LANDSCAPE EFFECTS ON BEE POLLINATORS IN A TROPICAL AGROECOSYSTEM

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ABSTRACT

Land-use change and intensification are among the most important drivers of species loss and the degradation of ecosystem functions. Agricultural areas occupy nearly 40% of the Earth's surface, thus efforts to mitigate the ecological effects of land-use intensification should focus in part on utilizing more sustainable food production practices that enhance species persistence within farms.

Bees (superfamily Apoidea) are widely considered the most important pollinators globally for both wild plant pollination and agricultural production. Global declines of managed and wild bees threaten the delivery of pollination services to agriculture.

In my first two chapters, I present results of research conducted in a coffee-dominated agricultural landscape in Costa Rica. I explore the extent to which coffee farm intensity (e.g., "sun" coffee vs. "shade" coffee) affects bee community dynamics. Chapter 1 focuses on how land-use intensity mediates the distribution and relative abundance of bee functional traits that are thought to be important for pollination. Chapter 2 explores how land-use context within an agroecosystem affects bee diversity and stability at the community scale. Both functional diversity, and diversity-stability relationships are community patterns that have been demonstrated to have a mechanistic relationship to ecosystem functioning (e.g., pollination).

We found that landscape context does influence functional trait distributions and relative abundance in bee communities in a coffee agroecosystem, implying that landscape context moderates the trait composition of bee communities. Further, we

found that the traits that responded to landscape elements are traits considered important for delivery of pollination services within farms. We also elucidate how landscape-scale intensification of coffee agroforestry practices reduces community-scale stability of bees by synchronizing their populations through time.

My third chapter is framed within the heuristic of "Social-Ecological Systems" as part of the University of Idaho's Integrative Graduate Education and Research Traineeship (IGERT) program. Here my co-authors and I show that natural resource management challenges may be aided by embarking on a thorough exploration of the spatio-temporal scales at which biophysical processes and natural resource governance operate, with an emphasis on spatio-temporal scale "mis-fit" (i.e., when biophysical processes that provision a resource are managed at improper scales).

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Social-Ecological Resilience and were a pleasure to interact with. I am most thankful to my family who made this possible through kind actions.

DEDICATION

This work is dedicated to Eva and Elliot. Your glorious spirits served as motivation during the most difficult times.

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CHAPTER 1

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1.1 ABSTRACT

Previous research suggests that the strength of the biodiversity-ecosystem process relationship is determined more by the distribution of relevant functional traits in a species community than simply the number of species present. In agroecosystems, many ecosystem processes (e.g., pollination) directly benefit farmers, and can therefore be considered "services". Thus, efforts to manage these services by enhancing biological diversity may present a "win-win" scenario for conservation scientists and farm owners. Many agricultural landscapes are composed of a patchwork of landscape elements (e.g., farms that employ various types of management practices, non-crop habitat patches, etc). Research within the domain of Countryside Biogeography has demonstrated that the configuration of these mosaic landscapes can have dramatic effects on biological diversity. However, while we know that landscape patterns can affect species richness, we know little about how these patterns affect functional diversity – which is a more mechanistic indicator of ecosystem processes.

Here we present results from a field study in a coffee agroforestry system in Costa Rica that elucidates the effects of landscape composition on bee functional diversity. We chose to focus on two characteristics of landscape mosaics that have been

shown to be important predictors of changes in biological diversity: (i) patch size, and (ii) matrix intensity. Because coffee in the region mass-blooms for a brief period once per year, we were able to explore how landscape effects changed based upon the strength of the contrast between landscape elements. That is, when coffee is mass-blooming, the ubiquitous presence of floral resources within coffee farms may reduce the effects of landscape elements on bee communities.

Bees were sampled in 19 forest patches along a gradient of patch size and matrix intensity in the Tarrazu region of Costa Rica. Our results show clearly that both patch size and matrix intensity affect bee functional diversity in forests embedded within coffee farms. In intensive landscapes (i.e., forest patches embedded within high-intensity matrices), forest patches never had high values of functional diversity, irrespective of forest patch size. Conversely, in less intensively managed landscapes, functional diversity increased considerably with relatively small increases in forest patch size. However, when coffee was mass-blooming, and the contrast between landscape elements was less pronounced, neither forest patch size nor matrix intensity was a significant predictor of bee functional diversity.

1.2 Introduction

Ecosystem services delivered to agriculture have been highlighted as a potential "win-win" scenario for maintaining viable agricultural production while conserving biodiversity (Gurr et al. 2003, Tscharntke et al. 2005, Daily and Matson 2008, Isaacs et al. 2009, Benayas and Bullock 2012). Mounting evidence suggests that remnant natural

areas embedded within agricultural landscapes (i.e., habitat patches within the intervening "matrix") serve as sources of organisms beneficial to agriculture (Ricketts 2004, Tscharntke et al. 2005, Bianchi et al. 2006). Natural areas tend to harbor higher levels of species diversity than managed agricultural areas, potentially enhancing ecosystem service delivery from natural areas to managed ones due to the positive relationship between biodiversity and ecosystem function (Tilman 2001, Hooper et al. 2005).

Pollination is a key ecosystem service for agriculture as it results in higher fruit, vegetable, and seed sets for the majority of the worlds' major entomophilous crops (Klein et al. 2007). Meta-analyses have shown that crop plants located close to natural areas are visited more often, and by more pollinator species, than crop plants more distant from natural areas (Garibaldi et al. 2011a). This "spillover" of wild bee pollinators from natural areas to managed ones enhances crop yields irrespective of the presence of managed honey-bees (Garibaldi et al. 2013), suggesting that some dimension of pollinator diversity is responsible for enhancing pollination functioning.

Two of the mechanistic explanations for why pollination function is higher with more diverse pollinator communities are: (i) portfolio or sampling effects, and (ii) niche complementarity and/or facilitation (Hooper et al. 2005, Tscharntke et al. 2005). In the context of pollination, species-rich communities (i.e., large species portfolio) may be more likely to contain pollinators that are particularly well suited to pollinate a specific plant (e.g., "trait matching" [Garibaldi et al. 2015]). With respect to niche complementarity, plant-pollinator relationships appear to show a high degree of

partitioning and foraging specialization (Blüthgen et al. 2007, Weiner et al. 2011), in turn affecting pollination function via niche differentiation.

The importance of both portfolio effects and complementarity is based upon the premise that the composition and range of organismal traits in a community (i.e., functional diversity) determine how ecosystems function (Tilman 2001). Functional diversity can be decomposed into at least two components: (i) "functional effect" diversity, and (ii) "functional response" diversity (Laliberté et al. 2010, Mori et al. 2012). "Functional response" diversity refers to the suite of functional organismal traits important for adaptations and/or responses to local environmental conditions. For example, small habitat patches may contain fewer species of small-bodied pollinators (often estimated based upon intertegular distance [ITD]) because small organisms are less likely to be capable of dispersing over large enough distances to augment limited resources typically associated with small habitats (Bommarco et al. 2010). Above-ground nesting bees are less susceptible to tillage than below-ground nesters (Williams et al. 2010) and small-bodied pollinators with short tongues are more affected by fire disturbance than long-tongued larger-scale dispersers (Moretti et al. 2009). In this way habitat loss and landscape context may differentially affect organisms based upon relevant life-history traits.

"Functional effect" diversity refers to the composition of traits in a community that affect ecosystem processes. For example, plant reproduction is mediated by a diverse suite of pollinator traits and behaviors, such as body size, tongue length, degree of sociality, flower handling, time of day of visitation, and differences in visitation to

different flower strata (Klein et al. 2003, Fontaine et al. 2006, Hoehn et al. 2008, Albrecht et al. 2012).

For pollinators, many "effect" traits are also "response" traits (e.g., tongue length, sociality, and body size). Thus, the composition of effect traits encountered within a pollinator community should be mediated by the interplay between response trait composition and environmental conditions. For example, if small, isolated habitat patches favour large-bodied pollinators, the dimension of functional effect diversity related to body size will be compressed relative to that of a larger habitat patch. Mori et al. (2012) clarify this relationship and demonstrate that functional response diversity ultimately controls ecosystem functioning through species complementarity. If there are strong overlaps between functional response and effect traits, it could be hypothesized that communities that contain low functional response diversity will necessarily have limited functional effect diversity.

From a landscape perspective, large, well connected habitat patches should contain species-rich communities relative to small isolated patches (Hanski 1998, Daily et al. 2001, Steffan-Dewenter et al. 2002, Kremen et al. 2004, Krauss et al. 2009). Because of the relationship between species richness and functional diversity (Tilman 2001, Hooper 2005), these large patches should have high levels of functional diversity. As patches get smaller, the effect of non-habitat becomes more pronounced, and matrix quality may be increasingly important for structuring communities within habitat patches (Donald and Evans 2006, Tscharntke et al. 2012).

Diversified farming systems, such as "high shade" coffee (*sensu* Moguel and Toledo 1999; Fig. 1.1), where coffee shrubs are grown within a complex canopy of

shade and crop plants, may enhance matrix quality by providing additional floral and nesting resources to pollinators (Vandermeer and Perfecto 2007, Perfecto and Vandermeer 2008, Jha and Vandermeer 2010, Garibaldi et al. 2014). While coffee is self-compatible, animal pollination is thought to increase fruit set and quality (Roubik 2002, Ricketts 2004, Klein et al. 2003, Garibaldi et al. 2011b), potentially setting up a "win-win" scenario for conservation and pollination service delivery. Numerous studies have demonstrated that low-intensive coffee management (e.g., farming that utilizes "high shade" management practices), results in higher planned and associated biodiversity at the farm scale (Perfecto and Vandermeer 2002, Perfecto et al. 2007, Philpott et al. 2008). However, it remains unclear the extent to which matrix quality affects biological diversity in adjacent habitat patches (Blitzer et al. 2012).

Our aim was to explore how landscape context and farm management practices interact to structure an aspect of biodiversity, namely functional diversity, that directly relates to the ecosystem function of pollination. From an applied perspective, understanding the importance of small habitat patches for harbouring pollinator communities should improve landscape-scale management for ecosystem services. Natural and semi-natural patches embedded within simplified landscapes are thought to be important for enhancing functional connectivity at landscape scales (Rozenfeld et al. 2008, Urban et al. 2009, Bodin and Saura 2010), suggesting that conservation of these areas as sources of ecosystem service delivery may also result in enhanced connectivity for a diversity of organisms at landscape scales. Moreover, clarifying the effects of matrix quality on functional diversity focuses management actions on

managed lands – precisely where interventions are likely most plausible (Donald and Evans 2006, Benton et al. 2007).

We sampled bees in a series of forest patches of varying size within a coffee agroforestry-dominated landscape in which farm management practices range from intensive to moderately extensive. We hypothesized that patches of semi-natural habitat (i.e., forest patches) will contain relatively high levels of biodiversity, and therefore functional diversity, but that this relationship will be mediated by matrix quality (i.e., coffee management intensity). We expected to find that bee community structure in forest patches strongly relates to the interaction between bee functional traits and landscape context, as has been found in other studies (Moretti et al. 2009, Bommarco et al. 2010, Williams et al. 2010). We extended this analysis to include an aspect of biodiversity, "functional diversity", that is potentially more relevant to ecosystem function (e.g., pollination) than simply species richness. Here we examine the effects of matrix quality and habitat size on bee functional response diversity, defined by the distribution of traits found within each bee community.

1.3 Materials and Methods

Study Sites and Regional Characteristics

Bees were sampled in forest patches within 5 counties (Cartago, Desamparados, Dota, León Cortez, and Tarrazu) in west central Costa Rica (Fig. 1.2). There are nearly 500 remnant forest patches in the area ranging in size from very small (< 1 ha) to very

large (> 2,000 ha); 90% of the forest patches are 1 – 10 ha in size. The predominant land-use in the area is coffee, which comprises about 65% of total land area (INECa 2014). Coffee management practices in the region are varied, but range from intensive "unshaded monoculture" to more extensive "commercial polyculture". Coffee blooms primarily once per year in the region, typically beginning in April and lasting approximately 3-5 weeks (L. Keesecker, *personal observation*); thus a mass of floral resources is available during a relatively short period of time annually.

A total of 19 forest patches, ranging in size from 0.3 to 16.4 hectares, was selected for sampling; all sampling locations were located between 1,200 – 1,800 m in elevation (Table 1.3). In 2013, bee sampling was conducted between February – March (pre-coffee flowering, dry season), April – May (during the coffee flowering, dry season), August – September ("shoulder" season, a mix of wet and dry season conditions, post coffee flowering), and October – November (wet season, post coffee flowering). In 2014, bee sampling was conducted during the same periods as in 2013, except that the wet season (October – November) was not sampled (Table 1.2). The order in which each set of 19 forest patches was sampled was randomized within each sample period across sample years to control for the influence of temporal biases. Bee traps (see below) were deployed for 5-day periods at each location in all seasons.

Data on rainfall and temperature were collected from regional weather stations (ICAFE 2015) and summarized over each of the collection periods. The average 6-day high temperature, and the total 6-day rainfall were calculated for each sample period (Table 1.3). Sample locations were associated with proximate weather stations (Frailes,

San Carlos, San Lorenzo, and Santa Maria) based upon shortest Euclidean distance; all forest patches were located within 5-km of at least one of the four weather stations.

Bee Traps

Bees were sampled using two types of passive sampling; Blue Vane traps (Stephen and Rao 2005) and pan traps. Blue Vane traps consist of a yellow base, filled with soapy water (odorless and colorless), with a blue funnel-like top through which organisms navigate into the yellow base; the funnel design prevents organisms from escaping once inside the yellow base. Pan traps, small plastic bowls with a mixture of water and colorless, odorless dish soap, were either painted with fluorescent blue or yellow paint, or were left white. For the Blue Vane traps, two types of trap configurations were used; terrestrial traps consisted of a bamboo pole (~ 2-m in height) fastened with a perpendicular post from which the Blue Vane traps could be suspended (Fig. 1.3). Aerial traps consisted of Blue Vane traps that were elevated using a rope and pulley into the canopy of the forest patches (Fig. 1.4). Heights of aerial traps (between 3-m – 20-m) varied based upon the height of the forest canopy. Pan traps (2 white, 1 blue, and 1 yellow) were positioned approximately 1 m above the ground using platforms, which were fastened to the terrestrial bamboo poles (Fig. 1.3); pan traps were not used as part of the aerial trap configuration. The elevation and aspect of each trap was calculated using the Spatial Analyst extension in ArcGIS 10.1 (ESRI 2012), based upon a 30-m resolution digital elevation model (DEM) of Costa Rica (INECb 2014).

Both Blue Vane traps and pan traps were filled to approximately half their respective volumes with the soapy water mixture. Small holes (~1-cm) were drilled midway around the circumference of both Blue Vane and pan traps to improve drainage and prevent overflow during rainy periods. Screen was placed on the outside of each hole to prevent the loss of specimens through the drain holes. For each forest patch the number of bee traps was scaled to patch area (2 terrestrial traps/ha; 1 aerial trap/ha). Because it is believed that light reflectance is an important factor in attracting bees to both Blue Vane and pan traps, canopy cover (a proxy for light penetration through the forest canopy) was estimated using a densiometer at each trap location. Bees were collected from each trap after each 5-day sample period and placed in small plastic bags filled with 70% isopropyl alcohol. Once processed, bees were coded with unique identifiers and pinned to dry.

Bees were exported to the US and identified to species or the nearest taxon at the USDA-ARS Bee Laboratory in Logan, UT. Intertegular distance (ITD), a proxy for body size (Cane 1987), was measured using a Keyence digital optical microscope (VHX-500F). Five female individuals from each species were used to measure ITD, and the average of these five measurements was used as the ITD for the entire group. For species with less than five individuals, all individuals were measured for ITD and then the value was averaged. For the few species where no females were captured, ITD for males was measured and used as the ITD for the entire species. Other life-history traits, such as feeding specialty, degree of sociality, and nest location, were determined based upon expert knowledge (Table 1.4) (Terry Griswold, *personal communication*).

Forest Patch Characteristics

Forest patch characteristics were measured using a combination of field surveys and satellite imagery. At each bee trap, 20-m transects, oriented east to west, were used to sample flowering plants within 1m of the transect. Because bee traps were located proportionally based upon forest patch size, the number of flowering plant transects (which originate at each bee trap location) increased with forest patch size (i.e., three 20-m transects/ha of forest). Plants were identified to species, or in some cases morphospecies, and the diameter at breast height was measured for every tree within each transect. Canopy cover was estimated at the endpoints of each transect using a densiometer.

Landscape Context

Matrix quality was determined using a Land-Use/Land-Cover (LULC) classification developed from Worldview-2 satellite imagery taken in 2012 within a 1-km buffer of 16 of the 19 focal forest patches (Table 1.1); imagery for the remaining three forest patches is currently unavailable. Several studies have shown that bee communities respond to landscape effects within ~ 1-km of sample locations (Steffan-Dewenter et al. 2002, Kremen et al. 2004), and this relationship has also been demonstrated for bees in Costa Rica (Brosi et al. 2007). Buffers for each forest patch were created using ArcGIS 10.1 (ESRI 2012).

The satellite imagery was used to classify LULC in the following categories: (1) sun coffee (i.e., coffee monoculture), (2) shade coffee (i.e., coffee polyculture that includes a relatively complex overstory, such as the intercropping of banana within farms), (3) urban, (4) pasture, and (5) exposed soil (Table 1.1). Forest patches were difficult to discriminate based upon the classification algorithm, thus forest patches were manually digitized based upon the imagery (de Jesús et al. 2016). Details of LULC classification can be found in de Jesús et al. (2016).

Land-use intensity was estimated based upon the proportion of a subset of LULC categories as follows:

$$LUI_i = 100 - F_i + 0.5Sh_i + .35S_i + 0.2P_i + 0.1BU_i$$

where, F_i, SH_i, S_i, P_i, and BU_i are the proportions of forest, "shade" coffee, "sun" coffee, pasture, and bare-urban, respectively within 1-km of each forest patch *i* (Table 1.1). Weighting coefficients for each land-use category are based upon expert opinion (Lonsdorf et al. 2009) on the effects of these categories on nesting and floral resources for bees. The coefficients used here are based upon those that Lonsdorf et al. (2009) used in their significantly predictive bee community models that were validated in a Costa Rican landscape with similar land-use types.

Shade Tree Inventory

Shade trees used within coffee farms were surveyed in 2015 within 108 sample plots in the region. Sample plots were located at distances between 50-m - 500-m from proximate forests. At each plot a 10-m x 10-m quadrat was established; within each

quadrat, all shade tree species identities were recorded by a parataxonomist (Table 1.5).

Statistical Analyses

Rao's quadratic entropy index (FD_Q) and community-weighted-mean (CWM) trait values were calculated for each forest patch, for each of 9 sampling events, using the FD package in the program R (R Development Core Team, 2014); all statistical models were created using the lme4 package in R (Bates et al. 2014). FD_Q is the "sum of distances between pairs of species in trait space, weighted by the product of their relative abundances" (Weiher 2001; pg 182). Thus, calculations of FD_Q require an inventory of species, their relative abundances, and their associated traits (e.g., tongue length, ITD, etc.) (Table 1.4). CWM is the mean value of a trait in a community based upon the relative abundance of species in a community that possess that trait (Lavorel et al. 2007).

To evaluate the effects of land-use intensity, forest patch size, and coffee flowering on FD_Q, we fit a linear mixed effects model with FD_Q as the response variable, and land-use intensity, forest size, and coffee flowering (binary; "yes" or "no") as explanatory variables. FD_Q index values were arcsine-square-root transformed, and forest patch size was log-transformed, to attain an approximately normal distribution for each variable. Because the number of traps varied based upon forest patch size, we included the number of traps as a random factor; thus model intercept estimates vary depending upon the number of traps used within each forest patch. Several models

were compared that used different types of variable interaction combinations. We used backwards step-wise model selection to identify the model with the highest predictive ability (Table 1.6).

Trait types dictated how CWM values were categorized; tongue length, nest location, social status, and feeding specialty are binary; ITD is continuous (Table 1.4). We fit separate models for each CWM trait category, where each trait was the response variable, and LUI, forest patch size, and coffee flowering were explanatory variables (Table 1.7). As with the FD_Q analysis, we also used backwards step-wise selection to identify models with the highest predictive ability for each trait category.

The species accumulation curve for the study area was generated using the specaccum function in the package "vegan" in the program R (R Development Core Team, 2014). The sample-based species accumulation curve, with replacement, was generated using the Coleman method (Coleman et al. 1982).

1.4 Results

We collected 2,455 individual bees from 92 species (Table 1.4). Each forest patch was sampled a total of nine times over the course of the study, which includes samples in each of the three predominant seasons ("wet", "dry", and "shoulder"), before, after, and during mass coffee flowering events (Table 1.2); each sample event included both aerial and terrestrial trapping methods. Over the course of the study, pan traps

were deployed for a total of over 4,000 sample days; Blue Vane traps were deployed for about 6,000 sample days. Pan traps collected only 606 individuals, while Blue Vane traps collected 1,849 individuals.

The species accumulation curve for the bee community did not saturate (Fig. 1.5), suggesting that we were not able to detect all species within the community. However, previous research on bee pollinators in Costa Rica has been limited similarly (Brosi et al. 2008). Different trapping methods captured different aspects of bee biological diversity in this study; Blue Vane traps generally captured a wider range of biodiversity (measured here by Shannon's index, H') within bee communities than pan traps (Fig. 1.6), while aerial and terrestrial Blue Vane traps captured different proportions of bee tribes (Fig. 1.7). Thus, while we were not able to sample the entire community, the distribution of species captured by the various trapping methods indicates a reasonable level of variation sufficient to make relatively generalizable inferences. Exploratory data analysis did not suggest that rainfall or temperature (Table 1.3) were related to FD_Q or CWM and therefore these weather variables are not included in the analysis.

Land-use intensity and forest patch size were predictive of FD_Q (Table 1.6). As hypothesized, the combination of low-intensive land-use within the matrix and large forest patch size contributed to high levels of bee functional diversity in forest patches (Fig. 1.8). However, this relationship varied depending upon whether the coffee plants were mass-blooming (Fig. 1.8, Table 1.6). The interaction between coffee flowering and land-use intensity was significant in the linear mixed effects model that was most predictive (Table 1.6), as indicated by Fig. 1.8.

For comparison, we used the same statistical modeling framework as with the FD_Q analysis, but with species richness and Shannon's index (H') as response variables. Both species richness and H' increased with forest patch size, and this relationship was also mediated by land-use intensity, though to a weaker degree than FD_Q (Figs. 1.9 & 1.10, Table 1.6); coffee flowering was not a significant predictor in either the species richness or H' models (Table 1.6).

Because FD_Q is an aggregate measure of functional diversity, we additionally ran separate analyses for each of the CWM trait categories in order to disentangle how landscape context affects individual trait values. Various combinations of coffee flowering, forest patch size, and land-use intensity were statistically significant predictors of CWM trait values (Table 1.7). Long-tongued bees dominated communities in intensively managed landscapes (Fig. 1.11), but the strength of this relationship depended upon whether coffee was mass-blooming or not. There were no statistically significant effects of either forest patch size, or land-use intensity, on weighted-mean nest location (Table 1.7).

In terms of inter-tegular distance, relationships with forest patch size and land-use intensity were highly non-linear (Fig. 1.12). Small forest patches located within intensive landscapes tended to have more large-sized bees, while small forest patches in landscapes where landscape intensity was low had more small-bodied bees.

Neither sociality (social/solitary) nor nest location (above-ground/below-ground) responded either land-use intensity or forest patch size (Table 1.7); both functional traits were significantly predicted by coffee flowering. Feeding speciality

(oligolectic/polylectic) was sensitive only to land-use intensity, with oligolectic feeders dominating in high intensive matrix types (Table 1.7, Fig. 1.13)

1.5 Discussion

Anthropogenic changes to ecosystems, such as land-use intensification for agriculture, have been shown to alter a variety of ecological processes and patterns (Vandermeer and Perfecto 2007, Kennedy et al. 2010). Here we present empirical evidence that suggests that land-use intensity affects how traits are distributed within bee communities in semi-natural habitat patches in simplified landscapes. Because species' traits are directly related to many important ecosystem processes (Roscher et al 2012, Wood et al. 2015), such as pollination (Fontaine et al. 2006, Hoehn et al. 2008, Frund et al. 2013), it is imperative that researchers understand how landscape context affects this aspect of biological diversity (Tscharntke et al. 2012).

Our primary hypothesis was that, while relatively small patches of semi-natural habitat may contain high levels of biodiversity, and therefore high levels of functional diversity, the relationship between patch size and biological diversity would be mediated by matrix intensity. Our results clearly demonstrate this pattern along several dimensions of functional diversity.

