Understanding the Impact of Land Use Change on Bee Populations and Ecosystem Services in the Seasonally Dry Tropics: An Interdisciplinary Approach

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by
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Authorization to Submit Dissertation

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Abstract

Over the past century, humans have made unprecedented changes to the world's ecosystems, causing global ecosystem service (ES) loss. More information on the relationship between land use and ES provision is needed to improve policy design and resource allocation in heterogeneous agroecosystems. In this study, we used a team-based interdisciplinary approach to understand the impact of land use change on ES in the Nicoya Peninsula of Costa Rica. This region has undergone dramatic land use changes in the past century, and recent reforestation has been attributed to socio-economic drivers as well as a combination of multi-scalar conservation policies, including Payments for Ecosystem Services (PES). We investigated the relative impact of human-dominated land uses on bee populations, which are a proxy for pollination services. We found that bee populations vary with altitudinal and seasonal changes, and that among low altitude land uses, teak plantations have significantly lower bee abundance, richness, diversity, and evenness than pastures. In addition, we observed changes in the relative abundance of functional groups, with large sized cavity-nesting bees, buzz pollinating bees, and moderate to small sized bee specialists being less represented in teak plantations compared to coffee agroforestry and pastures. To determine the value of these land uses to a group of non-landowners, we then explored a mixed-methods approach for the valuation of ES based on local ecological knowledge. We found that beekeepers perceive a loss of provisioning services (i.e., honey production) due to recent land use changes, and that they prefer native forests for beekeeping. We also found that they are most limited by access, rather than existing land cover in the region. To address the large scale of ES management, we reviewed current methods and future opportunities for applying remote sensing tools to the study of bees and other ES-providing insects. Finally, we explored the potential for using functional trait measurements, which are most often measured at the plot scale, for landscape-scale ES management. We discuss the proxies and metrics used to determine different types of ES based on functional trait measurements, and outline a framework for upscaling multiple ES to assess conservation policy.

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Dedication

This project is dedicated to the people who made Moscow and Hojancha places I could call home. An extra special thank you to:

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Ecosystem service loss and research needs

Over the past century, humans have made unprecedented changes to the world's ecosystems. While many of these changes have contributed to gains in human well-being and economic development, they also have had short and long-term negative feedbacks on human society, such as the loss of ecosystem services (ES). The concept of ES, defined as the benefits humans derive from functioning ecosystems, was designed to address the link between ecosystems and human well-being (Daily 1997, MEA 2005). ES include provisioning services, such as the production of lumber or food; regulating services, such as pollination or pest control; supporting services, such as carbon storage and nutrient cycling; and cultural services, such as recreational or spiritual use (Fig. 1). According to the Millennium Ecosystem Assessment (2005), many ES that are critical for human well-being are being degraded or used unsustainably worldwide.

Anthropogenic land use change is one of the main drivers of ES loss, and is occurring rapidly and on a global scale, largely due to the need to provide resources for a growing population (Foley et al. 2005). By the year 2000, crop and pastureland covered almost 50 million square kilometers, or 34.9% of non-ice covered land on the planet (Goldewijk et al. 2010). With rapid land conversion and subsequent ES loss, we need to have a better understanding of the ecological processes that drive ES provision (Kremen and Ostfeld 2012). The application of knowledge in ES-related ecological theory and practice can help policymakers and stakeholders to simultaneously meet human needs and conserve ecosystems (DeClerck et al. 2006) and maintain the ES needed for sustainable food security and human well-being.

Interdisciplinary approaches for studying ES

Questions related to the impact of land use and cover on ES provision require an interdisciplinary perspective because they depend on many different ecosystem functions, as well as an understanding of the value of and demand for services by human societies. This is due to several processes recently explored in ES literature, including ES trade-offs, where one ES is increased at the cost of another (Foley et al. 2005), and the differing spatio-temporal lags related to ecosystem function (Fremier et al. 2013). Understanding and managing ES provision also requires consideration of the relative value of these services to human societies (Liu et al. 2010). There is a rich literature on the social (Brown et al. 2015) and economic (Fisher et al. 2008) valuation of ES, which each include numerous methods for determining the importance, worth, or usefulness of land use types based on ES demand and provision. Useful approaches to ES problems depend not only on better understanding of the function of ecosystems, but also on novel methods to combine these disciplinary perspectives (Daily et al. 2009).

Repko and colleagues (2008) define interdisciplinary science as a process of answering a question or solving a complex problem by drawing on different disciplinary perspectives, and integrating them to create a more comprehensive understanding or cognitive advancement. There are several conceptual frameworks designed for interdisciplinary approaches to ES research as part of social-ecological systems (SES). Ostrom (2009) describes an SES as a composition of various sub-systems that are relatively separable from each other, but are interconnected so that each component feeds back on the others, as well as other connected SES. Her concept, based on political ecology, includes four core subsystems: resource units, resource system, governance system, and users. This and other SES frameworks and typologies (i.e., Daily et al. 2009, Helming et al. 2011) are designed to consider interconnected social and ecological concepts over local, regional, and national scales, helping to integrate ES provision and value into decision-making.

While interdisciplinary research methods have advanced significantly in the last decade, there is still considerable need for novel interdisciplinary approaches to understand ES in changing landscapes (Daily et al. 2009), and to improve collaboration between scientists and practitioners (Foley et al. 2005). We used both disciplinary and interdisciplinary methods to better understand the impact of land use change on ecosystem function and the outcomes for specific stakeholder groups in a social-ecological system.

Interdisciplinary objectives of the research team

The chapters in this dissertation are part of a larger team effort in the framework of an NSF-IGERT program. We approached questions about ES change in the study region as part of a dynamic SES in Costa Rica. Our team research objectives were to understand ES changes due to land use and cover change in the Nicoya Peninsula of Costa Rica, to determine the value of these changes for local stakeholders, and to provide practical information about ES changes to stakeholders and decision-makers in the study region.

There were several concepts and processes that we measured as part of the study (Fig. 2). In our study system, as outlined in the conceptual diagram, ES-focused conservation strategies and policy design have a direct impact on land use and cover change, which then result in changes to ES provision. ES outcomes must be measured using two perspectives: human perception of services, which can be measured in various socio-cultural or economic terms, and measurement of the ecosystem function itself using methods from the biophysical sciences. One of the key facets of the conceptual diagram is the need for assessment of service trade-offs and prioritization, for which scientists can provide information, but requires decision-making by policymakers and other stakeholders in the SES.

