

## RESEARCH ARTICLE

# Nesting sites of giant honeybees modulated by landscape patterns

Charlotte Pavageau<sup>1,2</sup>  | Cédric Gaucherel<sup>3</sup> | Claude Garcia<sup>1,2</sup> | Jaboury Ghazoul<sup>1</sup>

<sup>1</sup>ETH Zürich, Zürich, Switzerland

<sup>2</sup>CIRAD, Montpellier, France

<sup>3</sup>AMAP, INRA, CIRAD, CNRS, IRD, Université Montpellier, Montpellier, France

## Correspondence

Charlotte Pavageau

Email: charlotte.pavageau@usys.ethz.ch

## Funding information

IDP BRIDGES, Grant/Award Number: PITN-GA-2013-608422 – IDP BRIDGES; CIRAD

Handling Editor: Ainhoa Magrach

## Abstract

1. The composition of agro-ecological landscapes is thought to have important implications for the production of major crops through its effects on pollinator abundance and behaviour.
2. We explored the roles of land cover and land cover heterogeneity on bee nest distribution for the giant honeybee *Apis dorsata*, a key species for coffee pollination, in a complex agroforest landscape. We emphasized scaling and non-uniform effects by combining two different approaches of spatial analysis, the point-pattern analysis and surface-pattern analysis.
3. We found non-exclusive, positive effects of agroforests, forest fragments and land-cover heterogeneity on the presence and number of nests. The distribution of nests responded to habitat heterogeneity at small scale (<100 m), forest fragments at medium scale (<300 m) and to agroforest at larger scales (500 m to 2 km). Our multiple approaches highlight that the landscape effects were neither linear nor uniform within the study zone. Nests were consistently located in areas of medium agroforest density or medium to high forest density, but were absent where forest fragments are the most concentrated.
4. The agroforest matrix was particularly important in shaping the size of nest aggregates. Nests tended to be few when there is low tree cover at broad scale, while nests were numerous when agroforest patches are abundant within the bees' foraging range.
5. *Synthesis and applications.* Our study revealed that structurally complex landscapes appear to support bee populations. The spatial arrangement of different land covers affected honeybee nest distributions by providing nesting and foraging resources across multiple scales. The results suggest that continued intensification of small forest fragments and expansion of large monospecies plantations will be deleterious to the populations of giant honeybees *A. dorsata*. Fragmentation of the agroforestry matrix at small scales (100s m) does not, however, appear detrimental for *A. dorsata* as long as sufficient diversified resources are available at the landscape scale (kms).

## KEYWORDS

agro-ecological landscapes, agroforestry, *Apis dorsata*, honeybee, landscape analysis, nesting, pollination, spatial scale, Western Ghats, wild bees

## 1 | INTRODUCTION

Land-use intensification, habitat loss and fragmentation are thought to be driving a decline in bee populations in some regions (Kremen, Williams, & Thorp, 2002; Potts et al., 2010; Steffan-Dewenter & Westphal, 2008; though see, Ghazoul, 2015 as to the limitations of current knowledge). The extent to which such declines will result in pollinator-induced crop production deficits remains ill-defined, particularly in the tropics (Ghazoul, 2005, 2013). Tropical agroforestry landscapes are increasingly viewed as regions in which crop production needs could be balanced with those of conservation and ecosystem service provision (Jha et al., 2014; Perfecto & Vandermeer, 2008). Such landscapes are often characterized by a high spatial heterogeneity of land covers, various degrees of agricultural intensification, and varying extent and quality of remaining natural habitats. These heterogeneous landscape mosaics are thought to provide a wide variety of habitat conditions and resources for mobile species such as bees (Carre et al., 2009; Steffan-Dewenter, Munzenberg, Burger, Thies, & Tschardtke, 2002; Williams & Kremen, 2007). The link between land cover patterns, pollinator populations and pollination services remains somewhat contentious, in part because many studies have approached this issue at just a single scale of analysis. Processes affecting pollinator nesting and foraging behaviours might unfold at multiple scales, from the farm or forest stand through to the wider landscape. Consequently, a better understanding of how heterogeneous landscapes support bee populations at multiple spatial scales is necessary to evaluate the extent to which crop pollination services are vulnerable to future changes in land use and land cover, and to provide land managers with effective recommendations.

Among pollinators, wild species seem to provide more effective and stable pollination services (Garibaldi et al., 2013). In contrast to what is known about floral resource use and dependency, we know relatively little about the nesting requirements of wild pollinators, and especially about factors conditioning nesting choice (Kremen et al., 2007; Potts et al., 2005; Steffan-Dewenter & Westphal, 2008). The distribution of nests of wild social bee species constrains the spatial provision of pollination services, since flower visitation generally declines with increasing distance from the nest. It is thus of great interest to assess the influence of different factors on nest-site selection and to relate them to landscape characteristics at different scales. For instance, very little direct data exist on bee nest density (Kim, Williams, & Kremen, 2006; Knight et al., 2005). Nesting location is mainly influenced locally by the availability of suitable nesting habitats and of nesting resources, such as nest trees for open-nesting bee species, as well as the availability and diversity of floral resources within the foraging distance from the nests (Eltz, Bruhl, van der Kaars, & Linsenmair, 2002; Kremen et al., 2007; Samejima, Marzuki, Nagamitsu, & Nakasizuka, 2004). Depending on the case, the floristics parameters were either the main or the least limiting factor for nest density.

Overall, landscape composition influences pollinator abundance at multiple scales (Kennedy et al., 2013), as it modulates resource distribution and hence resource use. Structurally complex and heterogeneous landscapes provide higher diversity and spatiotemporal stability

of resources (Dunning, Danielson, & Pulliam, 1992; Tschardtke et al., 2012), as different habitats provide resources at different times of the year (Miguet, Gaucherel, & Bretagnolle, 2013). Forested habitats, particularly, provide a high abundance and diversity of important resources for bees (Ricketts et al., 2008), as shown for the giant Asian honeybee, *Apis dorsata* (Krishnan, Kushalappa, Shaanker, & Ghazoul, 2012). However, forests or (semi-)natural forested habitats represent a variety of ecosystems with various degrees of human modifications. This suggests a need for a finer characterization of forest types and their distribution in pollination studies. In South Indian coffee landscapes, agroforest coffee plantations and forest patches present similar but distinct tree cover and understorey layer characteristics (Ambinakudige & Sathish, 2009; Bhagwat, Kushalappa, Williams, & Brown, 2005).

In this study, we address how different landscape properties influence the distribution of nests of the giant Asian honeybee *A. dorsata*, a key pollinating species across Southeast Asia. In particular, *A. dorsata* is the main pollinator of economically important crops such as coffee (Krishnan et al., 2012). The spatial pattern of their nests has important implications for pollination services and thus for the livelihoods of smallholder coffee farmers. The issue of scale is critical for the analysis of landscape–population distribution interactions, since multiple processes operating across several scales affect population distribution in landscapes (Tews et al., 2004). In the case of *A. dorsata*, the local condition of the nesting sites and the availability of foraging resources at larger scales simultaneously influence the distribution of colonies (Boreux, Krishnan, Cheppudira, & Ghazoul, 2012). The large open nests of *A. dorsata* are usually found suspended from branches of large trees of preferred species, which probably ensures protection against predators or adverse conditions (Roy et al., 2011; Singh, Singh, & Singh, 2007). Given that the foraging range of *A. dorsata* can exceed 2 to 3 km (Dyer & Seeley, 1991), we expected nest distribution to respond to landscape properties at scales of 100 m to several kilometres. In addition, those effects might not be uniform across the landscape. To address the issues of scaling and spatial variation in landscape effects, we used two complementary approaches. First, we combined two types of landscape representation, point-pattern vs. surface pattern, associated with two different scales of variation in nest distributions. Second, we used multiscale tools of analysis for each representation, scrutinizing interactions between nest distributions and land cover across a continuous range of scales. Such approaches allow us to unravel different aspects of landscape–pollinator interactions (Dale et al., 2002; Graf, Bollmann, Suter, & Bugmann, 2005; Schroder & Seppelt, 2006). Using fully mapped data of nest positions and land cover, we tested three alternative (not mutually exclusive) hypotheses: density of nests is correlated with heterogeneity in land cover (H1), density of agroforests (H2) or density of forest patches (H3).