First, FD_Q, an aggregate measure of abundance-weighted distances between species in trait space (Weiher 2011), was sensitive to patch size, land-use intensity, and coffee flowering (Fig. 1.8). When coffee is in mass-bloom, and the contrast between landscape elements may therefore be less pronounced in terms of floral resources,

neither forest patch size nor LUI was an important predictor of FD_Q values. However, when coffee was not mass-blooming, FD_Q values responded to both patch size and land-use intensity in ways that align with theory. For example, the familiar island/ocean model of Island Biogeography predicts reductions in species richness in patches of small size. When land-use intensity is high, and therefore the matrix may essentially be perceived as an "ocean" of few floral and nesting resources, FD_Q estimates are low, particularly in small forest patches; as patch size increases, FD_Q also increases, but this relationship is more pronounced in less intensive landscapes (Fig. 1.8). FD_Q values are always relatively low, irrespective of forest patch size, when land use intensity surrounding the patch is high. Essentially, our results demonstrate that the influence of landscape configuration on community functional diversity is most relevant when there are stark contrasts in landscape elements.

Additionally, our results suggest that focusing solely on species richness or biological diversity indices (e.g., H') may mask how landscape factors affect ecosystem functioning. Both species richness and H' increased linearly with forest patch size, and exhibited relatively weak relationships with land-use intensity; neither measure responded to coffee flowering (Table 1.6, Figs. 1.9 & 1.10). Thus, in our study area, matrix effects are only weakly predictive of two common measures of diversity (i.e., richness and H') implying that the matrix functions like a homogeneous "ocean" in which forest patches are embedded. However, when we "scaled down" our analysis to focus on trait diversity (i.e., FD_Q), based upon traits that are mechanistically linked to matrix quality, we uncovered patterns that would have otherwise gone unnoticed.

Analysis of community-weighted-mean (CWM) values elucidates how each of the traits used to calculate FD_Q respond to landscape elements. Several, but not all, of the CWM trait values responded to matrix quality. Tongue length, ITD, and feeding specialty all responded to changes in land-use intensity (Table 1.7, Figs. 1.11, 1.12 & 1.13). Forest patches embedded within intensive landscapes favor long-tongued bees of moderate body size. These results align well with theory; long-tongued bees may be able to forage for floral resources from flowers with both deep and shallow tubes. Larger-bodied bees can often disperse farther than small-bodied bees (Greenleaf et al. 2007), thus, it can be hypothesized that larger-bodied bees should be less affected by habitat loss and matrix intensification than small-bodied bees; our results demonstrate this phenomenon (Fig. 1.12, Table 1.7).

Feeding specialty was also sensitive to matrix quality. When land-use intensity values are relatively low, bee communities are dominated by polylectic (i.e., generalist) feeders. At high values of land-use intensity the community switches and is dominated by oligolectic (i.e., specialist) feeders (Fig. 1.13). One possible explanation for this phenomenon is that high quality matrices provide a relatively diverse array of floral resources that can be exploited by generalists (Table 1.5). As land-use intensity values increase, and thus matrix quality decreases, there are fewer types of floral resources available. It is possible that specialized feeders outcompete generalist feeders for these resources, resulting in bee communities dominated by specialists.

From an applied perspective, our results suggest that small semi-natural areas (e.g., the forest patches in this study) in intensive landscapes may not contain sufficient levels of functional diversity to adequately function as pollination service providers

even if they "spillover" into managed agricultural areas. However, when landscape composition is less intensive, relatively small increases in forest patch size can have marked effects on bee FD_Q, and CWM trait categories (e.g., tongue length, body size, and feeding specialty). Our results suggest that "the matrix" does indeed mediate bee functional diversity via the interaction between matrix quality and semi-natural patch area.

A promising area of research is to clarify the extent to which the functional composition of bees (e.g., functional diversity) within semi-natural areas relates to the types of functional traits exhibited by bees actually visiting flowering crops. A key goal for future studies should be to quantify the effects of aggregate measures of functional diversity, such as FD_Q, on ecosystem functions, like pollination. As far as we are aware, no studies have attempted to measure this; however, our results on functional diversity patterns within semi-natural areas along a gradient of intensity should inform future work aimed at elucidating the effects of functional diversity "spillover" into managed systems.

Moreover, the fact that FD_Q, as well as several individual traits, responded to the mass flowering of a ubiquitous crop within the matrix, implies that there may be important temporal dynamics with respect to bee functional diversity at landscape scales. Future research aimed at disentangling how patch size and matrix quality interact to affect the temporal stability and/or asynchrony of functional traits would aid in our understanding of how functional traits are distributed through time.

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TABLE 1.1 SUMMARY OF FOREST PATCH CHARACTERISTICS. Forest patch characteristics for each of 19 sample patches. Land-use intensity is derived from the proportion of each Land-Use/Land-Cover (LU/LC) type within a 1-km buffer of each forest patch. Three of the forest patches were located in an area without existing imagery needed for LU/LC classification.

			Matrix Composition (% LU/LC)					
Forest No.	Elevation (m)	Size (ha)	Forest	"Shade" coffee	"Sun" coffee	Bare/Urban	Pasture	LUI
1	1493	1.1	6	40	31	7	16	59.25
2	1734	9	10	22	39	12	16	60.95
3	1425	2	4	53	22	7	15	58.1
4	1598	6.8	10	35	31	10	14	57.85
5	1718	1	3	45	28	8	16	60.7
6	1521	2.9	0	41	31	10	18	64.05
7	1578	3.7	7	39	29	7	18	59.05
8	1300	2	-	-	-	-	-	-
9	1645	3.2	5	47	21	9	17	59.85
10	1530	1.6	-	-	-	-	-	-
11	1795	2.2	6	37	35	6	16	59.45
12	1232	5.6	-	-	-	-	-	-
13	1413	0.3	0	30	23	20	25	69.95
14	1705	0.9	4	36	50	4	7	58.7
15	1663	1.7	12	36	33	7	13	55.15
16	1754	4.2	15	29	34	7	15	54.9
17	1503	16.4	7	29	40	10	13	60.9
18	1696	2.9	38	29	38	8	20	29.4
19	1669	1.2	7	52	24	5	12	55.7

TABLE 1.2 CALENDAR OF SAMPLE ACTIVITY

Season	Dry					Shoulder			Wet			Dry
Coffee Flowering			Flowering									
	Jan	Feb	March	April	May	June	July	Aug	Sept	Oct	Nov	Dec
Sample 2014		x	x	x	x			x	x	x	x	
Sample 2015		x	x	x	x	x		x	x			

TABLE 1.3 SUMMARY OF WEATHER DURING THE STUDY. Summary of rainfall and temperature across seasons and years (i.e., nine sample events) for each forest patch. Data for each forest patch was collected from weather stations within a 5-km radius of each patch. Bee traps were deployed over a 5-day period, thus weather data was summarized over the deployment day plus the 5-day sample period (i.e., total of 6-days).

	6-Day Average Maximum Temperature (C°)			6-Day Total Rainfall (mm)		
Forest No.	min	max	mean	min	max	mean
1	18	21.3	19.2	0	31.2	10.2
2	17.5	19.6	18.7	0	53.2	18.9
3	18	19.8	18.8	0	47.8	11.6
4	18	19.8	18.6	0	140.2	30.7
5	17.9	19.2	20.5	0	133.6	26.2
6	18.1	19	20.2	0	132	29.6
7	17.9	20.3	18.8	0	42.4	8.2
8	16.6	19.1	18	0.8	83.8	24.3
9	17.3	21.2	18.9	0	106.6	21.6
10	17	19.3	18	0	80.7	25.1
11	17.5	19.6	18.5	0	80.4	28.6
12	17.3	19.1	18.1	0.5	83.8	23.6
13	17.8	20.4	18.8	0	44.8	10.9
14	17.8	21.3	19.1	0	40	10.5
15	18	21.3	19.1	0	31.2	11.6
16	16.7	19.9	18.3	0	85.8	38.4
17	17.7	19.9	19	0.2	55.4	23
18	18.1	19.5	18.8	0	118.4	22.9
19	17.9	21.5	19.2	0	118.4	23.3

TABLE 1.4 BEE SPECIES AND TRAIT CHARACTERISTICS. List of bee species, and their associated functional trait values, collected over the course of the study. Inter-tegular distance (ITD) was measured directly using a digital optical microscope. The remaining functional traits were determined based upon expert knowledge (Terry Griswold, *personal communication*).

Family	Tribe	Genus_species	Mean ITD (µm)	Feeding Specialization	Tongue Length	Social Status	Nest Location	Abundance
Andrenidae		*Pseudopanurgus* Spp. 2	1561.8	Polylectic	long	solitary	above	1
Apidae	Anthophorini	*Deltoptila* Spp. 1	NA	Polylectic	long	solitary	above	1
	Apini	*Apis mellifera*	2375.5	Polylectic	long	social	above	59
	Bombini	*Bombus digressus*	3950.7	Polylectic	long	social	NA	1
		Bombus ephippiatus	4964.0	Polylectic	long	social	below	66
		Bombus pullatus	2949.4	Polylectic	long	social	above	3
		Bombus volluceloides	3991.3	Polylectic	long	social	NA	21
	Centridini	*Epicharis angulosa*	5130.0	Polylectic	long	solitary	below	76
	Ceratini	*Ceratina eximia*	1999.7	Polylectic	long	solitary	above	1
		Ceratina ignara	1260.1	Polylectic	short	solitary	above	8
		Ceratina Spp. 3	2004.4	Polylectic	long	solitary	above	79
		Ceratina Spp. 7	1050.2	Polylectic	short	solitary	above	3
		Ceratina trimaculata	845.0	Polylectic	short	solitary	above	1
	Emphorini	*Melitoma monozonula*	2503.8	Oligolectic	long	solitary	below	1
		Melitoma nudicauda	2513.3	Oligolectic	long	solitary	below	20
	Eucerini	*Melissodes tepaneca*	2182.8	Polylectic	short	solitary	below	1
		Melissoptila pinguis	1747.5	NA	short	solitary	below	2
		Peponapis apiculata	2767.3	Oligolectic	long	solitary	below	288
		Peponapis limitaris	2661.1	Oligolectic	long	solitary	below	38
		Thygater aethiops	3131.8	Polylectic	long	solitary	below	23
		Thygater cockerelli	2835.3	Polylectic	long	solitary	below	1
		Thygater columbiana	2527.6	Polylectic	long	solitary	below	5
		Thygater crawfordi	2884.3	Polylectic	long	solitary	below	64
	Euglossini	*Eufriesea concava*	4796.0	Polylectic	long	solitary	above	1
		Eufriesea mexicana	4544.3	Polylectic	long	solitary	above	1
		Euglossa cybelia	3285.6	Polylectic	long	solitary	above	4
		Euglossa deceptrix	3024.9	Polylectic	long	solitary	above	3
		Euglossa dilemma	3293.2	Polylectic	long	solitary	above	27
		Euglossa dodsoni	2636.5	Polylectic	long	solitary	above	1
		Euglossa flammea	3104.4	Polylectic	long	solitary	above	9
		Euglossa maculilabris	3008.8	Polylectic	long	solitary	above	5
		Euglossa townsendi	2965.1	Polylectic	long	solitary	above	2
		Eulaema cingulata	5300.0	Polylectic	long	variable	above	2
		Eulaema luteola	5694.0	Polylectic	long	variable	above	12
		Eulaema meriana	5630.0	Polylectic	long	solitary	above	1
		Eulaema mexicana	NA	Polylectic	long	solitary	below	1
		Eulaema polychroma	4830.0	Polylectic	long	variable	above	56
	Exomalopsini	*Exomalopsis* Spp. 1	2368.7	Polylectic	long	solitary	below	1
	Meliponini	*Lestrimelitta mourei*	NA	Polylectic	NA	social	above	2
		Melipona costaricensis	3738.5	Polylectic	long	social	above	1
		Meliwillea bivea	NA	Polylectic	long	social	NA	1
		Partamona orizabensis	NA	Polylectic	long	social	NA	28
		Scaptotrigona subobscuripennis	NA	Polylectic	long	social	above	12
		Trigona corvina	NA	Polylectic	long	social	above	11
		Trigona fulviventris	1284.0	Polylectic	short	social	above	988
	Tapinotaspidini	*Paratetrapedia* Spp.	2201.5	NA	long	solitary	below	1
		Paratetrapedia Spp. 2	NA	NA	long	solitary	below	1
	Xylocopini	*Xylocopa* Spp. 1	5276.0	Polylectic	long	solitary	above	1
		Xylocopa Spp. 2	6614.0	Polylectic	long	solitary	above	1
		Xylocopa tabaniformis	4243.5	Polylectic	long	solitary	above	101

TABLE 1.4 (CONTINUED)

Family	Tribe	Genus_species	Mean ITD (µm)	Feeding Specialization	Tongue Length	Social Status	Nest Location	Abundance
Colletidae	Caupolicanini	*Ptiloglossa guinnae*	3645.4	Polylectic	short	solitary	below	2
	Colletini	*Colletes* Spp. T	2023.3	NA	short	solitary	below	1
		Hylaeus Spp. 3	1458.0	Polylectic	short	solitary	above	1
Halictidae	Augochlorini	*Augochlora nominata*	1097.4	Polylectic	short	NA	below	1
		Augochlora sidaefoliae	1290.9	Polylectic	short	NA	above	7
		Augochlora smaragdina	NA	Polylectic	short	variable	variable	1
		Augochlora Spp. 1	1327.1	Polylectic	short	solitary	above	92
		Augochlora Spp. 15	1433.3	Polylectic	short	solitary	above	6
		Augochlora Spp. 17	1266.6	Polylectic	short	NA	above	1
		Augochlora Spp. A	1254.1	Polylectic	short	solitary	below	3
		Augochlora Spp. B	1302.2	Polylectic	short	solitary	below	1
		Augochloropsis metallica	1532.8	Polylectic	short	NA	below	1
		Augochloropsis Spp. 7	1666.1	Polylectic	short	solitary	below	1
		Caenaugochlora costaricensis	1981.2	Polylectic	short	solitary	below	2
		Caenaugochlora Spp. 10	1467.3	Polylectic	short	social	below	18
		Caenaugochlora Spp. 11	1666.6	Polylectic	short	NA	below	1
		Caenaugochlora Spp. 2	791.3	Polylectic	short	NA	below	1
		Neocorynura centroamericana	1513.0	Polylectic	short	NA	below	4
		Neocorynura pubescens	1321.9	Polylectic	short	NA	below	1
		Neocorynura rufa	1460.0	Polylectic	short	social	below	3
		Neocorynura Spp. 17	1025.5	Polylectic	short	solitary	below	4
		Neocorynura Spp. 6	NA	NA	short	solitary	below	1
		Pseudaugochlora sordicutis	2097.9	Polylectic	short	variable	below	40
	Halictini	*Agapostemon leunculus*	1683.3	Polylectic	short	semisocia	below	1
		Dinagapostemon Spp. 2	2005.8	unknown	short	solitary	below	2
		Dinagapostemon Spp. 3	2190.5	unknown	short	solitary	below	5
		Habralictus Spp. 8	973.5	unknown	short	solitary	below	1
		Lasioglossum jubatum	1225.2	Polylectic	short	solitary	below	1
		Lasioglossum katyae	1774.3	Polylectic	short	solitary	below	5
		Lasioglossum Spp.	NA	Polylectic	short	variable	below	3
		Lasioglossum Spp. 10	1265.4	Polylectic	short	social	below	135
		Lasioglossum Spp. 16	1024.0	Polylectic	short	solitary	below	11
		Lasioglossum Spp. 54	1119.5	Polylectic	short	social	below	3
		Lasioglossum Spp. 7	1291.3	Polylectic	short	NA	below	1
		Lasioglossum Spp. 8	1242.7	Polylectic	short	social	below	47
		Lasioglossum Spp. 9	1398.5	Polylectic	short	social	below	4
		Lasioglossum Spp. A	1132.5	Polylectic	short	social	below	1
		Lasioglossum Spp. B	NA	Polylectic	short	social	below	1
		Lasioglossum umbripenne	1033.2	Polylectic	short	social	below	1
Megachilidae	Megachilini	*Megachile* Spp. 1	4135.8	Polylectic	long	solitary	NA	1
		Megachile Spp. 3	2357.4	Polylectic	long	solitary	NA	1
		Megachile Spp. 4	2746.7	Polylectic	long	solitary	NA	1
								2455
								Total Abundance

TABLE 1.5 SHADE TREE SPECIES ENCOUNTERED WITHIN COFFEE FARMS. List of shade tree species encountered within 108 sample plots located within coffee farms in the study area.

Familiy	Genus	species	Common Name
Anacardiaceae	*Spondias*	spp. 1	Jacote
Asparagaceae	*Yucca*	spp. 1	Hitabo
Asparagaceae	*Yucca*	spp. 1	Yuca
Bignoniaceae	*Tabebuia*	spp. 1	Roble encino
Bignoniaceae	*Tabebuia*	spp. 2	Cortez
Boraginaceae		spp. 1	Lengua de Buey
Fabaceae	*Erythrina*	*poeppigiana*	Poro
Fabaceae	*Inga*	*vera*	Guaba
Lauraceae	*Cinnamomum*	spp. 1	Canela de Montaña
Lauraceae	*Nectandra*	spp. 1	Aguacate
Malvaceae	*Ochroma*	*pyramidale*	Balso
Moraceae	*Ficus*	spp. 1	Higueron
Moraceae	*Ficus*	spp. 2	Mato Palo
Musaceae	*Musa*	*paradisiaca*	Banano/Guineo
Myrtaceae	*Psidium*	*guajava*	Guayaba
Myrtaceae	*Eucalyptus*	spp. 1	Eucalypto
Podocarpaceae		spp. 1	Cipresillo
Rosaceae		spp. 2	Almendra
Rutaceae	*Citrus*	spp. 1	Naranja
Rutaceae	*Citrus*	spp. 2	Limon Dulce
Sapindaceae	*Cupania*	*rufescens*	Guabiya
Sapotaceae		spp. 1	Sapotillo
Solanaceae		spp. 1	Guitite
Solanaceae		spp. 2	Naranjilla
Urticaceae	*Cecropia*	*peltata*	Guarumo

TABLE 1.6 STATISTICAL MODELS AND MODEL PARAMETERS FOR BIOLOGICAL DIVERSITY VALUES. Summary of mixed-effects models where functional diversity (FD_Q), species richness, and a measure of biological diversity (H') are response variables. Full models represent mixed effects models that were the best fit; in all models the number of traps within each forest patch was treated as a random effect.

		Df	*AIC*	*LRT*	*P >=*
FD_Q	Full Model	*FD_Q ~ Forest Patch Size + LUI + Forest Patch Size:LUI + Forest Patch Size:Coffee Flowering + Forest Patch Size:LUI:Coffee Flowering + (1| no. traps)*			
	Forest Patch Size	1	-204.5	9.85	**0.001695****
	Forest Patch Size:LUI	1	-205.18	9.18	**0.002446****
	Forest Patch Size:Coffee Flowering	1	-208.8	5.56	**0.01840***
	Forest Patch Size:LUI:Coffee Flowering	1	-208.8	5.55	**0.01845***
Richness	Full Model	*Richness ~ Forest Patch Size + Forest Patch Size:LUI + (1| no. traps)*			
	Forest Patch Size	1	49.29	10.6	**0.001129****
	Forest Patch Size:LUI	1	44.05	5.36	**0.02065***
H'	Full Model	*H' ~ Forest Patch Size + Forest Patch Size:LUI + (1| no. traps)*			
	Forest Patch Size	1	39.05	9.96	**0.001596****
	Forest Patch Size:LUI	1	35.15	6.07	**0.01376***
	*, **, and *** correspond with P < 0.05, P < 0.01, and P < 0.001 for parameter estimates in the model. Df: degrees of freedom, AIC: Akaike information criterion, LRT:Likelihood ratio test				

TABLE 1.7 STATISTICAL MODELS AND MODEL PARAMETERS FOR COMMUNITY WEIGHTED MEAN VALUES. Summary of the mixed effects model results for five community-weighted mean traits in response to landscape effects. Full models represent mixed effects models that were the best fit; in all models the number of traps within each forest patch was treated as a random effect.

		Df	*AIC*	*LRT*	*P >=*
Community Weighted Mean (CWM)	Full Model	*Sociality ~ Coffee Flowering + (1| no. traps)*			
	Coffee Flowering	1	216.68	5.62	**0.01777***
	Full Model	*Feeding ~ LUI + (1| no. traps)*			
	LUI	1	61.46	9.42	**0.002142****
	Full Model	*Nest Location ~ Coffee Flowering + (1| no. traps)*			
	Coffee Flowering	1	170.65	11.35	**0.0007544*****
	Full Model	*ITD ~ Forest Patch Size:LUI + (1| no. traps)*			
	Forest Patch Size	1	81.41	4.35	**0.03707***
	LUI	1	83.65	6.58	**0.01031***
	Forest Patch Size:LUI	1	81.28	4.22	**0.04002***
	Full Model	*Tongue Length ~ LUI + Coffee Flowering + (1| no. traps)*			
	LUI	1	174.7	9.82	**0.00173 ****
	Coffee Flowering	1	170.11	5.23	**0.02219 ***

*, **, and *** correspond with P < 0.05, P < 0.01, and P < 0.001 for parameter estimates in the model. Df: degrees of freedom, AIC: Akaike information criterion, LRT:Likelihood ratio test

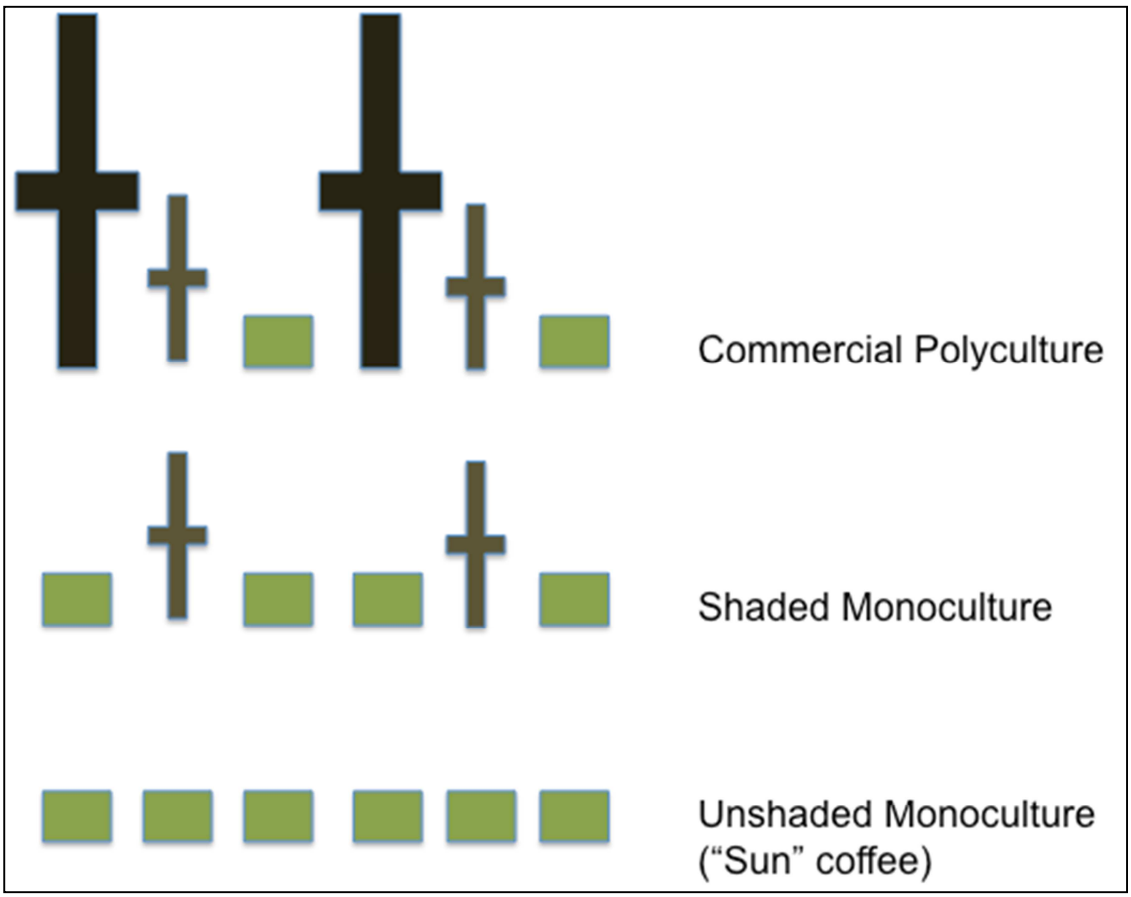

FIGURE 1.1 GRADIENT OF COFFEE MANAGEMENT PRACTICES IN THE STUDY AREA. Illustration of different intensities of coffee management (adapted from Moguel and Toledo 1999). Green boxes represent coffee plants, and different colored "t" shapes represent shade tree species (e.g., poro [*Erythrina*], banana [*Musa*], Eucalyptus, etc, in our study area; Table 1.5). The majority of the farms in the study area are managed along this spectrum. Landscapes in our study (19 x 1-km buffers, in which matrix land-use intensity [LUI] values were calculated) ranged from low to high proportions of both "sun" coffee management and commercial polyculture/shaded monoculture (Table 1.1).

