herbivory is well known, and recent empirical research suggests that tolerance is a widespread host response to parasitic infection, not only in plants but also in animals (Simms and Triplett 1994; Kover and Schaal 2002; Carr et al. 2006; Raberg et al. 2007; Boots 2008; Raberg et al. 2009). Genetic variation in tolerance has been evidenced in experimental systems (Rausher 2001; Kover and Schaal 2002), and genetic data are now unraveling molecular mechanisms of coevolution with virulence (Ayres and Schneider 2008).

In the coevolutionary perspective, the distinction between resistance and tolerance is a fundamental one, because resistance and tolerance have radically different ecological and epidemiological consequences and therefore generate very different evolutionary feedbacks on virulence (Roy and Kirchner 2000; Boots 2008). Resistance has a negative effect on parasites, whereas tolerance does not. As they live longer when infected, tolerant hosts increase the infectious period of the parasite. This means that selection for tolerance will tend to increase the prevalence of the disease. In contrast, the evolution of resistance, by definition, decreases parasite fitness and reduces the infection prevalence. Emerging theory has begun to shed light on the evolutionary implications of this fundamental ecological difference. Tolerance alleles are likely to be promoted by positive frequency-dependent selection (Roy and Kirchner 2000) and quantitative models have been developed to compare the cost for the host to evolve either resistance or tolerance against a nonevolving parasite (Miller et al. 2005). When tolerance evolves, the evolutionary feedback on the parasite can drive the evolution of high virulence (Restif and Koella 2003; Miller et al. 2006). Data and models show that selection can favor mixed defenses, combining resistance and tolerance (Mauricio et al. 1997; Fornoni et al. 2004; Restif and Koella 2004). This begs the question of how the evolution of high virulence promoted by tolerance feeds back on the evolution of both defenses, and ultimately how the concurrent evolution of resistance and tolerance shapes coevolution with virulence. Addressing these questions requires that previous theory be extended and unified in a model in which all three traits—resistance, tolerance, and virulence—can coevolve.

The model presented here combines the ecological process of host–parasite interaction with the evolutionary process fueled by heritable variation in virulence and defenses. Evolution of a trait changes the ecological state of the system and the epidemiology of infection, which feeds back on selection on all traits and thus entangles the evolutionary dynamics of the two species (Fig. 1A). The ecological model was designed to integrate several key physiological, environmental, and epidemiological factors of host and parasite population dynamics (Fig. 1B, C). At the physiological level, the resources allocated to the traits (virulence in the parasite, defenses in the host) are diverted from reproductive potential, and the corresponding reproductive cost functions can be accelerating as well as decelerating (Miller et al. 2005, Best et al. 2009). With respect to environmental and epidemiological factors, the model accounts for a free-living stage in the parasite population: infected hosts release parasite propagules. The propagules' longevity is determined in part by their "background mortality" that thus becomes an environmental factor of the coevolutionary process (Bonhoeffer et al. 1996; Day 2001). Infection occurs upon contact between a susceptible host and a propagule. Transmission depends upon a propagation factor—the rate at which an internalized parasite uses resources exploited from the host to produce infectious propagules; and the infection rate—the frequency of encounters between susceptible hosts and free-living parasites. The host population is regulated by density dependence of the birth rate, while the parasite population is kept from growing unbounded by the obligate nature of the interaction.

We organize the model analysis around three general questions: (1) How do physiological, environmental, and epidemiological parameters affect resistance–tolerance coevolution? (2) How does the nature of host defense—resistance versus tolerance—affect virulence evolution? (3) How does the concurrent evolution of all three traits alter the patterns of resistance–tolerance covariation predicted under fixed virulence and the response of virulence to variation in physiological, environmental, and epidemiological parameters? We answer these questions by examining two-trait (resistance–tolerance, virulence–resistance, virulence–tolerance) and three-trait (virulence–resistance–tolerance) evolutionary equilibria. Evolutionary convergence and stability of the equilibria is studied under the assumption of small, rare, and independent genetic variation in the traits. Finally, an invasion analysis is performed to examine the consequences of not-so-small and not-so-rare mutations for the maintenance of variation in virulence, resistance, and tolerance.

Model Construction and Analysis

We consider the coevolution of resistance, tolerance, and virulence between a host and an obligate endoparasite (Fig. 1). The parasite has a free-living, infectious stage. Transmission is purely horizontal (the consequences of vertical transmission have also been studied and will be presented elsewhere). Infection happens upon contact and there is no multiple infection. The endoparasite exploits its host's resources to produce infectious propagules in the free-living stage. Virulence is expressed in terms of endoparasite reproductive success at the expense of host survival.

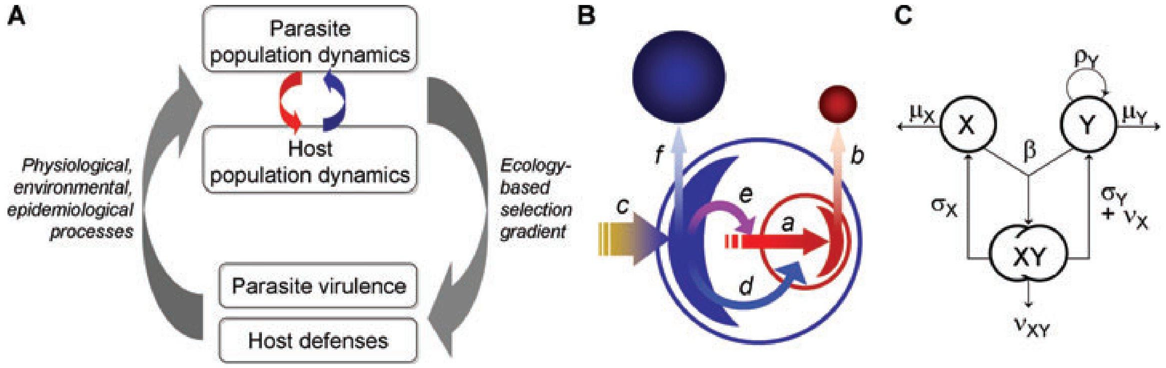

Figure 1. Theoretical principles and model structure. (A) Host–parasite coevolutionary dynamics driven by ecogenetic feedback. Resident trait values set the ecological state of the system, given physiological, environmental, and epidemiological parameters (assumed to be constant). The ecological state generates selective pressures on the genetic variation that arise from mutation in the resident populations. Thus, heritable variation in the individual traits changes the system's ecology, and variation in the ecology feeds back, via selection, on trait variation. Iteration of this ecogenetic feedback loop determines the long-term evolutionary dynamics of the adaptive traits. Note that variation in the trait(s) of one species will change the ecology of the whole system and therefore the selective pressures acting on genetic variation in this species and the other as well, thus entangling both species in a coevolutionary process. Similarly, physiological, environmental, and epidemiological parameters pertaining to one species may affect the whole ecology and thus the selective pressures experienced by both species. (B) Physiological model of virulence, resistance, and tolerance. A parasite (small red circle) is shown as internalized in its host (large blue circle). Metabolized resources that are potentially available for parasite and host reproduction are indicated by the small red and large blue crescents, respectively. Virulence is defined as the fraction of somatic (nonreproductive) energy that the host loses to the parasite (*a*). This energy discounted by the cost of virulence is available for production (*b*) of free-living parasites (small red sphere). The host acquires resources from the external environment (*c*). Metabolized resources can be invested in resistance (*d*) which decreases parasite survival; in tolerance (*e*) which reduces the negative impact of virulence on host survival. Metabolized resources discounted by the cost of investments in resistance and tolerance are available for production (*f*) of new susceptible hosts (large blue sphere). (C) Ecological model of host and parasite population dynamics. Susceptible hosts reproduce at (density-dependent) rate ρ_Y and die at rate μ_Y. Free-living parasites die at rate μ_X and infect hosts at rate β. Infected hosts die at rate ν_{XY}, produce free-living parasites at rate σ_X and susceptible hosts either by host reproduction (no vertical transmission) at rate σ_Y or by clearance and recovery (death of infecting parasite) at rate ν_X. We use a modified version of the original Kostitzin model in which the linear density dependence of birth that regulates the host population is replaced with a more realistic nonlinear (saturating) function of density (see van Baalen and Jansen 2001 for a similar adjustment).

Resistance increases the endoparasite's within-host mortality rate whereas tolerance reduces the host mortality risk caused by the parasite. The cost of a trait is paid in terms of reduced reproductive potential.

For given virulence, resistance and tolerance trait values, we construct the epidemiological model of the system; the model governs the ecological dynamics of the parasite and host populations. Next we allow for genetic variation in the traits. Deterministic equations for the coevolutionary dynamics of the traits are obtained under the assumption of small and rare mutations. The analysis of the selection gradient yields insights into the consequences of larger and more frequent mutations on the traits dynamics around evolutionary equilibrium.

ECOLOGICAL MODEL

The biological assumptions are translated mathematically by using an epidemiological SIS model that includes a free-living stage for the parasite (Bonhoeffer et al. 1996; Day 2001), and negative density dependence of the birth rate of susceptible and infected hosts (Kostitzin 1934; Wolin 1985); see Figure 1. The parasite species is denoted by X (population density X) Susceptible hosts have density Y and infected hosts have density Z. Parasitism is obligate in the sense that parasites cannot reproduce in their free-living stage. From the infected stage Z, hosts can give birth to susceptible individuals Y, and internalized parasites can give birth to free-living propagules X. The assumption of no vertical transmission implies that Z individuals cannot give birth to new Z individuals. Death of an infected host implies the death of the associated parasite X. Death of an infecting parasite can be caused by intrinsic mortality or by host resistance, and returns a recovered, susceptible host Y.

The model parameters are defined as follows. Free-living parasites X die at a per capita rate $\mu_X = \mu_{0X} + \mu_{1X}$, where μ_{0X} denotes the intrinsic mortality rate of X and μ_{1X} is the background mortality rate of X due to environmental hazards. Free-living parasites infect susceptible hosts at rate β according to the law of mass action on densities X and Y. Finally, new free-living parasites are produced from infected hosts at rate σ_X. The rate of change of free-living parasite density X is therefore given by

$$dX/\mathrm{d}t = -\mu_X X - \boldsymbol{\beta} XY + \sigma_X Z. \quad \text{(1A)}$$

Susceptible hosts reproduce at per-capita rate ρ_Y and die at per-capita rate $\mu_\mathrm{Y} = \mu_{0\mathrm{Y}} + \mu_{1\mathrm{Y}}$, where $\mu_{0\mathrm{Y}}$ is the host per-capita intrinsic mortality rate and $\mu_{1\mathrm{X}}$ is the host background mortality rate due to environmental hazards. Infection removes hosts from the susceptible population at rate β. New susceptible hosts are produced from infected hosts at per-capita rate $(\sigma_\mathrm{Y} + \nu_\mathrm{X})$ where σ_Y measures the rate of reproduction of infected hosts (there is no vertical transmission) and ν_X denotes the rate of mortality of an internalized parasite, which in effect clears the infection and returns a susceptible host. Hence the rate of change of susceptible host density Y is:

$$\mathrm{d}Y/\mathrm{d}t = (\rho_\mathrm{Y} - \mu_\mathrm{Y})Y - \boldsymbol{\beta} XY + (\sigma_\mathrm{Y} + \nu_\mathrm{X})Z. \quad \text{(1B)}$$

Finally, the density of infected hosts changes due to contact between X and Y (rate β), death of infecting parasite at per-capita rate ν_X, and death of infected hosts at per-capita rate ν_XY:

$$\mathrm{d}Z/\mathrm{d}t = \boldsymbol{\beta} XY - (\nu_\mathrm{X} + \nu_\mathrm{XY})Z. \quad \text{(1C)}$$

Equations (1A–C) thus determine the epidemiological dynamics of the system. The birth and death rates involved are potentially affected by parasite virulence and host defenses. Virulence, resistance, and tolerance are modeled as continuous traits, denoted by x_1, y_1, and y_2, respectively.