The Nicoya Peninsula social-ecological system

Land conversion in tropical regions has global implications. The tropics contain a disproportionately high number of the world's biodiversity hotspots (Myers et al. 2000) and tropical forests store much of the world's carbon stocks (Gibbs et al. 2007). The impact of land use and cover change is especially dramatic in tropical dry forest regions, where the majority of forest has been converted to pasture and agricultural land (Murphy and Lugo

1995). Dry forests are the most threatened of all the lowland tropical forests; as of 1988, less than 0.1% of dry tropical forests had conservation status, and the remaining forest mostly existed in habitat fragments and degraded patches (Janzen 1988). Despite this global trend, forest transitions in the dry tropics have occurred asymmetrically, and forests have begun to show signs of stability and some recovery in more developed countries such as Panama and Costa Rica (Redo et al. 2012).

For our interdisciplinary SES study, we worked in the Nicoya, Hojancha, Nandayure, and Puntarenas counties of the Nicoya Peninsula, located in Northwestern Costa Rica (Fig. 3). Except for Puntarenas, which is part of the Puntarenas province, these counties are within the Guanacaste province and the Tempisque Conservation Area. The peninsula, bordered by the Pacific Ocean to the west and the Gulf of Nicoya to the east, is a mix of seasonally dry and moist tropical ecological life zones (Calvo-Alvarado et al. 2009), with about 95 percent of the average 1,800mm of rainfall occurring from May to November (Mata and Echeverria 2004). The elevation within the peninsula ranges from sea level to ca. 900 meters. As of 2005, 43.6% of the peninsula was forested (Calvo-Alvarado et. al 2009).

The Nicoya Peninsula has recently undergone a dramatic land use and cover changes, and in some counties forest cover increased from 14% to 52% between 1970 and 2005 (Serrano 2005). Due to high beef prices and a growing cattle industry, extensive dry tropical forest in the peninsula was converted to pasture from the 1950s to mid 1970s (McLennan and Garvin 2012). FAO estimated Costa Rica’s deforestation rate between 1976 and 1980 to be 3.2% annually, the fifth highest rate globally (Sanchez-Azofeifa et al. 2001). This trend was reversed by the effects of a drop in international beef demand and prices combined with a severe El Niño-induced drought in the late 1970’s, resulting in extensive migration back to urban areas (Vallejo et al. 2006). As a result, many agricultural lands in the Nicoya Peninsula were abandoned, and a large proportion of pastureland regenerated into secondary forest.

Coincident with this demographic shift, local initiatives and national policy changes emerged that were conducive to reforestation in the peninsula. Locally, Monte Alto Natural

Reserve was set aside for conservation, and a community-managed water organization was formed to conserve water in light of the severe aforementioned drought. The local government agency Centro Agrícola Cantonal de Hojancha (CACH) was created, providing resources for reforestation and education for improved farm management techniques (Vallejo et al. 2006). The Costa Rican government implemented protected lands, forestry incentives, and tax incentives for reforestation investments, mostly in the late 1990s (Vallejo et al. 2006). The National Fund for Forest Finance (Fondo Nacional de Financiamiento Forestal - FONAFIFO) was created to mitigate deforestation. This fund allocates Payment for Environmental Services (PES). Since its creation, FONAFIFO has financed over 12,500 PES under thirteen modalities (FONAFIFO 2013).

Although Costa Rica is a pioneer of ES incentives (Pagiola 2008), there is a need for research on the impacts of the various changes that have occurred under these policies over the last few decades. Some of the PES-sponsored reforestation has occurred in the form of monoculture tree plantations (Vallejo et al. 2006). These tree plantations have been established on degraded pastures, but may have replaced potential re-growth of native secondary forests. Studies have also found that PES in Costa Rica may not have a significant impact on reforestation because several other national policies, including a law against deforestation, already regulate land cover (Sanchez-Azofeifa et al. 2007). From a social perspective, researchers have questioned the viability of these "win-win" conservation solutions (Muradian et al. 2013), for example showing that incentives are disproportionately offered to large farm and forest owners (Zbinden and Lee 2005).

Arguably most pressing, little is known about trade-offs between ES associated with payments for different land cover types (Foley et al. 2005, Jackson et al. 2005). PES in Costa Rica are provided for a "bundle" of several services, including mitigation of global warming gases, protection of water resources, biodiversity and conservation, and scenic beauty (Pagiola 2008). Because there is a lack of evidence for service trade-offs for target land cover types or land uses, research is needed to measure the services that are supported by current and potential future land uses.

Within Hojancha County, where much of our study took place, the most common land uses are forest (primary, secondary, and riparian, 52%), pastures (36%), and forest plantations (8%) (Serrano 2005, Vallejo et al. 2006). Teak (*Tectona grandis*, Family: Lamiaceae) is a tropical hardwood deciduous species native to Southeast Asia, and a popular plantation crop in tropical climates. Teak plantations are a common part of the landscape in the Nicoya Peninsula (Fig. 4), and are an increasingly popular reforestation strategy in the dry tropics (Hallet et al. 2011). Little is known about how provisioning of ES differs between secondary forest versus monoculture tree plantations, but in Costa Rica teak plantations are incentivized by PES as a type of reforestation. PES contracts are significantly related to the presence of tree plantations on farms in the Nicoya Peninsula (Cárdenas et al. 2014). Though it is established that plant diversity is lower in plantations, studies on other organisms and ecosystem function outcomes are needed to better understand the impact of teak plantations on incentivized ES (Hallett et al. 2011).

Our interdisciplinary team focused on three ES within common land use and cover types, including teak plantations, in the Nicoya Peninsula SES: biodiversity, carbon storage, and water storage. This dissertation is primarily focused on the effects of land use and cover change on biodiversity of native and domestic bee populations.