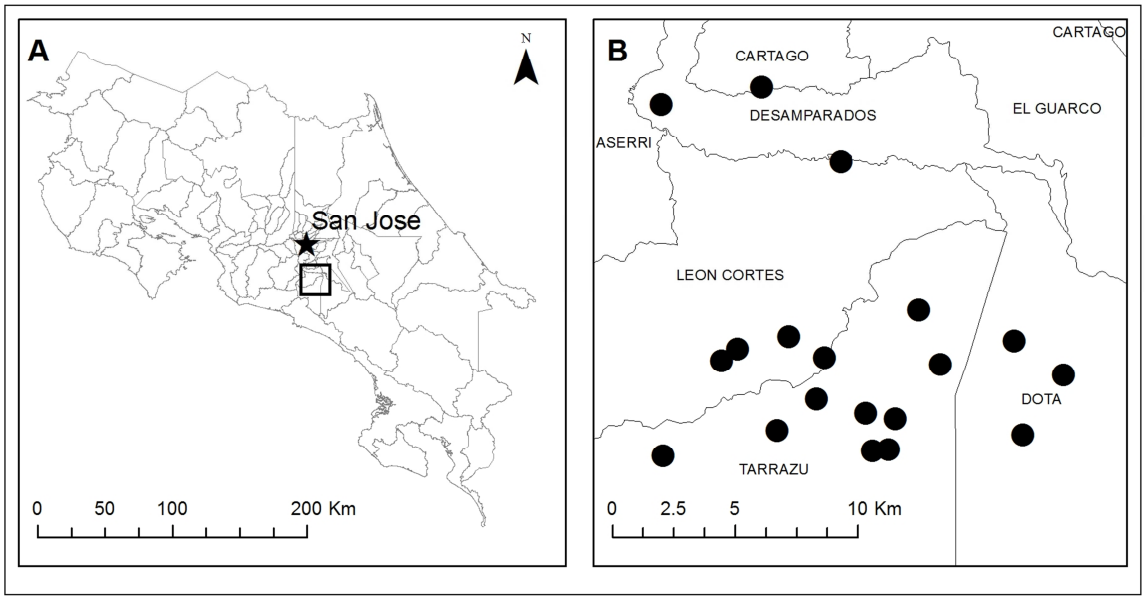

FIGURE 1.2 LOCATION OF STUDY AREA. Study area in Costa Rica (A) covers five counties (B) south of the capital, San Jose.

FIGURE 1.3 ILLUSTRATION OF TERRESTRIAL BEE TRAPPING. Photo of a terrestrial bamboo trap with 4 x pan traps and 1 x Blue Vane trap.

FIGURE 1.4 ILLUSTRATION OF AERIAL BEE TRAPPING. Aerial Blue Vane trap being suspended into the forest canopy by a rope and pulley.

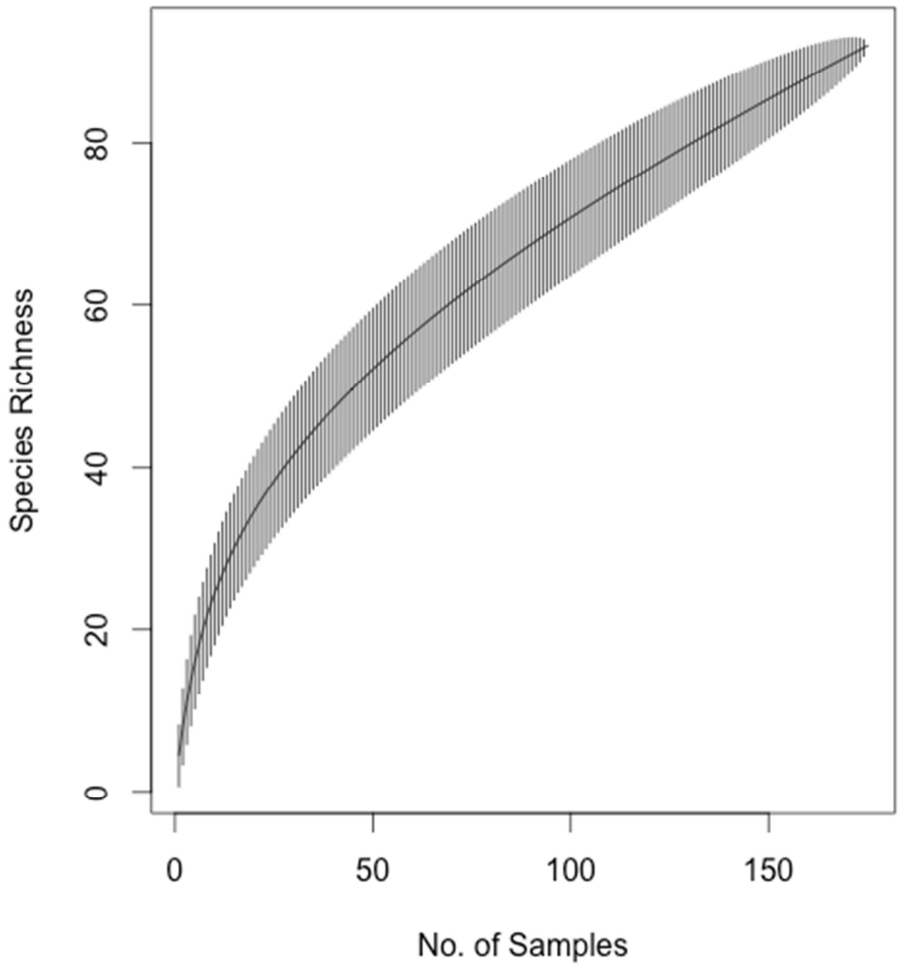

FIGURE 1.5 SPECIES ACCUMULATION CURVE OF BEES CAPTURED. Species accumulation curve of bees captured in the study; the curve does not saturate. The species accumulation curve for the study area was generated using the specaccum function in the package "vegan" in the program R (R Development Core Team. 2014). The sample-based species accumulation curve, with replacement, was generated using the Coleman method (Coleman et al. 1982).

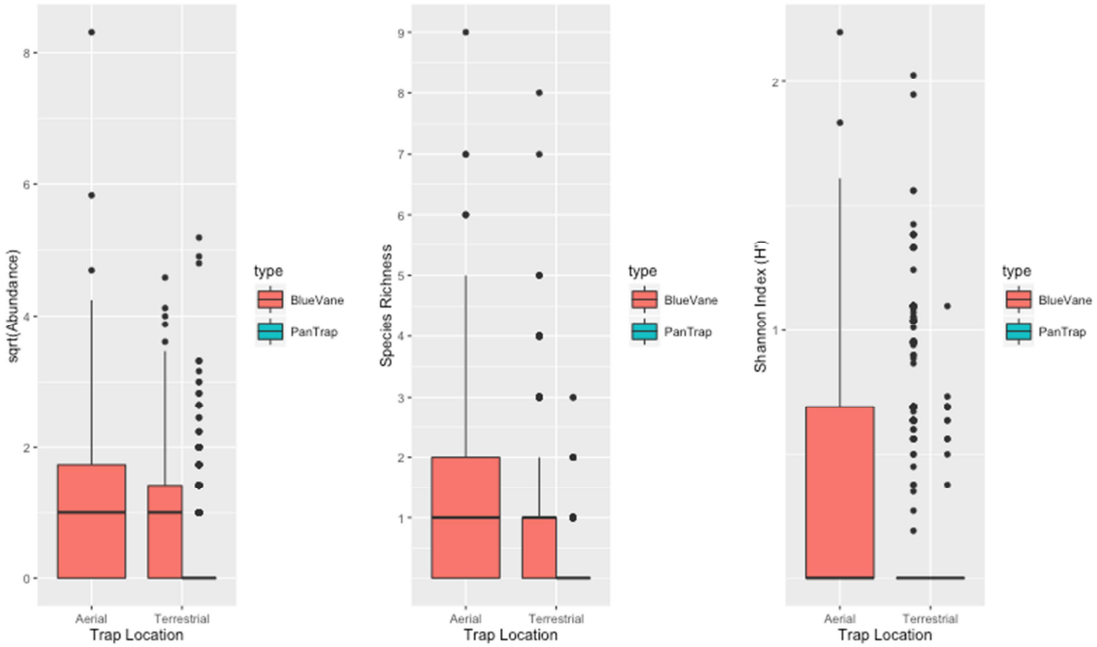

FIGURE 1.6 BIOLOGICAL DIVERSITY METRICS BY TRAP TYPE. Trap type (Blue Vane and pan trap) and trap location (aerial and terrestrial) appear to affect the abundance, richness, and diversity (H') of bees collected in the study. Blue Vane traps collect a more diverse suite of species, as measured by Shannon's index (H'), as well as higher species richness and abundance than pan traps. Data presented here are from each individual trap across all nine sample events in all 19 forest patches. Thus, because data were not pooled, there are many "zero" counts of abundance, richness, and H'.

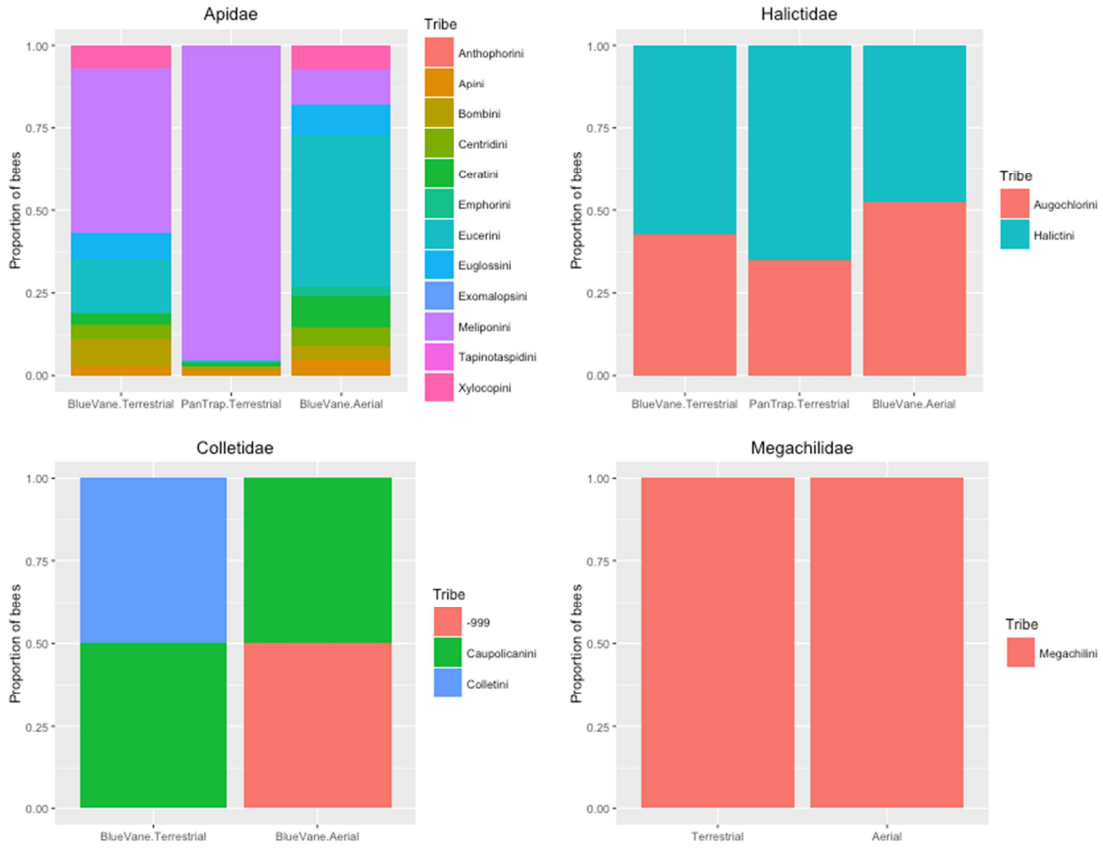

FIGURE 1.7 BEE FAMILIES CAPTURED BY TRAP TYPE. Aerial and terrestrial traps captured different proportions of bee species within forest patches. Employing both methods may have contributed to the diverse suite of functional traits encountered in the sample. The family Apidae contained the highest number of tribes sampled in the study. Within the families of Colletidae and Megachilidae species richness was low (5 species, and 3 species, respectively); thus it is not surprising that tribal diversity was also low. There were 47 species of Halictidae collected in our study, but they are all members of only two tribes. Graphs are of the four bee families represented in our study (Apidae, Colletidae, Halictidae, and Megachilidae) and the proportion of each family represented by individual tribes. x-axis labels (Blue Vane/pan trap; aerial/terrestrial) indicate how these patterns change depending upon trap type and location.

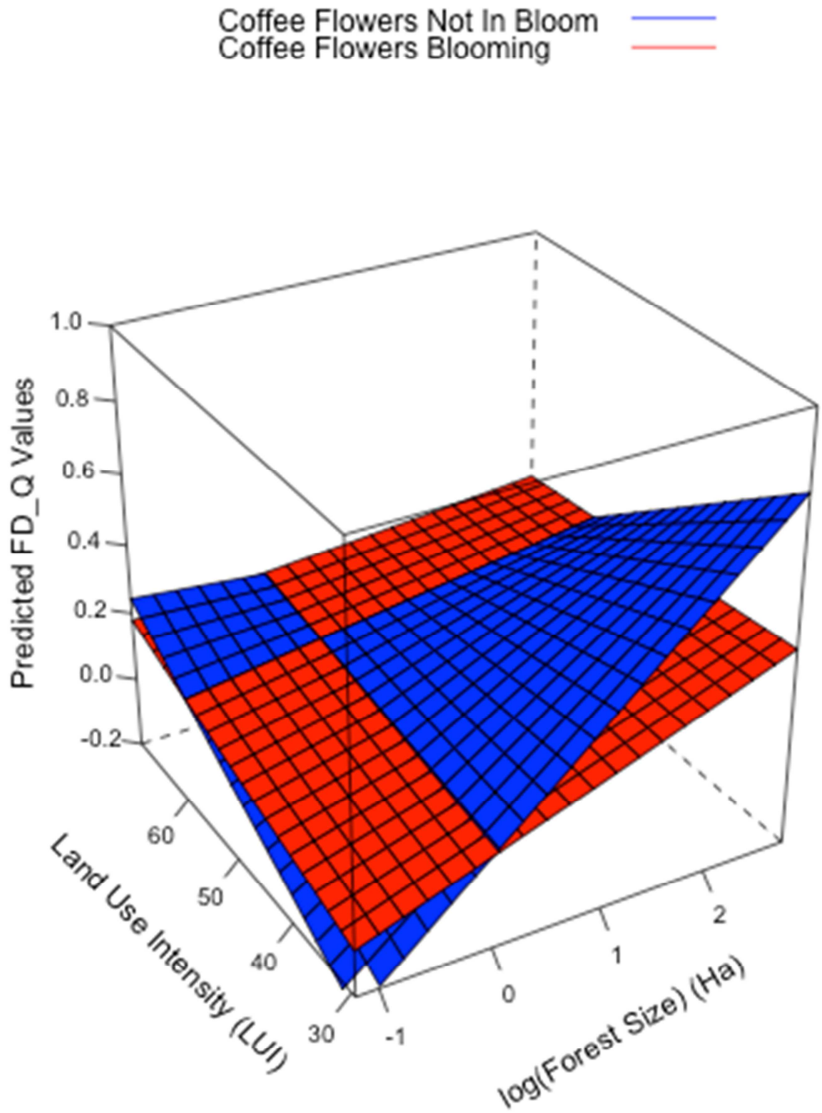

FIGURE 1.8 FUNCTIONAL DIVERSITY IN RELATION TO FOREST SIZE AND LAND-USE INTENSITY. Predicted relationship between land-use intensity (LUI), forest patch size, and FD_Q based upon the best-fit statistical model (Table 1.6). The relationship between landscape characteristics and FD_Q are only predictive when the coffee plants are not blooming, and thus the landscape elements have less contrast. When coffee is not blooming, the highest FD_Q values are found in low-intensive matrix types (low LUI) at intermediate to large patch sizes. In matrices with high land-use intensity, FD_Q values are never large.

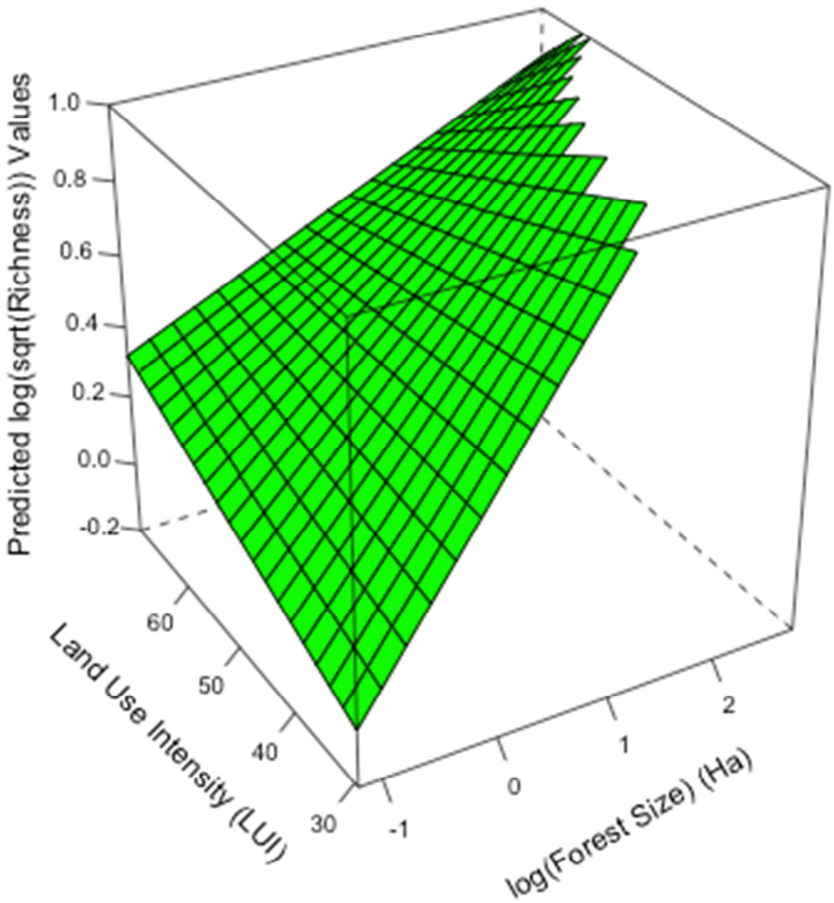

FIGURE 1.9 SPECIES RICHNESS IN RELATION TO FOREST SIZE AND LAND-USE INTENSITY. Predicted relationship between land-use intensity (LUI), forest patch size, and species richness based upon the best-fit statistical model (Table 1.6); there was no statistically significant relationship between species richness and flowering. Species richness increases with forest patch size, however, this relationship is mediated weakly by LUI.

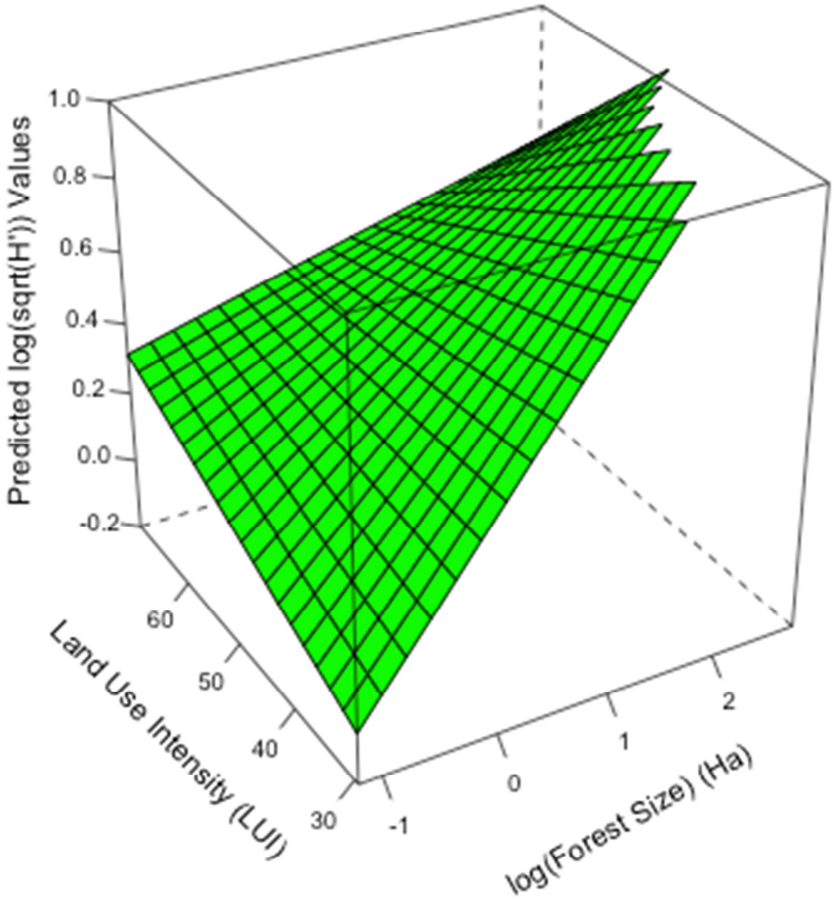

FIGURE 1.10 SHANNON'S INDEX IN RELATION TO FOREST SIZE AND LAND-USE INTENSITY. Predicted relationship between land-use intensity (LUI), forest patch size, and Shannon's index (H') based upon the best-fit statistical model (Table 1.6); there was no statistically significant relationship between species richness and flowering. Species richness increases with forest patch size, however, this relationship is mediated weakly by LUI.

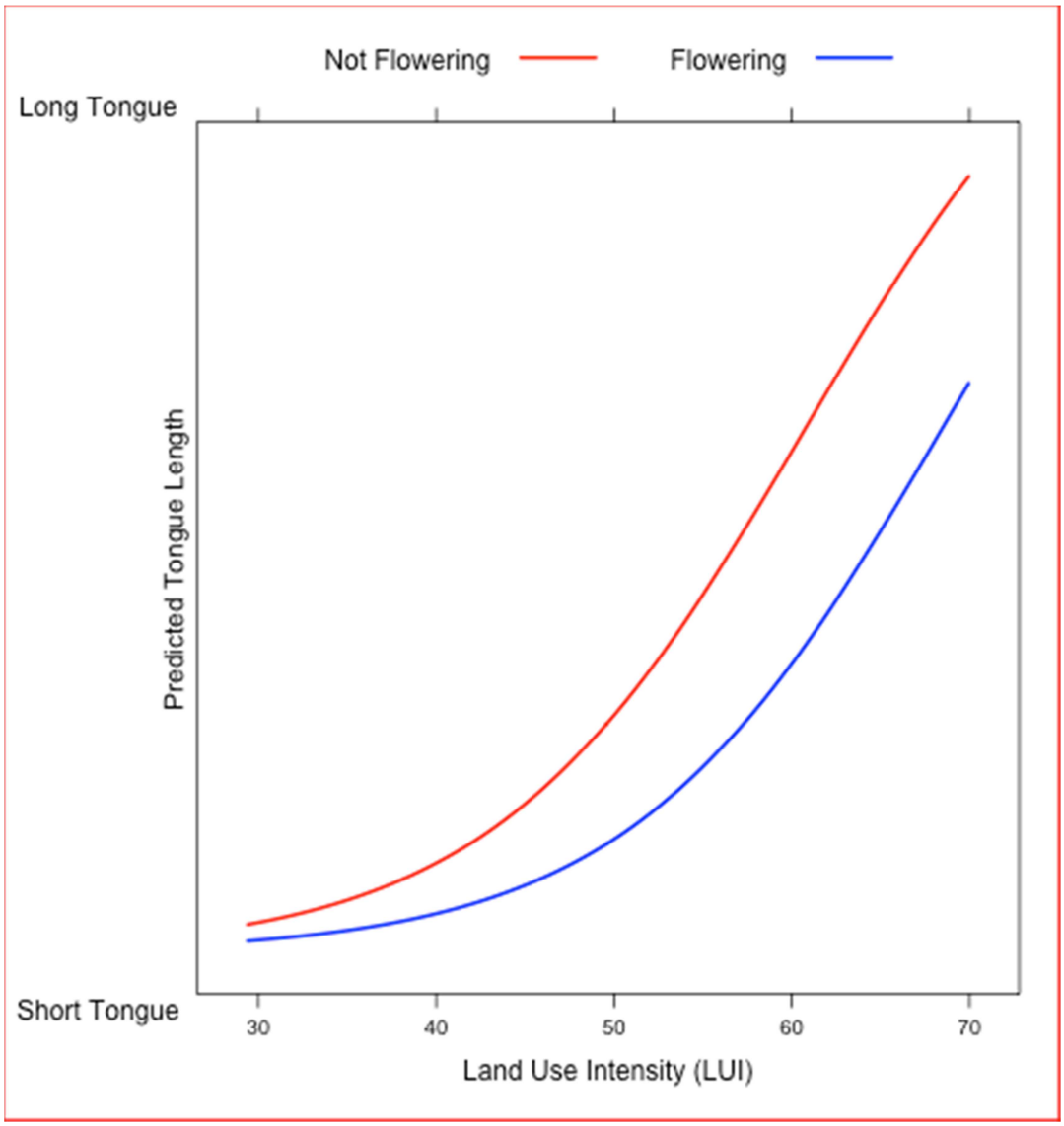

FIGURE 1.11 BEE TONGUE LENGTH IN RESPONSE TO LAND-USE INTENSITY. Predicted relationship between bee tongue length and land-use intensity (LUI) based upon the best-fit statistical model (Table 1.7). Bee communities were dominated by longue-tongued bees in intensive landscapes, though the strength of this relationship was mediated by mass coffee blooming. The y-axis shows the probability of CWM values as a function of LUI. As land-use increases (LUI increases), communities begin to be dominated by long-tongued bees. When coffee is not mass flowering, the threshold at

which LUI seems to differentiate between long- and short-tongued bees appears at lower levels of LUI.