## 2 | MATERIALS AND METHODS

### 2.1 | Study area and species

Our study area was located in South India, in the district of Kodagu, within the Western Ghats biodiversity hotspot (Myers, Mittermeier,

Mittermeier, da Fonseca, & Kent, 2000). The study focused on a 9.3 km wide area, covering 68 km<sup>2</sup> (12.251°N, 75.793°E; Figure 1). The landscape is largely covered by coffee plantations (60%) and rice fields (33%). Coffee is exclusively produced under shade. Small forest fragments cover only 1.5% of the study zone (all patches <10 ha, mean size = 1.6 ha), and are largely degraded compared to their initial stage (Bhagwat et al., 2005). Forest fragments shelter about 167 different tree species, compared to 162 tree species in coffee estates (Bhagwat et al., 2005). The average tree density is estimated at 325 ± 104 stems per hectare in coffee plantations and 1361 ± 599 stems per hectare in forest fragments, while the Shannon diversity index for trees is 2.71 in plantations and 3.29 in forest fragments (Ambinakudige & Sathish, 2009).

The rock bee *A. dorsata* accounts for 58% of the insects visiting coffee flowers in the region (Krishnan et al., 2012). *Apis dorsata* nests are often found in aggregations or more rarely singly on a tree. Their large body size (17–20 mm) allows them to typically forage up to 2–3 km (Dyer & Seeley, 1991).

## 2.2 | Landscape and nest data

In February–March 2014, we exhaustively mapped all the nests of *A. dorsata* in the study area. We localized the quite visible nests by visiting all forest fragments within the study zone, and by interviewing 283 planters on the presence of *A. dorsata* in their neighbourhood. The high nest-site fidelity of *A. dorsata* (Paar, Oldroyd, & Kastberger, 2000), combined with local farmer knowledge of nesting sites and previous mapping of nests (Krishnan, 2011) provided good prior knowledge of probable nest locations and allowed us to cross-check the comprehensiveness of the search. Nest locations were recorded with a Garmin GPSMAP 60CSx.

To characterize the landscape patterns, we used a land cover map of the study area, extended by a buffer zone of 2 km to minimize edge effects. The land cover map was derived from an IRS-P6 LISS IV image of 2008 at a resolution of 5.8 m at nadir. Land cover types were

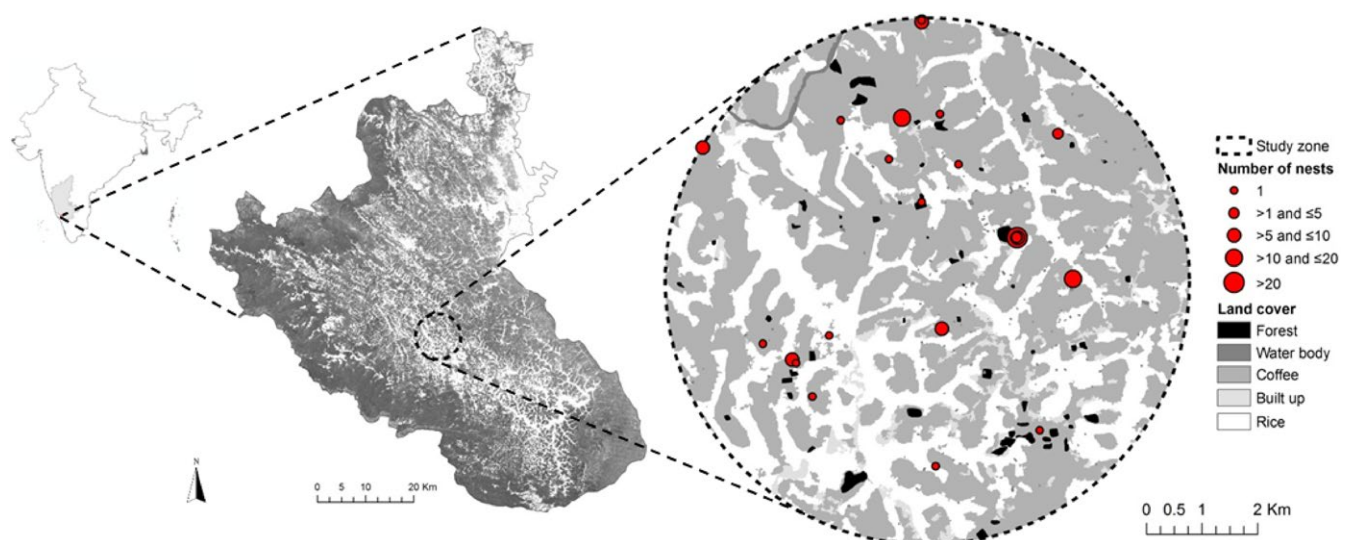
classified in five categories (coffee plantation, rice, built up, forest fragment and water body), corresponding to resources types potentially used by bees. The exact boundaries of the forest fragments were ground-truthed with GPS data collected during field work in 2014.

## 2.3 | Analysis of nest–landscape pattern interactions

We combined two approaches to explore the relationship between nest localization or nest density and landscape patterns at multiple scales, the point-pattern analysis and surface-pattern analysis. Both methods are well adapted for fully mapped data, as they are robust to spatial autocorrelation and are intrinsically scale-dependent, unlike classical GLM models (Gaucherel, Alleaume, & Hely, 2008; Schroder & Seppelt, 2006). Point-pattern analysis focuses on fine-scale interactions between individual objects (Goreaud & Pelissier, 2003), while surface-pattern analysis deals with larger gradient in nest density and land cover composition. In contrast to point-pattern, surface-pattern analysis allows better consideration for landscape configuration and spatial variations in the ecological interactions. In particular, surface-pattern analysis estimates correlation for each point of the landscape. For comparison purpose, we additionally performed a GLM on the number of nests and proportion of different land cover at different scales (see Appendix S1).

## 2.4 | Point-pattern analysis

We considered (1) the locations of nests and (2) the locations of patches of forest fragments and of coffee plantations as realizations of different spatial point processes. We first performed the Besag L function on the nest points (Diggle, 1983) with edge correction, and we defined 95% confidence levels of a homogeneous Poisson process. Values of L(r) above the upper bounds of the confidence envelope indicate clustering, and those below the lower bounds indicate regularity. We then distributed 10,000 random points in the study zone and



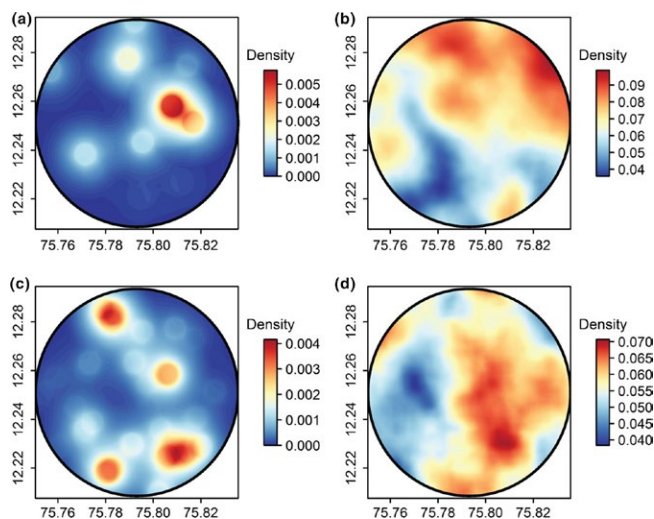
**FIGURE 1** Geographical location of the study area in the Kodagu district, South India, and positions of the nests within the study zone [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

assigned to them the corresponding land cover type. The intertype  $L_{12}$  function (Goreaud & Pelissier, 2003) was then calculated with 95% confidence levels of an independent process to explore the interactions (attraction–repulsion) between nests and land cover patches (either agroforests or forest fragments). A  $L_{12}$  function above the confidence envelope would reveal that forest fragments are more clustered around bee nests than expected by chance. To reduce the sensitivity of the results to the initial distribution of points, we calculated the mean  $L_{12}$  function on 10 random distributions of landscape points.