Bee populations as an ES proxy

Pollination is perhaps the most well studied ES provided by insects. Eighty-seven percent of all flowering plant species depend on animals to transfer pollen (Ollerton et al. 2011). Humans directly depend on animal pollination for food production and economic activities, as 35% of crop species worldwide depend on pollinators (Klein et al. 2007). Bees (Hymenoptera: Apoidea) are important pollinators that affect reproductive processes in wild species and crops in most landscapes (Steffan-Dewenter and Westphal 2008, Winfree 2013. This group of service providers is threatened by disturbances such as habitat loss, pesticide use, the spread of pathogens, and invasive species worldwide (Winfree et al. 2009, Potts et al. 2010). Thus, bees have become a model taxon for studying how environmental disturbances impact the provisioning of ES (Winfree 2013).

Understanding of changes in pollination services in response to habitat loss requires better data on the relationship of bee populations to local, regional, and landscape-scale variables (Winfree 2013, Zulian et al. 2013), particularly in under-studied ecosystems. Since most studies on pollinators have been done in landscapes with low proportions of remaining habitat (Winfree et al. 2011), they may not be generalizable to less studied landscapes, such as heterogeneous agroecosystems common in the developing tropics (Archer et al. 2014). Patterns correlating decreasing bee diversity to habitat loss are strongest in areas with little remaining habitat, while work done in more heterogeneous landscapes has often shown neutral or positive effects of human-dominated land uses, such as flowering crops, on bee diversity (Tscharntke et al. 2005, Holzchuh et al. 2008, Winfree et al. 2011). Existing research often treats different land uses as either "habitat" or "non-habitat" and does not consider the variety of nesting substrates and foraging resources that bees may utilize in less intensively managed agroecosystems (Winfree et al. 2007, Kennedy et al. 2013).

Furthermore, while land use and cover, management, and landscape context may impact pollination services from wild bee populations, managed bee colonies are used for pollination in many countries. The global demand for honeybee (*Apis mellifera*) pollination services is outpacing the honeybee stock, and decreasing populations have implications for crop production and biodiversity maintenance (Aizen and Harder 2009). With pollinator populations decreasing and increasing rates of colony collapse in managed honeybees (Potts et al. 2010), it is of pressing importance to understand how human activities influence bee populations (Vanbergen et al. 2013). It is critical to understand the value of different land use and cover types for beekeeping and potential impacts of land use and cover changes over time for managed pollinators.

Pollination services in the Nicoya Peninsula

We investigated the impacts of land use change in relation to bee populations because of the importance of this guild to pollination, honey production, and biodiversity maintenance in the Nicoya Peninsula. In the seasonally dry tropics, a large proportion of flowering plants depend on bee pollination. Native bees are the most important pollinators for the majority of trees in the peninsula, and large-bodied bees alone are the primary pollinators of almost 17% of all plants in the Nicoya peninsula (Frankie et al. 2004). Bees are also critical pollinators for local crops such as melon and mango (Losey and Vaughan 2006, Klein 2006), and improve the quantity and quality of coffee crops (Klein et al. 2003). There is evidence that bee abundance and diversity is decreasing (Frankie et al. 1997) and that the composition of bee populations changes with distance from native habitat in pastures (Brosi et al. 2007) in Costa Rica.

Domestic honeybees also play a crucial role in the Nicoya Peninsula SES. In the tropics, managed stingless bees (Hymenoptera: Apidae: Meliponini) and honeybees are used to produce honey. The majority of the 400-500 beekeepers in Costa Rica are located in the province of Guanacaste (J. von Veen, personal communication). Many of these beekeepers are in the Nicoya Peninsula, including the members of the largest beekeeping society in Costa Rica, ASOAPI (Asociación de Apicultores de Jicaral).

This dissertation describes research approaching the impacts of land use and cover change on bee populations from several perspectives within our interdisciplinary conceptual model (Fig. 5). In chapter two, *Understanding the impact of human-dominated land uses on bee populations in the seasonally dry tropics,* I investigated the impacts of land use change and distance from native habitat on bee abundance, richness, diversity, evenness, and the relative abundance of functional groups among common land uses in the Nicoya Peninsula. I found that bee population metrics are significantly lower in PES-incentivized teak plantations than coffee and pasture systems, and that the relative abundance of functional groups such as moderate to large flower-pollinating cavity-nesting bees, buzz pollinators, and moderate to small-sized specialists are lower in teak plantations relative to the other land uses.

In chapter three, *A mixed-methods approach for applying local ecological knowledge to ecosystem service valuation*, I examine beekeeper perceptions of land use change in the peninsula, and how they value different land uses for apiculture. Because the ES concept is inherently anthropogenic, it is important to integrate measurements of ES provisioning based on stakeholder perceptions. In the case of potential pollination services from bees, beekeepers hold valuable local ecological knowledge based on their experiences with land use and cover change. I found that beekeepers perceived a decrease in resources for their bees due to specific land use, cover, and management changes in the last 50 years. I also found, using mapping, that their perception of limitations in floral resources may be due to lack of access to their preferred land uses. Our novel mixed-methods approach can help apply local ecological knowledge to inform conservation policy.

The final two chapters are focused on concepts and methods to apply ES measurements at the plot scale to regional-scale conservation policies. Chapter four, *Remote sensing and ecosystem services: Current status and future opportunities for the study of bees and pollination-related services,* outlines remote sensing contributions to the study of ES from insects, and focuses on potential uses to study bee populations scales applicable to large-scale conservation efforts. Chapter five, *Spatial scaling-up of functional traits for ecosystem services: Concepts and methods*, is an interdisciplinary team effort and describes how multiple services can be addressed by policymakers based on functional trait-based ecological data. It addresses the challenges and opportunities of combining trait-based measurements of multiple ecosystem services to match management scales.