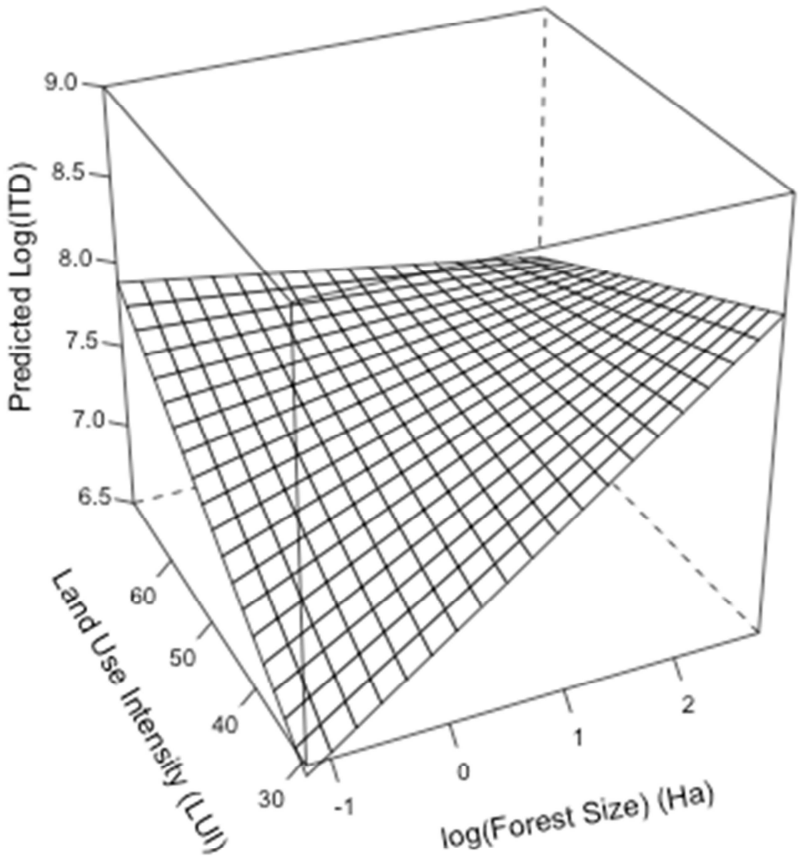

FIGURE 1.12 BEE INTER-TEGULAR DISTANCE IN RELATION TO FOREST SIZE AND LAND-USE INTENSITY. Predicted relationship between inter-tegular distance (ITD; a proxy for body size), land-use intensity (LUI), and forest patch size based upon the best-fit statistical model (Table 1.7). At low levels of matrix intensity (i.e., low values of LUI), increases in patch size result in larger ITD values. When LUI is high, the effect of forest patch size on ITD is less pronounced. Small forest patches in low-intensive matrices have lower ITD values than large patches in intensive matrix types.

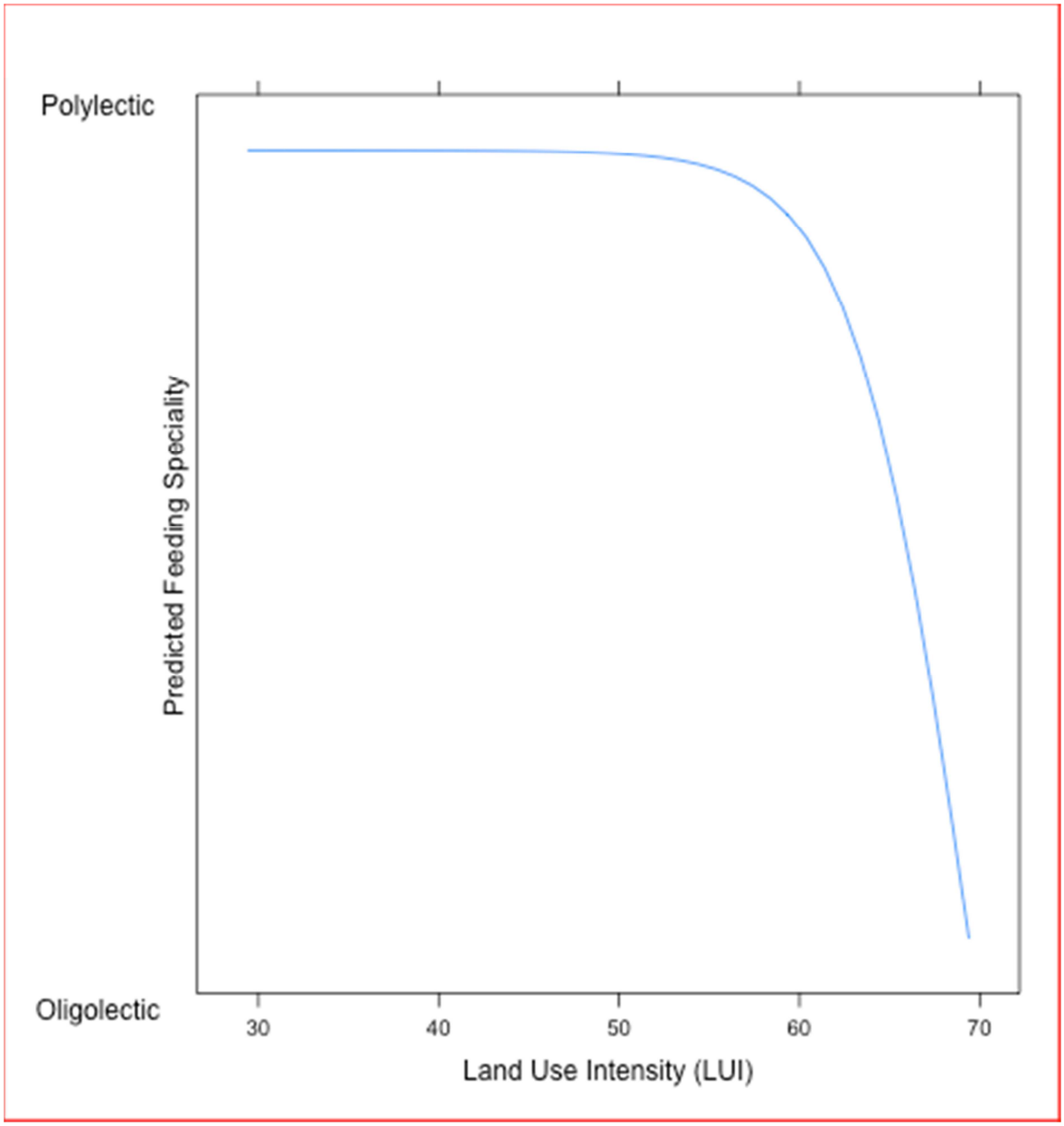

FIGURE 1.13 BEE FEEDING SPECIALTY IN RESPONSE TO LAND-USE INTENSITY. Predicted relationship between land-use intensity (LUI) and community-weighted mean (CWM) feeding speciality based upon the best-fit statistical model (Table 1.7). At low levels of LUI communities are dominated more by generalist (polylectic) species. As LUI

increases, and therefore matrix quality decreases, communities are dominated primarily by more specialized (oligolectic) feeders.

CHAPTER 2

LANDSCAPE ELEMENTS DRIVE BEE COMMUNITY STABILITY THROUGH CHANGES IN SPECIES RICHNESS AND ASYNCHRONY

2.1 ABSTRACT

Patterns of land-use change and intensification, such as for agriculture, often result in habitat loss, increased habitat fragmentation, and isolation of remnant habitat patches, all of which may fundamentally alter ecosystem functioning at community scales. While the relationship between some of these landscape patterns on biological diversity is known (e.g., species richness often declines as a function of patch size), less is known about how surrounding non-habitat (i.e., the "matrix") influences community-scale dynamics.

Here we explore how two landscape elements, patch size and matrix quality, affect community-scale stability of bee pollinators within a coffee agroforestry system in Costa Rica. First we examine the effects of these landscape elements on bee species richness. We then leverage recent advances in understanding of diversity-stability relationships to disentangle how landscape-mediated changes in bee species richness affect community stability. We further this analysis by investigating how the stability of functional traits is affected by landscape-scale patterns.

Our results indicate that reductions in patch size, as well as matrix intensification, result in reduced species richness at the community scale. Moreover,

reductions in species richness were associated within community instability, primarily driven by the relationship between richness and synchrony among bee communities. As species richness declined with matrix intensification and habitat loss, interspecific synchrony between bee populations increased, resulting in high levels of community instability. Despite this tendency, functional trait composition was relatively stable, suggesting a form of functional redundancy.

2.2 Introduction

The widespread effects of human activities on ecosystem functioning (EF) (e.g., nutrient cycling, plant and animal reproduction) around the world has led some to dub our current epoch as the "Anthropocene" (Crutzen 2002). Land-use change and intensification (e.g., for agriculture) are both important anthropogenic activities that mediate biological diversity and the delivery of ecosystem services (e.g., pollination and bio-control) (Foley et al. 2005, Tscharntke et al. 2005, Bianchi et al. 2006, Ricketts et al. 2008). While there has been an emphasis on the conservation of ecosystem services in the face of increased human-induced environmental pressure (Millenium Ecosystem Assessment 2003, Kremen and Ostfeld 2005, Chan et al. 2006), ecosystem service delivery ultimately depends on EF (Bennett et al. 2009, Duncan et al. 2015); thus conservation efforts should be targeted at the processes that embody particular EF of interest.

Several dimensions of biological diversity have been shown to mediate EF at the community scale. These include species richness (Loreau et al. 2001, Cardinale et al.

2002, Tilman et al. 2006), species evenness (Wilsey and Potvin 2000, Crowder et al. 2010), and patterns of population abundances (e.g., asynchrony) (Yachi and Lareau 1999, Hector et al. 2010).

Species richness may moderate EF, a concept typically referred to as the "diversity-stability" relationship (McCann 2000). Often the relationship between species richness and stability is positive (i.e., stability increases with species richness), a phenomenon known as the "portfolio" effect (Schindler et al. 2015, Thibaut and Connolly 2012). Portfolio effects are thought to reduce the risk of EF disruption because diverse ecosystem components (e.g., species assemblages) tend to stabilize EF (Schindler et al. 2015).

Patterns of land-use change and intensification often result in habitat loss, reductions in habitat size, increased habitat fragmentation, and isolation of remnant habitat "patches" (Forman 1995, Fahrig 2003, Turner 2005, Tscharntke et al. 2012). Many empirical studies have demonstrated that these effects alter fundamental ecological patterns and processes, such as population dynamics (Hanski 1998, Hunter 2002, Franzén and Nielson 2010), food web structure (Polis et al. 1997, Fortuna and Bascompte 2006, Tylianakis et al. 2007), and the distribution of functional traits within a community (Flynn et al. 2009, Bommarco et al. 2010, Laliberté 2010); thus it is now well understood that community-scale patterns and processes are moderated by landscape context (Tscharntke et al. 2012).

In light of this, recent attention has been focused on the role of non-habitat, or "the matrix", that surrounds focal habitat patches (Ricketts 2001, Dauber 2003, Vandermeer and Perfecto 2007, Perfecto and Vandermeer 2010). Empirical studies

demonstrate that habitat "islands" embedded within the matrix may harbor relatively high levels of biological diversity (Daily et al. 2001, Watling et al. 2011, Karp et al. 2011, Ökinger et al. 2010), and that organisms originating from these "islands" deliver ecosystem services within the matrix (Bianchi et al. 2006, Ricketts et al. 2008, Garibaldi et al. 2011). However, while many studies focus on the effects of organismal "spillover" from unmanaged habitat patches into the matrix (i.e., the delivery of ecosystem services to the matrix), very few studies have explored the effects of the matrix itself on community properties within habitat patches (Blitzer et al. 2012). For example, it is unknown whether habitat patches can continue to deliver biologically-mediated ecosystem services if they are embedded within highly simplified matrix types.

Here we explore the extent to which matrix intensification affects the community stability of bee pollinators, which are important taxa for the delivery of pollination services to agriculture (Klein et al. 2007, Kremen et al. 2007, Garibaldi et al. 2013) in small remnant natural areas. After Thibaut and Connolly (2012) we measure community stability as the product of population asynchrony and an abundance-weighted measure of species-level stability. We sampled bees within remnant natural forest patches embedded within an agricultural landscape composed primarily of coffee farms. We hypothesized that patches embedded within intensive matrix types (e.g., "sun" coffee) have lower levels of bee community stability; conversely, we predicted that bee community stability would increase as matrix quality was extensified (e.g., via shaded coffee polycultures) (Fig. 2.1).

2.3 METHODS

Study Sites and Regional Characteristics

Bees were sampled in forest patches within 5 counties (Cartago, Desamparados, Dota, Leon Cortez, and Tarrazu) in west central Costa Rica (Fig. 2.2). There are nearly 500 remnant forest patches in the area ranging in size from very small (< 1 ha) to very large (> 2,000 ha); 90% of the forest patches are 1 – 10 ha. The predominant land-use in the area is coffee, which comprises about 65% of total land area (INECa 2014). Coffee management practices in the region are varied, but range from intensive "unshaded monoculture" to more extensive "commercial polyculture" (*sensu* Moguel and Toledo 1999). Coffee blooms annually in the region, typically beginning in April and lasting approximately 3-5 weeks (L. Keesecker, *personal observation*); thus, a mass of floral resources is available during a relatively short period of time annually.

A total of 19 forest patches, ranging in size from 0.3 to 16.4 hectares, was selected for sampling; all forest patches were located between 1,250 – 1,800 masl (Table 2.1). In 2013, bee sampling was conducted between February – March (pre-coffee flowering, dry season), April – May (during the coffee flowering, dry season), August – September ("shoulder" season, a mix of wet and dry season conditions, post coffee flowering), and October – November (wet season, post coffee flowering). In 2014, bee sampling was conducted during the same periods as in 2013, except that the wet season (October – November) in 2014 was not sampled (Table 2.2). The order in which each set of 19 forest patches was sampled was alternated for each sample period

across sample years to control for the influence of temporal biases. Bee traps (see below) were deployed for five-day periods at each location in all seasons.

Precipitation and temperature data were collected from regional weather stations (ICAFE 2015) and summarized over each of the collection periods. Sample locations were associated with proximate weather stations based upon shortest Euclidean distance; all forest patches were located within 5-km of at least one of the four weather stations.

The average 6-day high temperature, and the total 6-day rainfall were calculated for each sample period (Table 2.3). Bee traps were deployed over a 5-day period, thus weather data was summarized over the deployment day plus the 5-day sample period (i.e., total of 6-days). To reduce the number of variables included in statistical models, Principal Components Analysis (PCA) was used to combine rainfall and temperature into one aggregate weather variable (i.e., by using the first principal component of the PCA).

Bee Traps

Bees were sampled using two types of passive sampling; Blue Vane (SpringStar, WA, USA) traps (Stephen and Rao 2005) and pan traps. Blue Vane traps consist of a yellow base, filled with soapy water (odorless and colorless), with a blue funnel-like top through which organisms navigate into the yellow base; the funnel design prevents organisms from escaping once inside the yellow base. Pan traps, small plastic bowls (~ 8 in. diameter) with a mixture of water and colorless, odorless dish soap, were either

painted with fluorescent blue or yellow paint, or were left white. For the Blue Vane traps, two trap configurations were used; terrestrial traps consisted of a bamboo pole (~ 2m in height) fastened with a perpendicular post from which the Blue Vane traps could be suspended, approximately 1.5 m from the ground surface (Fig. 2.3). Aerial traps consisted of Blue Vane traps that were elevated using a rope and pulley into the canopy of the forest patches (Fig. 2.4). Heights of aerial traps (between 3 – 20 m) varied based upon the height of the forest canopy. Pan traps (2 white, 1 blue, and 1 yellow) were positioned approximately 1 m above the ground using platforms fastened to the terrestrial bamboo poles that held the Blue Vane traps (Fig. 2.3); pan traps were not used as part of the aerial trap configuration. The elevation and aspect of each trap was calculated using the Spatial Analyst extension in ArcGIS 10.1 (ESRI 2012), based upon a 30-m resolution digital elevation model (DEM) of Costa Rica (INECb 2014).

Both Blue Vane trap reservoirs and pan traps were filled to approximately half their respective depths with the soapy water mixture. Small holes (~1 cm) were drilled midway around the circumference of both Blue Vane and pan traps to prevent overflow during rainy periods. Screen was placed on the outside of each hole to prevent the loss of specimens through the drain holes. For each forest patch the number of bee traps was scaled to patch area (2 terrestrial traps/ha; 1 aerial trap/ha). Because it is believed that light reflectance is an important factor in attracting bees to both Blue Vane and pan traps, canopy cover (a proxy for light penetration through the forest canopy) was estimated using a densitometer (Concave Model C, Forestry Suppliers) at each trap location. Bees were collected from each trap after each 5-day sample period and placed

in small plastic bags filled with 70% isopropyl alcohol. Once processed, bees were coded with unique identifiers and pinned to dry.

Bees were exported to the US and identified at the USDA-ARS Bee Laboratory in Logan, UT. Intertegular distance (ITD), a proxy for body size (Cane 1987), was measured using a Keyence digital optical microscope (VHX-500F). Five female individuals from each species were used to measure ITD, and the average of these five measurements was used as the ITD for each species. For species with fewer than five specimens, the average of all specimens was used as the ITD for each species. For the few species where no females were captured (< 5 species), ITD for males was measured and used as the ITD for the species (Terry Griswold, *personal communication*). Other life-history traits, such as tongue length, feeding specialty, degree of sociality, and nest location, were categorical and determined based upon expert knowledge (Terry Griswold, *personal communication*) (Table 2.4).

Landscape Context

Matrix quality was determined using a Land-Use/Land-Cover (LULC) classification developed from Worldview-2 satellite imagery taken in 2012 (Digital Globe 2015) within a 1-km buffer of 16 of the 19 focal forest patches; imagery for the remaining three forest patches is unavailable so these three sites could not be used in analyses of matrix effects. The imagery was used to classify LULC into the following categories: (1) sun coffee (i.e., coffee monoculture), (2) shade coffee (i.e., coffee polyculture that includes a relatively complex overstory, such as the intercropping of

banana within farms), (3) urban, (4) pasture, and (5) exposed soil. Forest patches were difficult to identify using the imagery classification algorithm used for delineating the other land-use categories, thus forest patches were manually digitized based upon the imagery (de Jesús et al. 2016). Details of LULC classification can be found in de Jesús et al. (2016).

Matrix intensity was estimated based upon the proportion of LULC categories as follows:

$$LUI_i = (F_i) + (0.5 * Sh_i) + (0.35 * S_i) + (0.2 * P_i) + (0.1 * BU_i)$$

where F_i, Sh_i, S_i, P_i, *and* BU_i are the proportions of sun coffee, shade coffee, pasture, bare-urban, and forest (respectively) within 1-km of each forest patch *i*. Weighting coefficients in this formula for each land-use category are based upon expert opinion (Lonsdorf et al. 2009) on the effects of these categories on nesting and floral resources for bees.

Statistical Analyses

Population synchrony (ϕ), average species-level population variability (CV_n^s), and community variability (CV_n^c) were calculated, after Thibaut and Connolly (2012), for each forest patch, for multiple sampling events over the course of two years (five sample events in 2014; four sample events in 2015), using the program R (R Development Core Team. 2014). The coefficient of variation for the entire community (CV_n^c) was calculated as:

$$CV_n^c = \sqrt{\Phi} * CV_n^s \qquad \text{(Eq. 1)}$$

also after Thibaut and Connolly (2012), where superscript *c* indicates a community-level property, superscript *s* indicates a species-level quantity, and *n* refers to the number of species within a community.

First, we fit a series of linear mixed effects models with species richness as a response variable and forest patch size and land use intensity as explanatory variables. Because we hypothesized that landscape factors mediate diversity, and that diversity in turn drives temporal patterns of population dynamics, we then fit a series of linear mixed effects models where ϕ, CV_n^s, and CV_n^c respond to species richness.

Because the number of traps varied based upon forest patch size, we included the number of traps as a random factor (Bolker et al. 2009); thus, model intercept estimates vary depending upon the number of traps used within each forest patch. Because data were not pooled across sample years, the sample year was also included as a random factor (Zuur et al. 2009). Several models were compared that used different types of variable interaction combinations. We used backwards step-wise model selection to identify the model with the highest predictive ability based on Akaike information criterion scores (AIC). All linear mixed effects models were fit using the lme4 package (Bates et al. 2014) in the program R (R Development Core Team, 2014).

Functional diversity was measured using Rao's quadratic entropy index (Rao_Q), which was calculated for the community within each forest patch across each of the nine sample events. Rao_Q is the "sum of distances between pairs of species in trait space, weighted by the product of their relative abundances" (Weiher 2001; pg 182).

Thus, calculations of Rao_Q require an inventory of species, their relative abundances, and their associated traits (e.g., tongue length, ITD, etc.) (Table 2.4).

To determine which trait value dominated a community in a sample, community-weighted-mean (CWM) trait values were also calculated for each forest patch across sample events. CWM is the mean value of a trait in a community based upon the relative contribution of species in a community that possess that trait (Lavorel et al. 2007).

The stability of functional trait composition was measured differently depending upon the nature of the trait. For continuous measures, such as Rao_Q and ITD, stability was measured as the mean/variance ratio of pooled values within a sample event. For categorical variables, the number of changes in CWM values across sample events divided by the total number of sample events was used to measure stability. This measure of stability is bound between 0, when CWM values do not change across sample events, and 0.888 (8 CWM changes/9 sample events) when CWM values change every sample period. Population-level stability for each species ($Stab_s$) was measured using the mean\variance ratio of abundances, within each sample event, for each species containing > 10 individuals in the entire sample. Trait stability ($Stab_t$) was calculated by pooling species abundances by trait values within each sample event, and calculating mean/variance ratio for each category.

2.4 Results

We collected 2,594 individual bees from 94 different species. Each forest patch was sampled a total of nine times over the course of the study, which includes samples

in each of the three predominant seasons ("wet", "dry", and "shoulder"), before, after, and during mass coffee flowering events (Table 2.2); each sample event included both aerial and terrestrial trapping methods. Over the course of the study, pan traps (terrestrial) were deployed for a total of over 4,000 sample days; Blue Vane traps (terrestrial and aerial) were deployed for about 6,000 sample days. Pan traps collected only 627 individuals, while Blue Vane traps collected 1,967 individuals.

Species richness was positively related to forest patch size across both years in our study (Table 2.5, Fig. 2.5). Parameter estimates for both models of the effects of forest size on species richness (forest patch size; forest patch size + land use intensity) were similar (~1.3 additional species per hectare of forest patch; Table 2.5). Including elevation, canopy cover, and weather variables in the linear mixed effects model increased model AIC values; these variables were not included in any of the mixed effects models because they always increased model AIC values (Table 2.5).

Land use intensity of the matrix had a negative effect on species richness across both years (Table 2.5; Fig. 2.6). The model incorporating forest patch size and matrix land use intensity together was significant (Table 2.5). Thus, when land use intensity was high (i.e., characterized by a large proportion of intensive coffee cultivation) and forest patch size was small, bee species richness was reduced relative to large forest patches embedded within low intensive landscapes.

Synchrony, measured by the statistic ϕ, was negatively affected by species richness, indicating that individual populations were more asynchronous in more species rich assemblages (Table 2.5; Fig. 2.7). Community-level variation, measured by CV_n^c, was related negatively to species richness (Table 2.5; Fig. 2.9). In contrast,

species richness was not a significant predictor of weighted average population variability (CV_n^s) (Table 2.5; Fig. 2.8).

There was no significant relationship between land use intensity and the stability of total community functional diversity, measured by the mean\variance ratio of Rao_Q (L = 0.89, *P* = 0.343; Fig. 2.10). The mean-variance ratio of ITD was not related to land use intensity values (L = 1.45, *P* = 0.218; Fig. 2.10). Stability of categorical traits (tongue length, feeding specialty, nest location, and sociality) was not significantly related to land use intensity (Fig. 2.11).