Virulence is defined as the process whereby the parasite exploits the host to produce free-living propagules from the infected stage. Mathematically, we use the intrinsic expected lifetime of the host, $1/\mu_{0\mathrm{Y}}$, as a measure of the host "somatic energy" that the parasite may exploit; and we define parasite virulence as the fraction, x_1, of host somatic energy that the parasite actually exploits to produce propagules. Host somatic energy is converted into parasite production with a conversion coefficient, γ, that we call propagation factor, and the efficiency of the conversion is discounted by the physiological cost of virulence. By setting $\phi = \gamma/\mu_{0\mathrm{Y}}$, and parameterizing the cost function of virulence by $\theta_{\mathrm{x}1}$, the parasite production rate can be written as

$$\sigma_\mathrm{X} = \phi x_1 (1 - x_1)^{\theta_{x1}}. \quad \text{(2)}$$

Inside the host, the parasite is exposed to host resistance, the effect of which is modeled as a mortality factor that adds to the parasite's intrinsic mortality rate. Thus, for a given degree y_1 of host resistance, the mortality rate of the parasite in the complex stage is

$$\nu_\mathrm{X} = \mu_{0\mathrm{X}} + \omega_{\mathrm{y}1} y_1, \quad \text{(3)}$$

where $\omega_{\mathrm{y}1}$ measures the efficiency of resistance.

The effect of virulence on the host is to increase mortality in the complex stage—an increase that the host can mitigate by investing resources into tolerance. The mortality increase is proportional to x_1; the proportionality factor, $\omega_{\mathrm{x}1}$, is called virulence efficiency. The host tolerance, as measured by the continuous trait y_2, limits the mortality increase with an efficiency factor denoted by $\omega_{\mathrm{y}2}$. Hence, the mortality rate of the complex as a function of virulence x_1 and tolerance y_2 is:

$$\nu_\mathrm{XY} = \mu_{0\mathrm{Y}} + \mu_{1\mathrm{Y}} + \omega_{x1} x_1 / (1 + \omega_{\mathrm{y}2} y_2). \quad \text{(4)}$$

The host pays the physiological cost of resistance and tolerance in terms of reduced reproduction. Thus, the per-capita birth rate ρ_Y of free-living hosts equals the intrinsic birth rate $\rho_{0\mathrm{Y}}$ discounted by a density-dependent regulatory factor, and by the multiplicative costs of resistance y_1 and tolerance y_2. The shape of resistance and tolerance cost functions is fixed by parameters $\theta_{\mathrm{y}1}$ and $\theta_{\mathrm{y}2}$. Hence

$$\rho_\mathrm{Y} = \rho_{0\mathrm{Y}} (1 - y_1)^{\theta_{y1}} (1 - y_2)^{\theta_{y2}} / (1 + \kappa(Y + Z)), \quad \text{(5)}$$

where the Beverton–Holt density-dependent regulatory factor $1/(1 + \kappa(Y + Z))$ reflects competition within and between free-living host and complex stages with equal intensity κ. In the absence of vertical transmission, the birth rates of the host susceptible and infected stages are assumed to be equal:

$$\sigma_\mathrm{Y} = \rho_\mathrm{Y}. \quad \text{(6)}$$

The actual shape of costs in natural systems remains poorly known. General life-history theory (e.g., Rueffler et al. 2006), and models of host defense evolution in particular, have emphasized the critical influence of the accelerating versus decelerating profile of the cost function on the evolution of the corresponding character. This influence was demonstrated by Miller et al. (2005) for the evolution of tolerance, by Best et al. (2009) for the evolution of avoidance coevolving with virulence, and by Restif and Koella (2004) for the evolution of mixed, resistance/tolerance defenses. Our choice of power functions for the direct costs of virulence and defenses (eqs. 2 and 5) is grounded in previous models (e.g., Sasaki 2000, Restif and Koella 2004) and the simplest mathematically to explore the effect of the cost profile by tuning a single parameter (θ).

EVOLUTIONARY DYNAMICS

We use the adaptive dynamics framework (Metz et al. 1992; Dieckmann and Law 1996; Champagnat et al. 2006) to model the coevolution of virulence, x_1, resistance, y_1, and tolerance, y_2, and investigate the effect on the traits' coevolution of three classes of parameters: physiological, environmental, and epidemiological (Table 1). Physiological factors include the costs of traits ($\theta_{\mathrm{x}1}$, $\theta_{\mathrm{y}1}$, $\theta_{\mathrm{y}2}$) and traits' efficiencies ($\omega_{\mathrm{x}1}$, $\omega_{\mathrm{y}1}$, $\omega_{\mathrm{y}2}$). Environmental

Table 1. Model parameters and default values. All rates are measured with respect to the time unit of the ecological model, eq. (1A–C).

	Symbol	Parameter	Default value
Parasite	x_1	Investment in virulence	0.75
	ω_{x1}	Virulence efficiency	5
	μ_{0X}	Intrinsic mortality rate	1
	μ_{1X}	Background mortality rate	0
	γ	Propagation factor	50
	θ_{x1}	Exponent of the cost function of virulence	0.25
Host	y_1	Investment in resistance	0
	y_2	Investment in tolerance	0
	ρ_{0Y}	Intrinsic birth rate	10
	κ	Competition coefficient	5.10^{-5}
	μ_{0Y}	Intrinsic mortality rate	1
	μ_{1Y}	Background mortality rate	0
	ω_{y1}	Resistance efficiency	5
	ω_{y2}	Tolerance efficiency	2.5
	θ_{y1}	Exponent of the cost function of resistance	0.1
	θ_{y2}	Exponent of the cost function of tolerance	0.25
Other	β	Infection rate	1.10^{-5}
	k	Trait evolutionary rate	1.10^{-7}

factors include background mortalities (μ_{1X}, μ_{1Y}). Epidemiological factors include infection rate (β) and propagation factor (γ).

The coevolutionary process is described by a sequence of mutation–selection steps in phenotypic trait space (Metz et al. 1996; Champagnat et al. 2006). Each selection step is determined by the invasion fitness of a mutant host or parasite phenotype interacting with the resident host–parasite system in stationary ecological (epidemiological) state (Metz et al. 1992). Successful invasion by a mutant changes the ecological state of the system, which entails that subsequent host or parasite mutants will experience a different selection gradient. This feedback between heritable variation in any one trait and the ecology-based selection gradient of all traits entangles the evolutionary dynamics of the two interacting species (Fig. 1A).

Combinations of traits where the selection gradient equals zero are called (co)evolutionary equilibria and represent potential rest points for the coevolutionary process. Whether evolutionary equilibria predict adaptations that can be expected in real systems critically depends on their attractivity, that is, whether they can be reached by the mutation–selection process from some ancestral conditions. If mutations are rare and have small effects, and if the resident system is always at ecological equilibrium, then the attractivity of evolutionary equilibria can be analyzed by using the so-called canonical equations of the adaptive traits dynamics (Dieckmann and Law 1996). This is the approach followed here (see Appendix).

First, the ecological model is analyzed. We use a combination of analytical and numerical tools to check that the host–parasite system is at ecological equilibrium (provided it is ecologically viable) across the entire phenotypic trait space for all parameter intervals considered in this study (see Fig. S1 for representative numerical results). Then we numerically solve the canonical equations of adaptive dynamics for a range of initial conditions (i.e., ancestral trait values) that sample the whole phenotypic trait space. This yields the (unique) evolutionary equilibrium and establishes its global attractivity for at least some range of host and parasite evolutionary rates that includes their default values (Table 1). Finally, we test the invasion stability of the evolutionary equilibrium by relaxing the small-and-rare mutation assumption of the canonical equations.

This computational routine can be used to study the system's coevolutionary dynamics with respect to any set of parameter values. For each parameter there is a default value (Table 1), and all physiological, environmental, and epidemiological parameters that are relevant to our biological questions are varied across intervals that contain their default value. The model analysis aims at determining how the evolutionary equilibria vary and covary in response to variation in each relevant parameter. Answers to our focal questions are obtained by doing this for the full model in which virulence, resistance, and tolerance coevolve (VRT model), and for three submodels: the RT model, in which resistance and tolerance coevolve while virulence is fixed; the VR and VT models, in which virulence coevolves either with resistance or with tolerance.

Results

COEVOLVING RESISTANCE AND TOLERANCE: EMERGING PATTERNS OF VARIATION AND COVARIATION

We identify conditions that favor resistance or tolerance by investigating numerically how the RT model responds to changes in parameter values (Fig. 2). When comparing evolved traits among populations that differ by one parameter, we say that evolution promotes "supplementary defenses" if defenses show positively correlated responses to selection: a change in the parameter causes both defenses to increase (or decrease) evolutionarily. This is actually the case with virulence: increasing virulence generally selects resistance and tolerance in the same direction (Fig. 2A). We say that evolution promotes "complementary defenses" if the response of tolerance and resistance to selection are negatively correlated: evolution trades off one defense for the other.

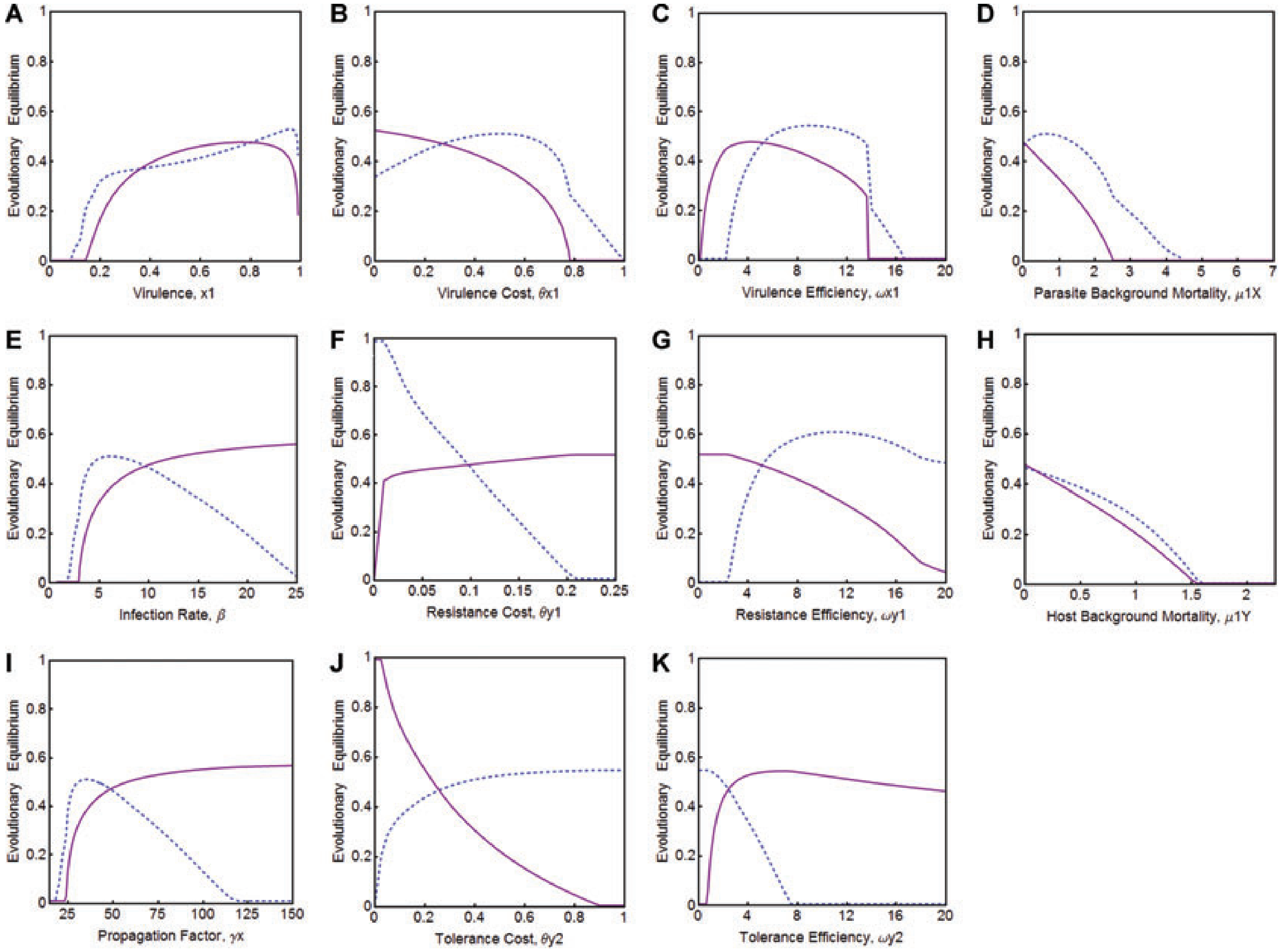

Figure 2. Coevolved resistance and tolerance with respect to physiological, epidemiological, and environmental parameters (RT model). Dashed blue line: resistance. Solid purple line: tolerance. In each panel, all nonvarying parameters are fixed to default values (Table 1). The infection rate is scaled by 10^6. See Figures S2–S4 for a sensitivity analysis of patterns C, D and E with respect to virulence efficiency, parasite background mortality, and infection rate, respectively.