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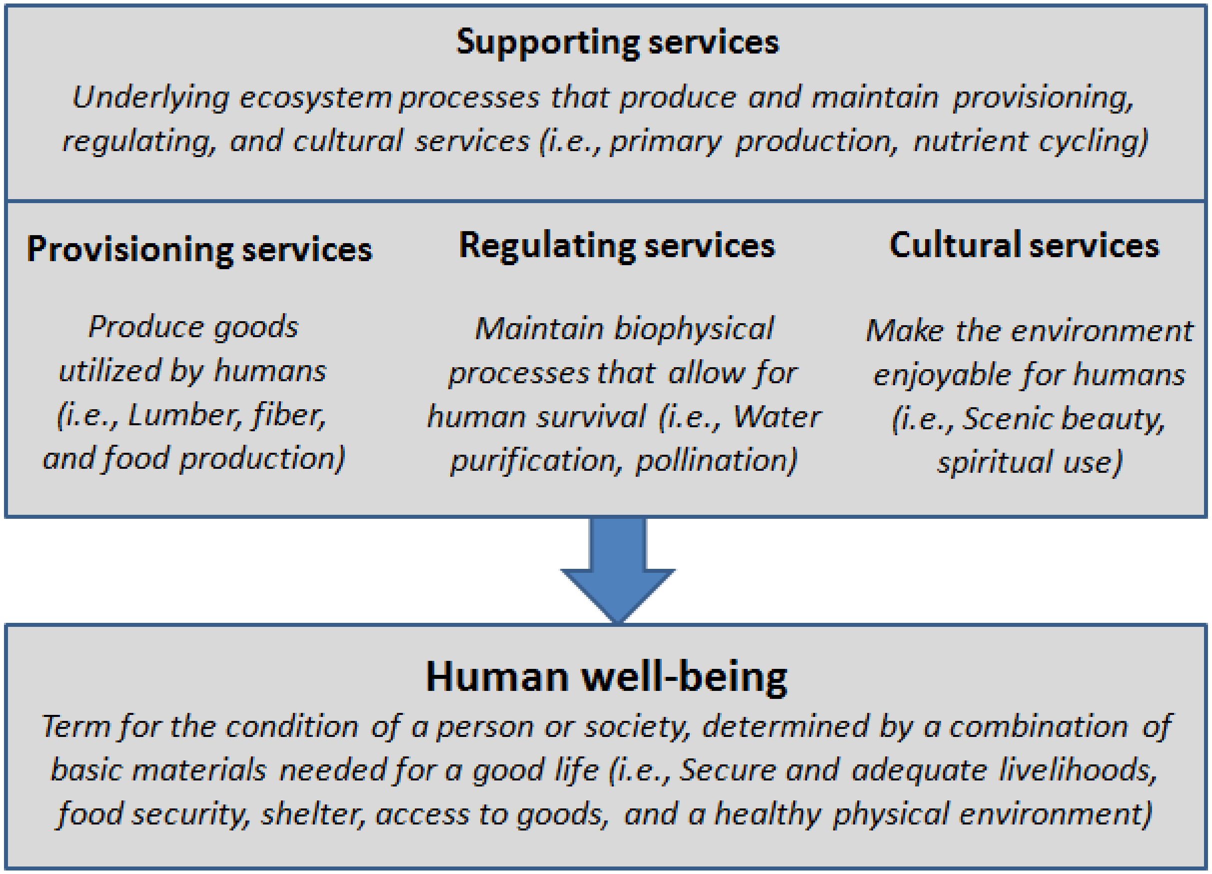

Supporting services

Underlying ecosystem processes that produce and maintain provisioning, regulating, and cultural services (i.e., primary production, nutrient cycling)

Provisioning services

Produce goods utilized by humans (i.e., Lumber, fiber, and food production)

Regulating services

Maintain biophysical processes that allow for human survival (i.e., Water purification, pollination)

Cultural services

Make the environment enjoyable for humans (i.e., Scenic beauty, spiritual use)

Human well-being

Term for the condition of a person or society, determined by a combination of basic materials needed for a good life (i.e., Secure and adequate livelihoods, food security, shelter, access to goods, and a healthy physical environment)

Figure 1. Organization of ecosystem services with their connections to human well-being. Adapted from MEA 2005.

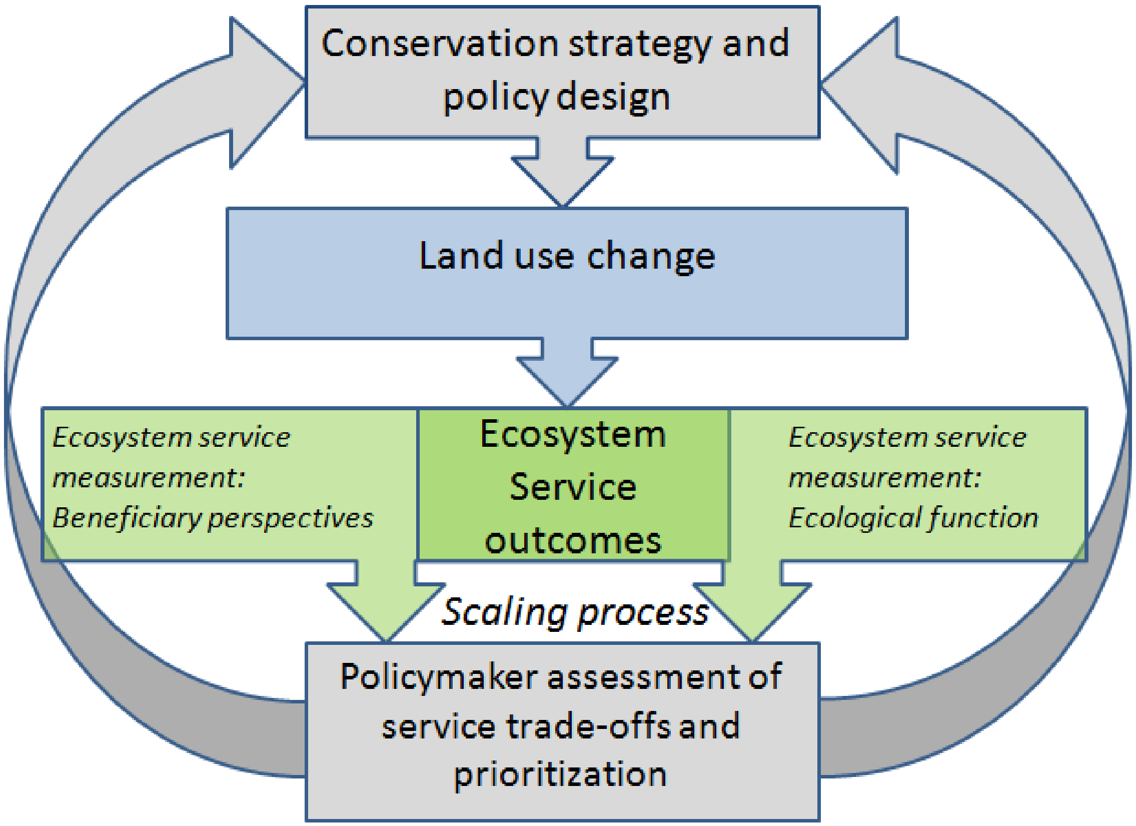

Figure 2. Conceptual diagram for assessing the impact of land use change on ecosystem services in the context of the Nicoya Peninsula social-ecological system. This study was focused on ecosystem service measurement (in green) and scaling processes for applying those measurements to service assessments.