The distribution of species' population-level stability ($Stab_s$) was relatively uniform excepting two species, *Peponapis apiculata* and *Trigona fulviventris* (Fig. 2.12), suggesting that community stability was not dominated by a few highly stable species. There were differences in pooled trait stability ($Stab_t$) by trait value; below-ground nesting bees were more stable than above-ground nesting bees (t = -2.438, df = 26.209, *P* = 0.0218) (Fig. 2.13). However, long-tongued bees were not more stable than short-tongued bees (t = -1.1199, df = 34.666, *P* = 0.270) (Fig. 2.13) and solitary bees were more not more stable than social bees (t = -1.6825, df = 32.596, *P* = 0.102) (Fig. 2.13). Differences in $Stab_t$ were not explored by feeding specialty due to low sample size among oligolectic bees (no. oligolectic species = 4) (Table 2.4).

2.5 Discussion

We explored the effects of two landscape-scale factors, patch size and matrix quality, on species richness. We then examined how landscape-mediated changes in

species richness affect several dimensions of community dynamics for bee communities in a fragmented coffee agroecosystem. Our results demonstrate that species richness declines as patch size decreases and matrix quality is reduced and that this reduction in species richness ultimately reduces community-level stability via the effects of species richness on synchrony (Fig. 2.14).

Because synchrony depends upon how summed species co-variances scale with individual population variances (Thibaut and Connolly 2012), low synchrony values therefore indicate that (i) either co-variances are low with respect to species variances, or (ii) species variances are large relative to co-variances. In assemblages characterized by low species richness, species abundances were either more correlated through time (i.e., co-variances are large), had large species-specific variances, or both, relative to species rich assemblages.

Community variability (CV_n^c) is highest (and thus stability lowest) when populations are synchronous and summed species-level variances are large relative to species mean abundances (i.e., CV_n^s is large) (Thibaut and Connolly 2012). In our study, species richness enhanced community stability (i.e., low CV_n^c values), primarily due to the positive relationship between species richness and asynchrony. Species richness was ultimately lowest in patches of small size embedded within intensive matrices, demonstrating the effects of landscape pattern on community-scale stability. Such a process may be of interest in agroecosystems, many of which depend upon wild animal pollination (Klein et al. 2007). That is, our and other results suggest fragmented habitat patches may serve as sources of beneficial pollinators if they are of sufficient

size and surrounded by low-intensive agriculture (Bianchi et al. 2006, Ricketts et al. 2008).

The stability of bee functional diversity and bee traits was not associated with landscape patterns in our study. Rao_Q, a multidimensional metric of total functional diversity, was not associated with changes in either matrix intensification or forest patch size. This pattern suggests that trait stability is conferred through functional redundancy among bee communities within forest patches. It is possible that despite reductions in species richness and community stability associated with small patches embedded within intensified matrices, overall trait space remains relatively unchanged over time (i.e., across sample periods). This may also reflect the fact that only four traits were used to calculate Rao_Q, and many of these traits were binary (e.g., long tongue vs. short tongue) and therefore trait space was more likely to be occupied than if it was more finely divided.

Trait stability, measured for each of four traits, was not associated with either matrix intensification or forest patch size. Here, as for Rao_Q, we found no evidence that landscape patterns affect the stability of functional traits, despite landscape-mediated changes in richness. One possible explanation for this is that the community is assembled in such a way that reductions in species richness are more or less uniformly affecting the distribution of traits (i.e., measured by CWM) within each community.

Our results suggest that the population stability of the most dominant species (> 10 individuals in the entire study) was relatively uniformly distributed across species. There was little variation in population stability among species. This could account for the lack of a relationship between CV_n^s and species richness we found in our study in

the sense that the range of mean\variance ratios was not large among dominant species, and CV_n^s is weighted by abundance.

Overall our results highlight that landscape pattern affects community stability through changes in species richness. The primary mechanism through which richness positively affected community stability (the portfolio effect) was via community synchrony (Fig. 14). Synchrony is of interest in the context of bees, mostly obligate mutualist partners of angiosperms, because asynchronous fluctuations of bee pollinators are often needed to sustain the range of temporal patterns among flowering plant communities (Rathcke and Lacey 1985). Our results suggest that intensifying agroecosystems results in species loss within embedded semi-natural areas, and that this loss threatens the ability of these areas to serve as sources of stable pollinator communities important to agriculture.

Though habitat loss (i.e., reduction of forest patch size) and matrix intensification both reduced species richness, overall trait stability was generally unaffected, suggesting a pattern of functional redundancy. That is, when species are lost, communities become more synchronous and less stable, but functional traits generally do not become less stable. Trait synchrony was not measured here, because there is currently no existing metric with which to measure it. It would be of future interest to understand this aspect of temporal dynamic in light of "trait matching" between bee pollinators and flowering plants and its positive effect on fruit set (Garibaldi et al. 2015).

From an applied perspective, semi-natural areas contained relatively stable bee trait distributions regardless of landscape context. Thus, while landscape elements

affected species richness, that effect did not translate into changes in trait stability. From the perspective of food production, the traits of interest would be functional effect traits, of which we included three: tongue length, sociality, and ITD, neither of which had stability values that tracked matrix intensification or forest patch size. However, we were unable to measure trait synchrony and it therefore remains unknown how this important aspect of trait diversity may relate to community synchrony. Despite this limitation, our results suggest that community-scale dynamics relevant to ecosystem function, such as the stability of bee communities, depend upon landscape context. Thus, future efforts to maintain stable bee pollinator communities in agroecosystems will benefit from taking a landscape perspective.

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TABLE 2.1 SUMMARY OF FOREST PATCH CHARACTERISTICS. Forest patch characteristics for each of 19 sample patches. Land-use intensity is derived from the proportion of each Land-Use/Land-Cover (LU/LC) type within a 1-km buffer of each forest patch (see equation in Methods). Three of the forest patches were located in an area without existing imagery needed for LU/LC classification.

			Matrix Composition (% LU/LC)					
Forest No.	Elevation (m)	Size (ha)	Forest	"Shade" coffee	"Sun" coffee	Bare/Urban	Pasture	LUI
1	1413	0.3	0	30	23	20	25	69.95
2	1705	0.9	4	36	50	4	7	58.7
3	1718	1	3	45	28	8	16	60.7
4	1493	1.1	6	40	31	7	16	59.25
5	1669	1.2	7	52	24	5	12	55.7
6	1530	1.6	-	-	-	-	-	-
7	1663	1.7	12	36	33	7	13	55.15
8	1425	2	4	53	22	7	15	58.1
9	1300	2	-	-	-	-	-	-
10	1795	2.2	6	37	35	6	16	59.45
11	1521	2.9	0	41	31	10	18	64.05
12	1696	2.9	38	29	38	8	20	29.4
13	1645	3.2	5	47	21	9	17	59.85
14	1578	3.7	7	39	29	7	18	59.05
15	1754	4.2	15	29	34	7	15	54.9
16	1232	5.6	-	-	-	-	-	-
17	1598	6.8	10	35	31	10	14	57.85
18	1734	9	10	22	39	12	16	60.95
19	1503	16.4	7	29	40	10	13	60.9

TABLE 2.2 CALENDAR OF SAMPLE ACTIVITY.

Season	Dry					Shoulder			Wet			Dry
Coffee Flowering			Flowering									
	Jan	Feb	March	April	May	June	July	Aug	Sept	Oct	Nov	Dec
Sample 2014		x	x	x	x			x	x	x	x	
Sample 2015		x	x	x	x	x		x	x			

TABLE 2.3 SUMMARY OF WEATHER DURING THE COURSE OF THE STUDY. Summary of rainfall and temperature across seasons and years (i.e., nine sample events) for each forest patch. Data for each forest patch were collected from weather stations within a 5-km radius of each patch.

	6-Day Average Maximum Temperature (C°)			6-Day Total Rainfall (mm)		
Forest No.	min	max	mean	min	max	mean
1	18	21.3	19.2	0	31.2	10.2
2	17.5	19.6	18.7	0	53.2	18.9
3	18	19.8	18.8	0	47.8	11.6
4	18	19.8	18.6	0	140.2	30.7
5	17.9	19.2	20.5	0	133.6	26.2
6	18.1	19	20.2	0	132	29.6
7	17.9	20.3	18.8	0	42.4	8.2
8	16.6	19.1	18	0.8	83.8	24.3
9	17.3	21.2	18.9	0	106.6	21.6
10	17	19.3	18	0	80.7	25.1
11	17.5	19.6	18.5	0	80.4	28.6
12	17.3	19.1	18.1	0.5	83.8	23.6
13	17.8	20.4	18.8	0	44.8	10.9
14	17.8	21.3	19.1	0	40	10.5
15	18	21.3	19.1	0	31.2	11.6
16	16.7	19.9	18.3	0	85.8	38.4
17	17.7	19.9	19	0.2	55.4	23
18	18.1	19.5	18.8	0	118.4	22.9
19	17.9	21.5	19.2	0	118.4	23.3

TABLE 2.4 BEE SPECIES AND TRAIT CHARACTERISTICS. List of bee species, and their associated functional trait values, collected over the course of the study. Inter-tegular distance (ITD) was measured directly using a digital optical microscope. The remaining functional traits were determined based upon expert knowledge (Terry Griswold, *personal communication*).

Family	Tribe	Genus_species	Mean ITD (µm)	Feeding Specialization	Tongue Length	Social Status	Nest Location	Abundance
Andrenidae		*Pseudopanurgus* Spp. 2	1561.8	Polylectic	long	solitary	above	1
Apidae	Anthophorini	*Deltoptila* Spp. 1	NA	Polylectic	long	solitary	above	1
	Apini	*Apis mellifera*	2375.5	Polylectic	long	social	above	59
	Bombini	*Bombus digressus*	3950.7	Polylectic	long	social	NA	1
		Bombus ephippiatus	4964.0	Polylectic	long	social	below	66
		Bombus pullatus	2949.4	Polylectic	long	social	above	3
		Bombus volluceloides	3991.3	Polylectic	long	social	NA	21
	Centridini	*Epicharis angulosa*	5130.0	Polylectic	long	solitary	below	76
	Ceratini	*Ceratina eximia*	1999.7	Polylectic	long	solitary	above	1
		Ceratina ignara	1260.1	Polylectic	short	solitary	above	8
		Ceratina Spp. 3	2004.4	Polylectic	long	solitary	above	79
		Ceratina Spp. 7	1050.2	Polylectic	short	solitary	above	3
		Ceratina trimaculata	845.0	Polylectic	short	solitary	above	1
	Emphorini	*Melitoma monozonula*	2503.8	Oligolectic	long	solitary	below	1
		Melitoma nudicauda	2513.3	Oligolectic	long	solitary	below	20
	Eucerini	*Melissodes tepaneca*	2182.8	Polylectic	short	solitary	below	1
		Melissoptila pinguis	1747.5	NA	short	solitary	below	2
		Peponapis apiculata	2767.3	Oligolectic	long	solitary	below	288
		Peponapis limitaris	2661.1	Oligolectic	long	solitary	below	38
		Thygater aethiops	3131.8	Polylectic	long	solitary	below	23
		Thygater cockerelli	2835.3	Polylectic	long	solitary	below	1
		Thygater columbiana	2527.6	Polylectic	long	solitary	below	5
		Thygater crawfordi	2884.3	Polylectic	long	solitary	below	64
	Euglossini	*Eufriesea concava*	4796.0	Polylectic	long	solitary	above	1
		Eufriesea mexicana	4544.3	Polylectic	long	solitary	above	1
		Euglossa cybelia	3285.6	Polylectic	long	solitary	above	4
		Euglossa deceptrix	3024.9	Polylectic	long	solitary	above	3
		Euglossa dilemma	3293.2	Polylectic	long	solitary	above	27
		Euglossa dodsoni	2636.5	Polylectic	long	solitary	above	1
		Euglossa flammea	3104.4	Polylectic	long	solitary	above	9
		Euglossa maculilabris	3008.8	Polylectic	long	solitary	above	5
		Euglossa townsendi	2965.1	Polylectic	long	solitary	above	2
		Eulaema cingulata	5300.0	Polylectic	long	variable	above	2
		Eulaema luteola	5694.0	Polylectic	long	variable	above	12
		Eulaema meriana	5630.0	Polylectic	long	solitary	above	1
		Eulaema mexicana	NA	Polylectic	long	solitary	below	1
		Eulaema polychroma	4830.0	Polylectic	long	variable	above	56
	Exomalopsini	*Exomalopsis* Spp. 1	2368.7	Polylectic	long	solitary	below	1
	Meliponini	*Lestrimelitta mourei*	NA	Polylectic	NA	social	above	2
		Melipona costaricensis	3738.5	Polylectic	long	social	above	1
		Meliwillea bivea	NA	Polylectic	long	social	NA	1
		Partamona orizabensis	NA	Polylectic	long	social	NA	28
		Scaptotrigona subobscuripennis	NA	Polylectic	long	social	above	12
		Trigona corvina	NA	Polylectic	long	social	above	11
		Trigona fulviventris	1284.0	Polylectic	short	social	above	988
	Tapinotaspidini	*Paratetrapedia* Spp.	2201.5	NA	long	solitary	below	1
		Paratetrapedia Spp. 2	NA	NA	long	solitary	below	1
	Xylocopini	*Xylocopa* Spp. 1	5276.0	Polylectic	long	solitary	above	1
		Xylocopa Spp. 2	6614.0	Polylectic	long	solitary	above	1
		Xylocopa tabaniformis	4243.5	Polylectic	long	solitary	above	101

TABLE 2.4 (CONTINUED)

Family	Tribe	Genus_species	Mean ITD (µm)	Feeding Specialization	Tongue Length	Social Status	Nest Location	Abundance
Colletidae	Caupolicanini	*Ptiloglossa guinnae*	3645.4	Polylectic	short	solitary	below	2
	Colletini	*Colletes* Spp. T	2023.3	NA	short	solitary	below	1
		Hylaeus Spp. 3	1458.0	Polylectic	short	solitary	above	1
Halictidae	Augochlorini	*Augochlora nominata*	1097.4	Polylectic	short	NA	below	1
		Augochlora sidaefoliae	1290.9	Polylectic	short	NA	above	7
		Augochlora smaragdina	NA	Polylectic	short	variable	variable	1
		Augochlora Spp. 1	1327.1	Polylectic	short	solitary	above	92
		Augochlora Spp. 15	1433.3	Polylectic	short	solitary	above	6
		Augochlora Spp. 17	1266.6	Polylectic	short	NA	above	1
		Augochlora Spp. A	1254.1	Polylectic	short	solitary	below	3
		Augochlora Spp. B	1302.2	Polylectic	short	solitary	below	1
		Augochloropsis metallica	1532.8	Polylectic	short	NA	below	1
		Augochloropsis Spp. 7	1666.1	Polylectic	short	solitary	below	1
		Caenaugochlora costaricensis	1981.2	Polylectic	short	solitary	below	2
		Caenaugochlora Spp. 10	1467.3	Polylectic	short	social	below	18
		Caenaugochlora Spp. 11	1666.6	Polylectic	short	NA	below	1
		Caenaugochlora Spp. 2	791.3	Polylectic	short	NA	below	1
		Neocorynura centroamericana	1513.0	Polylectic	short	NA	below	4
		Neocorynura pubescens	1321.9	Polylectic	short	NA	below	1
		Neocorynura rufa	1460.0	Polylectic	short	social	below	3
		Neocorynura Spp. 17	1025.5	Polylectic	short	solitary	below	4
		Neocorynura Spp. 6	NA	NA	short	solitary	below	1
		Pseudaugochlora sordicutis	2097.9	Polylectic	short	variable	below	40
	Halictini	*Agapostemon leunculus*	1683.3	Polylectic	short	semisocia	below	1
		Dinagapostemon Spp. 2	2005.8	unknown	short	solitary	below	2
		Dinagapostemon Spp. 3	2190.5	unknown	short	solitary	below	5
		Habralictus Spp. 8	973.5	unknown	short	solitary	below	1
		Lasioglossum jubatum	1225.2	Polylectic	short	solitary	below	1
		Lasioglossum katyae	1774.3	Polylectic	short	solitary	below	5
		Lasioglossum Spp.	NA	Polylectic	short	variable	below	3
		Lasioglossum Spp. 10	1265.4	Polylectic	short	social	below	135
		Lasioglossum Spp. 16	1024.0	Polylectic	short	solitary	below	11
		Lasioglossum Spp. 54	1119.5	Polylectic	short	social	below	3
		Lasioglossum Spp. 7	1291.3	Polylectic	short	NA	below	1
		Lasioglossum Spp. 8	1242.7	Polylectic	short	social	below	47
		Lasioglossum Spp. 9	1398.5	Polylectic	short	social	below	4
		Lasioglossum Spp. A	1132.5	Polylectic	short	social	below	1
		Lasioglossum Spp. B	NA	Polylectic	short	social	below	1
		Lasioglossum umbripenne	1033.2	Polylectic	short	social	below	1
Megachilidae	Megachilini	*Megachile* Spp. 1	4135.8	Polylectic	long	solitary	NA	1
		Megachile Spp. 3	2357.4	Polylectic	long	solitary	NA	1
		Megachile Spp. 4	2746.7	Polylectic	long	solitary	NA	1
								2455
								Total Abundance

TABLE 2.5 STATISTICAL MODELS AND MODEL PARAMETERS FOR COMMUNITY-SCALE RICHNESS AND STABILITY MEASURES. Summary of linear mixed effects model analysis for the effects of landscape elements on species richness, and the effects of species richness on synchrony, CV_n^s, and CV_n^c. The number of traps used in each forest patch, and the year in which samples were taken, were used as random effects in the models.

Model	*Parameter*	*Df*	*AIC*	*LRT*	*Estimate*	*St. Error*	*P <=*
Richness ~ Forest Patch Size + (1|Year) + (1|No. Traps)							
	Forest Patch Size	1	191.09	17.302	1.2696	0.1888	**0.001**
Richness ~ Land Use Intensity + (1|Year) + (1|No. Traps)							
	Land Use Intensity	1	191.09	6.0567	-0.1666	0.0649	**0.0139**
Richness ~ Forest Patch Size + Land Use Intensity + (1|Year) + (1|No. Traps)							
	Forest Patch Size	1	187.03	19.2227	1.28019	0.17054	**0.001**
	Land Use Intensity	1	175.79	7.9774	-0.17444	0.05971	**0.0047**
φ ~ Richness + (1|Year) + (1|No. Traps)							
	Richness	1	7.7812	4.4577	-0.01443	0.006917	**0.0347**
CV_n^s ~ Richness + (1|Year) + (1|No. Traps)							
	Richness	1	21.534	1.5805	-0.0108	0.008763	0.2087
CV_n^c ~ Richness + (1|Year) + (1|No. Traps)							
	Richness	1	38.233	3.7703	-0.02367	0.01274	0.0522

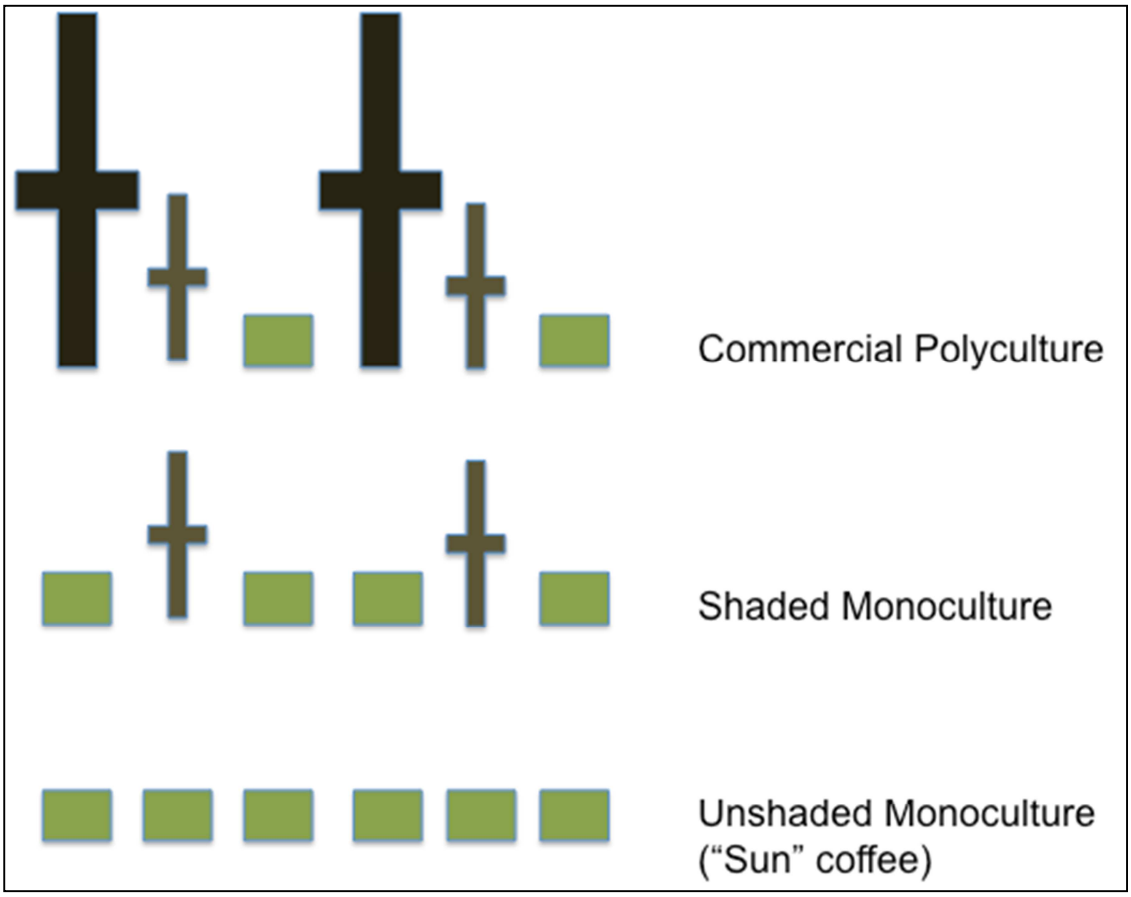

FIGURE 2.1 GRADIENT OF COFFEE MANAGEMENT PRACTICES IN THE STUDY AREA. Illustration of different intensities of coffee management (adapted from Moguel and Toledo 1999). Green boxes represent coffee plants, and different colored "t" shapes represent shade tree species (e.g., poro [*Erythrina*], banana [*Musa*], Eucalyptus, etc, in our study area; Table 2.5). The majority of the farms in the study area are managed along this spectrum. Landscapes in our study (19 x 1-km buffers, in which matrix land-use intensity [LUI] values were calculated) ranged from low to high proportions of both "sun" coffee management and commercial polyculture/shaded monoculture (Table 2.1).

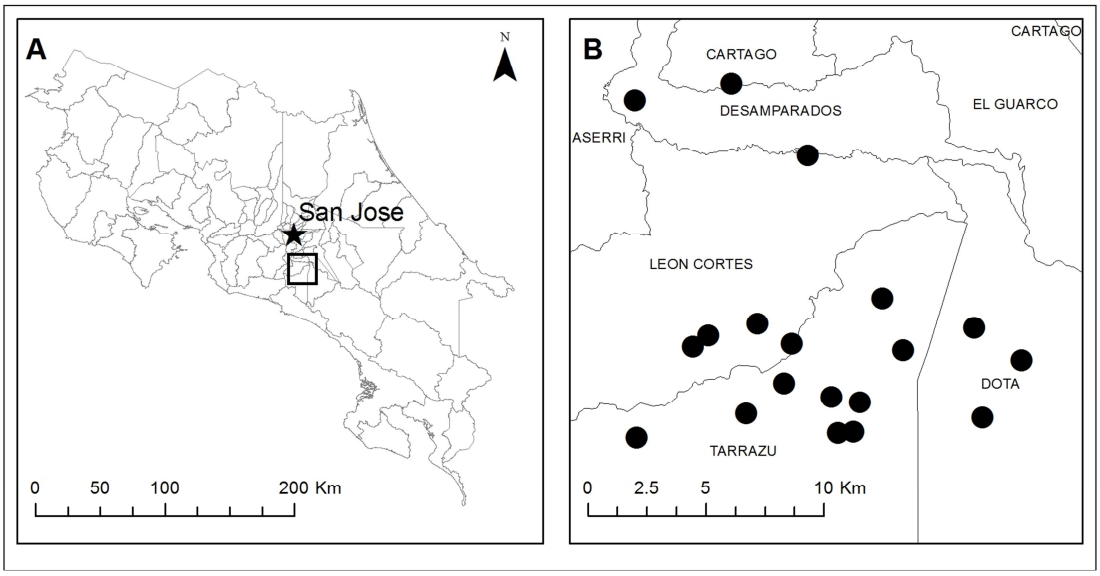

FIGURE 2.2 LOCATION OF STUDY AREA. Study area in Costa Rica (A) covers five counties (B) south of the capital, San Jose.

FIGURE 2.3 ILLUSTRATION OF THE TERRESTRIAL BAMBOO TRAPS USED IN THE STUDY. Photo of a terrestrial bamboo trap with 4 x pan traps and 1 x Blue Vane trap.