## 2.5 | Surface-pattern analysis: MHM and CMP methods

We first calculated continuous surface variables using the multiscale heterogeneity map (MHM) method (Gaucherel, 2007). The MHM method calculates for each pixel of study area a pattern index (e.g. the density of a specific land cover type) at increasing scales (i.e. using different sizes of moving windows around the central pixel). It then produces a map of the mean value of the index at successive scales, and thus a distance-weighted density estimate (Dormann et al., 2007). This method overcomes the problem of scale sensitivity of local spatial variables such as density or heterogeneity indices (Gaucherel, 2007; Gaucherel et al., 2010). Here, we calculated the multiscale density of nests and three landscape metrics: (1) the multiscale density of agroforests; (2) the multiscale density of forest fragments; (3) a multiscale heterogeneity map with five land cover categories. Heterogeneity is measured by a connectivity index, which takes into account both the composition and the configuration of land covers. It is defined as  $H = RC - 1$ , with RC the relative contagion expressed as (Li & Reynolds, 1993):

$$RC = 1 + \sum_{i=1}^n \sum_{j=1}^n P_{ij} \frac{\ln(P_{ij})}{2 \ln(n)}$$



**FIGURE 2** Multiscale map of (a) nest density (MHM), (b) agroforest density, (c) forest fragment density and (d) heterogeneity index, calculated for successive scales from 100 m to 4 km [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

where  $P_{ij}$  is the probability of patch type  $i$  being adjacent to patch type  $j$ . This heterogeneity index is expected to increase with land cover diversity in a specific surrounding.

In a second phase, we compared the MHM map of nest density and the three MHM maps of landscape indexes, using the surface-pattern Correlation Map and Profile (CMP) method (Gaucherel et al., 2008). This method is based on a comparison made among moving windows centred on each pixel (for both maps) of the study zone. A cross-correlation index, defined as a coefficient of linear correlation, can thus be extracted from the moving windows, and for different widths (scales) of the moving window.

We computed correlation maps at successive spatial scales from 100 m to 4 km, chosen to take account of both the effects of fine stochastic patterns and broader gradients in the landscape. We then computed a multiscale map as the average of all monoscale maps, as well as a scaling profile as the mean cross-correlation index value over the whole study zone. Consequently, this method simultaneously explores spatial and scaling relationships, and thus detects local relative variations in the patterns as well as larger scaling effects. The absence of correlation may be interpreted as independent patterns. We finally analysed in more detail areas presenting high significant negative and positive correlation values.

## 3 | RESULTS

### 3.1 | Distribution of bees

We found 112 nests in the study zone of 68 km<sup>2</sup>, either aggregated on the same tree or not (Figure 1, 10 solitary nests and 8 aggregates >4 nests). Nests were found in forest fragments (38% of the nests) or in coffee plantations (62% of the nests), with an average density of 1.6 nests/km<sup>2</sup>. The aggregated pattern of the nests was confirmed by the significantly positive value of the empirical  $L(r)$  function (Figure 3a). The characteristic scale of aggregation was 30 m, though the  $L(r)$  function for nests remains positive even at larger scales (>2.2 km). This could correspond to some heterogeneity in the pattern or to larger scale trend, as shown in the multiscale map of nest density (Figure 2a).

### 3.2 | Point-pattern analysis

The  $L_{12}$  intertype function shows a positive attraction between the nests and the agroforest patches from 20 to 1,650 m, as the  $L_{12}$  function is significantly higher than expected by chance (Figure 3b). Moreover, the strength of the attraction between the nests and the agroforest patches exhibits two local peaks at 140–300 m (secondary peak) and at 1,500 m (main peak). The observed values of the  $L_{12}$  intertype function between the nests and the forest fragments are also higher (more aggregated) than expected under a null model of complete independence, at distances between 33 and 1,100 m (Figure 3c). The positive interaction of forest fragments on nests peaks at 385 m, with a weak negative effect at large distance (>1,640 m). We conclude that *A. dorsata* nests and agroforests tend to be positively correlated

both at small and large distances, while *A. dorsata* nests interact positively with forest fragments at fine scales only (up to 385 m).

### 3.3 | Surface-pattern analysis

The previous  $L_{12}$  functions assume that the point process is stationary. The intertype function provides a quantitative description of the interaction between nests and tree-covered patches averaged across the entire landscape, and thus fails to reveal spatial variations contrary to the CMP method. The average cross-correlation CMP index between agroforest and nest densities is very low at all scales (CMP  $\sim 0.06$ ). Nonetheless, the local presence of high positive and negative correlations at each spatial scale contradicts the simple hypothesis that nests are always found in areas with high density of agroforests (Figures 4 and 5). Two patterns emerge when analysing separately areas with high positive and high negative correlations at all scales (Figure 5). On the one hand, high positive correlations ( $>0.6$ ) cover 10% of the landscape. Those areas are characterized by medium values of nest density (Figure 5c), but lower values of agroforest density relative to the whole landscape (Figure 5e;  $p < .001$ ). Positive correlations indicate that, in those regions, when nest density decreases (or as the distance to the nest increases), the agroforest density is also further decreasing from 100 m to 4 km (from low density to very low density of agroforest). On the other hand, high negative correlations ( $<-0.6$ ) are found for 12% of the study area. They are located around areas of high nest concentrations and are characterized by high nest density values (Figure 5c) and high density of agroforests (Figure 5e;  $p < .001$ ). Hence, the density of agroforests increases as the nest density decreases. Areas with local positive and negative correlations are clearly differentiated by, respectively, low and high values of the agroforest density (Figure 5c). Those results are robust, and remain similar with reduced threshold values (CMP =  $\pm 0.2$ ).

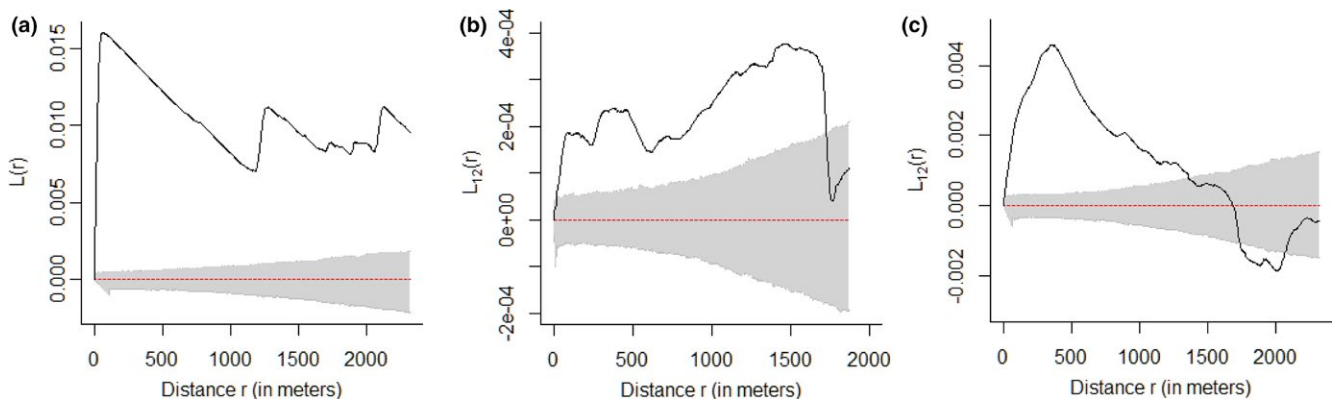
The overall cross-correlation index between the density of nests and the density of forest fragments is positive and relatively high at all scales (CMP  $\sim 0.3$ ). Distinct negative and positive correlations again

are detected in the landscape, but positive correlations cover a larger portion of the study zone (40% of the landscape; Figure 6a). This features an overall positive effect of forest fragments on the nests from 100 m onwards. The profile of CMP correlation is quite stable with increasing scales, typical of a fine-scale interaction. Positive correlations are detected for all values of forest density  $<0.003$  and all values of nest density (Figure 6b,c). We confirmed the positive influence of forest fragments on nest distribution, yet not where forest fragments are the most concentrated (no significant correlation detected when the density of forest fragments  $>0.003$ , Figure 6c). The results are in line with the Ripley intertype function.