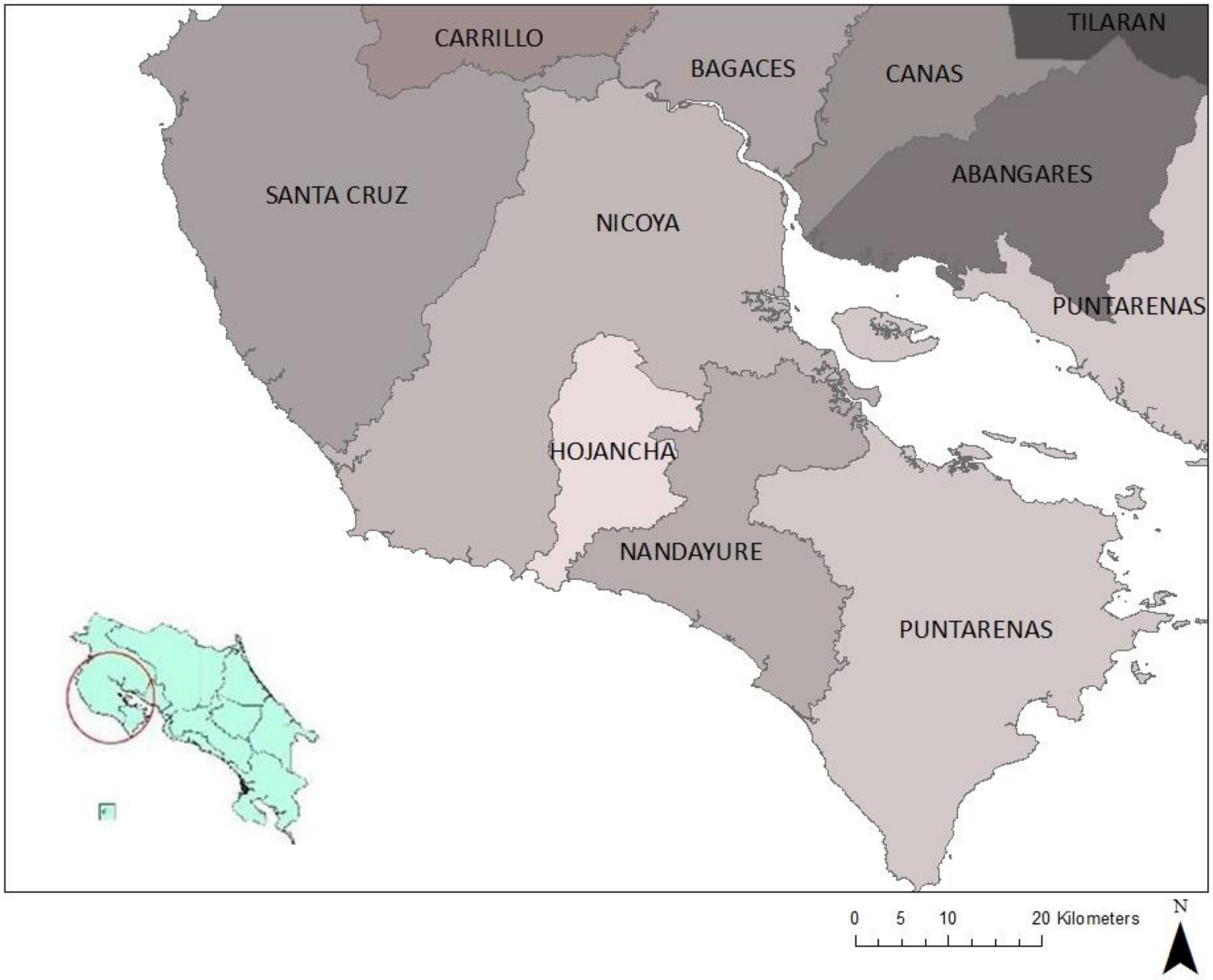

Figure 3. The Nicoya Peninsula is located in northwestern Costa Rica (inset). This study was primarily focused on Nicoya, Hojancha, and Nandayure counties. Map created from data in the 2008 Costa Rica Atlas.

Figure 4. Examples of extensive teak plantations (lighter green) in the Nicoya Peninsula. These plantations are located in Lajas (left) and Santa Marta (right), Hojancha County.