FIGURE 2.4 ILLUSTRATION OF THE AERIAL TRAPS USED IN THE STUDY. Aerial Blue Vane trap being suspended into the forest canopy by a rope and pulley.

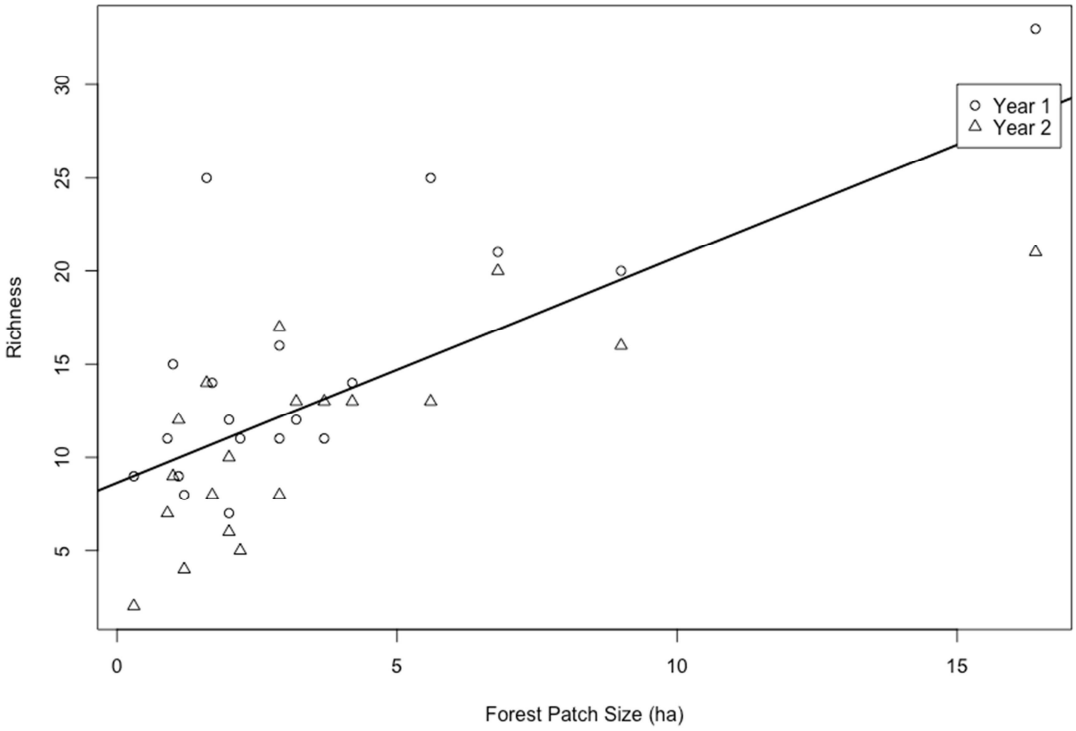

FIGURE 2.5 RELATIONSHIP BETWEEN FOREST PATCH SIZE AND BEE SPECIES RICHNESS.

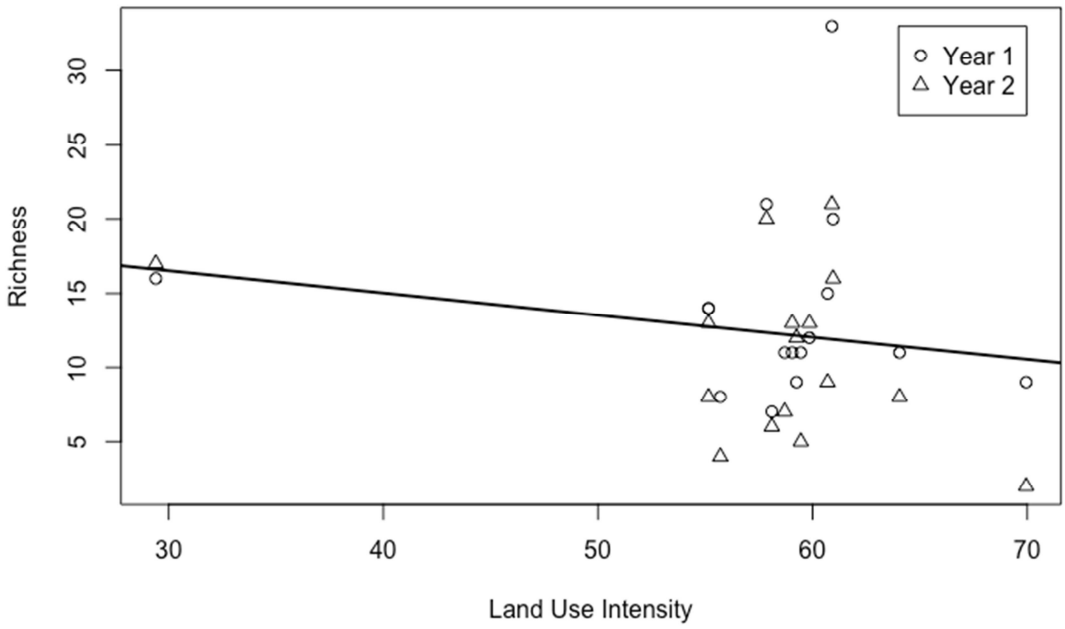

FIGURE 2.6 RELATIONSHIP BETWEEN LAND-USE INTENSITY IN THE "MATRIX" ON BEE SPECIES RICHNESS.

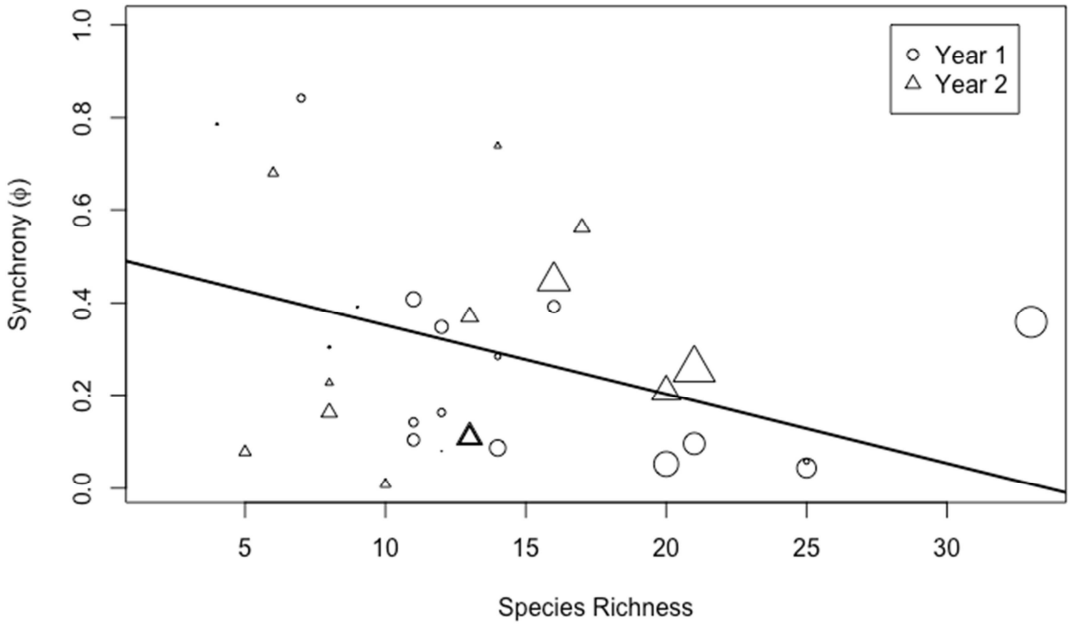

FIGURE 2.7 RELATIONSHIP BETWEEN BEE SPECIES RICHNESS AND BEE COMMUNITY SYNCHRONY (ϕ). Symbols are scaled small to large based on forest patch size.

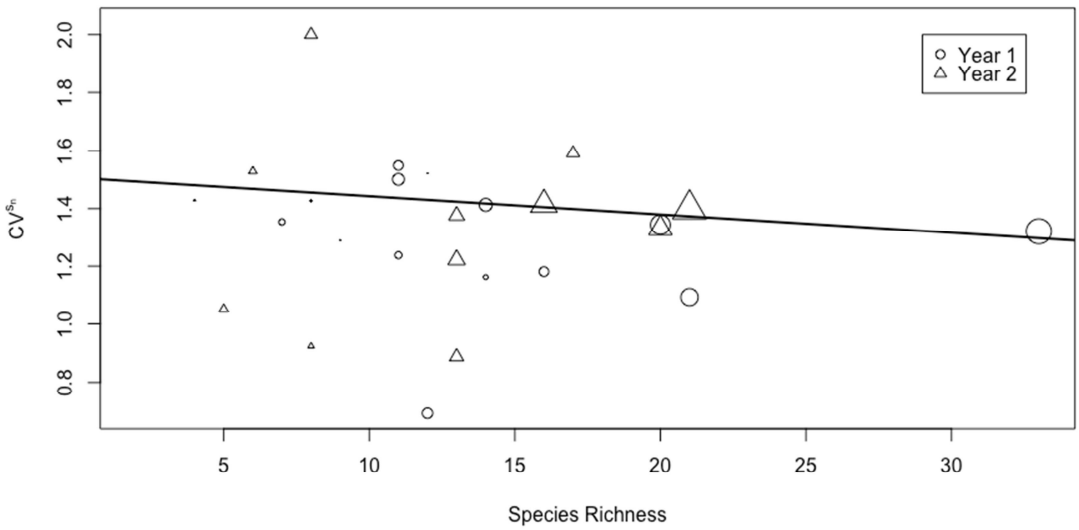

FIGURE 2.8 RELATIONSHIP BETWEEN BEE SPECIES RICHNESS AND AVERAGE SPECIES LEVEL POPULATION VARIABILITY (CV_n^s). Symbols are scaled small to large based on forest patch size.

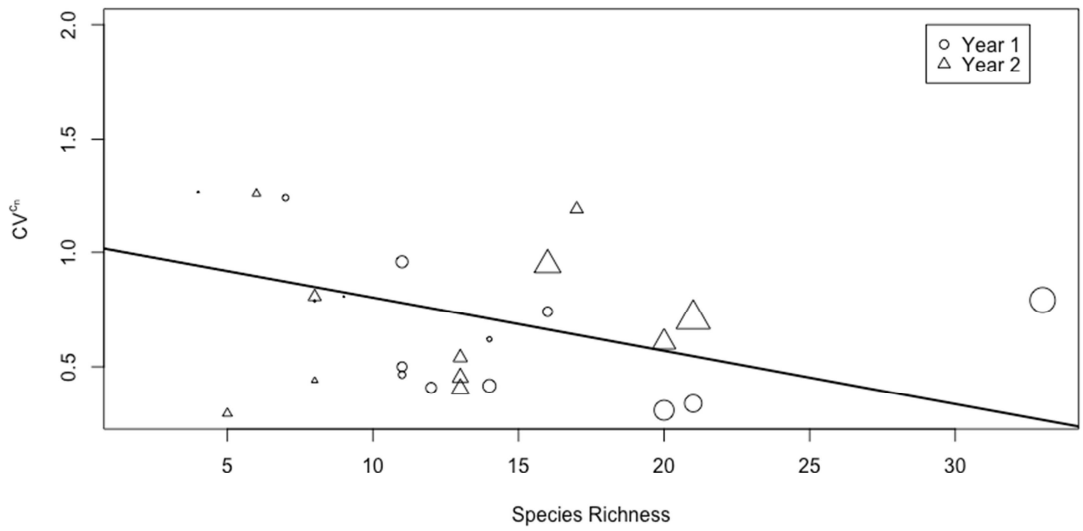

FIGURE 2.9 RELATIONSHIP BETWEEN BEE SPECIES RICHNESS AND COMMUNITY-SCALE VARIABILITY (CV_n^c). Symbols are scaled small to large based on forest patch size.

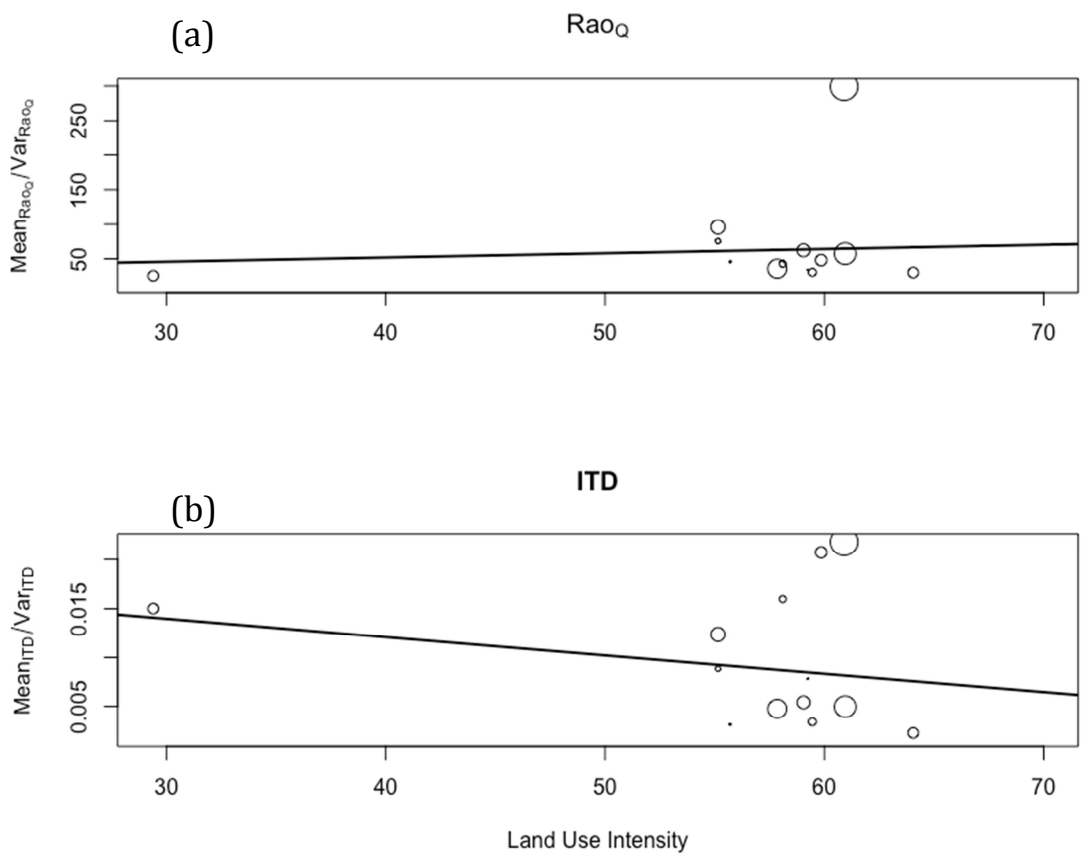

FIGURE 2.10 RELATIONSHIP BETWEEN LAND-USE INTENSITY IN THE "MATRIX" AND THE STABILITY OF RAO$_Q$ AND INTER-TEGULAR DISTANCE. Relationship between land use intensity in the "matrix" and (a) the stability of Rao$_Q$, and (b) the stability of ITD. Symbols are scaled small to large based on forest patch size.

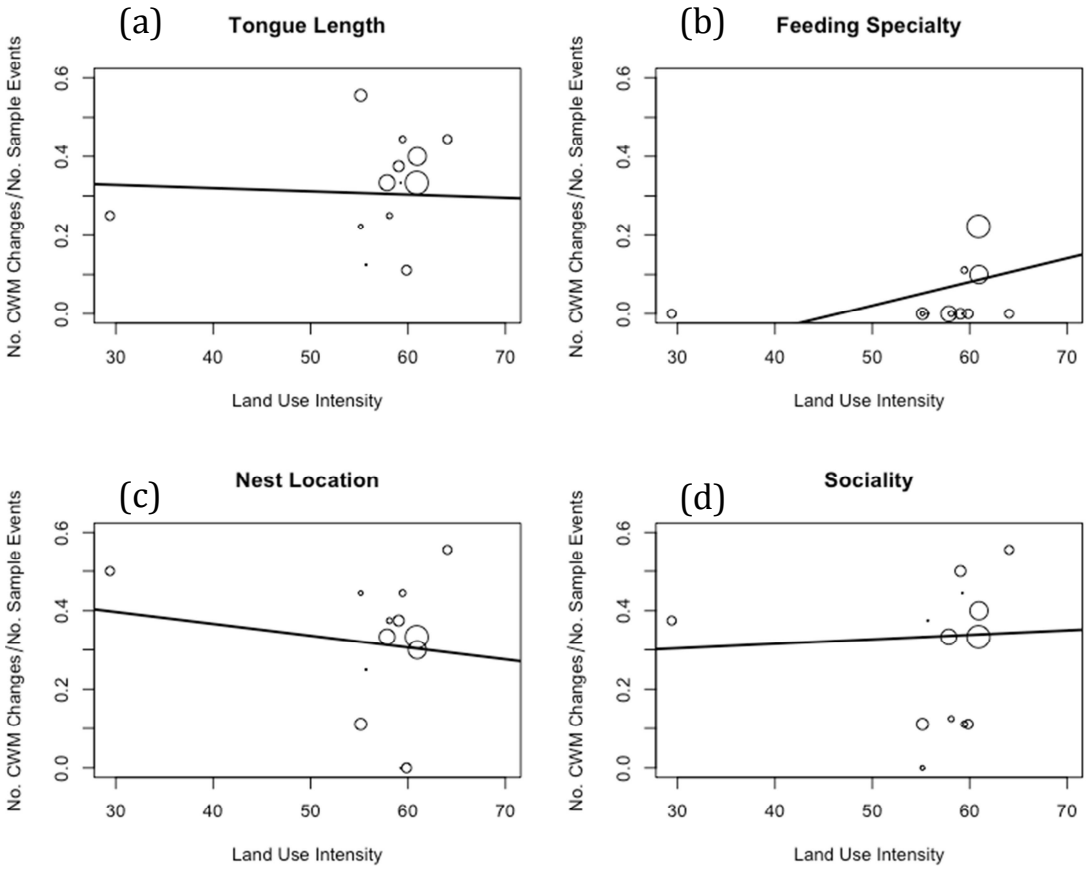

FIGURE 2.11 RELATIONSHIP BETWEEN LAND-USE INTENSITY IN THE "MATRIX" AND COMMUNITY WEIGHTED MEAN TRAIT STABILITY. Relationship between land use intensity in the "matrix" and the CWM variability of four traits: (a) tongue length, (b) feeding specialty, (c) nest location, and (d) sociality (Table 2.4). Symbols are scaled small to large based on forest patch size.

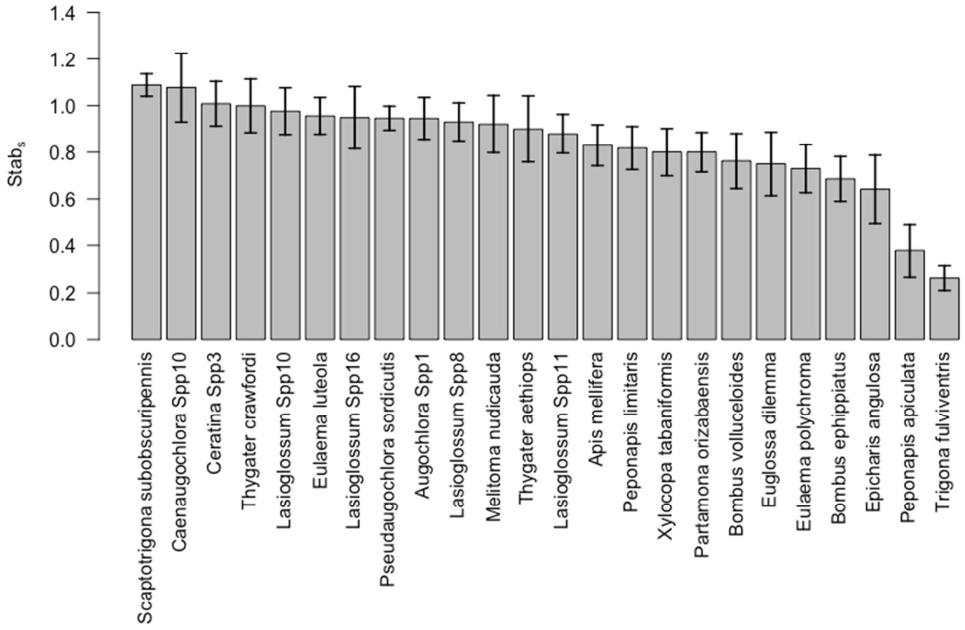

FIGURE 2.12 POPULATION STABILITY OF THE MOST ABUNDANT BEE SPECIES. Mean-variance population stability, $Stab_s$, for all species in which total abundance exceeded ten in the entire sample. Values are means (±1 SE).

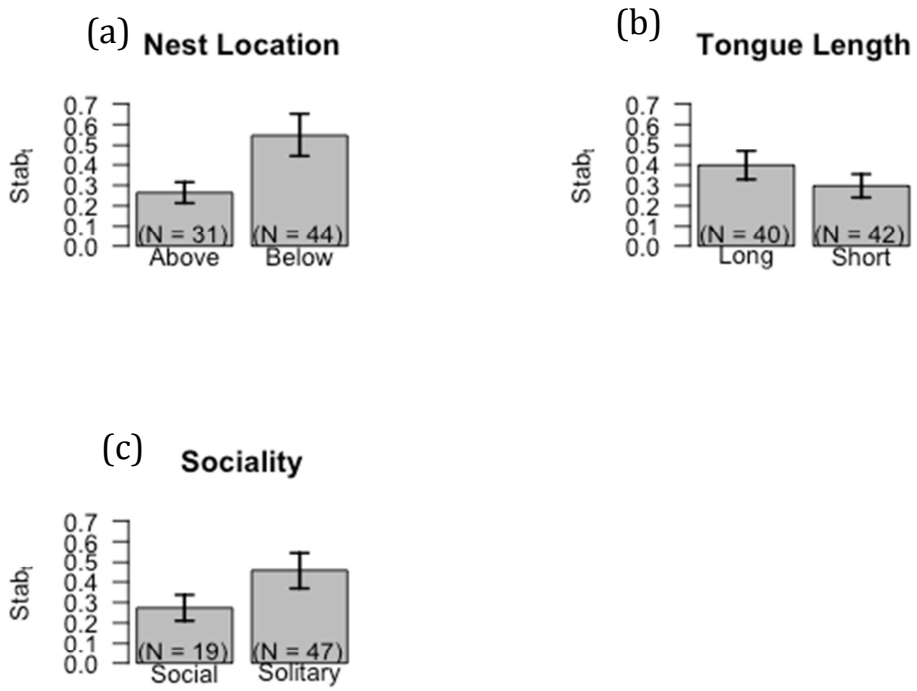

FIGURE 2.13 TRAIT STABILITY BY TRAIT CATEGORY. Mean-variance trait stability, $Stab_t$, by trait category: (a) nest location, (b) tongue length, and (c) sociality. Values are means (±1 SE) and N is the number of species.

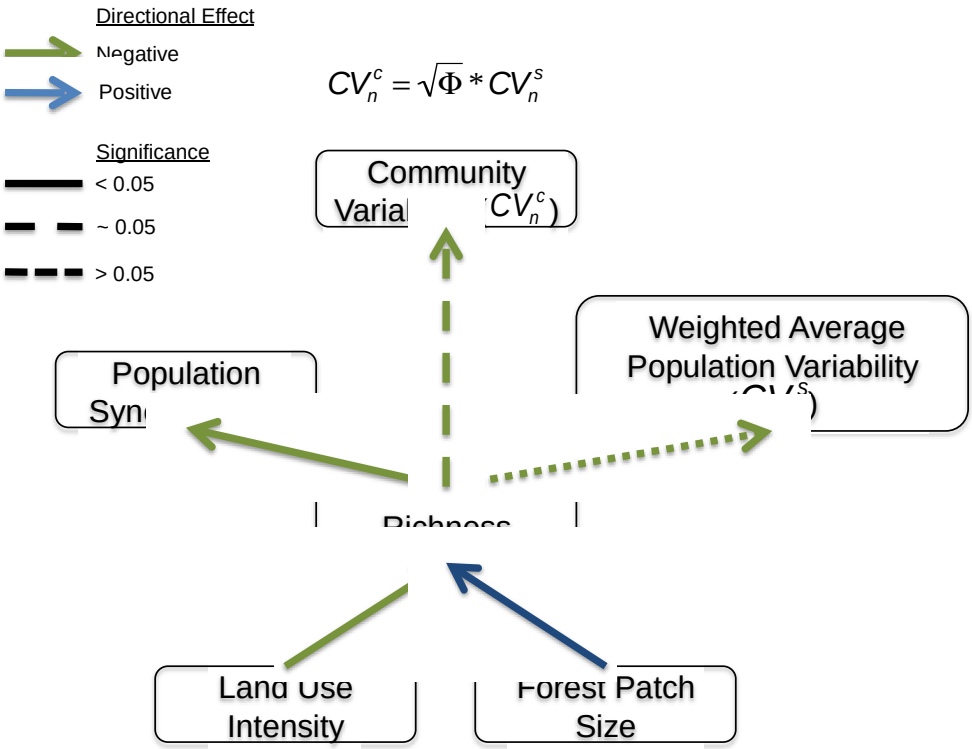

FIGURE 2.14 ILLUSTRATION OF THE EFFECTS OF LANDSCAPE ELEMENTS ON COMMUNITY DYNAMICS. Results from linear mixed effects models describing relationships between landscape-scale elements (forest patch size, land use intensity within the "matrix") and species richness. Community variability, CV_n^c, is negatively correlated with species richness, suggesting that landscape patterns drive community stability via changes in species richness. The effect of richness on CV_n^c appears to have been primarily due to the negative relationship between species richness and synchrony (ϕ).