The distinction between supplementary and complementary defenses leads to recognize two evolutionary routes toward pure strategies. One route involves selection for low defense altogether when defenses are supplementary: both defenses decrease, and a pure strategy is established after one defense trait has reached zero. The other route involves "all-or-nothing" selection when defenses are complementary: one defense trait increases whereas the other decreases, and a pure strategy is established once the latter has reached zero. To analyze the occurrence of evolutionary complementarity versus supplementarity, and conditions under which pure versus mixed strategies evolve, we fixed virulence to a high value ($x_1 = 0.75$) at which a mixed strategy of strong resistance and strong tolerance evolves for parameters set to their default values (Fig. 2A). Then we examined the consequences of varying physiological, environmental, and epidemiological parameters (Fig. 2B–K), one at a time. After having identified the key parameters to which the evolution of resistance and tolerance was most sensitive, we tested the generality and robustness of all univariate responses (Fig. 2) by simultaneously varying all key parameters (Figs. S2–S4).

Except for high values of resistance efficiency (Fig. 2G), variation in the cost or efficiency of defenses results in evolutionary complementarity. Pure resistance evolves when the efficiency of resistance or the cost of tolerance is high (Fig. 2G, J). Pure tolerance evolves when the efficiency of tolerance or the cost of resistance is high (Fig. 2F, K). Pure tolerance also evolves by complementarity under high infection rate (Fig. 2E) or high propagation factor (Fig. 2I). These epidemiological conditions put the host at high risk of infection, which disfavors investment in resistance while promoting tolerance.

All other instances of pure defense involve resistance evolving by supplementarity. Pure resistance thus evolves under low virulence (Fig. 2A), high virulence cost (Fig. 2B), or high virulence efficiency (Fig. 2C). When virulence is low or the cost of virulence is high, selection for defense is weak, and investment in tolerating a parasite that causes little harm is disfavored, hence pure resistance. When virulence efficiency increases, resistance becomes selectively advantageous over tolerance, hence a pattern of complementarity, up to a threshold beyond which the total fitness benefit of defense declines—the host "gives up" evolutionarily, hence a supplementary pattern in which tolerance falls faster, leading to pure resistance.

Pure resistance also evolves under low infection rate (Fig. 2E) or low propagation factor (Fig. 2I). These conditions reduce the risk for a free host to be infected. Selection for defense weakens as a consequence, hence a fitness advantage to shorten the association by expressing resistance and no tolerance. Finally, pure resistance evolves under high parasite or host background mortality rates (Fig. 2D, H). Under low infection rate or low propagation factor, increasing background mortality in hosts or parasites relaxes selection on defenses and promotes evolutionary supplementarity. High background mortality in the host makes tolerance—that is, an increase in host survival—of little selective value, hence the evolution of pure resistance. High background mortality in the parasite selects against that host strategy—tolerance—which would "protect" the parasite from background mortality factors.

When mixed strategies evolve, the RT model can be used to explore patterns of evolutionary covariation of resistance and tolerance among populations that differ in physiological, epidemiological, or environmental conditions (Fig. 3). In general, evolutionary covariation arises from shared selection pressures (i.e., the same selective pressure applies on both traits) and selective interactions (one trait influences selective pressures on the other) (e.g., Le Galliard et al. 2005). Evolutionary supplementarity implies a positive correlation between resistance and tolerance, whereas evolutionary complementarity means a trade-off between resistance and tolerance.

For fixed virulence, variation in host or parasite background mortality rates drives essentially positive correlations between resistance and tolerance (Fig. 3F for variation with respect to parasite background mortality rate; the response curves to host background mortality rate are very similar and not shown), that is, evolutionary supplementarity. The background mortality rates basically scale up or down the selective pressures on both traits and hence on their values at coevolutionary equilibrium.

In contrast, both complementarity and supplementarity can evolve in response to variation in a single physiological or epidemiological parameter, provided that variation occurs across wide enough a range. Sign reversals are therefore expected in the evolutionary correlations obtained by comparing populations that have adapted to conditions differing in one of these parameters:

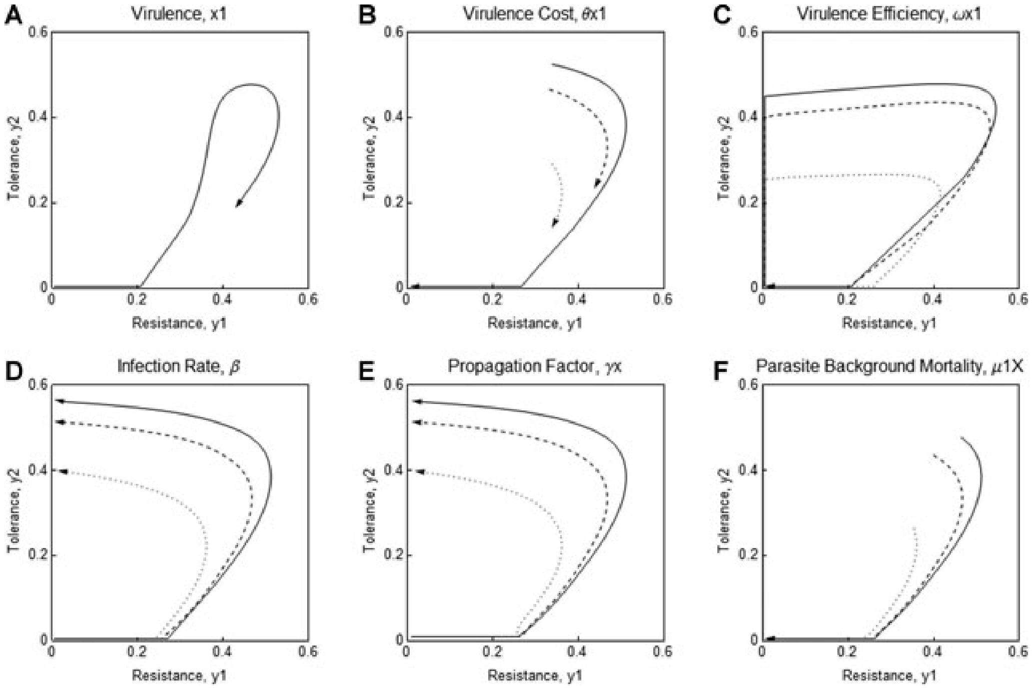

Figure 3. Resistance–tolerance evolutionary correlations in response to variation in virulence and associated physiological parameters (A–C), epidemiological parameters (D, E) and environmental parameters (F). Each curve shows the value of resistance (y_1) and tolerance (y_2) at evolutionary equilibrium in the RT model. In B–F, curves are plotted for different parasite virulence : 0.25 (dotted), 0.5 (dashed), and 0.75 (plain). In each panel, all nonvarying parameters are fixed to default values (Table 1).

virulence cost, virulence efficiency, infection rate, and propagation factor (Fig. 3B–E). These parameters are direct (the latter two) or indirect (the former two) influences of parasite prevalence, and prevalence indeed plays a key role in driving the correlation reversals. Below some threshold on prevalence, both resistance and tolerance are selected for, and their responses correlate positively as long as variation in the underlying parameter keeps prevalence below that threshold. Above the threshold, the risk of reinfection becomes so high that resistance is selected against; as long as the risk of parasite-induced mortality is not too high, selection remains positive on tolerance, hence a trade-off between resistance and tolerance.

These results altogether show, first, that the evolution of resistance and tolerance responds in intuitive and expected ways to the traits' physiological parameters (costs and efficiencies) (Fig. 2F, G, J, and K); in contrast, the cost and the efficiency of virulence have strong impact on the parasite population dynamics that feed back and drive highly nonlinear patterns of variation in host defenses (Figs. 2B,C and 3B,C). Second, both epidemiological parameters (infection rate and propagation factors) have very similar influences on resistance and tolerance (Figs. 2E,I and 3D,E). Third, deterioration of environmental conditions that result in increasing host or parasite background mortality will beget similar decline in resistance and tolerance (Fig. 2D, H), with the exception of an increase of resistance when parasite background mortality increases across low values (Figs. 2D and 3F). In conclusion, most variation in resistance and tolerance that is not explained by the traits' cost and efficiency is accounted for by three key parameters: virulence efficiency, infection rate, and parasite background mortality. The robustness of univariate patterns of resistance and tolerance (Fig. 2) thus depends on the strength of the interaction effects between the key parameters. These interaction effects turn out to be weak (Figs. S2–S4): the univariate response of resistance and tolerance to each key parameter is affected essentially linearly by simultaneously varying the other two key parameters. Thus, the evolutionary patterns shown in Figure 2 and our conclusions for the evolution of pure and mixed defenses hold in general.

HOW IS VIRULENCE AFFECTED BY COEVOLUTION WITH RESISTANCE VERSUS TOLERANCE?

When host and parasite coevolve, the evolutionary equilibrium virulence is influenced by the trait's physiological parameters as expected: virulence decreases as virulence cost or virulence efficiency increases (results not shown). Because no correlation is assumed between virulence and transmission, variation in the infection rate or propagation factor has no effect on virulence when virulence evolves alone (results not shown). Yet the infection rate and propagation factor do influence virulence when parasites and hosts coevolve. Increasing the contact rate (or propagation factor) across low values favors a rapid increase in virulence along with a sharp increase of host defense, either resistance (Fig. 4A) or tolerance (Fig. 4B). The increase of virulence and tolerance saturates at high infection rates (Fig. 4B) whereas coevolved virulence and resistance reach a peak and then decline (Fig. 4A). Interestingly, the same variation in resistance can correlate with a wide change in virulence across low infection rates, or a narrow change in virulence across high infection rates.

With higher infection rate or propagation factor, the infection probability is larger and selection favors parasites that invest less in virulence, for two reasons: they pay a lower cost of virulence, and the lesser damage they cause to their host results in a longer infection time, hence a larger production of propagules. The coevolving resistance then also decreases with increasing the infection rate or propagation factor (Fig. 4A). In contrast, within a range of low infection rate (Fig. 4A), more contact will select for more virulence and more resistance. With infrequent contact, the probability for a host, once recovered, to be reinfected is low, which favors investment in resistance, hence stronger selection for virulence. Because the proportion of susceptible hosts

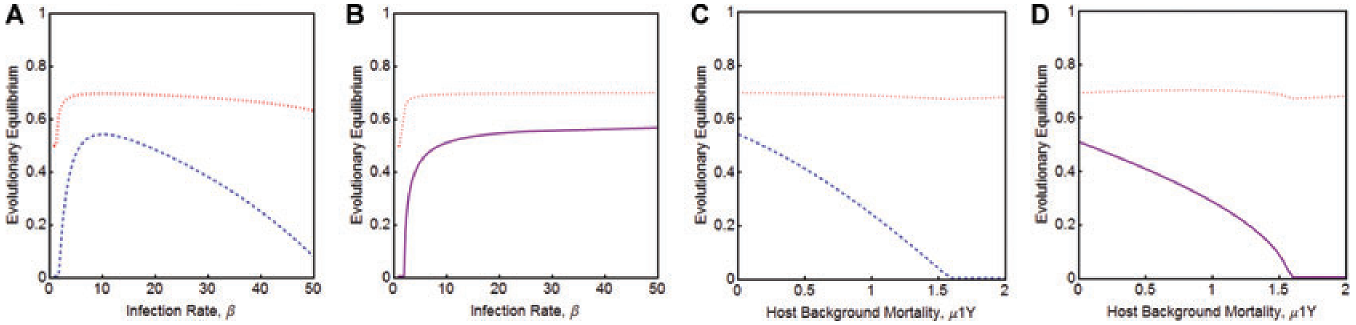

Figure 4. Virulence coevolving with resistance (A and C, VR model) or tolerance (B and D, VT model), with respect to infection rate and host background mortality. Dotted red line: virulence. Dashed blue line: resistance. Solid purple line: tolerance. All nonvarying parameters are fixed to default values (Table 1). The infection rate is scaled by 10^6. See Figures S5–S8 for a sensitivity analysis of these patterns with respect to virulence efficiency, parasite background mortality, and infection rate.

remains high (because of infrequent contact and likely recovery), the increase in virulence is not counter-selected.