Similar to the effect of forest fragments, the overall correlation between landscape heterogeneity and nest density is positive at all scales (CMP  $\sim 0.25$ ; Figure 2a,d and Figure S2 in Appendix S2). The pattern of nest density is significantly and positively correlated to the pattern of land cover heterogeneity on a large fraction of the landscape. This indicates a nesting preference for areas with high heterogeneity of land cover types at all scales and in particular at small scales.

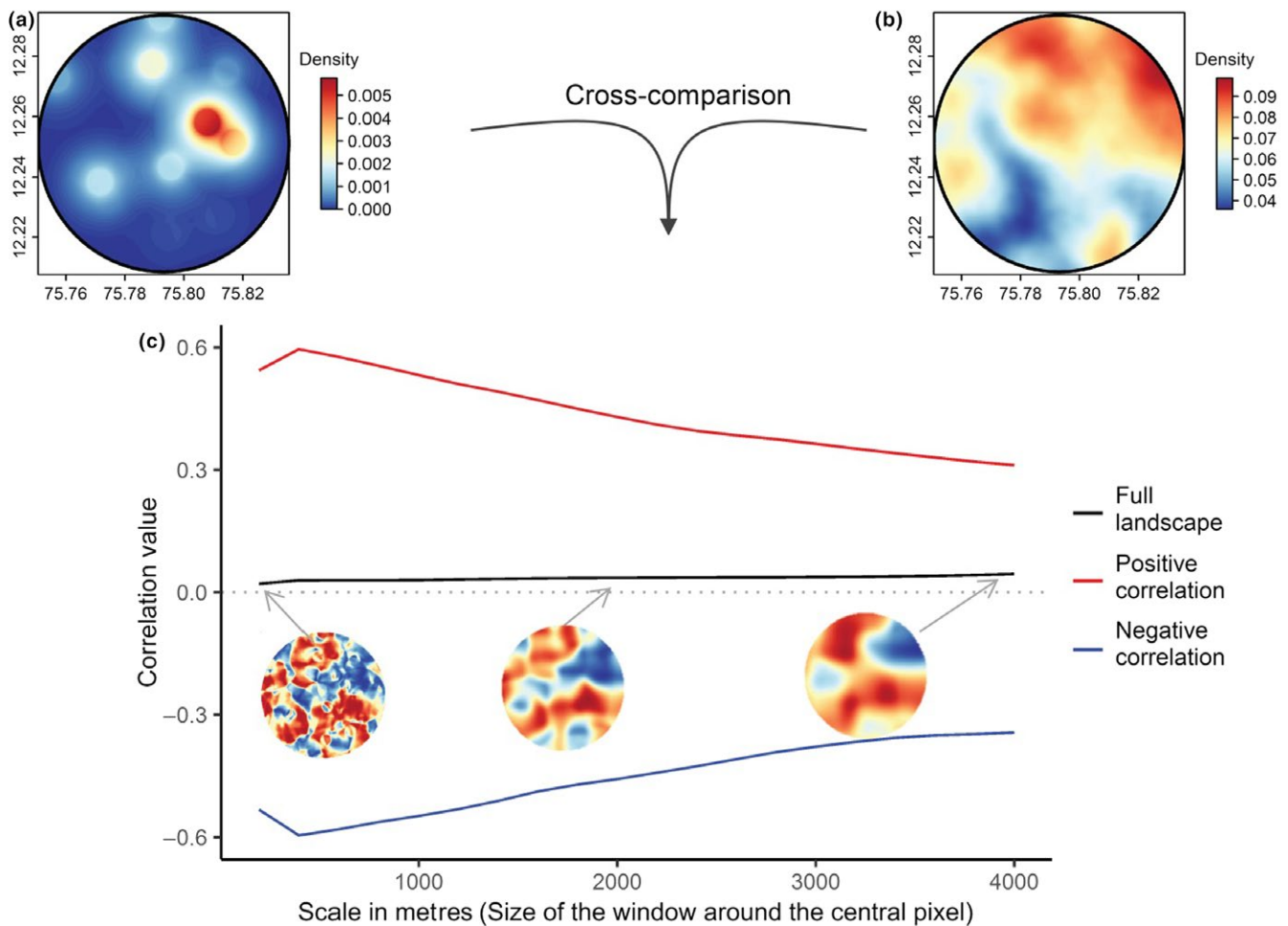
## 4 | DISCUSSION

The present study provides a new direct estimation of the density of wild nests of a key pollinator, *A. dorsata*, and how nest distribution relates to different land cover types across a variety of spatial scales. The average density of 1.6 nests/km<sup>2</sup> is comparable to indirect estimates of nest density in protected areas in the Western Ghats (Roy et al., 2011) and shows that *A. dorsata* can persist in human-modified landscapes. By combining spatial point-pattern and surface-pattern analyses, we further demonstrated that the nest distribution responded to multiple landscape properties at multiple scales simultaneously. In particular, both the agroforestry matrix and forest fragments influence the presence of nests, although the scale and direction of the interactions vary across the two land covers and are not uniform across the study zone. This implies that robust multiscale approaches



**FIGURE 3** (a) Besag  $L(r)$  univariate function for the nests. Besag  $L_{12}$  intertype function (b) between nests and agroforests, and (c) between nests and forest fragments. The solid lines represent observed values, the horizontal dotted lines represent the expectation under complete spatial randomness (theoretical) for (a) or complete spatial independence for (b) and (c), and the grey lines represent the 95% local confidence interval based on 999 simulations of a Poisson process or of an independent process [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]





**FIGURE 4** Results of the comparison between (a) the MHM density of nests and (b) the MHM density of agroforests, using the CMP method. (c) cross-correlation profile through spatial scales from 100 to 4 km. The black line represents the average cross-correlation value over the whole landscape at each scale, the red and blue lines represent the positive and negative correlations. The monoscale cross-correlation maps for 100 m, 2 km and 4 km are displayed. Hot and cold colours relate to positive and negative correlation, respectively [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

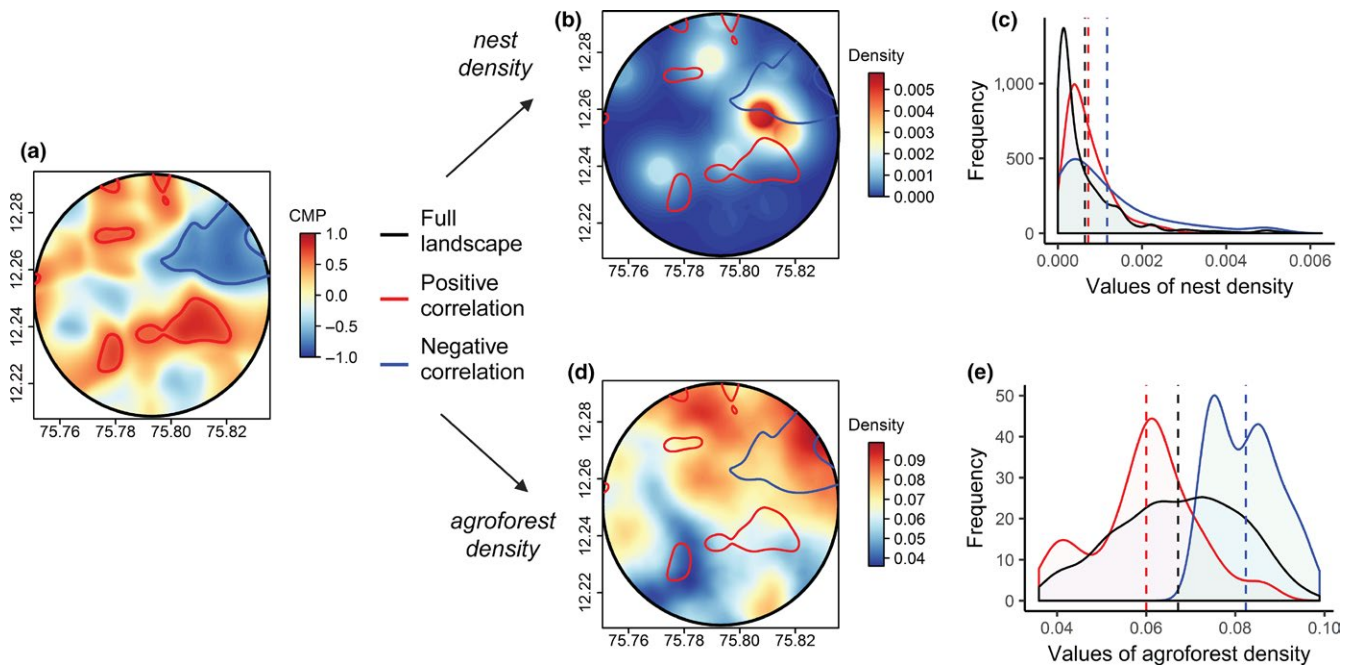
are needed to understand the distribution of social bees in complex landscape (Gaucherel et al., 2010; Graf et al., 2005).