CHAPTER 3

RECONCILING RESOURCE MANAGEMENT WITH THE LANDSCAPE: AN APPROACH TO IDENTIFY SCALE MIS-FIT IN SOCIAL-ECOLOGICAL SYSTEMS

3.1 ABSTRACT

Scale mis-fit occurs when natural resources are not managed at the spatial or temporal scale at which they are provisioned. Issues of scale mis-fit abound in social-ecological systems. They can hinder efforts to effectively manage resources and threaten resilience of the larger ecosystem, thus affecting societal well-being and livelihoods. Here, we present an approach to identify issues of scale mis-fit. Our approach can be used to define a specific natural resource problem, determine the scales at which relevant biophysical processes and management actions occur, assess spatial and temporal scale mis-fits, and identify potential solutions. We provide two case studies of drinking water resource management in Costa Rica and the Pacific Northwest United States as applications of our approach to natural resource management. While our case studies focus on a subset of water resources, the approach we present is broadly applicable to an array of social-ecological systems.

3.2 INTRODUCTION

Humans rely on natural resource provision for many facets of life, including sustenance, energy, livelihoods, recreation, and shelter. Effective management of natural resources is crucial to ensure their sustained use. Natural resource provision results from complex ecosystem interactions occurring across spatial and temporal scales, but resource use by society often occurs without understanding of the multi-scale biophysical processes that produce the resource or the complex response to management (Levin 1992). As a result, this lack of understanding is often exacerbated when management of natural resources occurs at different scales than those at which natural resources are provisioned and has been recognized within a variety of social-ecological systems (SES) and governance approaches (Ludwig and Smith 2005, Cumming et al. 2006, Dore and Lebel 2010, Termeer et al. 2010, Carmona-Torres et al. 2011, Apostolopoulou and Paloniemi 2012, Johnson et al. 2012, Paloniemi et al. 2012, Vervoort et al. 2012, Cumming et al. 2013).

Failing to manage natural resources at the appropriate scales can compromise both the long-term availability of the resource and the functioning of the larger SES (Lee 1993, Cumming et al. 2006, Wilson 2006, Dore and Lebel 2010, Moss and Newig 2010, Johnson et al. 2012, Fremier et al. 2013). Therefore, effective management of natural resources requires reconciling complex biophysical and social interactions that occur across different temporal and spatial scales within an SES (Gunderson and Holling 2002, Cash et al. 2006, Cumming et al. 2006) to fit management actions to the scales at which biophysical processes are provisioning the natural resource.

The SES perspective to natural resource management has emerged from the recognition that: (i) interactions and feedbacks between the biophysical processes that

provision resources and actions related to their management commonly occur, (ii) unexpected changes in natural resource availability are common (e.g., due to natural and social system dynamics), and (iii) management actions aimed at adapting to changes in natural resource flows, rather than maintaining constancy, are necessary to sustain natural resource availability (Folke 2006). Thus, the SES framework requires holistic approaches to management that integrate system components (social and ecological) and their interactions to analyze and elucidate problems of natural resource sustainability (Liu et al. 2007, Ostrom 2009). Interdisciplinary SES approaches provide a unique opportunity to analyze complex environmental problems from varying perspectives and to investigate a problem more thoroughly (Newell 2001).

Scale mis-fit commonly exists and has been recognized within SES; however, systematic approaches to identify scale mis-fit are lacking. Therefore, we present an integrated approach to analyze natural resource problems using a scale mis-fit lens that deconstructs components of an SES while enhancing understanding of complex interactions within the system. Users of this approach determine the scales at which relevant biophysical and governance processes occur to identify spatial and temporal scale mis-fit and propose potential solutions to a natural resource problem in an effort to align management actions to the relevant biophysical scales.

We suggest that framing complex natural resource issues explicitly in terms of spatial and temporal scales may allow for new insights to identify, analyze, and resolve natural resource problems in SES. By defining a system based on the scales of biophysical processes that sustain natural resources and the scales of management actions that influence these processes, the complex interactions between the

biophysical and human components of the SES can be reduced to fundamental elements underlying a specific natural resource problem. This clarity may reveal critical mis-fits in the scales of biophysical processes and management actions, highlighting possible improvements for natural resource problems. For example, natural cycles of forest loss and regeneration take much longer than historical management practices of wildfire suppression allowed. Recognizing this as a temporal scale mis-fit places more focus on defining management actions that allow forests to burn at a recurrence interval that better aligns with natural forest regeneration processes.

Our approach is designed for researchers, managers, and other practitioners to become aware of spatial and temporal scale mis-fits within various SES and identify solutions to address problems arising from them. The overall goal of this approach is to advance management by understanding the integrated biophysical and governance context of natural resource problems and applying that understanding to management actions. Systematically identifying sources of scale mis-fit and outlining solution options will assist users in achieving this goal. We recognize that no simple or single solution exists for resolving scale mis-fit complexity. However, this approach can be useful across a wide variety of SES to identify scale mis-fits and possible solutions without suggesting panaceas (Bovens and Hart 1996, Brunner et al. 2005, Ostrom et al. 2007).

Scale Mis-Fit Definitions

Scale is a fundamental aspect of social, physical, and biological systems and is considered a unifying concept between different academic traditions (Silver 2008).

Scale has previously been studied and defined in the literature (see Gibson et al. 2000, Young 2002, Cash et al. 2006, Cumming et al. 2006), and we adopt the definition "dimensions used to measure and study any phenomenon" (Gibson et al. 2000, p. 218) However, both within scientific literature and colloquially, scale is also used as an overarching term to refer to points along a spatial or temporal scale. We adopt this common terminology. For example, the terms "national scale" and "local scale" (i.e., jurisdictional boundaries) and the term "watershed scale" refer to different geographically defined areas on a spatial scale; different time frames (e.g., decades or minutes) refer to different points along a temporal scale. Box 3.1 presents several key definitions related to scale that we have adopted for this approach.

Box 3.1. Key definitions and explanation related to scale mis-fit
Scale: "The spatial, temporal, quantitative, or analytical dimensions used to measure and study any phenomenon." (Gibson et al. 2000, p. 218)
Spatial scale: The geographically-defined area where biophysical, management, or governance processes occur in a system.
Temporal scale: The amount of time it takes for biophysical, management, or governance processes to occur in a system.
Scale mis-fit: When adequate management actions do not occur at the spatial scales (i.e., geographic areas) or temporal scales (i.e., amount of time) most relevant to the biophysical processes provisioning the resource.

Here, biophysical processes are the interactions between two or more components of a natural system that contribute to the provisioning of a resource. We use the term biophysical explicitly to include both biological and physical components of an SES. The term management specifically refers to the actions of overseeing resource provision and usage. Management actions are the implementation of rules and regulations that are determined by governance processes, which occur through the

larger social system (Parkes et al. 2010). Governance processes extend beyond formal government and include the actions of all individuals and institutions involved in making decisions and establishing rules and norms that influence a natural resource (Richards and Smith 2002, Graham et al. 2003, Armitage and Plummer 2010).

We define scale mis-fit as a discrepancy between the scales of biophysical processes and management actions (Box 3.1). Spatial and temporal scale mis-fits exist when adequate management actions do not occur at the spatial scales (i.e., geographic areas) or temporal scales (i.e., amount of time) most relevant to the biophysical processes provisioning the resource. Although governance processes occur at multiple scales, resolving scale mis-fit problems necessitates adequate management actions at the spatial and temporal scales most relevant for the biophysical processes specific to the natural resource problem of concern.

Sources and Consequences of Scale Mis-Fit

Scale mis-fit in SES may arise from a variety of causes. Note that the terms "mis-fit" and "mismatch" are often used synonymously; we prefer the term "mis-fit" because it does not imply the existence or feasibility of an exact match between scales and/or processes. Cumming et al. (2006) categorize sources of scale mis-fit (referred to by the authors as "scale mismatch") as mainly social, ecological, or coupled social-ecological, clarifying that mis-fit can be caused by environmental factors, the organizations responsible for management, or interactions between them. These authors provide examples of environmental sources of scale mis-fit including natural cycles within

ecological communities (e.g., due to disease outbreaks or predator-prey interactions) or unexpected environmental responses to management. They also describe social drivers of scale mis-fit as changes in land tenure, technology, human population growth, markets, infrastructure, and values. Others have further described the sources of scale mis-fit as rooted specifically in the governance system, such as imperfect knowledge about the biophysical system being managed (Hessl 2002, Apostolopoulou and Paloniemi 2012), constraints within the institutions charged with management (Paloniemi et al. 2012), short-term economic returns overshadowing environmental processes in policy development (Ludwig and Smith 2005, Dore and Lebel 2010, Ahlborg and Nightingale 2012, Paloniemi et al. 2012), and difficulty in adapting legislation and agency practices to meet environmental needs (Gibson et al. 2000, Young 2002). In our view, the primary source of scale mis-fit is a failure to fully understand and consider the scales of biophysical processes provisioning a resource and to subsequently align management actions and governance processes accordingly.

A lack of understanding or recognition of the most relevant scales at which biophysical processes provision a resource can hinder efforts to align resource management with these processes (Cash et al. 2006). For instance, Johnson et al. (2012) explored potential causes of sea urchin declines in Maine, USA in the late twentieth century. They concluded that the small-scale biophysical processes most important for maintaining sustainable sea urchin fishery levels (local migration of sea urchins to areas in which they were easily harvested) were not adequately incorporated into state-scale fishery co-management policies, resulting in persistent sea urchin decline. In another example in the western United States, management actions designed with a

temporal understanding discordant with cross-scale ecological dynamics, including forest dynamics, grazer population dynamics, and fire regime, have also have been blamed for decline of forests (Holling 1986, Hessl 2002). Furthermore, since natural systems rarely follow socio-political boundaries, consequences of management actions in one region can have transboundary effects. For example, upstream river degradation can influence downstream water quality, flood occurrence, and fisheries (Fremier et al. 2013). While it is increasingly evident that effective resource management necessitates that social processes are consistent with the scales of related biophysical processes (Cleveland et al. 1996), scale mis-fit continues to exist within many SES and contribute to many environmental problems (Young 2002).

Toward an Approach to Identify and Address Scale Mis-Fit

Many examples of natural resource problems resulting from scale mis-fit in SES exist in the literature (Wilson 2006, Dore and Lebel 2010, Ahlborg and Nightingale 2012, Apostolopoulou and Paloniemi 2012, Johnson et al. 2012, Kane 2012, Vervoort et al. 2012). However, systematic identification and analysis of scale mis-fit is lacking. Moreover, identifying problems related to mis-fit prior to natural resource decline or system collapse is more effective to prevent and mitigate problems than retrospective analysis. Cumming et al. (2006) concluded that once identified, resolving scale mis-fit first requires an awareness of how scale contributes to problems within an SES, followed by the development of a range of potential solutions. We build on this conclusion by proposing that systematic problem definition should be the first step

towards diagnosing and potentially resolving issues of scale mis-fit and presenting a process for identifying scale mis-fit.

Our approach to identify and analyze scale mis-fit integrates concepts from existing theoretical frameworks, mainly the policy sciences (Lasswell 1968, Clark 2002) and social-ecological resilience (Cumming et al. 2005, Walker and Salt 2006, Walker and Salt 2012). Both frameworks have been used to map biophysical and social processes within SES (Walker et al. 2002, Rutherford et al. 2009, Wilshusen 2009, Brunner and Lynch 2010, Walker and Salt 2012), and our approach incorporates insights from specific aspects of each of them. The policy sciences framework offers a problem definition process as a starting point for natural resource managers to guide their analysis and resolution of complex problems (Clark 2002, Lynch et al. 2013, Hammer 2013). Resilience theory, with its origins in describing non-linear behaviors in biophysical systems (Holling 1973), offers tools to assess complex dynamics in coupled SES (Walker and Salt 2006). These frameworks help define a system based on available knowledge and we propose applying this knowledge specifically to identify issues of scale mis-fit and potential ways of improving alignment of management actions to the relevant scales of resource-sustaining biophysical processes. In our approach, we reiterate the emphasis that both of these frameworks place on promoting participatory processes to engage multiple stakeholders in research and practical applications of analyzing these dynamics in SES (Clark 2002, Walker et al. 2002, Walker and Salt 2012).

Much of the published literature related to scale mis-fit in SES focuses primarily on the effects of scale mis-fit in natural resource provisioning (Gunderson and Holling 2002, Cumming et al. 2006, Moss & Newig 2010, Carmona-Torres et al. 2011, Ahlborg

and Nightingale 2012, Johnson et al. 2012, Vatn and Vedeld 2012, Vervoort et al. 2012). Identifying effective solutions to problems within SES often requires addressing scale mis-fit, although tools to identify and analyze scale mis-fit are lacking. The only approach that we have found in the literature to identify scale mis-fit is presented by Ludwig and Smith (2005) based on Walker et al. (2002). Their four-step approach to address scale mis-fit uses resilience analysis in Australian rangelands. The steps include: (i) mapping the scales at which key processes and components of the SES occur, (ii) evaluating potential trajectories of the SES, (iii) assessing the effects of scale mis-fits driving uncertainty in trajectory predictions, and (iv) gauging how different methods for correcting scale mis-fits may affect management actions. We expand on this approach by beginning with focused problem orientation, followed by a systematic appraisal of the relevant scales for both the biophysical processes that provision a natural resource and the management actions pertinent to the stated problem.

3.3 An Approach to Identify Scale Mis-Fit

Our stepwise approach to identify and address scale mis-fit in SES is presented in Box 3.2 as a series of six steps, where each step builds on understanding gained in previous steps. The approach is designed to focus on one specific natural resource problem, although many problems may exist within an SES. We see great value in using professionally facilitated, interactive processes engaging multiple stakeholders to complete these steps.

Box 3.2. A six-step approach to identify, analyze and address scale mis-fit

Step 1. Define the problem related to the natural resource of concern.

a) What is the natural resource of concern in the system?
b) What is the specific problem related to this resource?

Step 2. Describe biophysical processes that provision the resource.

a) What biophysical processes are relevant for providing the resource?
b) Where do these processes occur on the landscape? (spatial scales)
c) How much time does it take for these processes to occur? (temporal scales)
d) What are the spatial and temporal scales most relevant to address the specified problem?

Step 3. Describe how humans influence biophysical processes contributing to the resource.

How do human activities influence the biophysical processes at the most relevant spatial and temporal scales (from Step 2d)?

Step 4. Describe management actions and governance processes that influence the resource.

a) What institutions (governmental and non-governmental) play a role in managing these human activities, and what management actions do they take?
b) What governance processes determine these management actions?
c) Where geographically are management actions focused? (spatial scale)
d) What time frames do management actions address? (temporal scale)

Step 5. Assess spatial and temporal scale mis-fits.

a) Do adequate management actions (Step 4) occur at the biophysically relevant spatial and temporal scales (Step 2)?
b) What spatial and/or temporal scale mis-fits exist?

Step 6. Identify potential solutions to address scale mis-fits.

a) What management actions are needed at the relevant spatial and/or temporal scales to address the scale mis-fits identified?
b) What governance processes are needed to achieve these management actions?
c) What barriers exist under current laws and policies and what process would be necessary to overcome these barriers?
d) What potential solutions could be implemented over short-, medium-, and long-terms?

3.4 Scale Mis-Fit in Water Resource Management

We found our approach useful for examining case studies in water resource management, where scale mis-fit exists prominently (Cash et al. 2006, Dore and Lebel 2010, Moss and Newig 2010) but has not been resolved effectively (Poff et al. 2003). As

with other natural resources, the biophysical processes that influence water resources occur at multiple spatial scales ranging from small-scale molecular processes (e.g., interactions between chemical pollutants) to large-scale basin, continental, or global-level processes (e.g., groundwater flow and climate, flood, and drought regimes). Management actions often are not aligned with the scales of these biophysical processes. For example, political boundaries generally do not follow watershed boundaries, making watershed management more complex when crossing multiple jurisdictions. Moreover, defaulting to a focus at the watershed scale could ignore or fail to prioritize biophysical processes that occur at different scales, such as climate regimes or groundwater recharge, which do not generally adhere to topographic watershed boundaries (*sensu* Vatn and Vedeld 2012).

One example of an effort to address issues of scale in water resource management problems is Integrated Water Resource Management (IWRM). IWRM promotes both a watershed vision for management actions (Agarwal et al. 2000) and integration of governmental authority over various activities that impact the water resource (Cosens and Stow 2014). However, water resource problems are often very unique and cannot utilize one standard solution (Biswas 2004). While IWRM is an attempt to address water issues at the most appropriate biophysical spatial scale (i.e., the watershed), some point out that the watershed is not always the most appropriate scale of addressing governance processes (Cohen and Davidson 2011). In addition, despite the prevalence of scale issues in water resource systems, IWRM principles do not specifically address the issue of scale mis-fit. IWRM is designed to address fragmentation in management of human activities that affect the same connected water

resource. While this may at times address scale issues, they are not the focus. Ultimately, given the multiple spatial and temporal scales that are involved in water resources, water management must address scale mis-fit issues to be effective and to produce long-term results. In addition, participatory methods that engage multiple stakeholders have been particularly effective in establishing opportunities to overcome scale mis-fit (Dore and Lebel 2010) and in enabling vertical integration, linking the levels of water governance (Knuppe and Pahl-Wostl 2011). We demonstrate how our approach promotes integration and multi-scale considerations in two water resource management case studies.

3.5 Case Studies: Water Resource Management in Costa Rica and the PAcific Northwest USA

We present two case studies focused on drinking water management to demonstrate the utility of our approach in analyzing SES problems. By presenting these case studies, we aim to contribute to the continuing development of heuristic approaches to identify, understand, and resolve scale mis-fit. The first case is based in Costa Rica and was developed through interdisciplinary teamwork of four doctoral students in the Joint Doctoral Program between the Tropical Agricultural Research and Higher Education Center (CATIE) and the University of Idaho (UI). The second case is based in the western United States and draws from long-term involvement of the University of Idaho in scientific studies on regional water resources, as well as interdisciplinary studies by faculty and students in the UI Waters of the West Program.

With both case studies, we present relevant background information before using our scale mis-fit approach to analyze the SES.

Costa Rica Case Study Background

The Costa Rica case study focuses on drinking water quality in rural communities in the Cartago Province of central Costa Rica. This case study draws from findings from interviews with community organizations and government agencies involved in drinking water management and a survey and workshop with community drinking water organizations in the study region. Drinking water quality remains largely unknown, although potentially hazardous contaminants, such as agrochemicals, are used within the watershed and are likely entering community water sources. Throughout the country, local community-based drinking water organizations (CBDWOs, or ASADAs and CAAR in Spanish) are responsible for overseeing the management and provision of drinking water in rural communities. In this region, drinking water is piped directly from springs and most CBDWOs use chlorine treatments to reduce the risk of bacterial contamination. Water quality testing is conducted once every six months to two years, if at all. In addition, common land uses within the contributing area include agriculture and pasture, and contaminants from these practices threaten water quality. The Water Law (Costa Rica Government 1942)

and the Environmental Law (Costa Rica Government 1995) mandate forested protection zones of 200 m and 100 m radii, respectively, around the spring. Most citizens are uncertain about which radius to use, and enforcement of the two laws is minimal. Moreover, these protection zones are not based on scientific evidence. The upstream area contributing to a spring (springshed) lies largely unprotected, while the majority of the protected area lies downstream of the spring in areas that do not contribute groundwater to the spring flow (Figure 3.1). Therefore, much of the springshed is not protected under the two laws. We use the term springshed to refer to the area of land in which water infiltrates into the ground and exits at a common spring source. We differentiate springshed from watershed, which is typically determined by topography, since springs mainly rely on only groundwater sources that may not follow topographic relief.

As a result of the discrepancy between the protection areas and the boundaries of the springsheds, CBDWOs often are not aware of the influence that the springshed has on water quality and do not monitor activities that occur in these regions. Due to limited or non-existent water quality testing, CBDWOs and users lack information about the quality of their drinking water sources. Potential threats that exist in the springshed interfere with the ability of CBDWOs to provide potable drinking water for local communities. In some cases these threats may pose hazardous to community members' health. Limited financial and human resources prevent communities and government agencies from conducting studies to identify where groundwater recharge occurs, to determine whether water contamination is occurring within the springshed, and to establish effective management plans.

Six-step Approach Applied to the Costa Rica Case

Using the six-step approach presented in Box 3.2, we analyze the SES related to drinking water in the Cartago province of Costa Rica.

Step 1: Drinking water quality is a significant concern within rural communities of Costa Rica. Water quality monitoring is infrequent, and understanding of groundwater recharge zones for the springs is limited, preventing CBDWOs from identifying both potential contaminants and the human actions that are responsible for contamination. This uncertainty about water quality jeopardizes human health.

Step 2: Many biophysical processes influence the provision of clean drinking water, including climate processes (precipitation) and hydrogeologic processes (infiltration, groundwater flow, and spring water discharge). Precipitation occurs at a regional scale, while the interactions between infiltrated water, groundwater, and spring water occur at the scale of the springshed. Precipitation occurs on the order of minutes to hours, while infiltration and shallow groundwater flow to springs occur on the order of hours to months, depending on springshed size, soil parameters, and precipitation intensity and magnitude. In order to address the problem of focus, the relevant spatial scale is the springshed, while the relevant temporal scale is in the range of hours to days.

Step 3: Human activities primarily influence water quality through land use management practices. Within the springsheds, which are not protected by the Water Law (1942) or Environmental Law (1996), many concerning land uses occur, such as intensive agriculture and cattle grazing. Agrochemicals applied to crops and fecal coliforms from cattle manure can enter soils and flow to the spring on the temporal scale of hours to days.

Step 4: Several institutions are responsible for management actions and governance processes in this region. The National Institute for Water and Sewage (ICAA, or AyA in Spanish) is responsible for providing CBDWO administrative support; they also provide occasional training and limited financial resources. The Ministry of Energy and the Environment (MINAE) developed and enforces the Environmental Law (Costa Rica Government 1995) that stipulates the 100 m radius protection area around drinking water sources. The Water Law (Costa Rica Government 1942) stipulates the 200 m radius (Figure 1). The CBDWOs act on the local community scale to develop spring sources, maintain infrastructure for water delivery, collect fees, and finance maintenance of the system. Spatially, management actions are limited to areas directly around the springs, although very few springs are fully protected by the mandated 100 and 200 m radius zones. Temporally, the relevant management actions, water quality tests, generally occur on a scale from once every six months (most frequent) to once every two years (least frequent), or sometimes not at all.

Step 5: The relevant biophysical spatial scale is the springshed, where recharge contributes to spring flow. Land use within the springshed, including agriculture and cattle grazing, threatens water quality, but management actions to regulate these practices, when undertaken, usually only occur within the 100 to 200 m surrounding the springs. Of the limited management practices undertaken to mitigate the effects of land use on water quality, many are targeted in locations outside of the springshed, downslope of the spring in the area that does not contribute to spring flow. Therefore, there is a spatial scale mis-fit between the scale of drinking water management with the scale of the biophysical processes that provision the resource. Management actions also do not occur at the temporal scales most relevant for drinking water provisioning. Water quality tests are conducted infrequently, but potential threats to water quality (e.g., agrochemicals and fecal coliforms) are possibly occurring in the springshed, ranging on the order of minutes to days (Figure 3.2). Therefore, the limited testing that is conducted has a high probability of not identifying any acute contaminants that pass through the system; this results in a temporal scale mis-fit.

Step 6: To address these scale mis-fits, management actions are needed at the springshed scale, and governance processes should focus on establishing the springshed as the protection area for management focus. Delineation of springshed boundaries requires significant resources given the difficulty of determining the extent of groundwater contribution to springs. However, the watershed, based on topographic boundaries, may be initially considered, given the likelihood of significant overlap with the springshed. Also, the watershed is a more feasible and cost-effective scale to begin

protecting. More frequent water quality monitoring aligned with the temporal scale of infiltration and shallow groundwater flow rates is also needed to identify potential rapid changes on the landscape that lead to contamination of drinking water supplies.