An increase in the host's background mortality selects for higher virulence when virulence evolves alone (results not shown). When virulence and defense coevolve, the effect of host background mortality on virulence is often minor, whereas the coevolving defense, either resistance or tolerance, decreases dramatically as mortality increases (Fig. 4C, D). According to the nonlinear response of virulence and defense to infection rate (Fig. 4A, B), we expected a more pronounced correlated response of virulence and defense to mortality at low infection rate and this is indeed the case (Figs. S5–S8), but only when virulence coevolves resistance (Figs. S5 and S7), and the pattern is further influenced by virulence efficiency (Figs. S6A–C and S7A–C). Thus, the prediction of virulence increasing with host background mortality only holds when virulence coevolves with resistance, and under the condition of low infection rate and low virulence efficiency.

THREE-WAY COEVOLUTION OF RESISTANCE, TOLERANCE, AND VIRULENCE

Three-way coevolution preserves all qualitative predictions of evolutionary supplementarity and complementarity and the resistance–tolerance trade-off (Fig. 5), but causes several important quantitative changes (Figs. 5 and 6). Three-way coevolution generally selects for more virulence (Fig. 6A–E) and less tolerance (Fig. 6K–O). Compared to two-way tolerance–virulence coevolution, tolerance decreases faster in response to increasing host or parasite background mortality (Fig. 6N, O), leaving resistance as a pure defense at levels of background mortality lower than in two-way coevolutionary scenarios (Fig. 6I, J). Compared to two-way resistance–virulence coevolution, resistance is affected chiefly in its response to variation in epidemiological parameters. Thus, as the infection rate or propagation factor increases, resistance becomes strongly counter-selected and tolerance is favored as pure defense (Fig. 6G, H, L, and M).

Relative to the infection rate (or propagation factor), virulence is maximized at a contact rate where the total investment in defense also peaks (involving significant resistance and close-to-maximum tolerance, Fig. 5A, B), but in general there is no tendency for three-way coevolution to maximize parasite virulence and host defenses concurrently. With respect to virulence efficiency, virulence increases as virulence efficiency decreases while both defenses coevolve to zero (Fig. 5D). With respect to host or parasite background mortality, virulence remains high and shows little variation while defenses coevolve from high to null as background mortalities increase from zero (Fig. 5E, J).

In fact, all patterns of coevolutionary variation are possible. Virulence is predicted to increase correlatively with resistance increasing and tolerance decreasing when the cost of resistance decreases (Fig. 5F) or resistance efficiency increases (Fig. 5G). Virulence increasing in correlation with resistance decreasing and tolerance increasing is expected in response to variation in the cost of tolerance (Fig. 5H), or across low tolerance efficiency (Fig. 5I), or across intermediate virulence efficiency (Fig. 5D). A positive correlation of virulence, resistance, and tolerance is predicted in response to variation in virulence cost (Fig. 5C), or low infection

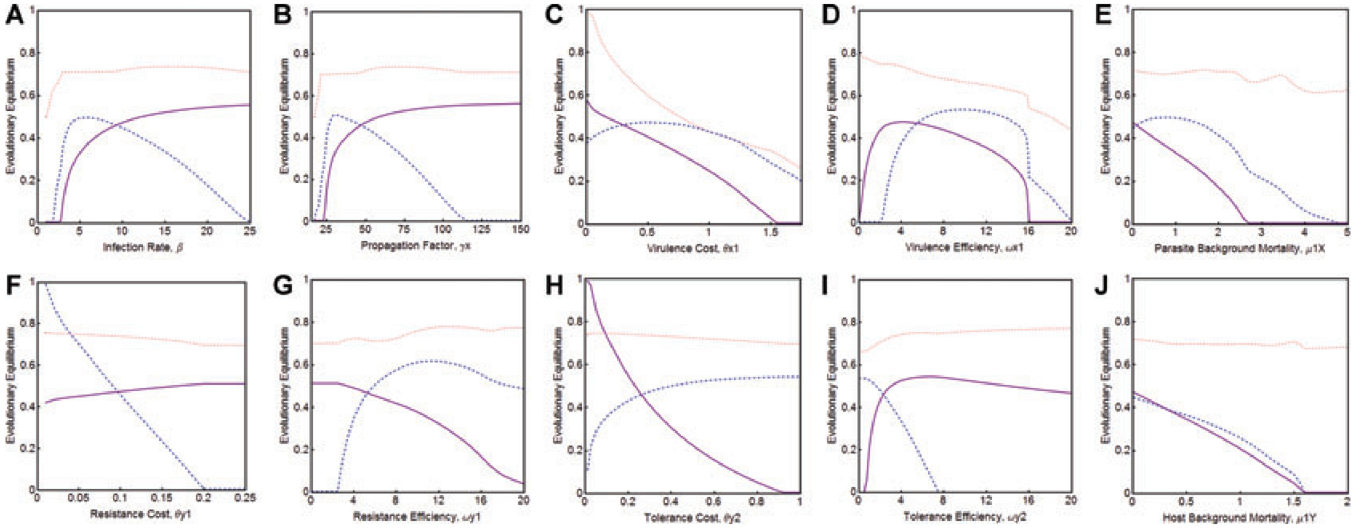

Figure 5. Coevolved virulence, resistance, and tolerance (VRT model) with respect to epidemiological, physiological, and environmental parameters. Dotted red line: virulence. Dashed blue line: resistance. Solid purple line: tolerance. No vertical transmission ($x_3 = y_3 = 0$). All nonvarying parameters are fixed to default values (Table 1). The infection rate is scaled by 10^6. See Figures S9 and S10 for a sensitivity analysis of VRT model with respect to virulence efficiency and infection rate.

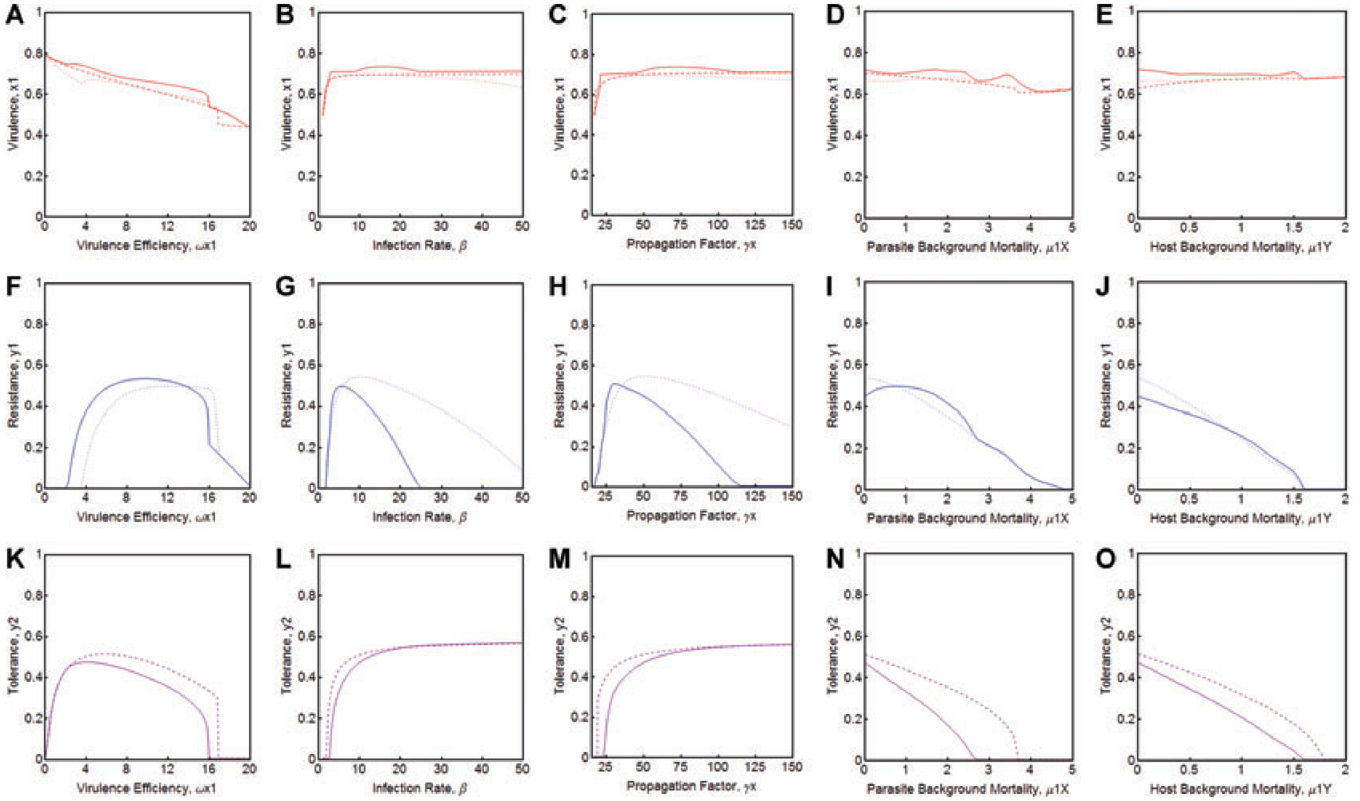

Figure 6. Coevolved virulence, resistance, and tolerance in the two-trait and three-trait models. Coevolved virulence–resistance (dotted curves, VR model), virulence–tolerance (dashed, VT model), and virulence–resistance–tolerance (solid, VRT model) are shown with respect to five underlying parameters: virulence efficiency, infection rate, propagation factor, parasite background mortality, and host background mortality. (A–E), Comparing evolved virulence between VR, VT, and VRT models. (F–J), Comparing evolved resistance between VR and VRT models. (K–O), Comparing evolved tolerance between VT and VRT models. All nonvarying parameters are fixed to default values (Table 1). The infection rate is scaled by 10^6.

rate or propagation factor (Fig. 5A, B), or high virulence efficiency (Fig. 5D).

Quantitatively, the key factors of virulence evolution are the cost of virulence, the efficiency of virulence, and both epidemiological parameters at low values (infection rate and propagation factors) (Figs. 5A–D and 6A–C; Figs. S9 and S10). The indirect effect of the host's physiological parameters, mediated by eco–evolutionary feedbacks, is always relatively small (Figs. 5F–J and 6E). In contrast, the physiological parameters of the parasite have strong quantitative effects on the evolution of host defenses (Figs. 5A–E and 6F, I, K, N; Fig. S10). Comparing resistance–tolerance coevolution (Fig. 2) and three-trait coevolution (Fig. 5) shows that eco–evolutionary feedbacks work synergistically to reinforce two-trait evolutionary patterns: The resistance–virulence pattern in response to decreasing virulence cost for fixed virulence (Fig. 2B) mirrors the pattern predicted for increasing virulence under fixed cost (Fig. 2A); when all three traits coevolve, decreasing the cost of virulence does promote an increase in virulence, and resistance and tolerance responds as predicted by combining the selective responses seen in Figure 2A and B.

EFFECT OF NOT-SO-SMALL AND NOT-SO-RARE MUTATION

Evolutionary equilibria in all four models (RT, VR, VT, VRT) are globally attractive and globally stable over all ranges of parameters that we investigated (Fig. 7, Figs. S12–S20). Global attractivity means that evolutionary equilibria can be reached by small and rare mutational steps from any combination of ancestral trait values (provided that the system is ecologically viable for these ancestral traits), including the "mellowest" ancestral stage of interaction, in which the parasite exploits its host with the minimum virulence that ensures ecological viability, and the host expresses no defense. Global stability means that no mutation in a single trait can invade the system once at evolutionary equilibrium.