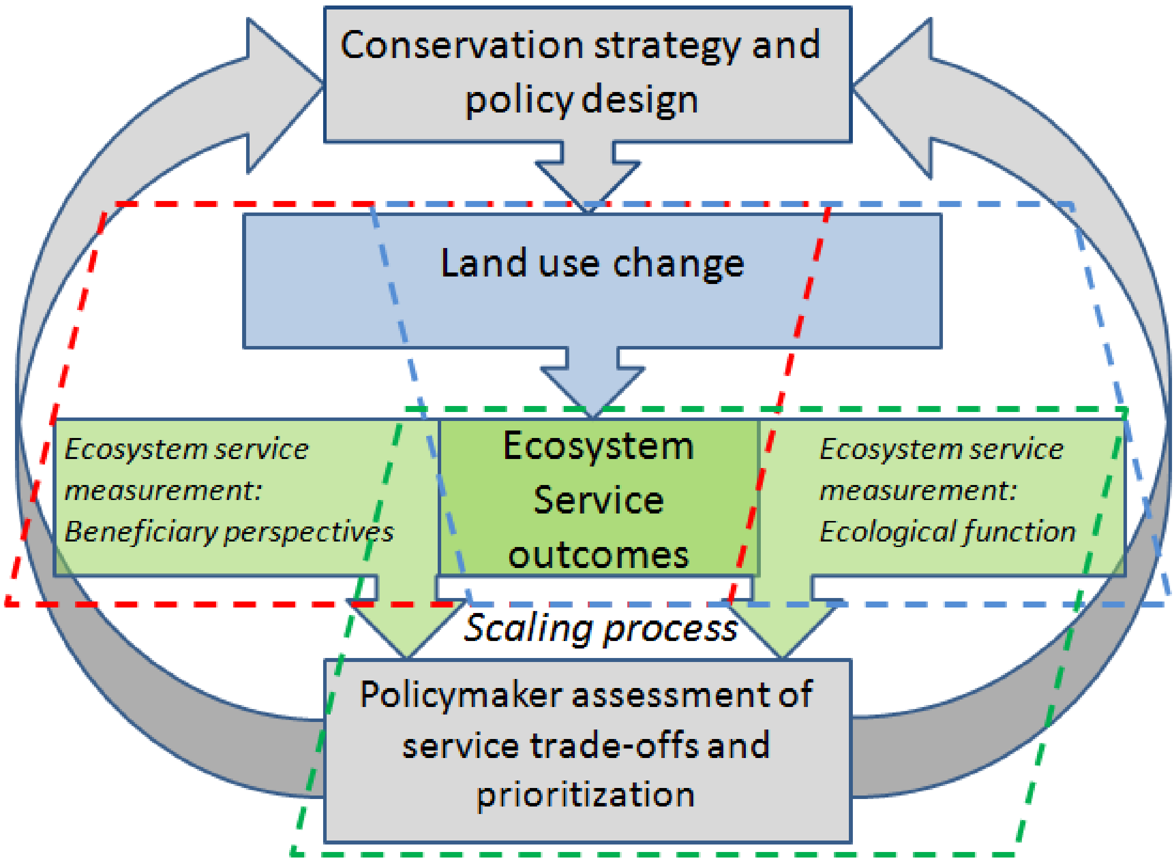

Figure 5. Though all chapters consider the social and ecological context of the Nicoya Peninsula, particularly as related to ecosystem services-based conservation policy design, each chapter has a specific focus within the interdisciplinary conceptual diagram. The dotted lines represent the contributions from chapter two (blue), three (red), four and five (green).

Chapter 2: Understanding the Impact of Human-Dominated Land Uses on Bee Populations in the Seasonally Dry Tropics

Abstract

Human dominated land uses make up a large and growing proportion of global land cover, but many questions remain regarding the relative impact of these land uses on ecosystem service provision. This is particularly true in the heterogeneous agroecosystems of the developing tropics. In this study, we investigated the relative impact of coffee agroforestry, pastures, and teak plantations on bees, which are important pollination service providers in the seasonally dry region of northwestern Costa Rica. We collected bees in each land use using blue vane traps (2013-2014) and pan traps (2014) at 0, 100, and 200 meters from adjacent forest edges. We found that bee abundance, richness, diversity, and evenness varied along seasonal and altitudinal gradients. We also found that while high altitude pastures and coffee plantations mostly had similar bee communities, bee population metrics were lower in teak plantations than pastures of the same altitude class. In addition, we found that bee diversity was higher at the edge of the forest in teak plantations compared to interiors, while differences in distance from forest were not observed in the other land uses. Differences in bee population metrics in teak as compared with pasture may be due to lower abundance and richness within three functional groups: small- to moderate-sized flower specialist bees, moderate- to large-sized cavity-nesting bees, and buzz-pollinating bees. Key findings from this work can inform the allocation of Payments for Ecosystem Services modalities that incentivize reforestation via teak plantations, as such payments may have the unintended consequence of decreasing important groups of pollinating bees compared to other human-dominated land uses.

Introduction

Human-modified land uses, such as croplands, pastures, and managed forests cover a large and growing proportion of global terrestrial surface area (DeFries et al. 2004). Conversion from native habitat to human-dominated land uses has been described as one of the main causes for the loss of ecosystem services (ES), the benefits that humans derive from functioning ecosystems (Daily 1997, MEA 2005). While conservation strategies, such as the establishment and maintenance of protected areas, exist to prevent further loss of ES, it is important to understand the extent to which certain human-dominated land uses hold potential for supporting biodiversity (Harvey et al. 2011) and ecosystem function (Blitzer et al. 2012). There are several examples of human-dominated land uses that support ES provision, particularly in less intensively managed, heterogeneous landscapes (Ricketts et al. 2001, Daily 2009). More research is needed to better understand the relative impact of different human-dominated land uses on ES provision.

It is particularly necessary to study the effects of human activity on ES provided by "mobile agents" (Kremen et al. 2007). Mobile agents are organisms that deliver services locally, but move within and among habitats, thus their biology and community composition are impacted at local and landscape scales (Kremen et al. 2007). Local management for these agents can have benefits at the landscape scale. Animal pollination is an example of a mobile agent-based ES, and it has recently gained attention as a service that is threatened or declining in some regions of the world (Winfree et al. 2009). Animal pollination is important for 35% of crop production (Klein et al. 2007) and 87% of wild plant reproduction (Ollerton et al. 2011) worldwide, so understanding the impact of human-dominated land uses on animal pollinators is critical to maintain functioning ecosystems.

Wild bees are the primary animal pollinators in most regions of the world (Klein et al. 2007, Kremen et al. 2007). Pollination from bees has served as a model for understanding the impact of land use change on mobile agents of ES, but significant knowledge gaps remain (Kremen et al. 2007, Winfree 2013). While studies have found that populations of bees may be threatened by habitat loss and land use intensification (Steffan-Dewenter et al. 2005, Potts et al. 2010), these studies have usually been done in landscapes with a very low proportion of remaining habitat (Winfree et al. 2009, Winfree 2013, Archer et al. 2014). In less intensively managed agroecosystems, results have been more varied (Brosi et al. 2007, Winfree et al. 2007, Holzschuh et al. 2008, Winfree et al. 2011), as these land uses may provide a variety of nesting substrates and foraging resources for bees (Tscharntke et al. 2005, Winfree et al. 2011, Kennedy et al. 2013).