Potential short-term solutions include delineating watershed boundaries for all springs and conducting targeted sampling after rainfall events when occurrence of contaminants might be greatest. Two medium-term solutions could include 1) developing a monitoring plan to capture the appropriate spatial extent and temporal variability of the biophysical processes to sustain consistent, clean drinking water for the communities, and 2) forming regional bridging organizations (i.e., a watershed management group) among CBDWO water managers to promote water quality training, shared knowledge, communication, and collective garnering of financial resources. Two potential long-term solutions are to 1) modify existing laws and enforcement mechanisms to establish appropriate upslope spring protection areas and focus management actions at the watershed scale and 2) determine groundwater contributions to the springs for management at the springshed scale.

Overview of the Six-Step Approach in Costa Rica

Applying the six-step approach to this SES in Costa Rica reveals a predominant issue of spatial scale mis-fit involved in drinking water management, as management actions do not exist at springshed levels. The spatial scale of biophysical processes responsible for water provisioning (i.e., the springshed) is not sufficiently considered in the design of Costa Rican drinking water management policy. Use of this approach

indicates that several potential options exist for community members to address water quality in this region, including short-term efforts that can provide insight into the problem while longer-term solutions are refined and implemented. Results of our approach also emphasize the importance of monitoring water resource dynamics at the appropriate temporal scale. The strategy of focusing water protection efforts at the springshed scale, monitoring spring water quality more frequently, and sharing this information throughout a local CBDWO network would establish community knowledge to inform short-term actions in lieu of long-term policy that will require significant time to reform. Therefore, a change in the spatial and temporal scale of management actions would more closely align the governance actions with the biophysical processes for water provision in this particular case as well as in other cases facing similar issues.

Palouse Basin Case Study Background

The Palouse Basin case study focuses on groundwater availability in the Palouse Basin located in the Inland Northwest of the United Sates (Figure 3.3). The majority of water from the basin is pumped from the Grande Ronde, a deep fractured basalt aquifer that provides groundwater for domestic and industrial users located in the Idaho and Washington states. Significant concern exists over aquifer levels, which have been declining at a rate of 20-45 cm per year for the past 60 years (see Figure 3.4; Beall et al. 2011, Moran 2011) with no direct evidence of aquifer recharge (Belknap 1999). Water

allocation occurs at the state level in the United States (California Oregon Power Co. v. Beaver Portland Cement Co. 1935, Tarlock 2011), but the Washington/Idaho state line divides the Grande Ronde Aquifer. Idaho state law prohibits aquifer mining, defined as water pumping rates that exceed the rate of natural groundwater recharge (Idaho Statutes 42-237a(g)). Therefore, the occurrence of aquifer mining as defined by law cannot be determined without knowing the recharge rate, which has not been determined in this case. Washington state law is less specific but prohibits pumping beyond the source's yield capacity (RCW 90.44.070), which has not yet been scientifically determined for this aquifer. Continued need for a scientific answer to the questions of the exact size and recharge rate of the aquifer has diverted attention from developing plans to reduce pumping rates, reinforcing the spatial and temporal mis-fits.

With approval of Congress, federal law allows the creation of an interstate authority that crosses state lines and allows the region to control management of their water system as one unit. However, studies show that decision makers in the region have rejected this approach based on fear that federal approval will complicate management (Richartz 2011). The Palouse Basin Aquifer Committee (PBAC) was established in 1967 as a voluntary entity bridging the state divide and has been instrumental in facilitating voluntary conservation measures. However, PBAC lacks management and enforcement authority for conservation goals in the region.

Six-Step Approach Applied to the Palouse Basin Case

Using the six-step approach presented in Box 3.2, we analyze the SES related to the Palouse Basin.

Step 1: The resource of concern is groundwater from the Grande Ronde Aquifer. The water level of the aquifer has been declining significantly for the last 60 years. However, uncertainties remain over whether the aquifer is recharging and if the basin will experience a water shortage, since the recharge rate has not been scientifically determined. Existing local policies encourage voluntary conservation measures. State law requirements for curtailment of pumping on a "mined" aquifer have not been met in either state in which the aquifer occurs. Political will to develop alternative drinking water sources is lacking, as any viable surface water sources are shared by the two states.

Step 2: The biophysical processes that influence the aquifer include climate processes (precipitation) and hydrogeologic processes (primarily infiltration and aquifer recharge). Precipitation occurs at a regional scale, whereas infiltration and recharge occur on the aquifer scale. A shallow aquifer provides water to portions of one city and its recharge occurs on a scale of hours to months. The occurrence of recharge to the primary deep aquifer is unknown, but movement of recharge, if any, into production zones is clearly not occurring in a timeframe to prevent aquifer decline. In order to address the problem of focus, the relevant spatial scale is the aquifer, while the relevant temporal scale is unknown, but longer than the current period of record (60 years).

Step 3: Municipal groundwater pumping accounts for the most significant use of water from the aquifer and pumping rates increase with population growth. Groundwater pumping is likely occurring at a rate greater than recharge to the production zone given declines in the level of the aquifer over the last 60 years.

Step 4: The aquifer extends across the Washington-Idaho border and, as a result, is managed independently by the two states, invoking jurisdictional complexity. The PBAC, composed of representatives of the communities reliant on the aquifers and representatives of each state in an advisory capacity, was established to bridge efforts at the aquifer scale. The PBAC promotes information sharing and establishment of joint conservation goals, including the 1993 Groundwater Management Plan (GWMP). Although suggested management actions such as the GWMP are not legally binding, generally communities have complied. Although the rate of aquifer decline has slowed since implementation of the GWMP, aquifer levels continue to decline (Figure 3.4).

In the state of Idaho, Statute 42-237a(g) prohibits aquifer mining exceeding the groundwater recharge rate (a standard that cannot be met if recharge is unknown), while Washington law (RCW 90.44.080) prohibits pumping an aquifer beyond its "safe yield." The relevant spatial scale of management actions includes the four cities that pump water from the aquifer and the state scale at which management is dictated. The temporal scale of management actions ranges from daily (pumping) to years (for development of city and university plans) to decades (for development and implementation of legislation).

Step 5: Currently there is no legally binding governance or management at the aquifer scale, which is the scale at which groundwater resources are provisioned, resulting in a spatial scale mis-fit. However, PBAC forms a bridging organization between the states of Idaho and Washington at this scale. The rate of aquifer recharge has not been determined and steady decline of the aquifer level over time suggests that the rate of extraction is greater than the rate of recharge at least to the production zone of municipal wells, indicating that a temporal mis-fit is occurring. The limited scientific investigations of recharge rate preclude imposing legal restrictions on pumping rates. The high cost associated with such research has inhibited the necessary scientific studies. Stakeholder attention primarily focuses on the state-defined spatial mis-fit and the need for further scientific study. However, application of this approach indicates that the temporal scale is far more important.

Step 6: Strategies to overcome scale mis-fit in the Palouse Basin must address the problem of declining groundwater reserves at the aquifer scale and at a temporal scale that matches the discrepancy between the recharge rate to the production zone and rate of groundwater decline. Adequate investment to develop new water sources is paramount. Continued effort to determine recharge rates is warranted, although they have proved unsuccessful to date. The basin may be better served by determining the maximum depth of production through test wells and consideration of the economics of pumping from that depth. Based on maximum depth of pumping, the timeframe for aquifer decline to this point (assuming current rate of decline) and thus the need for supplemental resources may be determined.

One potential short-term strategy to address these issues is the establishment of a facilitated forum where scientists and decision makers can discuss relevant issues and identify the roles of science and policy in addressing existing problems. Over several years, a medium-term strategy to incorporate university-based research to determine maximum economic pump depth and possibly aquifer recharge rates could provide student training and valuable knowledge to the regional groundwater problem. Efforts to identify alternative water sources and design, permit, and develop compliance measures for new water sources could move forward. Potential long-term strategies include determining a more robust means for communities to work together across the state line, potentially through empowering PBAC, and coordinating appropriate pumping levels of the aquifer based on scientific evidence.

Overview of the Six-Step Approach in the Palouse Basin

Applying the six-step approach in the Palouse Basin reveals a spatial scale mis-fit in this SES. Given that a state line divides the Grande Ronde Aquifer, management occurs within jurisdictional boundaries that do not overlap with the most appropriate spatial scale, the aquifer scale, for regional groundwater resources. While the scale at which PBAC is focused aligns well with the biophysical scale at which water is provisioned in the Palouse Basin, the organization has no enforcement authority. However, this spatial scale mis-fit overshadows and tends to mask the temporal scale mis-fit, which lies at the heart of the problem. The main source of the water resource problems in this region is that the withdrawal rate exceeds the

timeframe in which aquifer recharge occurs within the production zone. Since legislation in both states requires scientific determination of the general recharge rate in order to legally limit pumping, costly and lengthy studies are needed before adequate water conservation practices will be implemented. Using our approach in this case study helps users identify the temporal scale mis-fit occurring and place more focus on potential short-term solutions to mitigate the effects of waiting for necessary long-term solutions.

3.6 Applicability of the Six-Step Approach for the Case Studies

The case studies demonstrate a useful approach to identify, further understand problems associated with, and discuss alternative solutions for scale mis-fit. In the Costa Rica case, by framing the management problem in terms of spatial and temporal scales, potential avenues for improving resource governance and defining management actions emerged. Our approach revealed feasible means to address water quality issues in drinking water. CBDWOs are spending human and financial resources to manage protection areas that do not contribute to the quality of spring water in the region. Resources would be more effectively used to protect those areas that have the most influence on drinking water quality. Delineating watersheds in lieu of springsheds provides an essential and feasible starting point for aligning the spatial scale of management actions with the spatial scale most relevant (and practical) for water resource provisioning.

Ultimately, identifying the scale mis-fit between management actions and biophysical processes of an SES exposes potential vulnerability that may threaten the ability of an SES to provision an adequate supply of resources. Addressing this weakness could strengthen the SES to address ongoing large-scale issues including increasingly common problems associated with climate change and population growth.

Restatement of the Palouse Basin aquifer issue from a scale mis-fit perspective distilled the complex problem to an awareness of specific spatial and temporal mis-fit in water resource governance. Focusing on both spatial and temporal scales clarified the multi-scale nature of the problem and highlights the need for cross-scale collaborations. Using our approach revealed that a critical temporal mis-fit issue is likely masked by the obvious spatial mis-fit created by the political border dividing the aquifer. Significant attention is being placed on the political boundaries rather than focusing on the likely decline of the aquifer, precluding more appropriate sustainable management of groundwater resources. Our approach identified that more knowledge of the system could potentially improve mismanagement. The lack of management actions at the basin scale and the lack of a long-term, legally binding conservation plan contribute to uncertainty about the future availability of drinking water in the Palouse region.

These two cases provide examples of how our approach is useful for identifying and understanding issues of scale mis-fit within SES. The steps in our approach provide a process for navigating environmental problems by first focusing on a specific natural resource problem and then framing the problem explicitly in terms of the scales of both biophysical and governance processes, thereby making the problem more manageable to tackle without ignoring system complexity. When addressing complex problems with

an interdisciplinary systems approach, it is often difficult to strike a balance between holistically understanding a problem that involves multiple interactions and feedbacks and deconstructing the problem into individual components. With this approach we intend to provide an entry point for breaking a problem down into manageable components through an analysis that acknowledges system complexity while identifying specific vulnerabilities. This approach is applicable to other contexts, both in water resource management and with other natural resource problems where spatial and temporal scales are of particular relevance and will be useful to researchers, managers, and other practitioners involved in natural resource management.

3.7 Discussion

This six-step approach to analyzing scale mis-fit has several unique aspects. First, a focus on scale facilitates mutual understanding among researchers and stakeholders with different disciplinary orientations. This focus is of particular importance given the need for interdisciplinary approaches to SES (Redman et al. 2004, Lang et al. 2012) that can be hampered by the inherent difficulty of interdisciplinary collaboration (Eigenbrode et al. 2007, Morse et al. 2007). Second, specifically emphasizing the scales of resource provision and management offers an opportunity to identify "critical causes," when they are related to scale, of natural resource problems that are not always intuitive or obvious in SES. Third, this approach explicitly places a concurrent emphasis on both spatial and temporal scales, as well as biophysical and governance systems, which are critical for effective natural resource management.

Lastly, our approach encourages users to identify a range of possible solutions over different time frames rather than focusing on a single solution to resolve problems of scale mis-fit.

We also recognize the need to address potential weaknesses of this approach. For example, solutions to address scale mis-fit are often complex and not straightforward. After identifying an existing scale mis-fit, one cannot simply "align the scales" to "fix" the problem. For example, where a problem is identified in an SES, creating or changing legislation might better protect resources and prove to be necessary to address the scale mis-fit. However, as new legislation requires a long-term vision, waiting for changes in legislation without additional short-term actions to address problems could allow them to worsen. More importantly, uncertainty requires a more nimble approach than legislative action in a governance structure that fits the scale of today's problem but may prove inadequate in the future. Therefore, short- and medium-term mitigation strategies that address certain aspects of a problem could be explored concurrently with comprehensive long-term approaches. We propose that considering multiple solutions for different time frames will avoid issues that occur when focusing on one solution for a specific time frame.

Potential solutions and governance approaches need to be tailored for each resource and unique SES (Vatn and Vedeld 2012). Therefore, we envision that this approach will require in-depth, participatory discussions involving multiple stakeholders relevant for a specific case. Given that identifying solutions to scale mis-fit is complex, we would like to highlight that Step 6 is intended to encourage users of this approach to consider potential solutions to specifically address identified scale mis-fits.

However, further work would be needed to identify a range of potential options that would satisfy multiple stakeholders' interests and to analyze the benefits and drawbacks of each solution. In addition, some factors influencing natural resource use, such as culture, history, religion, or economics, may not be explicitly addressed in this approach and may need further consideration in some cases. We encourage users to apply other relevant conceptual models, frameworks or analytical tools in conjunction with this approach specific to scale mis-fit.

3.8 Conclusion

Issues of scale mis-fit, when natural resources are not managed or governed at the scale at which they are provisioned, exist in a wide variety of SES. Lack of understanding the scales at which biophysical processes influence natural resource provisioning can lead to misalignment of management actions influencing resources. Identifying effective solutions to problems within SES often requires addressing scale mis-fit, although limited tools to identify and analyze scale mis-fit have been developed. We propose a systematic, approach for identifying, analyzing, and addressing scale mis-fit in environmental problems, based upon the premise that many natural resource problems are ultimately caused by a misalignment of the scales of management to the scales of resource provisioning.

The two case studies presented, from Costa Rica and the Inland Northwest region of the United States, highlight the applicability of our approach in two different social-ecological contexts related to water resource management. However, this

approach for interdisciplinary investigation of spatial-temporal phenomena will be useful to analyze natural resource problems across a variety of SES contexts. We encourage others to test and refine this scale mis-fit approach for a range of natural resources issues, such as species, forest, and marine management, in various SES contexts to aid in its development and practical application. While identification of scale mis-fit is an imperative step towards reconciling natural resource management with biophysical processes occurring on the landscape, additional work is particularly necessary to identify and implement solutions to address scale mis-fit problems.

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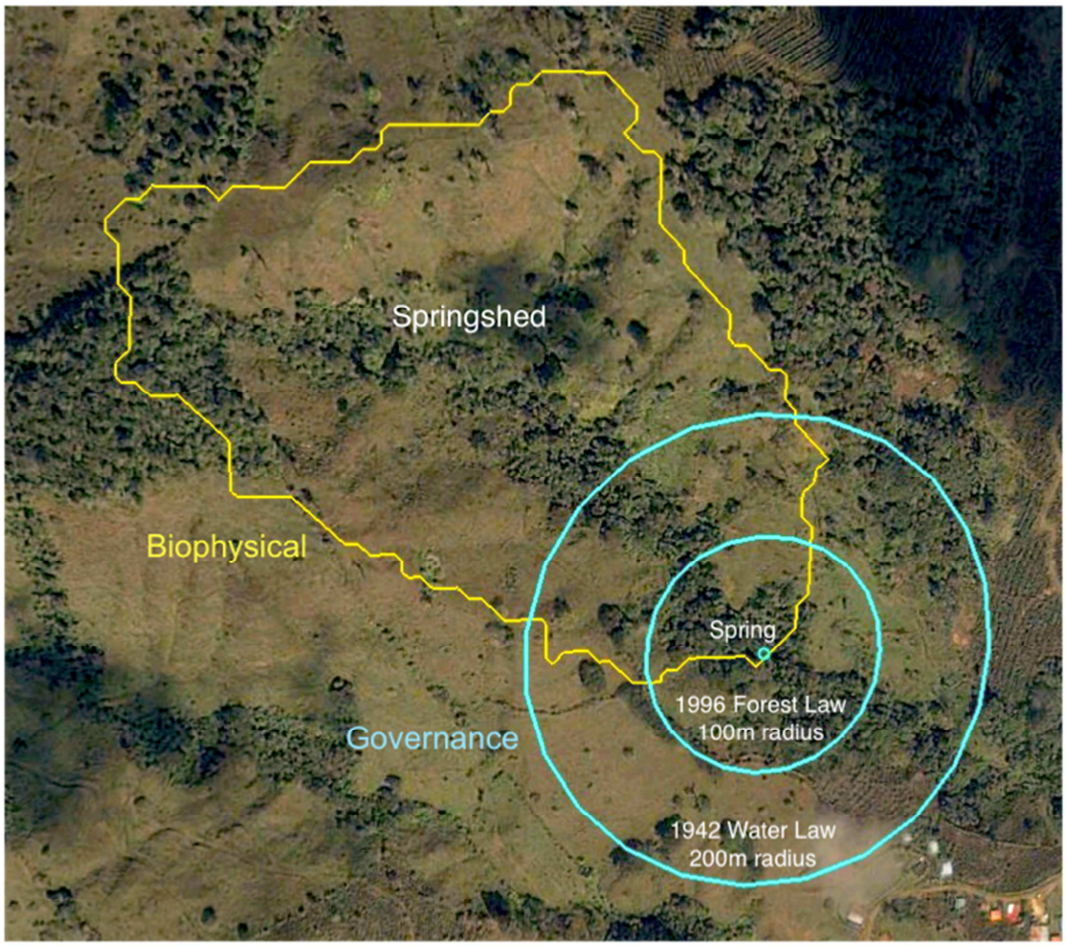

FIGURE 3.1 ILLUSTRATION OF A SPATIAL SCALE MIS-FIT IN THE COSTA RICA CASE STUDY. Illustration of a spatial scale mis-fit between the upstream area contributing to spring discharge (the potential springshed, yellow polygon) and the mandated protection buffers surrounding the spring (blue polygons) managed by a CBDWO in the Cartago Province of Costa Rica. Management actions primarily occur within the protection buffers, which do not fit the spatial scale of the biophysical processes that provision the drinking water (i.e., within the springshed) (Map data ©2013 Google, Digital Globe).

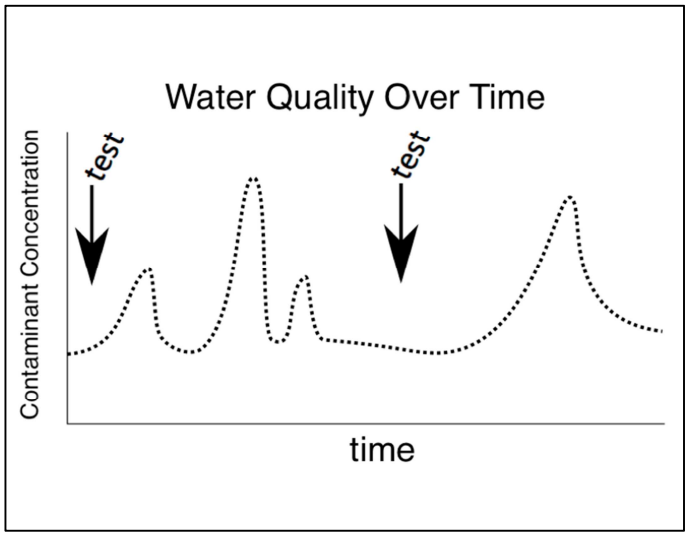

FIGURE 3.2 ILLUSTRATION OF TEMPORAL SCALE MIS-FIT IN THE COSTA RICA CASE STUDY. Conceptual illustration of a temporal scale mis-fit between the frequency of water quality testing and the probable changes in water contaminant concentration over time. CBDWOs in Costa Rica typically sample water for contaminants less than twice per year, and thus the tests are not likely revealing the suitability of the water for drinking.

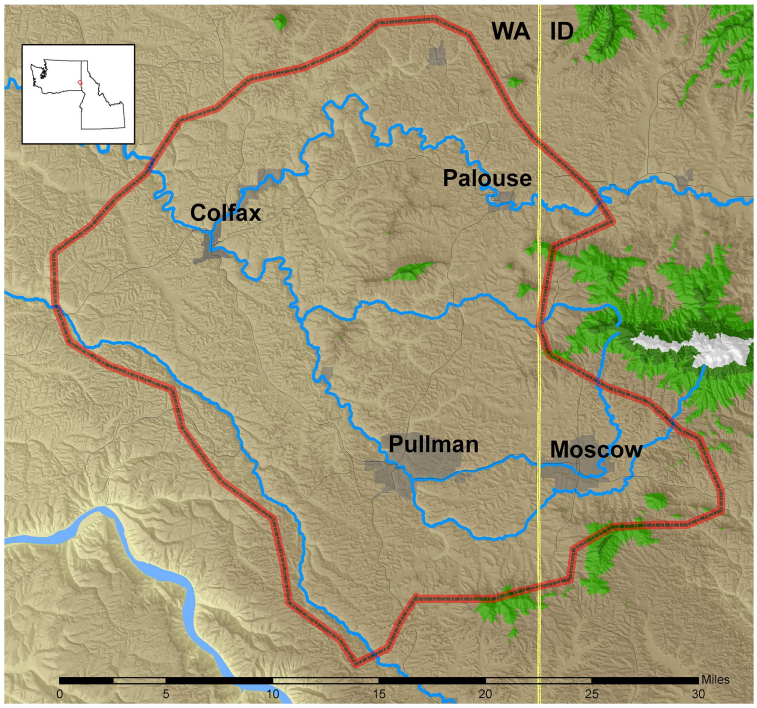

FIGURE 3.3 ILLUSTRATION OF SPATIAL SCALE MIS-FIT IN THE PACIFIC NORTHWEST USA CASE STUDY. Palouse Basin showing boundary between Idaho and Washington (yellow line) and the approximate boundary of the Grande Ronde aquifer (red line) located within both states. The inset shows where the aquifer is located within both states.

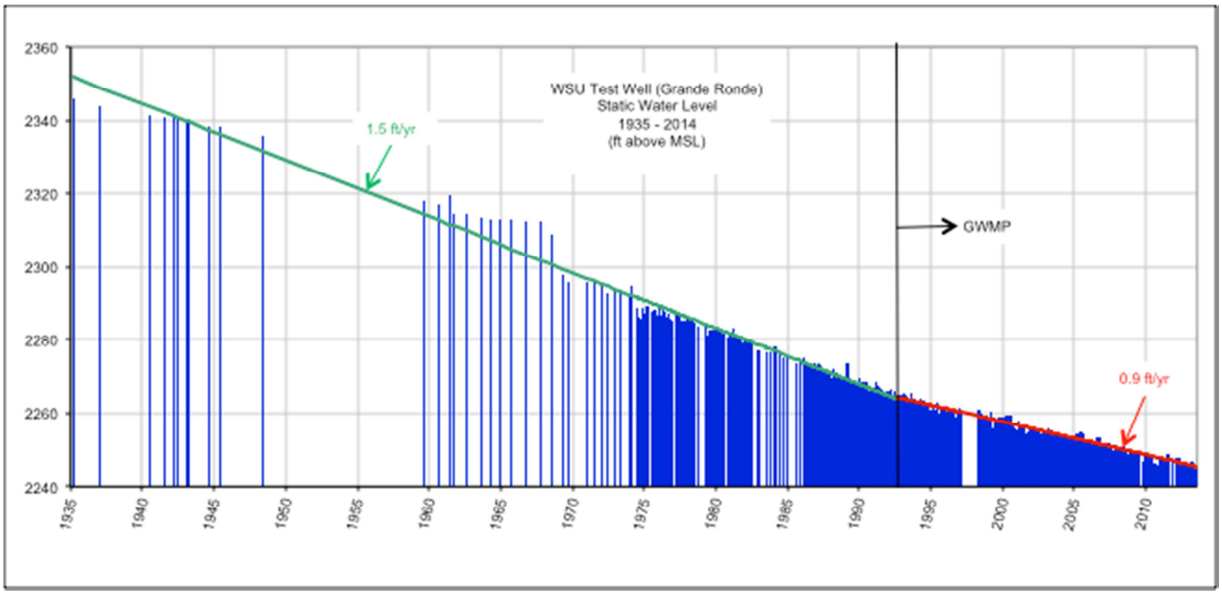

FIGURE 3.4 HISTORIC GROUNDWATER LEVELS FROM THE PACIFIC NORTHWEST USA CASE STUDY. Static water levels in the WSU Test Well. Green and red regression lines show decrease of levels prior to and after 1993, respectively, when the Groundwater Management Plan (GWMP) was developed by PBAC.