#### 4.1 | Landscape complexity and supplementation hypothesis

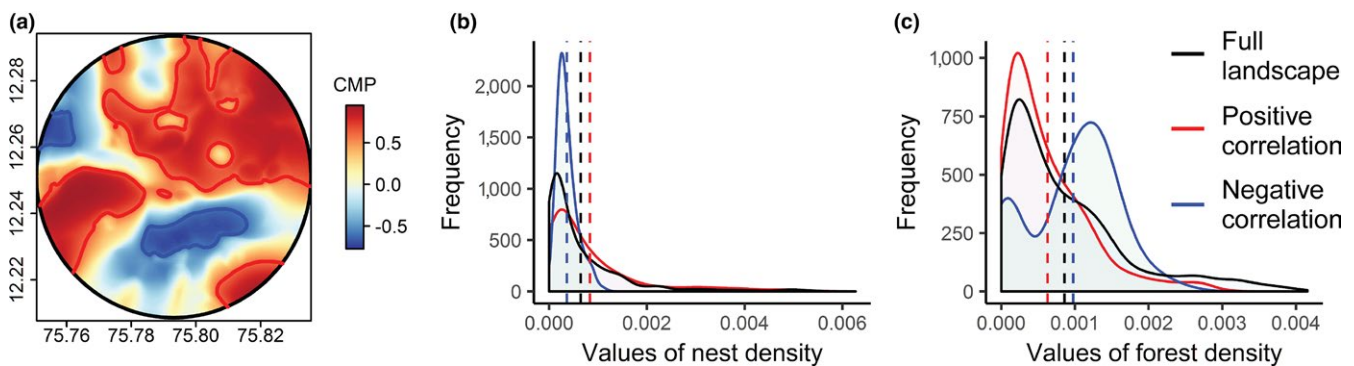
Our results showed that landscape complexity, in particular the spatial arrangement of forest fragments and coffee plantations at various scales, is related to the settlement of *A. dorsata* nests. The  $L_{12}$  intertype function analyses revealed significant positive effects of forest fragments and agroforests on the presence of nests at local scales (100 to 300 m, confirmed by the GLM method in Appendix S1). This scale of interaction is associated with immediate nesting conditions. Coffee plantations and forest fragments both provide substantial amounts of large native trees, key nesting resources for *A. dorsata* (Sivaram, Roopa, Shubharani, & Suwannapong, 2012; Thomas et al., 2009). More than half of the nests were found in agroforests, contradicting previous studies that suggest that *A. dorsata* preferentially nest in natural forest patches (Krishnan et al., 2012;

Roy et al., 2011; Thomas et al., 2009), although in relation to the proportion of each land cover in the landscape, the density of nests in forest fragments is higher (chi-test,  $p < .001$ ), suggesting more favourable nesting conditions. Forest fragments experience lower anthropogenic disturbance and have higher density and diversity of suitable large nesting trees than coffee plantations (Ambinakudige & Sathish, 2009; Bhagwat et al., 2005). This pattern is not, however, consistent across the landscape, as the CMP analysis revealed that while nests were associated with smaller forest fragments at local scales, they were absent in the vicinity of the largest aggregates of forest fragments (Figure 6c, absence of significant correlation for high values of forest fragments).

The intertype  $L_{12}$  function also showed a significant positive spatial association between nests and agroforests up to 140–300 m, and again at 1,500 m, while nests responded to forest fragment aggregations at scales less than 400 m only (Figure 3). The influence of agroforests and forest fragments differed across scales, and might be explained by differences in availability and quality of foraging resources. Forest fragments provide a wider diversity of foraging



**FIGURE 5** (a) Multiscale correlation map, computed by averaging CMP monoscale maps over the whole range of scales (from 100 m to 4 km). Areas of high positive correlation are surrounded in red (CMP > 0.6) and high negative correlation in blue (CMP < -0.6). (b) and (d) Locations of positive and negative correlation areas on the initial maps of nest and agroforest densities. (c) and (e) Distribution of values of nest density and agroforest density, in the whole landscape (in black), in areas of high negative correlation (in blue) and in areas of high positive correlation (in red). The dotted vertical lines show the mean values of the distribution [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]



**FIGURE 6** (a) Multiscale correlation map from the comparison between the density of nests and the density of forest fragment. Areas of high positive correlation are surrounded in red (CMP > 0.6) and high negative correlation in blue (CMP < -0.6). (b) and (c) Distribution of values, respectively of density of nests and density of forest fragments, in the whole landscape (in black), in areas of high negative correlation (in blue) and in areas of high positive correlation (in red) [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

resources, hosting about 167 different tree species, a majority of them being bee pollinated (Bhagwat et al., 2005; Krishnan, 2011; Sivaram et al., 2012). Nonetheless, these forest patches cover very small areas of the landscape and their importance as foraging locations might therefore be much reduced. The fine- to broader-scale positive effect of agroforests might be explained by the availability of substantial foraging resources from shade trees. According to Krishnan (2011), coffee plantations present on average 80 to 120 bee pollinated trees in flower per hectare from more than 100 different species during the stay of *A. dorsata* in the landscape between January and June. The composition of each plantation and phenology of each species

are unique and bees might thus mix pollen and nectar from different plantations at various distances and at different period of time. This hypothesis is supported by other studies on bees (Sivaram et al., 2012; Williams & Tepedino, 2003). The diversity and abundance of native shade trees in coffee plantations and forest fragments might ensure spatiotemporal stability of nectar and pollen availability.

*Apis dorsata* nests were also associated with coffee agroforest regions where local habitat heterogeneity was high (CMP methods, confirmed by the GLM method in Table S1 in Appendix S1). In other words, bee nests are observed in coffee plantations that occurred close to natural forest patches, waterbodies, rice paddies and built-up

areas (see also Steffan-Dewenter et al. (2002), Winfree, Griswold, and Kremen (2007) for similar results in other agricultural contexts). The positive effect of land cover heterogeneity, as a proxy for resource heterogeneity, also suggests that *A. dorsata* responds positively to spatially separated resources and/or is not affected by the fragmentation of land cover. Although causation cannot strictly be inferred from our correlation statistics, the significance of the pattern observed across methods supports the hypothesis that *A. dorsata* responds to landscape supplementation and complementation (Dunning et al., 1992; Tschantke et al., 2012), where different patch types host different kinds of required resources, substitutable or not, used for different purposes or present at different periods of the year. Further data on resources and seasonal and annual population dynamics of *A. dorsata* would be an important next research step to confirm how complex landscapes facilitate resource use by honeybees.

## 4.2 | Importance of the agroforestry matrix

Our results reaffirm the importance of the agroforestry matrix to maintain the ecological function of pollination in the landscape (Perfecto & Vandermeer, 2008). The fine- to broader-scale positive effect of agroforests complements previous works on pollination in coffee landscapes that have tended to focus on the more local scale effects of the matrix (Jha & Vandermeer, 2010; Klein, Steffan-Dewenter, & Tschantke, 2003). The point-pattern analysis and surface-pattern analysis showed that nest presence and density are correlated to agroforests, not only at a single scale but across a characteristic range of scales, which is determined by the bee foraging range (Figures 3b and 4c). The apparent absence of response to agroforests at intermediate scales (between 300 and 1,000 m) might be explained by the fragmented nature of the tree cover, since the average extent of tree-covered regions is around 300 m (Figure 7) and might reveal the tolerance of honeybees to habitat fragmentation (Kennedy et al., 2013).