More frequent and/or larger mutations may have dramatic effects on evolutionary dynamics (see Champagnat et al. 2006 for general theory, and e.g., Pugliese 2002 and Best et al. 2009 for examples pertaining to host–parasite systems). Here, we took a first step in studying these effects by examining the invasion structure of the trait space when the host and the parasite are at their expected coevolutionary equilibrium (models VR, VT, and

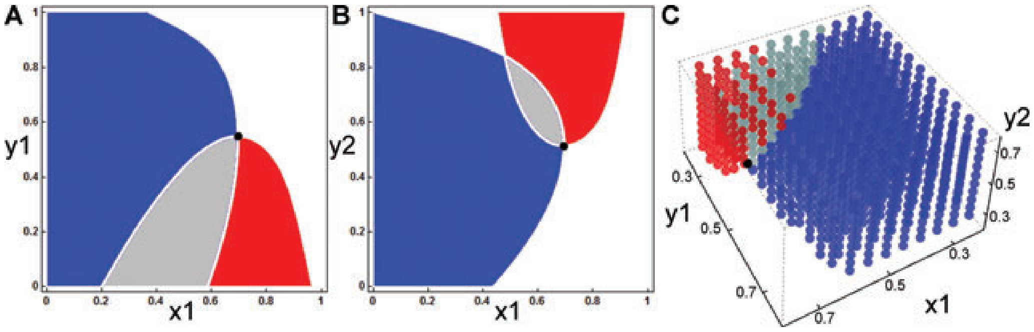

Figure 7. Invasibility of the evolutionary equilibrium (black circle) by mutant traits. Colored regions indicate combinations of trait values for which at least one mutant can invade. When a mutant parasite and a mutant host simultaneously arise in the red region: the mutant parasite invades whereas the mutant host goes extinct; in the blue region: the mutant host invades whereas the mutant parasite goes extinct; in the gray region: both mutant parasite and mutant host invade; in the white region: neither one can invade. The convexity of the regions of mutant parasite invasion (red and gray) and mutant host invasion (blue and gray) and their, respectively, horizontal and vertical tangent spaces (line or plane) at evolutionary equilibrium indicate that the evolutionary equilibrium is always a global ESS in the classical game-theoretical sense. (A) Virulence–resistance coevolution (VR model). (B) Virulence–tolerance coevolution (VT model). (C) Virulence–resistance–tolerance coevolution (VRT model). All parameters are set at their default values (Table 1). Figures S15–S20 provide a sensitivity analysis of (A), (B), and (C) with respect to virulence efficiency, parasite background mortality, and infection rate.

VRT). Although the coevolutionary equilibrium is globally stable against any mutant (small or large) expressed in any single trait, a rather different picture emerges when a mutant parasite and a mutant host assume a nonnegligible probability of arising in the same short interval of evolutionary time—that is, when we relax the rare mutation assumption of adaptive dynamics theory. Then one of four events happens: (1) both mutants go extinct; (2) the mutant parasite invades and replaces the resident parasite while the mutant host goes extinct; (3) the mutant host invades and replaces the resident host while the mutant parasite goes extinct; (4) both mutant parasite and mutant host invade and displace both resident populations. Thus, in cases (2)–(4) the coevolutionary equilibrium appears vulnerable to invasion provided that the probability of mutations co-occurring in the parasite and the host is nonzero. This is likely to be the case if the parasite has a much higher mutation probability than the host, which is commonly observed in natural host–parasite interactions; then probability that the parasite mutates whenever the host population does is high.

Cases (2) and (3) are remarkable instances of "evolutionary catalysis" (Nowak and Sigmund 1992): one mutant goes to fixation whereas the other goes extinct, but the former would have failed to invade without the presence of the latter. The unsuccessful mutant is "catalytic" in the sense that it is initially rare, it gives a foothold to the other mutant and thereby begets a potentially large evolutionary change in the other species, but eventually it leaves no trace in the system. This mutation catalysis phenomenon is significant because it entails that "evolutionary spikes" can be expected in the trait dynamics of one species without any noticeable change in the trait of the other species. Indeed on the evolutionary timescale, mutation catalysis will result in potentially large changes in the defense of the host while the parasite virulence remains at evolutionary equilibrium, and large changes in the parasite virulence while the host defenses remain at evolutionary equilibrium. Because the coevolutionary equilibrium is globally attractive, from the peak of a spike the small mutation–selection process will drive the trait of the spiking species back to its evolutionary equilibrium. If mutation are not so small and not so rare, in particular if mutation steps are frequent enough in the parasite and mutation variance is large enough in the host, then highly variable virulence and defenses may evolve.

More quantitative insights can be gained from the numerical analysis of the models (Fig. 7, Figs. S15–S20). The invasion structure of the trait space, that is, the distribution of cases (1)–(4), changes little in response to varying parameters to which evolutionary equilibria are most sensitive (virulence efficiency, infection rate, background mortalities). When virulence coevolves with resistance (VR model, Figs. 7A, S15, and S16), mutant parasites that are slightly less virulent than the evolutionary equilibrium will catalyze invasion by a wide range of host mutants, including mutants with low or even zero resistance (blue and gray areas in Figs. 7A, S15, and S16). Likewise, the invasion of parasite mutants can be catalyzed by host mutants that are less resistant than the evolutionary equilibrium, but the range of virulence that may be reached (both lower and higher than evolutionary equilibrium virulence) is comparatively narrower than it is for resistance (red and gray areas in Figs. 7A, S15, and S16). Evolutionary spikes of higher resistance (blue area in Figs. 7A, S15, and S16) or higher virulence (red area in Figs. 7A, S15, and S16) are predicted, the magnitude of which is sensitive primarily to parasite background mortality (Figs. S15 and S16). Invasion by co-occurring mutants that are more virulent and more resistant may not happen (in Figs. 7A, S15, and S16 the north-east quadrant from coevolutionary equilibrium is always blank).

A horizontally mirrored image obtains for virulence–tolerance evolution (VT model, Figs. 7B, S17, and S18). Less-virulent mutant parasites will catalyze invasion by a wide range of host tolerance (blue and gray areas in Figs. 7B, S17, and S18); evolutionary spikes of reduced tolerance are expected around coevolutionary equilibrium (blue area in Figs. 7B, S17, and S18). Likewise, more tolerant mutant hosts will catalyze invasion by a wide range of parasite virulence (red and gray areas in Figs. 7B, S17, and S18); evolutionary spikes of increased virulence are expected around evolutionary equilibrium (red area in Figs. 7B, S17, and S18), the magnitude of which increases with higher virulence efficiency (Figs. S17 and S18), higher parasite background mortality (Fig. S17), or lower infection rate (Fig. S18). Invasion by co-occurring mutants that are more virulent and less tolerant may not happen (in Figs. 7B, S17, and S18 the south-east quadrant from coevolutionary equilibrium is always blank).

The results for two-trait coevolution are entirely preserved in the three-trait (VRT) model (Figs. 7C, S19, and S20), and there are several new phenomena rooted in the three-dimensionality of the trait space. Mutant catalysis is now possible between a mutant parasite that is more virulent than at coevolutionary equilibrium and a mutant host that is both more resistant and more tolerant, or less resistant and less tolerant (Fig. 7C). Thus, three-trait coevolution makes even more likely the occurrence of evolutionary spikes in virulence. The likelihood and magnitude of evolutionary spikes in virulence are complex functions of virulence efficiency, infection rate, and parasite background mortality (Figs. S19 and S20): they increase with virulence efficiency, all the more as the parasite background mortality is higher (Fig. S19); they decrease with increasing the infection rate when parasite background moratlity is low (Fig. S20A–C), but peak at intermediate infection rate when parasite background mortality is higher (Fig. S20D–F).

Discussion

We presented a simple yet general eco–evolutionary model of host–parasite interaction that unifies and extends previous theory of parasite virulence and host defense. On the ecological timescale, physiological, environmental, and epidemiological processes determine the dynamics of populations of parasites and hosts with constant traits values. On the evolutionary timescale, long-term trait dynamics result from genetic variation in the traits (due to mutation) and selection pressures generated by the ecological state of the system.

The model was analyzed with the aim of better understanding (1) adaptive patterns of resistance and tolerance in hosts, (2) the evolution of virulence depending on the nature of the coevolving defense in the host, and (3) how the coevolution of virulence and both defenses differ from virulence–resistance and virulence–tolerance coevolution.

Our analysis of the ecological model shows that across the entire trait and parameter space the host–parasite interaction either drives the species to a stable equilibrium of coexistence, or causes extinction of the parasite or both species. Our evolutionary analysis identifies the efficiency of virulence, the infection rate, and the parasite background mortality as key factors of the evolutionary process that generally have strong, nonlinear effects on virulence and defenses. A detailed numerical study with respect to these key parameters indicates that the evolutionary process generally has a single equilibrium in the (two- or three-dimensional) trait space; that the equilibrium is always globally attractive through small and rare mutational steps for at least some range of host and parasite evolutionary rates around their default values; and that the equilibrium is globally stable against invasion by single-trait mutation, that is, an “ESS” (Evolutionarily Stable State) in the classical game-theoretical sense (Hofbauer and Sigmund 1998).

Thus, we could analyze evolutionary patterns of variation and covariation in virulence, resistance, and tolerance by examining the response of evolutionary equilibria to univariate changes of a large number of underlying physiological, epidemiological, and environmental parameters, and then testing the sensitivity of the results to concurrent changes of the three key parameters. Our predictions on the coevolution of virulence, resistance, and tolerance can therefore be taken as robust and general, relative to our physiological, ecological, and evolutionary assumptions.

EMPIRICAL SCOPE OF THE MODEL

The structure of the model is general and may apply, straightforwardly or by bringing in additional details, to a wide range of host–parasite/pathogen systems. In the context of theoretical evolutionary epidemiology at large, our model is closely related to earlier theory for spore-producing pathogens (e.g., Bonhoeffer et al. 1996; Day 2002). Transmission via the release of infectious propagules in the environment (rather than direct host–host contact) is found in many pathogens, with a great diversity in virulence and survival. Bonhoeffer et al. (1996) listed parasitic plants of the genus *Striga*, plant-parasitic nematode, several spore-forming bacteria, and viruses of the nuclera-polyhedrosis and granulosis families, as examples of highly virulent parasites with long-lived free-living propagules; microsporidian parasites typically produce long-living spores and range from high to low virulence; there are virulent pathogens whose transmission stages are very short-lived, for example, the measles virus, the endospores of the honey bee pathogenic bacteria *Bacillus larvae*, or the conidia of the caterpillar-infecting fungus *Nomurae rileyi*; in protozoans such as *Trichomonadida*, only the nonpathogenic species possess long-lived transmission stages. Thus, there is considerable diversity in virulence and propagule survival in nature, hence a fertile terrain for theory and the search of causal patterns.

Rather than trying to match any particular system, the model structure was chosen for its relevance to our questions—in particular, the evolution of virulence when parasite-induced mortality can be mediated by host tolerance. Having a parasite free-living stage and direct costs of both tolerance and virulence allows to analyze the coevolution of virulence and defenses while taking into account selection pressures on the parasite and the host that are independent (direct costs of virulence, resistance and tolerance) or interactive (mortality cost for the parasite, mitigated by the host's investment in tolerance). Having a free-living stage sets a "worst-case scenario" for the evolution of host defenses (other than avoidance) because the host has no direct control over the survival or the effect of parasites when they are free-living. The free-living stage also avoids limiting the model to host-to-host transmission, and instead parameterize (with the infection rate and parasite background mortality) a continuum of transmission routes from "quasi host-to-host" (high infection rate and short-lived parasite free stage), to rare host exposure to long-lived propagules (low infection rate, low parasite background mortality).