The connection between bee communities and pollination service provision has been demonstrated for several bee population metrics, which serve as proxies for direct measurement of pollination services in cropping or natural systems. Bee richness improves the resilience of pollination services (Winfree and Kremen 2009), and more diverse bee communities result in higher crop production (i.e., Klein et al. 2003) and more stable pollination services (Garibaldi et al. 2011). The link between diversity and pollination is likely due to functional differences between groups of bees (Hoehn et al. 2008, Fründ et al. 2013, Gagic et al. 2015). Functional differences in bee communities increase the persistence of diverse plant communities (Fontaine et al. 2006), improve crop yield (Hoehn et al. 2008, Tscharntke et al. 2008, Martins et al. 2015) and buffer pollination services from environmental changes (Brittain et al. 2013, *but see* Winfree and Kremen 2009). Several studies have demonstrated that ecological and life history traits, which are used to determine functional groups, mediate bee response to environmental disturbances (Moretti et al. 2009, Williams et al. 2010).

The human-modified tropics are particularly suited to understanding responses of organisms to moderate land use change, as much of the native habitat has been converted to low-intensity, small-scale agricultural land uses (Murphy and Lugo 1995). Dry forests are the most threatened of all the lowland tropical forests (Janzen 1988) and native bee populations in the dry tropics may have declined in recent years due to habitat loss (Frankie et al. 1997). The majority of research on bee populations has been done in North America and Europe (Winfree et al. 2011, Archer et al. 2014), so less is known about bee ecology in the subtropics and tropics (Steffan-Dewenter et al. 2005).

It is particularly important to understand the impact of land use on ES providers in these under-studied regions because innovative conservation policies are already being employed on private lands in many developing tropical countries (Pattanayak et al. 2010).

Costa Rica is one of the pioneers of Payments for Ecosystem Services (PES) schemes, which are incentives provided to landowners for maintaining certain land use, cover, or management types, called modalities, that provide ES (FONAFIFO 2013). Thes modalities are expected to provide a bundle of ES, including mitigation of global warming gases, protection of water resources, biodiversity and conservation, and scenic beauty (Pagiola 2008). Costa Rica currently incentivizes several land use and land management modalities, such as forest protection, agroforestry, and reforestation with tree plantations (FONAFIFO 2013). Studies in Costa Rica have shown that PES contracts for landowners are significantly correlated with the presence of non-native teak (*Tectona grandis)* plantations on farms (Cárdenas et al. 2014).

In this study, we compared bee population metrics in common land uses: coffee (*Coffea arabica)* agroforestry, teak plantations, and pastures, in a highly heterogeneous landscape in the Nicoya Peninsula of Costa Rica. We asked two questions: 1) How do bee communities differ among pastures, teak plantations, and coffee agroforestry systems, and 2) How do bee populations differ with distance from native habitat within these land uses?

For the first question, we hypothesized that bee abundance, richness, diversity, and evenness would be lowest in teak plantations, which typically contain low diversity and resource heterogeneity for animals in Central America (Hallet et al. 2011). Bees are the main pollinators of teak in its native range (Tangmitcharoen et al. 2006, 2009), but teak blooms during the wet season in Costa Rica, when fewer bees are active. Several studies have found that invertebrate diversity, specifically, is lower in tree plantations compared to other land uses in Central America (Stephens and Wagner 2007). It is still unknown what type of habitat or resources teak provides to bees in regions where it has been introduced.

We also hypothesized that bee abundance, richness, diversity and evenness would be highest in coffee plantations and intermediate in pastures. Coffee plantations in the region contain flowering coffee bushes, which are visited by diverse bee species. Local coffee management also includes maintaining diverse shade tree species (Appendix 1), which enhance functional diversity of bee populations (Jha and Vandermeer 2010). While pasture does not provide nectar resources, it typically contains live fences and shade trees that support animal diversity (Milder et al. 2010, Harvey et al. 2011).

In addition, we hypothesized that the relative abundance of different functional groups would vary among land use types. We expected to find that large flower pollinating bees, such as the large cavity nesters and buzz pollinators, would be more common in land uses that contain native trees with large inflorescences and nesting cavities (coffee and pasture). We also expected ground nesting bees to be relatively more common in pasture, where there is less management to disturb nesting sites.

For the second question, we hypothesized that bee abundance would be similar, but bee richness, diversity, and evenness would decrease with distance from native habitat in all land uses. This hypothesis is based on studies showing that spillover from forested habitats provide sources of pollinating bees for tropical agricultural crops (Klein et al. 2003, DeMarco and Coelho 2004, Ricketts 2004). In addition, studies have shown similar abundance, but changing bee community composition with distance from native habitat patches in tropical pastures (Brosi et al. 2007). We expected to find that this pattern would be more pronounced in teak plantations, followed by pasture and coffee, because of the distinct floral and nesting resources available in each land use.

Finally, we expected to find a shift in relative abundance of functional groups with distance from the forest edge. Brosi et al. (2007) observed that certain tribes of native bees, such as the stingless bees, become less abundant with distance from forested habitat in seasonally dry Costa Rica. We also expected that this trend will differ between land uses, with the relative abundance of functional groups being most distinct between the forest edge and non-edge traps in teak plantations.

Methods

Study region

This study was conducted in the Nicoya Peninsula of Northwestern Costa Rica (Fig. 1). The peninsula, bordered by the Pacific Ocean to the west and the Gulf of Nicoya to the east, is a mix of seasonally dry and moist tropical ecological life zones (Calvo-Alvarado et al. 2009), with about 95 percent of the average 1,800mm of rainfall occurring from May to November (Mata and Echeverria 2004). The elevation within the peninsula ranges from sea level to approximately 900 meters.

The Nicoya Peninsula has undergone substantial land use change as a result of deforestation and subsequent land abandonment and reforestation after the 1970s. In Hojancha County, forest cover increased from 14% to 52% between 1970 and 2005 (Vallejo et al. 2006). Currently, Hojancha County and the surrounding peninsula contain a heterogeneous land cover of secondary forest regrowth, pastures, tree plantations, and some agricultural crops (Calvo-Alvarado et al. 2009).