The CMP method revealed some modulations in the effect of the agroforestry matrix on nest distribution at larger scale. Although nests were consistently located in areas of moderate tree cover (Figure 5e), we highlighted two contrasting large-scale effects of agroforests in different parts of the landscape. In one region, agroforest tree cover increased with increasing distance from large aggregates of nests at scale over a few kilometres. Conversely, in another region of the landscape, agroforest tree cover decreased with increasing distance from small nest aggregates (Figure 5c,e). In other words, the broad-scale tree cover environment is high around large aggregates of nests and much lower around small aggregates. These results imply a positive feedback likely played by the tree cover on the presence of giant honeybee nests at broad scales (Figure 7). The nests tend to be isolated or few when the amount of tree-covered patches at broader scale is insufficient whereas the nests are numerous when the amount of agroforest patches are important within bees' foraging range. Subtle variations in tree cover appear to modulate population size of pollinators at the landscape scale. This again supports the idea that the agroforestry matrix contributes to spatiotemporal resource supplementation and complementation, an important element of population survival and reproduction (Miguet

et al., 2013; Riedinger, Mitesser, Hovestadt, Steffan-Dewenter, & Holzschuh, 2015). In addition, unlike forest fragments, coffee plants are characterized by temporary pulses of floral resources over a few weeks in February and March. This readily available and abundant resource (Sivaram et al., 2012) has been shown to coincide with the migration and settlement of *A. dorsata* nests between January and June (Krishnan, 2011). Similar studies have shown the importance of the availability of rich food sources for large aggregates of *A. dorsata* during the migration and nest establishment period (Singh et al., 2007).

In summary, we found similar, non-exclusive, positive effects of agroforests, forest fragments and land cover heterogeneity on the presence and number of nests in the landscape. Our multiscale approach highlights that effects are neither linear, nor uniform within the landscape, as shown by the low average value of CMP across the study zone or by the absence of nests in areas of highest density of forest fragments. It also involves different scales of response (fine scales for forest fragments and land cover heterogeneity, and broad scales for agroforests; Figure 7). Thus, the perspective that forests and natural habitats uniformly benefit bee presence (Garibaldi et al., 2011; Klein, Cunningham, Bos, & Steffan-Dewenter, 2008; Ricketts et al., 2008) appears to be more complex in heterogeneous landscapes, at least for *A. dorsata*.

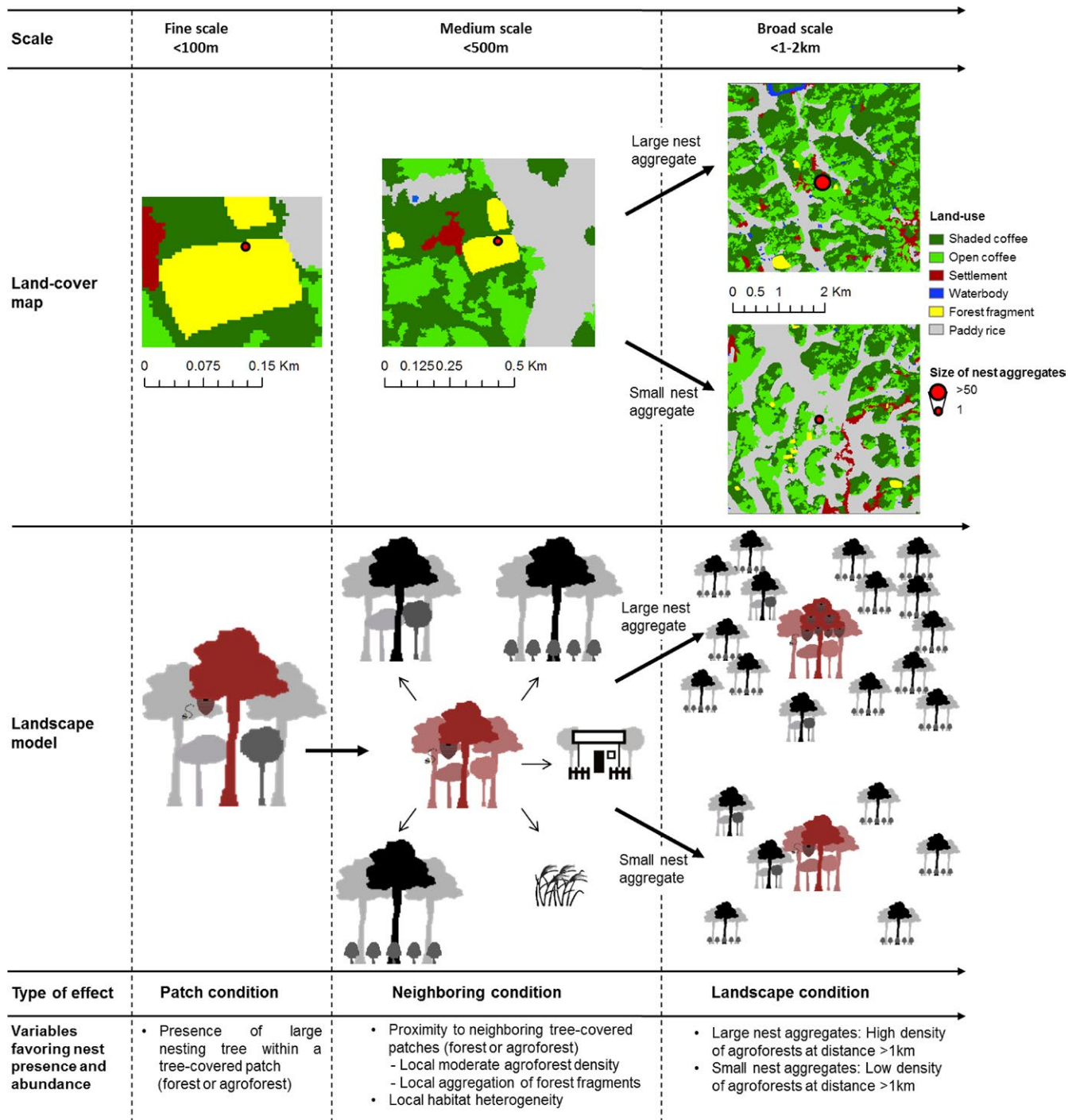
## 4.3 | Implications for landscape management

Despite significant contributions of honeybee pollination to coffee production (Krishnan et al., 2012), specific measures to protect wild populations are not common in local management practices (Ghazoul, 2007). The landscape analysis proposed in this study highlighted important implications for landscape management and pollination services. The heterogeneity in the spatial distribution of nests and presence of large aggregates, a tendency also observed among other eusocial bees (Singh et al., 2007; Wattanachaiyingcharoen, Wongsiri, & Oldroyd, 2008), is likely to translate into uneven pollination benefits for coffee farmers.

The study stresses the importance of considering multiple scales for management. At the agroforest scale, retaining large native shade trees would increase the availability of nesting resources and the spatiotemporal stability of foraging resources. Given that the size of individual plantations is much smaller (a few ha) than the foraging area covered by *A. dorsata* (around 1,000 ha), the benefits of conserving tree diversity would only be realized if it is scaled up across many plantations in the landscape.

Maintaining a complex heterogeneous landscape, including the preservation of remnant natural forest patches, would also favour *A. dorsata* populations. Other studies have also emphasized the need to retain small fragments of natural habitat within agricultural landscapes to support bee populations (Kremen et al., 2002), while our results additionally emphasize the value of landscape mosaic (Perfecto & Vandermeer, 2008). The results of the surface-pattern analysis on forest fragments showed that the presence of forest fragment is not systematically associated with the presence of nests; the conservation of forest fragments is thus not a sufficient condition for conserving pollinators. On the other hand, the fragmentation of tree cover at small scales (100s of metres) does not





**FIGURE 7** Synthesis of the multiple multiscale effects of tree-covered patches (coffee plantations and forest fragment) and land cover heterogeneity on the presence of nests. The spatial arrangement of land covers, as a proxy for nesting substrate, nesting sites and foraging resources, influences both nest presence and population size at different scales [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

appear detrimental for *A. dorsata*, as long as sufficient and diverse resources are available at the landscape scale (kms). Finally, the study allowed us to identify areas of conservation importance that sustain large aggregates of *A. dorsata* nests. Due to site fidelity of *A. dorsata* from 1 year to the next (Krishnan et al., 2012; Paar et al., 2000), those are the areas where trade-off between livelihood and conservation could be lean in towards conservation for the sake of the maintenance of populations of pollinators.