What the model's current structure does not include is explicit within-host dynamics. This does not imply, however, that systems with parasites that proliferate inside their host are excluded from the scope of the model. Rather, the parasite's within-host birth-and-death process is treated as a "blackbox," the outcome of which is encapsulated in two parameters, the propagation factor (γ) and recovery rate (ν_X). This "blackbox treatment" is sufficient, in fact, to answer many evolutionary questions that have been addressed using epidemiological models with "nested" within-host dynamics (Mideo et al. 2008). The reason is that for these questions and models the nesting was "inessential": The within-host dynamical model provides a mechanistic description of virulence, recovery and transmission processes and these feed into the epidemiological model at the level of the host population; but no reciprocal feedback operates from the between-host dynamics down to the within-host level in these studies.

As emphasized by Mideo et al. (2008), host–parasite evolutionary theory in which within-host dynamics are truly "essential" awaits further development. To this end, models like ours that account for a free-living stage appear to be well suited. For example, the density of free-living propagules may alter inoculum size; if inoculum size influences the progression of disease within a host, this would then lead to a feedback from between-host to within-host dynamics (Schmid-Hempel and Frank 2007). With virulence modeled mechanistically as exploitation of host resources, and free-living parasite population dynamics modeled explicitly, our framework sets the stage for advancing theory in which the processes of within-host resource dynamics, multiple infection, and competition among parasitic strains interact and make nesting essential.

EVOLUTION OF PURE DEFENSES

As emphasized by Roy and Kirchner (2000), even though resistance and tolerance may have equivalent short-term benefits for individual hosts, the traits feed back on and reshape selection pressures in opposite ways. There is a negative feedback between the prevalence of resistant hosts and their fitness advantage, which may limit the evolution of resistance; there is a positive feedback between the prevalence of tolerant hosts and their fitness advantage, which may promote the evolution of tolerance. Thus, one expects the evolution of resistance and tolerance to be critically influenced by the system's epidemiology—the abundance and survival of hosts, the prevalence of infection, and the dynamics of transmission. These factors depend in turn on the phenotype of the parasite itself: virulence is known to shape the evolution of costly resistance (Anderson and May 1982) and tolerance as well (Restif and Koella 2003; Miller et al. 2005).

As expected, the physiological costs and benefits of resistance and tolerance are key determinants of the evolution of pure defenses. Resistance or tolerance evolves as a pure defense by supplementarity when the efficiency of that trait is high, and by complementarity when the cost of the other trait is high. Pure tolerance is also expected to evolve by complementarity under high risk of transmission due to a large infection rate or propagation factor. Pure resistance is expected to evolve by supplementarity under low infection rate or propagation factor, and under high host or parasite background mortality. Three-way coevolution of resistance and tolerance with virulence tends to broaden the range of parameters over which evolution promotes pure defenses.

The evolution of pure defenses thus appears not to be restricted to the special cost functions (constant or linear and additive) that have been considered in previous studies of resistance–tolerance coevolution (Mauricio et al. 1997; Roy and Kirchner 2000; Tiffin 2000; Restif and Koella 2004). The prediction that very low infection rate or propagation selects completely against tolerance matches Restif and Koella's (2003) results based on a tolerance–virulence coevolutionary model. But in contrast with their analysis, our two-trait and three-trait coevolutionary models consistently predict the evolution of high levels of tolerance as a pure defense under high infection rate or high propagation factor.

EVOLUTIONARY CORRELATION BETWEEN RESISTANCE AND TOLERANCE

Plant defense combining resistance and tolerance has received growing attention since the study of inbred lines of *Ipomoea purpurea* by Fineblum and Rausher (1995) revealed a negative correlation between resistance against and tolerance of herbivory. Yet no general pattern of covariation seems to hold, even within species. In contrast to Fineblum and Rausher (1995) and Baucom and Mauricio (2008), other populations of *I. purpurea* showed no trade-off between defense strategies against herbivory (Tiffin and Rausher 1999) or pathogens (Simms and Triplett 1994). Likewise, tolerance and resistance were uncorrelated among inbred lines of *Arabidopsis thaliana* (Mauricio et al. 1997; Weinig et al. 2003). Further studies found negative correlations in plant–pathogen (e.g., Kover and Schaal 2002) and recently in animal–pathogen (Raberg et al. 2007) systems, whereas Carr et al. (2006) found no evidence for a trade-off between resistance and tolerance to Cucumber mosaic virus in *Mimulus guttatus*. Interestingly, Fornoni et al. (2003) observed an environment-dependent correlation between resistance and tolerance against herbivory in two natural populations of *Datura stramonium*. Our comparison of evolutionary patterns across physiological, environmental, and epidemiological conditions shows that resistance and tolerance can vary in similar or opposite directions and that the direction of covariation can revert in response to even a single physiological, environmental, or epidemiological factor—a conclusion that backs up and extends Restif and Koella's (2004) model.

Specifically, the evolution of complementary defenses, hence a resistance–tolerance trade-off, is predicted as a general and consistent response to variation in the cost of either trait. Variation of resistance or tolerance efficiency up to a threshold also drives the evolution of complementary defenses, hence the trade-off; above the threshold on either efficiency, evolution favors supplementary defenses, hence a positive correlation between resistance and tolerance. Such a sign reversal in the resistance–tolerance evolutionary correlation is found also in response to variation in the infection parameters (infection rate and propagation factor), in line with Restif and Koella's (2004) previous results.

Variation in the cost of virulence also begets sign reversal of the resistance–tolerance correlation. In contrast, as virulence efficiency varies, the correlation is essentially "piecewise positive:" positive but relatively flat for low virulence efficiency; positive and steep across higher virulence efficiency. Finally, variation in host or parasite background mortality drives the evolution of supplementary defenses, hence a positive, strong correlation between resistance and tolerance.

EVOLUTION OF VIRULENCE

Evolutionary theory traditionally defines virulence as induced host mortality. However, a more mechanistic definition of virulence can help incorporate finer details about the interaction between an individual parasite and its individual host and among multiple strains within the host (e.g., André et al. 2003; Alizon and van Baalen 2005, 2008; Mideo et al. 2008). We took such a mechanistic stance on virulence and defined it as the degree of exploitation of host resources (see Day 2002 for a similar approach). Exploitation mechanistically increases host mortality (because the host is deprived from somatic resources), and we defined "virulence efficiency" to measure the intensity of this impact.

In addition to the indirect cost of virulence generated by disease-induced mortality, the model accounts for the direct cost that the parasite may pay for greater exploitation of the host's resources. A direct cost of virulence is assumed in the population genetic theory of virulence (gene-for-gene models of virulence–resistance coevolution), where the benefit of a virulence allele for the parasite is discounted by the direct cost of carrying and expressing the allele. Sasaki's model (2000) provides a good example, and his fitness cost function ($\exp(-n.c)$ wheren n is the number of virulence alleles and c is the cost per allele), is mathematically very similar to our power function (eq. 2). Empirical evidence for such costs is conclusive although scant (e.g., Vera Cruz et al. 2000).

In contrast, quantitative evolutionary theory has largely ignored the direct cost, probably because of the use of a phenomenological, rather than mechanistic, definition of virulence. The basis for such costs, however, has been recognized. Direct costs may be generated physiologically by a more energy-demanding molecular or cellular machinery to acquire and process a larger amount of resources from the host (a classical assumption of life-history theory of resource acquisition/resource allocation evolution). This was addressed in some detail by Gilchrist et al. (2004) in their analysis of within-host viral fitness. In viruses, higher protein translation rates associated with higher propagule production may go with an increased probability of misfolding proteins. Misfolded proteins involved in reverse transcription may have lower enzymatic activities and shorter intracellular half-lives, and misfolded envelope proteins may have a lower target cell binding rate. Either effect may cause the production of infectious propagules to decline if translation occurs faster. Propagule production would thus peak at an intermediate rate of exploitation, which is what the cost function (eq. 2) describes. Another possible underlying mechanism is toxin production (Day 2002): greater exploitation of the host may be achieved by the production of molecular compounds that compromise the host immune system and increase host mortality as a side effect; there must be a cost, however, to the production of toxins, and the net benefit for the parasite may thus again reach its maximum at an intermediate level of toxin production.

The physiological cost of virulence may also follow indirectly from the increased morbidity of the host: as the host suffers greater exploitation, its very ability to acquire resources may be impaired, hence a reduced net income for the parasite. Morbidity costs were taken into account phenomenologically by Day (2001) by linking them to the contact rate; our approach is slightly more mechanistic, in the sense that morbidity costs would impact the parasite production rate, which might then alter the pattern of contacts (depending on the emerging host and parasite population dynamics). One of Day's (2001) important conclusions was that morbidity costs can drive the evolution of intermediate virulence even in the absence of a mortality cost. In general, virulence evolution will be influenced by the combined effects of mortality costs and direct costs. This distinction was important to us because it makes it possible to study the relative effects of two selective pressures on virulence, one that actually depends on the host's coevolving defense—tolerance—and one that is independent of host defense (direct cost).

The model reveals nonmonotonic patterns of virulence coevolving with resistance and tolerance. As larger infection rate or propagation factor drives progressively higher risk of transmission, virulence increases sharply under the synergistic effect of coevolution with (rising) resistance, and tolerance; then virulence increases slowly in a coevolutionary pattern dominated by a selective interaction with tolerance; past some threshold on infection rate or propagation factor, the selective balance shifts and favors the influence of (falling) resistance, causing virulence to decrease, until resistance is completely counter-selected and tolerance is left as pure defense—then both virulence and tolerance essentially plateau.

Earlier models predicted the evolution of more virulent parasites in response to increasing host background mortality (Anderson and May 1979; Lenski and May 1994; van Baalen and Sabelis 1995; Ebert and Weisser 1997; Gandon et al. 2001). We found host physiological and environmental parameters in general, and host background mortality in particular, to have little effect on virulence, relative to the dominant influence of the physiological parameters of virulence (cost and efficiency) and the epidemiological parameters at low level of transmission (low infection rate or propagation factor). The relatively small sensitivity of evolved virulence to host parameters results primarily from the coevolutionary response of host defenses, which mitigates the effect of host parameters on virulence selection gradient (see Appendix S1 and Figs. S21–S28 therein). In particular, the quantitative response of virulence to increasing host background mortality suggests a complex interplay of selective forces acting on virulence and defenses, with net selection on virulence possibly changing sign depending on whether each defense is high, low, or zero. We also note that the related prediction of less virulence when parasite background mortality increases (Ewald 1993, 1994; Hochberg et al. 2000) was not systematically upheld. As parasite background mortality increases to high values, defenses are completely counterselected, which can select for more virulence.

According to previous theory, more virulence was expected to evolve when host resistance coevolves (e.g., Gandon et al. 2002). This model shows that in general, at evolutionary equilibirum, virulence coevolving with tolerance is lower than virulence coevolving with resistance, which is itself lower than virulence coevolving with both tolerance and resistance. Evolutionary patterns of virulence and defenses are generally complex, even under two-way coevolution (Restif and Koella 2003). Under three-way coevolution, there is a general tendency for systems that evolve more resistance and more tolerance also to evolve more virulence. However, more virulence in the parasite does not always coevolve with more defense in the host. More virulence can evolve correlatively with more resistance and less tolerance (when the cost of resistance decreases or resistance efficiency increases), or with less resistance and more tolerance (with the cost of tolerance, across low tolerance efficiency, or across intermediate virulence efficiency). Thus, groups of populations or species that experience different physiological factors may evolve the same evolutionary trade-off between defenses and yet opposite patterns of virulence covariation.

MUTATION DYNAMICS AND NONEQUILIBRIUM EVOLUTION

In this model, the adaptive dynamics always admitted a single, globally attracting point equilibrium. For given physiological, epidemiological, and environmental parameters, the evolutionary equilibrium was computed by numerical integration of the canonical equations of the adaptive traits dynamics (see Appendix), with an array of initial conditions (i.e., the traits ancestral values) that spanned the whole ecologically viable region of the trait space (see Fig. S1 for examples) and with evolutionary rates scaled to 1 for both species. Evolutionary rates compound (1) the probability that an offspring carries a mutation that alters the adaptive trait, and (2) the variance of the distribution of mutational effects on the trait. In real systems, the parasite or pathogen may have a higher mutation probability (1) and a smaller range of mutational effects (2) relatively to the host; as a consequence, there is no obvious assumption to make about the host's and parasite's evolutionary rates as defined and used in adaptive dynamics models. Moreover, the canonical equations of adaptive dynamics (see Appendix, eqs. A.1 and A.2) account for faster evolutionary change when generation time is shorter or reproductive population size is larger, both factors that are function of the ecological and evolutionary state of the system, and thus dynamical.