#### ACKNOWLEDGEMENTS

This work was funded by the EU Project PITN-GA-2013-608422 – IDP BRIDGES “Bridging Plant Sciences and Policy” and by the contribution of CIRAD, France. We thank the French Institute of Pondicherry for their support. We are grateful to all the people who helped in field work and land owners for allowing us to visit their plantations and forest plots. We thank two anonymous reviewers for their useful comments.

## AUTHORS' CONTRIBUTIONS

J.G., C.P. and C.Gar. conceived the ideas and designed methodology; C.P. collected the data; C.P. and C.Gau. analysed the data; C.P., C.Gau. and J.G. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

## DATA ACCESSIBILITY

Data are available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.132g8> (Pavageau, Gaucherel, Garcia, & Ghazoul, 2017).

## ORCID

Charlotte Pavageau  <http://orcid.org/0000-0003-3221-4372>

## REFERENCES

- Ambinakudige, S., & Sathish, B. N. (2009). Comparing tree diversity and composition in coffee farms and sacred forests in the Western Ghats of India. *Biodiversity and Conservation*, 18, 987–1000. <https://doi.org/10.1007/s10531-008-9502-5>
- Bhagwat, S. A., Kushalappa, C. G., Williams, P. H., & Brown, N. D. (2005). The role of informal protected areas in maintaining biodiversity in the Western Ghats of India. *Ecology and Society*, 10, 40.
- Boreux, V., Krishnan, S., Cheppudira, K. G., & Ghazoul, J. (2012). Impact of forest fragments on bee visits and fruit set in rain-fed and irrigated coffee agro-forests. *Agriculture Ecosystems & Environment*, 172, 42–48.
- Carre, G., Roche, P., Chifflet, R., Morison, N., Bommarco, R., Harrison-Cripps, J., ... Vaissiere, B. E. (2009). Landscape context and habitat type as drivers of bee diversity in European annual crops. *Agriculture Ecosystems & Environment*, 133, 40–47. <https://doi.org/10.1016/j.agee.2009.05.001>
- Dale, M. R. T., Dixon, P., Fortin, M. J., Legendre, P., Myers, D. E., & Rosenberg, M. S. (2002). Conceptual and mathematical relationships among methods for spatial analysis. *Ecography*, 25, 558–577. <https://doi.org/10.1034/j.1600-0587.2002.250506.x>
- Diggle, P. J. (1983). *Statistical analysis of spatial point patterns*. London, UK: Academic Press.
- Dormann, C. F., McPherson, J. M., Araujo, M. B., Bivand, R., Bolliger, J., Carl, G., ... Wilson, R. (2007). Methods to account for spatial autocorrelation in the analysis of species distributional data: A review. *Ecography*, 30, 609–628. <https://doi.org/10.1111/j.2007.0906-7590.05171.x>
- Dunning, J. B., Danielson, B. J., & Pulliam, H. R. (1992). Ecological processes that affect populations in complex landscapes. *Oikos*, 65, 169–175. <https://doi.org/10.2307/3544901>
- Dyer, F. C., & Seeley, T. D. (1991). Dance dialects and foraging range in 3 Asian honey-bee species. *Behavioral Ecology and Sociobiology*, 28, 227–233.
- Eltz, T., Bruhl, C. A., van der Kaars, S., & Linsenmair, K. E. (2002). Determinants of stingless bee nest density in lowland dipterocarp forests of Sabah, Malaysia. *Oecologia*, 131, 27–34. <https://doi.org/10.1007/s00442-001-0848-6>
- Garibaldi, L. A., Steffan-Dewenter, I., Kremen, C., Morales, J. M., Bommarco, R., Cunningham, S. A., ... Klein, A. M. (2011). Stability of pollination services decreases with isolation from natural areas despite honey bee visits. *Ecology Letters*, 14, 1062–1072. <https://doi.org/10.1111/j.1461-0248.2011.01669.x>
- Garibaldi, L. A., Steffan-Dewenter, I., Winfree, R., Aizen, M. A., Bommarco, R., Cunningham, S. A., ... Klein, A. M. (2013). Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *Science*, 339, 1608–1611. <https://doi.org/10.1126/science.1230200>
- Gaucherel, C. (2007). Multiscale heterogeneity map and associated scaling profile for landscape analysis. *Landscape and Urban Planning*, 82, 95–102. <https://doi.org/10.1016/j.landurbplan.2007.01.022>
- Gaucherel, C., Alleaume, S., & Hely, C. (2008). The comparison map profile method: A strategy for multiscale comparison of quantitative and qualitative images. *IEEE Transactions on Geoscience and Remote Sensing*, 46, 2708–2719. <https://doi.org/10.1109/TGRS.2008.919379>
- Gaucherel, C., Balasubramanian, M., Karunakaran, P. V., Ramesh, B. R., Muthusankar, G., Hely, C., & Couteron, P. (2010). At which scales does landscape structure influence the spatial distribution of elephants in the Western Ghats (India)? *Journal of Zoology*, 280, 185–194. <https://doi.org/10.1111/j.1469-7998.2009.00652.x>
- Ghazoul, J. (2005). Buzziness as usual? Questioning the global pollination crisis. *Trends in Ecology & Evolution*, 20, 367–373. <https://doi.org/10.1016/j.tree.2005.04.026>
- Ghazoul, J. (2007). Challenges to the uptake of the ecosystem service rationale for conservation. *Conservation Biology*, 21, 1651–1652.
- Ghazoul, J. (2013). Pollination decline in context. *Science*, 340, 923–924. <https://doi.org/10.1126/science.340.6135.923-b>
- Ghazoul, J. (2015). Qualifying pollinator decline evidence. *Science*, 348, 981–982. <https://doi.org/10.1126/science.348.6238.981-b>
- Goreaud, F., & Pelissier, R. (2003). Avoiding misinterpretation of biotic interactions with the intertype K-12-function: Population independence vs. random labelling hypotheses. *Journal of Vegetation Science*, 14, 681–692.
- Graf, R. F., Bollmann, K., Suter, W., & Bugmann, H. (2005). The importance of spatial scale in habitat models: Capercaillie in the Swiss Alps. *Landscape Ecology*, 20, 703–717. <https://doi.org/10.1007/s10980-005-0063-7>
- Jha, S., Bacon, C. M., Philpott, S. M., Mendez, V. E., Laderach, P., & Rice, R. A. (2014). Shade coffee: Update on a disappearing refuge for biodiversity. *BioScience*, 64, 416–428. <https://doi.org/10.1093/biosci/biu038>
- Jha, S., & Vandermeer, J. H. (2010). Impacts of coffee agroforestry management on tropical bee communities. *Biological Conservation*, 143, 1423–1431. <https://doi.org/10.1016/j.biocon.2010.03.017>
- Kennedy, C. M., Lonsdorf, E., Neel, M. C., Williams, N. M., Ricketts, T. H., Winfree, R., ... Kremen, C. (2013). A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. *Ecology Letters*, 16, 584–599. <https://doi.org/10.1111/ele.12082>
- Kim, J., Williams, N., & Kremen, C. (2006). Effects of cultivation and proximity to natural habitat on ground-nesting native bees in California sunflower fields. *Journal of the Kansas Entomological Society*, 79, 309–320. <https://doi.org/10.2317/0507.11.1>
- Klein, A. M., Cunningham, S. A., Bos, M., & Steffan-Dewenter, I. (2008). Advances in pollination ecology from tropical plantation crops. *Ecology*, 89, 935–943. <https://doi.org/10.1890/07-0088.1>
- Klein, A. M., Steffan-Dewenter, I., & Tscharntke, T. (2003). Pollination of *Coffea canephora* in relation to local and regional agroforestry management. *Journal of Applied Ecology*, 40, 837–845. <https://doi.org/10.1046/j.1365-2664.2003.00847.x>
- Knight, M. E., Martin, A. P., Bishop, S., Osborne, J. L., Hale, R. J., Sanderson, A., & Goulson, D. (2005). An interspecific comparison of foraging range and nest density of four bumblebee (*Bombus*) species. *Molecular Ecology*, 14, 1811–1820. <https://doi.org/10.1111/j.1365-294X.2005.02540.x>
- Kremen, C., Williams, N. M., Aizen, M. A., Gemmill-Herren, B., LeBuhn, G., Minckley, R., ... Ricketts, T. H. (2007). Pollination and other ecosystem services produced by mobile organisms: A conceptual framework for the effects of land-use change. *Ecology Letters*, 10, 299–314. <https://doi.org/10.1111/j.1461-0248.2007.01018.x>
- Kremen, C., Williams, N. M., & Thorp, R. W. (2002). Crop pollination from native bees at risk from agricultural intensification. *Proceedings of the National Academy of Sciences of the United States of America*, 99, 16812–16816. <https://doi.org/10.1073/pnas.262413599>