However, the evolutionary rates of adaptive dynamics are relative to the slow timescale of the model, that is, the evolutionary timescale as opposed to the ecological timescale. In host–parasite systems, this timescale separation may break down when mutation dynamics and ecological dynamics overlap (Day and Gandon 2007). We have taken a first step to understanding the consequences of not-so-rare (and not-so-small) mutations by examining the consequences of multiple mutants arising around evolutionary equilibrium. It turns out that invasion of a mutant catalyzed by the presence of another, eventually unsuccessful mutant, is a common outcome. "Evolutionary spikes" of virulence or defense may often result, whereby a large mutant in one trait invades whereas the other traits essentially remain at evolutionary equilibrium. The model predicts evolutionary spikes to be significant source of variation in virulence in populations in which the infection rate is low, virulence efficiency is high, and parasite background mortality is high. A related phenomenon has been described by Best et al. (2009) in a model of virulence coevolving with avoidance. When the parasite has a higher mutation rate than the host, virulence was found to vary considerably on its way to the system's evolutionary equilibrium. Thus, Best et al.'s (2009) model and ours predict substantial transients in virulence of parasites with rapid mutation, and this may explain some of the bursting variation in parasite virulence that we see in nature. This may have practical implications for the control of disease emergence and the management of virulence (Dieckmann et al. 2002; Ebert and Bull 2003).

IMPLICATIONS FOR THE EVOLUTIONARY MANAGEMENT OF INFECTIONS

Evolutionary management of an infection seeks to interfere with or even redirect the evolution of host–parasite systems to achieve some desired practical goals—such as low virulence in the pathogens or pests, and high resistance or high tolerance in their hosts (Dieckmann et al. 2002). In agriculture for example, there is a growing interest in the use of parasite-tolerant crop plants as alternatives to chemical control. In this model, there are at least six parameters that may be amenable to management. On the one hand, epidemiological measures can alter the rate of contact, propagation factor, and background mortality rate of the parasite, thus modifying the pattern of transmission. On the other hand, virulence efficiency, resistance efficiency, and tolerance efficiency may be targeted by drug treatments.

Miller et al. (2006) cautioned that parasite evolution in response to host tolerance may lead to higher prevalence with lower, but still significant damage to the host. The results of the three-trait coevolutionary model further illuminates such conflicting effects and potential pitfalls of the evolutionary management of infections. Designing and using drugs that reduce virulence efficiency will select for more resistance and more tolerance provided that virulence efficiency is not knocked down too low; but in general reducing virulence efficiency will select parasites that are more virulent (Figs. 5D and 6A,F,K). Increasing resistance efficiency seems also problematic, as this would select strongly against tolerance, favor more virulent parasites, and could even lead to decreased resistance (Fig. 5G); similar consequences would follow from increasing tolerance efficiency (Fig. 5I). On the epidemiological side, management action would have to be strong enough to reduce the infection rate or propagation factor drastically to beget an evolutionary fall of virulence; but this would happen at the cost of a dramatic loss of resistance and tolerance occurring first (Figs. 6B, C, G, H, L, and M). Increasing the rate of mortality of free-living parasites may yield only a slim reduction in virulence while selecting strongly against both resistance and virulence (Figs. 5E and 6D, I, N).

Thus, coevolution of virulence and both defenses is unfavorable to evolutionary management compared to predictions from two-trait models, by promoting more virulence in general, and by accelerating the loss of defenses in response to management action on epidemiological, physiological, or environmental parameters. Evolutionary transients due to mutant catalysis and evolutionary spikes add to the "moving target" challenge raised by virulence evolution (Best et al. 2009). Put in a spatially heterogeneous context, these effects may prove disastrous if more virulent strains and less-defended hosts end up encountering in areas that are not covered by the management plan. To be effective, evolutionary management programs would have to combine actions on several parameters simultaneously, and optimize their implementation in time and space.

Conclusions and Perspectives

Our model provides a unified framework to study the concurrent evolution of resistance, tolerance, and virulence. The results are consistent with previous findings that provided partial insights into the coevolutionary process: greater tolerance evolved as a single trait (Miller et al. 2005) or coevolved with resistance (Restif and Koella 2004) in response to increasing transmission risk; resistance (coevolved with tolerance) maximized at intermediate transmission risk (Restif and Koella 2004); greater defense (resistance or tolerance) evolving as a single trait (Miller et al. 2005) or coevolving with virulence (Restif and Koella 2003) in response to decreasing host background mortality; negative correlation evolving between resistance and tolerance without assuming any physiological trade-off between the traits at the individual level (Restif and Koella 2004). Echoing the conclusions drawn from earlier models, our results emphasize the strong evolutionary effects of physiological costs of virulence and defenses, and thus reiterate the need to devote more experimental work to measuring these costs (Boots and Begon 1993; Antonovics and Thrall 1994; Bowers et al. 1994; Restif and Koella 2004).

The model yields several novel predictions that contrast with previous theory. This is because the model analysis addressed the concurrent evolution of all three traits, and studied their response to variation in a broad set of physiological, epidemiological, and environmental parameters. These predictions include: (1) Compared to two-way coevolutionary scenarios (virulence coevolving with resistance or tolerance), three-trait coevolution generally favors more virulence and less tolerance, and enlarges the range of parameters over which pure defenses evolve. (2) The key factors of adaptive variation in virulence are physiological virulence parameters (cost, efficiency) and epidemiological parameters (infection rate, propagation factor). The host's physiological and environmental parameters have relatively little influence on virulence evolution. In particular, the expectation that decreasing host background mortality selects against virulence is matched only when virulence efficiency and transmission risk are low. (3) Maximum virulence evolves at intermediate transmission risk, at which both coevolving resistance and tolerance reach high levels. (4) More virulence may evolve in response to increasing host background mortality, but only when virulence efficiency and transmission risk are low. (5) Evolutionary correlations between defenses (resistance and tolerance) can switch sign in response to variation in single physiological or epidemiological parameters. (6) The same negative correlation between resistance and tolerance (evolutionary trade-off) may coevolve with monotonically increasing or monotonically decreasing virulence, depending of the underlying factor of variation. (7) In spite of the global attractivity and stability of coevolutionary equilibria, mutant-catalyzed invasion and large "evolutionary spikes" of virulence and defenses are expected around equilibrium.

The results illustrate the complexity of interactions between selective pressures acting on multiple traits, and feedbacks between epidemiological and evolutionary dynamics. In particular, physiological parameters involved in the cost or benefit of one trait can have selective effects that propagate to the evolutionary dynamics of the other traits. These indirect effects may dominate in magnitude over direct effects: variation in resistance or tolerance efficiency parameters have much less direct effects on selected resistance or tolerance, respectively, as they have on the other defense trait and on virulence. Moreover, the counterselection of one defense may have abrupt and unexpected consequences for the coevolution of the other defense and virulence. Implications for the evolutionary management of infections are potentially severe.

Our model analysis and conclusions point to three directions for future research. First, our analysis has confirmed the importance of the feedbacks between adaptive change in tolerance and epidemiological change in prevalence (Roy and Kirchner 2000). This suggests that acquired immunity by the host is a factor—not considered in this model—that could have profound consequences for the evolution of tolerance, and therefore resistance and virulence. Immunity could be modeled first as an additional parameter in the model, and then as an adaptive trait that would be expressed at an additional cost to the host (e.g., Gilchrist and Sasaki 2002, André and Gandon 2006).

Second, our analysis focused on evolutionary outcomes as predicted by evolutionarily attractive and stable equilibria. When mutation occurs on a fast enough timescale (in one or both species), mutant catalysis can trigger evolutionary spikes that keep the system away from evolutionary equilibrium. Whether different ecological or epidemiological assumptions might lead to the persistent coexistence of multiple phenotypes, hence the evolution of polymorphism, warrants further investigation. For example, in their model of virulence-clearance coevolution, Best et al. (2009) found that density dependence acting on the host birth rate may oppose evolutionary branching in virulence, whereas density dependence acting on host death rate is conducive to virulence branching. A role for evolutionary branching to explain highly polymorphic virulence was advocated also by Svennungsen and Kisdi (2009). Evolutionary branching may also explain the coexistence of different strains of resistance in the host (Miller et al. 2005). Host and parasite mutation rates play an important role in determining the actual occurrence of evolutionary branching once the ecological conditions permit branching (Kisdi 1999; Best et al. 2009). Variation in the mutation rates may also affect the attractiveness of the evolutionary equilibrium, by turning the equilibrium into an evolutionary cycle (Dieckmann and Law 1996; Khibnik and Kondrashov 1997; Dercole et al. 2006a) or a more complex evolutionary attractor (Dercole et al. 2006b; Dercole and Rinaldi 2008). Investigating such a possibility would shed light on the consequences of tolerance for the Red Queen cycle of adaptation and counter-adaptation that is known to evolve under certain conditions between virulence and resistance (Khibnik and Kondrashov 1997; Dercole et al. 2006b).

In a related vein, our analysis assumed genetic independence of variation in the host defenses. This approach is appropriate to predict the patterns of trait covariation resulting purely from adaptive responses to physiological, environmental, or epidemiological factors, and thus to tease these patterns apart from potential effects of genetic constrains. Furthermore, genetic covariance, although not changing the evolutionary equilibria, may alter their long-term stability properties (Dieckmann and Law 1996; Dercole and Rinaldi 2008). There is empirical evidence that resistance and tolerance can be genetically linked (Stowe 1998; Ayres and Schneider 2008) or vary pleiotropically, for example, when a single trait combines tolerance and resistance, such as slow rusting in cereal crops (Vanderplank 1984). Quantitative analysis of such genetic covariance is still lacking. The tools of ecological genomics will help tackle this challenge, but even in plants, where tolerance has long been studied, genes conferring disease tolerance have yet to be identified at the molecular level (Rausher 2001; Raberg et al. 2009). Theoretical analyses, by identifying the characteristics of systems in which genetic covariation should have strong coevolutionary consequences, will help and guide this empirical endeavor.

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Appendix: Ecological and Evolutionary Analysis

ECOLOGICAL DYNAMICS

The ecological model is an SIS model with a free-living parasite stage and no direct host-to-host parasite transmission. The equations are adapted from Kostitzin's model (Kostitzin 1934) in which the linear density dependence of birth that regulates the host population is replaced with a more realistic nonlinear (saturating) function of density (see van Baalen and Jansen 2001 for a similar adjustment). Writing densities explicitly in the right-hand side of equations (1A–C) we have

$$
\begin{aligned}
\frac{dX}{dt} &= -\mu_X X - \beta XY + \sigma_X Z \\
\frac{dY}{dt} &= \left(\frac{\hat{\rho}_Y}{1+\kappa(Y+Z)} - \mu_Y\right) X - \beta XY \\
&\quad + \left(\frac{\hat{\rho}_Y}{1+\kappa(Y+Z)} + \nu_X\right) Z \\
\frac{dZ}{dt} &= \beta XY - (\nu_X + \nu_{XY})Z,
\end{aligned}
$$

where $\hat{\rho}_Y$ is a function of host traits given by eq. (5). Straightforward algebra on this system of equations shows that there are at least two and at most four ecological equilibria (i.e., equilibria with nonnegative X, Y, and Z values):

- If the parasite population is in demographic deficit, that is, $\sigma_X < \nu_X + \nu_{XY}$, then there are exactly two ecological equilibria: (0, 0, 0) that is, extinction of the whole system, and the host-only equilibrium $(0,\ (\hat{\rho}_Y/\mu_Y - 1)/\kappa,\ 0)$.
- If $\sigma_X > \nu_X + \nu_{XY}$, nonzero X at equilibrium can take on one or two values $\bar{X}$. Then $\bar{Y}$ and $\bar{Z}$ are uniquely determined by $\bar{Y} = ((\nu_X + \nu_{XY})/\beta)\,(\mu_X/(\sigma_X - \nu_X - \nu_{XY}))$ and $\bar{Z} = \beta\bar{X}\bar{Y}/(\nu_X + \nu_{XY})$.