- Krishnan, S. (2011). *Pollinator services and coffee production in a forested landscape mosaic* (PhD Thesis), ETH Zurich.
- Krishnan, S., Kushalappa, C. G., Shaanker, R. U., & Ghazoul, J. (2012). Status of pollinators and their efficiency in coffee fruit set in a fragmented landscape mosaic in South India. *Basic and Applied Ecology*, 13, 277–285. <https://doi.org/10.1016/j.baae.2012.03.007>
- Li, H. B., & Reynolds, J. F. (1993). A new contagion index to quantify spatial patterns of landscapes. *Landscape Ecology*, 8, 155–162. <https://doi.org/10.1007/BF00125347>
- Miguet, P., Gaucherel, C., & Bretagnolle, V. (2013). Breeding habitat selection of Skylarks varies with crop heterogeneity, time and spatial scale, and reveals spatial and temporal crop complementation. *Ecological Modelling*, 266, 10–18. <https://doi.org/10.1016/j.ecolmodel.2013.06.029>
- Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, 403, 853–858. <https://doi.org/10.1038/35002501>
- Paar, J., Oldroyd, B. P., & Kastberger, G. (2000). Giant honeybees return to their nest sites. *Nature*, 406, 475–475.
- Pavageau, C., Gaucherel, C., Garcia, C., & Ghazoul, J. (2017). Data from: Nesting sites of giant honeybees modulated by landscape patterns. *Dryad Digital Repository*, <https://doi.org/10.5061/dryad.132g8>
- Perfecto, I., & Vandermeer, J. (2008). Biodiversity conservation in tropical agroecosystems – A new conservation paradigm. *Annals of the New York Academy of Sciences*, 1134, 173–200. <https://doi.org/10.1196/annals.1439.011>
- Potts, S. G., Biesmeijer, J. C., Kremen, C., Neumann, P., Schweiger, O., & Kunin, W. E. (2010). Global pollinator declines: Trends, impacts and drivers. *Trends in Ecology & Evolution*, 25, 345–353. <https://doi.org/10.1016/j.tree.2010.01.007>
- Potts, S. G., Vulliamy, B., Roberts, S., O'Toole, C., Dafni, A., Ne'Eman, G., & Willmer, P. (2005). Role of nesting resources in organising diverse bee communities in a Mediterranean landscape. *Ecological Entomology*, 30, 78–85. <https://doi.org/10.1111/j.0307-6946.2005.00662.x>
- Ricketts, T. H., Regetz, J., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C., Bogdansk, A., ... Viana, B. F. (2008). Landscape effects on crop pollination services: Are there general patterns? *Ecology Letters*, 11, 499–515. <https://doi.org/10.1111/j.1461-0248.2008.01157.x>
- Riedinger, V., Mitesser, O., Hovestadt, T., Steffan-Dewenter, I., & Holzschuh, A. (2015). Annual dynamics of wild bee densities: Attractiveness and productivity effects of oilseed rape. *Ecology*, 96, 1351–1360. <https://doi.org/10.1890/14-1124.1>
- Roy, P., Leo, R., Thomas, S. G., Varghese, A., Sharma, K., Prasad, S., ... Davidar, P. (2011). Nesting requirements of the rock bee *Apis dorsata* in the Nilgiri Biosphere Reserve, India. *Tropical Ecology*, 52, 285–291.
- Samejima, H., Marzuki, M., Nagamitsu, T., & Nakasizuka, T. (2004). The effects of human disturbance on a stingless bee community in a tropical rainforest. *Biological Conservation*, 120, 577–587. <https://doi.org/10.1016/j.biocon.2004.03.030>
- Schroder, B., & Seppelt, R. (2006). Analysis of pattern-process interactions based on landscape models – Overview, general concepts, and methodological issues. *Ecological Modelling*, 199, 505–516. <https://doi.org/10.1016/j.ecolmodel.2006.05.036>
- Singh, R. P., Singh, A. K., & Singh, R. P. (2007). The effect of the availability of bee forage and environmental conditions on the nesting of *Apis dorsata* Fabr. *Journal of Apicultural Research*, 46, 276–281.
- Sivaram, V., Roopa, P., Shubharani, R., & Suwannapong, G. (2012). Pollen analysis in honeys collected from Karnataka region of Nilgiri Biosphere, South India. *Journal of Apiculture*, 27, 223–231.
- Steffan-Dewenter, I., Munzenberg, U., Burger, C., Thies, C., & Tscharntke, T. (2002). Scale-dependent effects of landscape context on three pollinator guilds. *Ecology*, 83, 1421–1432. [https://doi.org/10.1890/0012-9658\(2002\)083\[1421:SDEOLC\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[1421:SDEOLC]2.0.CO;2)
- Steffan-Dewenter, I., & Westphal, C. (2008). The interplay of pollinator diversity, pollination services and landscape change. *Journal of Applied Ecology*, 45, 737–741.
- Tews, J., Brose, U., Grimm, V., Tielborger, K., Wichmann, M. C., Schwager, M., & Jeltsch, F. (2004). Animal species diversity driven by habitat heterogeneity/diversity: The importance of key-stone structures. *Journal of Biogeography*, 31, 79–92. <https://doi.org/10.1046/j.0305-0270.2003.00994.x>
- Thomas, S. G., Varghese, A., Roy, P., Bradbear, N., Potts, S. G., & Davidar, P. (2009). Characteristics of trees used as nest sites by *Apis dorsata* (Hymenoptera, Apidae) in the Nilgiri Biosphere Reserve, India. *Journal of Tropical Ecology*, 25, 559–562. <https://doi.org/10.1017/S026646740900621X>
- Tscharntke, T., Tylianakis, J. M., Rand, T. A., Didham, R. K., Fahrig, L., Batary, P., ... Westphal, C. (2012). Landscape moderation of biodiversity patterns and processes – eight hypotheses. *Biological Reviews*, 87, 661–685. <https://doi.org/10.1111/j.1469-185X.2011.00216.x>
- Wattanachaiyingcharoen, W., Wongsiri, S., & Oldroyd, B. P. (2008). Aggregations of unrelated *Apis florea* colonies. *Apidologie*, 39, 531–536. <https://doi.org/10.1051/apido:2008045>
- Williams, N. M., & Kremen, C. (2007). Resource distributions among habitats determine solitary bee offspring production in a mosaic landscape. *Ecological Applications*, 17, 910–921. <https://doi.org/10.1890/06-0269>
- Williams, N. M., & Tepedino, V. J. (2003). Consistent mixing of near and distant resources in foraging bouts by the solitary mason bee *Osmia lignaria*. *Behavioral Ecology*, 14, 141–149. <https://doi.org/10.1093/beheco/14.1.141>
- Winfree, R., Griswold, T., & Kremen, C. (2007). Effect of human disturbance on bee communities in a forested ecosystem. *Conservation Biology*, 21, 213–223. <https://doi.org/10.1111/j.1523-1739.2006.00574.x>

## SUPPORTING INFORMATION

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

**How to cite this article:** Pavageau C, Gaucherel C, Garcia C, Ghazoul J. Nesting sites of giant honeybees modulated by landscape patterns. *J Appl Ecol*. 2018;55:1230–1240. <https://doi.org/10.1111/1365-2664.13069>