When $\sigma_X > \nu_X + \nu_{XY}$, ecological equilibrium $\bar{X}$ assumes one or two values depending on whether the discriminant of a polynomial equation of degree 2 is null or positive. The polynomial, the zeros of which return the $\bar{X}$ values, is

$$
\begin{aligned}
P(X) = {}& \hat{\rho}_Y(1+\zeta X) \\
& - (\mu_Y + \zeta\nu_{XY} X)[1 + (\kappa\mu_X/(\zeta\sigma_X - \beta))(1+\zeta X)].
\end{aligned}
$$

Local stability analysis of each ecological equilibrium involves the Jacobian matrix of the system, $\mathbf{J} = [J_{ik}]$ with $1 \le i, k \le 3$. We have

$$
\begin{aligned}
& J_{11} = -\mu_X - \beta Y, \quad J_{12} = -\beta X, \quad J_{13} = \sigma_X, \\
& J_{21} = -\beta Y, \quad J_{22} = -\mu_Y - \beta X + \hat{\rho}_Y/[1+\kappa(Y+Z)]^2, \\
& J_{23} = \beta + \hat{\rho}_Y/[1+\kappa(Y+Z)]^2, \\
& J_{31} = \beta Y, \quad J_{32} = \beta X, \quad J_{33} = -(\nu_X + \nu_{XY}).
\end{aligned}
$$

At ecological equilibrium (0, 0, 0), the Jacobian eigenvalues are $-\mu_X, -(\nu_X + \nu_{XY}), \hat{\rho}_Y - \mu_Y$. Hence the condition for local stability of (0, 0, 0): $\hat{\rho}_Y < \mu_Y$, that is, deficit in the host's demographic potential. At the host-only ecological equilibrium, some straightforward algebra shows that one eigenvalue is always real negative, and the other two are the roots of the degree 2 polynomial with positive discriminant, with at least one of the two (real) roots that is negative. The condition for local stability of the host-only equilibrium follows:

$$
(\nu_X + \nu_{XY})\mu_X/\beta \ < \ (\sigma_X - \nu_X - \nu_{XY})(\hat{\rho}_Y/\mu_Y - 1)/\kappa.
$$

To check the existence of one or two internal equilibria of host–parasite ecological coexistence and establish their local stability, systematic numerical analysis can be performed throughout the entire trait space $0 \le x_1, y_1, y_2 \le 1$, for any given set of physiological, environmental, and epidemiological parameter values. Exact expressions for the equilibrium or equilibria and for the corresponding Jacobian eigenvalues were obtained by symbolic computation using *Mathematica*®6 software (Wolfram Research Inc.). Numerical testing was then performed for a broad range of parameter values, with six theoretically possible outcomes: there are two internal equilibria and both, only one, or none are (is) locally stable; there is only one internal equilibria and it is locally stable, or not; or there is no internal equilibrium, that is, no host–parasite coexistence (in which case possible equilibria are host-only and extinction). Extensive simulations showed that only two outcomes are realized: one locally stable internal equilibrium, or no coexistence. A sample of numerical examples are provided in Figure S1, where parameters that turn out to have the greatest evolutionary influence are investigated.

EVOLUTIONARY DYNAMICS

Evolutionary dynamics of the adaptive traits are driven by the traits' selection gradient, which obtains from calculating the population growth rate of a mutant host or parasite in a resident host–parasite system at ecological equilibrium. The population dynamics of a mutant parasite with density $\tilde{X}$ interacting with a resident population of susceptible hosts (density Y) are governed by

$$
\begin{aligned}
\frac{d\tilde{X}}{dt} &= -\mu_X \tilde{X} - \beta\tilde{X}Y + \sigma_{\tilde{X}}\tilde{Z} \\
\frac{d\tilde{Z}}{dt} &= \beta\tilde{X}Y - (\nu_{\tilde{X}} + \nu_{\tilde{X}Y})\tilde{Z},
\end{aligned}
$$

where $\tilde{Z}$ denotes the density of hosts infected by mutant $\tilde{X}$. Likewise the dynamics of a susceptible population of mutant host with density $\tilde{Y}$ interacting with a resident parasite population (density X) are governed by

$$
\begin{aligned}
\frac{d\tilde{Y}}{dt} &= (\rho_{\tilde{Y}} - \mu_Y)\tilde{Y} - \beta X\tilde{Y} + (\sigma_{\tilde{Y}} + \nu_{\tilde{Y}})\tilde{Z} \\
\frac{d\tilde{Z}}{dt} &= \beta X\tilde{Y} - (\nu_X + \nu_{X\tilde{Y}})\tilde{Z},
\end{aligned}
$$

where we (slightly abusively) denote again by $\tilde{Z}$ the density of mutant hosts that are infected by resident parasite X.

Mutant populations are initially small and their impact on the resident populations at ecological equilibrium is negligible. Linearization of the resident-mutant dynamical system around the resident ecological equilibrium, $(\bar{X}, \bar{Y}, \bar{Z})$, yields the following equations for mutant population growth from small density:

$$
\frac{d}{dt}\begin{pmatrix}\tilde{X}\\ \tilde{Z}\end{pmatrix} = \mathbf{L}_{\tilde{X}}\begin{pmatrix}\tilde{X}\\ \tilde{Z}\end{pmatrix}
$$

where

$$\mathbf{L}_{\tilde{X}} = \begin{pmatrix} -\mu_X - \beta\bar{Y} & \sigma_{\tilde{X}} \\ \beta\bar{Y} & -(\nu_{\tilde{X}} + \nu_{\tilde{X}Y}) \end{pmatrix}$$

and

$$\frac{d}{dt}\begin{pmatrix} \tilde{Y} \\ \tilde{Z} \end{pmatrix} = \mathbf{L}_{\tilde{Y}}\begin{pmatrix} \tilde{Y} \\ \tilde{Z} \end{pmatrix}$$

where

$$\mathbf{L}_{\tilde{Y}} = \begin{pmatrix} (\rho_{\tilde{Y}} - \mu_Y) - \beta\bar{X} & \sigma_{\tilde{Y}} + \nu_X \\ \beta\bar{X} & -(\nu_X + \nu_{X\tilde{Y}}) \end{pmatrix}.$$

A first-order approximation of the invasion fitness $\lambda_{\tilde{X}}$ of mutant $\tilde{X}$ is given by

$$\lambda_{\tilde{X}} = \frac{-(\nu_{\tilde{X}} + \nu_{\tilde{X}Y})}{\mathrm{Tr}_{\tilde{X}}}\left[-\mu_X + \beta\bar{Y}\left(\frac{\sigma_{\tilde{X}}}{\nu_{\tilde{X}} + \nu_{\tilde{X}Y}} - 1\right)\right]$$

where $\mathrm{Tr}_{\tilde{X}}$ is the trace of the matrix $\mathbf{L}_{\tilde{X}}$. Likewise, invasion fitness $\lambda_{\tilde{Y}}$ of mutant $\tilde{Y}$ is

$$\lambda_{\tilde{Y}} = \frac{-(\nu_X + \nu_{X\tilde{Y}})}{\mathrm{Tr}_{\tilde{Y}}}\left[(\rho_{\tilde{Y}} - \mu_Y) + \beta\bar{X}\left(\frac{\sigma_{\tilde{Y}}}{\nu_X + \nu_{X\tilde{Y}}} - 1\right)\right],$$

where $\mathrm{Tr}_{\tilde{Y}}$ is the trace of the matrix $\mathbf{L}_{\tilde{Y}}$.

Let the right and left eigenvectors of matrix $\mathbf{L}_{\tilde{X}}$ be denoted by $\mathbf{U}_{\tilde{X}} = (U_{1\tilde{X}}\ ,\ U_{2\tilde{X}})$ and $\mathbf{V}_{\tilde{X}} = (V_{1\tilde{X}}\ ,\ V_{2\tilde{X}})$, with the normalizations $U_{1\tilde{X}}\ +\ U_{2\tilde{X}} = 1$ and $U_{1\tilde{X}}V_{1\tilde{X}}\ +\ U_{2\tilde{X}}V_{2\tilde{X}} = 1$. We use corresponding notations for the host. Then, the probabilities of nonextinction of the mutant parasite and mutant host are, respectively,

$$\mathrm{P}_{\tilde{X}} = \frac{\lambda_{\tilde{X}}}{\sigma_{\tilde{X}}U_{2\tilde{X}}V_{2\tilde{X}}}$$

$$\mathrm{P}_{\tilde{Y}} = \frac{\lambda_{\tilde{Y}}}{\sigma_{\tilde{Y}}U_{2\tilde{Y}}V_{2\tilde{Y}}}$$

(Athreya and Ney 1972; see also Theorem 1 in Athreya 1993, and Law and Dieckmann 1998).

The canonical equations for the adaptive dynamics of the parasite's trait x_1 and the host's trait y_i ($i = 1$ or 2) follow:

$$\frac{dx_1}{dt} = k_{x_1}\ \sigma_X\bar{Z}\ \frac{\partial P_{\tilde{X}}}{\partial\tilde{x}_1} \tag{A.1}$$

$$\frac{dy_i}{dt} = k_{y_i}\ (\rho_Y\bar{Y} + \sigma_Y\bar{Z})\ \frac{\partial P_{\tilde{Y}}}{\partial\tilde{y}_i}, \tag{A.2}$$

where partial derivatives with respect to mutant traits ($\tilde{x}_1$,$\tilde{y}_i$) are evaluated at the resident trait values. In each equation, the *k* coefficient is the trait's evolutionary rate, which compounds mutation probability per birth, and mutation step variance. The effective speed of evolutionary change is determined by the evolutionary rate times the total reproductive rate ($\sigma_X\bar{Z}$ in eq. A.1 and $(\rho_Y\bar{Y} + \sigma_Y\bar{Z})$ in eq. A.2).

Numerically, for any given set of parameter values, we implemented a sampling scheme (grid) that spanned the entire trait space, and for each point on the grid, that is, each combination of resident trait values, the ecological equilibrium was computed (see previous section), and the selective pressures were then evaluated. The results of these evaluations over the grid were interpolated to recover a continuous (polynomial) selection gradient. The interpolation was then used for the numerical integration of the canonical equations (by means of standard Runge–Kutta method). Finally, the convergence of the solutions to a single equilibrium was tested by varying the initial conditions across the grid.

Supporting Information

The following supporting information is available for this article:

Figure S1. Ecological equilibria across virulence–resistance–tolerance trait space. Effect of virulence efficiency (ω_{x1}), infection rate (β), and parasite background mortality (μ_{1X}).
Figures S2–S10. Univariate evolutionary patterns of resistance, tolerance, and virulence as predicted by RT, VR, VT, and VRT models: Sensitivity analysis with respect to virulence efficiency, infection rate, and host or parasite background mortality.
Figure S11. Resistance–tolerance correlation evolving in response to variation in parasite parameters under three-way coevolution (VRT model).
Figures S12–S14. Invasibility of the resistance–tolerance evolutionary equilibrium by mutant traits (RT model): Sensitivity analysis with respect to virulence efficiency, infection rate, and parasite background mortality.
Figures S15–S20. Invasibility of virulence–resistance (VR model), virulence–tolerance (VT model), and virulence–resistance–tolerance (VRT model) evolutionary equilibria by mutant traits: Sensitivity analysis with respect to virulence efficiency, infection rate, and parasite background mortality.
Appendix S1. On the sensitivity of virulence to host parameters. Includes:

Figure S21: Effect of host background mortality on virulence evolved in the absence of host coevolution compared to virulence coevolved with host defenses.
Figures S22, S23: Coevolved virulence and host defenses with respect to direct and indirect costs of virulence.
Figure S24: Effect of relative strength of direct and indirect costs of virulence on coevolved virulence and host defenses with respect to infection rate and host background mortality.
Figures S25, S26: Effect of direct cost of virulence and virulence–transmission conventional trade-off on coevolved virulence and host defenses with respect to infection rate and host background mortality.
Figures S27, S28: Effect of direct cost of virulence and nonlinearity in the indirect cost on coevolved virulence and host defenses with respect to infection rate and host background mortality.

Supporting Information may be found in the online version of this article.