Native bees provide the majority of pollination services to native plants in this region (Frankie et al. 2004). About 54% of native trees and 77% of non-tree native plants in the Nicoya Peninsula depend on bees, wasps, or flies for pollination (Frankie et al. 2004). Large bees, such as those in genera *Centris, Epicharis, Mesoplia, Mesocheira, Xylocopa,* and *Euglossa,* are especially important for flowering trees. The majority of these bees breed and nest during the dry season (Frankie et al. 1983), which corresponds with the blooming period of regional trees. Small bees, such as members of the Megachilidae and Halictidae families, and the stingless bees in the Apidae family, are also important pollinators, especially for non-tree flowering plants (Frankie et al. 2004).

Several regional crops depend on or benefit from pollination by bees. There is evidence that the fruit set and quality of coffee improves with bee visitation (Klein et al. 2003). Melon (*Cucumis melo)*, another common crop in the peninsula, is heavily dependent on bee pollination (Lugo and Vaughan 2006), and a major focus of bee research (Kremen et al.

2004). In addition, a number of bee-pollinated fruit trees like mango and avocado are grown in plantations or in home gardens for home consumption (Galbraith, personal observation).

Site selection

To test our hypotheses, we sampled bee populations in coffee agroforestry, pasture, and teak plantations over a two-year period (March 2013-November 2014). We sampled pastures on high and low altitude ranges to pair them with coffee and teak, respectively, due to the altitude difference between typical coffee agroforestry and teak plantations in the peninsula (Appendix 1). We selected five replicates of each of the four land use types. Sites spanned the Hojancha and Nicoya counties of the Nicoya Peninsula, from the drier gulf to the more humid Pacific coast (Fig. 1). To look at the influence of distance from forest on bee populations, we selected sites that had at least one edge adjacent to native forest habitat. We set traps in a straight line at 0, 100, and 200 meters from the native habitat patch. Due to the non-symmetrical configuration of typical farms, we categorized these traps as "edge" versus "non-edge" trap classes rather than looking at linear distance from habitat.

Data collection

We used Blue Vane Traps (BVT) (Stephen and Rao 2005) from 2013-2014 and pan traps (Droege 2015) in 2014 only. Each of the three trap locations per site included a BVT and three pan traps (one each: yellow, blue, and white). We set the traps, left them open for 72 hours, then collected them for specimen processing. We completed ten sampling periods (Appendix 2), including four sampling dates in 2013 with BVTs only (two dry and two wet season sampling periods). In 2014, we sampled with both trap types for three dry and three wet season periods. The late dry season sampling dates were coordinated with the coffee blooming period, which occurs after the first rain of the year. The mid-wet season sampling dates were coordinated with teak bloom, which occurred between June and July.

To deal with frequent heavy rains during the wet season, we inserted drains in BVTs by drilling holes at the bottom of each trap and then gluing fine insect netting over the holes. This allowed water to drain from the traps while insects remained. We set all BVTs at floral height. In teak, this required placing a rope over the upper branches of the tree, then raising the traps so they were near inflorescences. In coffee, we raised BVTs on wooden posts so they were suspended at the top of coffee bushes. In pasture, the traps were placed on shorter wooden posts to sit at approximately chest height. In all cases, the traps had similar visibility and sun exposure.

We used a soapy solution in the pan traps, and filled them to ca. 3 cm below the edge of the bowls. We inserted slits at the top of the bowls to allow for excess liquid to drain slowly without losing specimens in the case of heavy rain. We added salt to the soapy water solution to preserve specimens during the trapping period. Pan traps were placed at a uniform 1.5 meters from the ground on raised platforms in all land uses. We used fencing around the traps to decrease the occurrence of animal disturbances in pastures.

After collection, the specimens were washed, pinned and labeled, then frozen inside boxes to prevent molding or insect damage until they could be transferred to the U.S. All specimens were identified to the lowest possible taxon, either species or morphospecies, at the National Biodiversity Institute in Costa Rica and the USDA Bee Lab in Logan, Utah.

Bee poulation metrics

We determined abundance as the total number of bees trapped per site per sampling period. We calculated genus richness as the total number of genera observed per land use per site per sampling period, and morphospecies richness, which is a very good proxy for species richness (Oliver and Beattie 1996). To determine diversity, we used the Shannon diversity index, ($-\sum_n^i p_i \, ln p_i$), where p_i represents the proportion of individuals of species *n* relative to the total number of individuals collected per plot and sampling period. For evenness, we used the Shannon equitability index, where Shannon diversity is divided by the natural log of the total number of species collected per plot and sampling period.

We divided bees into functional groups based on categories from Frankie et al. (2004) and expanded the categories using expert knowledge and published literature. Fourteen functional groups were established based on bee size, sociality, foraging habits, specialization, and nesting substrate (Table 1).

Statistical analyses

We plotted cumulative genus and morphospecies curves over sampling periods to determine how effective our sampling was for capturing overall genus and morphospecies richness in the region. We plotted these curves with BVT and pan trap data separately to investigate the relative sampling efficiency of the two trapping methods.

We used Generalized Linear Mixed Models (GLMM) to compare bee population metrics among landuses in high (540-780 MASL) and low (15-350 MASL) altitude land classes. Altitude, season, or land classifications were fixed effects, while sites within these classifications were random. All computations were done using SAS 9.4, procedure GLIMMIX. For all analyses, we used the mean of the population metrics among the five site replicates. Due to missing points caused by animal disturbance, pan trap data were weighted by frequency. To test the impact of distance from forest on bee population metrics, we used GLMM comparing mean abundance, richness, diversity, and evenness in two distance classes: traps near the forest edge and traps 100 m or more distant from the edge (non-edge traps). We weighted the trap distance classes by frequency to correct for the greater number of non-edge trap samples. We tested effects of season, distance class, and interaction for all combined land uses, then for each land use individually.

We used nonmetric multidimensional scaling (NMDS, SAS 9.4 PROC MDS) to visualize the dissimilarity in relative abundance of bee funtctional groups among sites and with distance from the forest edge. NMDS is a method for graphically demonstrating the dissimilarity between variables in a reduced number of dimensions based on the pairwise distances between sites given the metrics of interest. It then positions the sites graphically in an assigned number of dimensions to maximize the rank correlation between the pairwise inter-site distances of the population metric and those of the graphical ordination (Quinn and Keough 2002).

We combined functional group data from BVT and pan trap results, then used a double square root transformation to stabilize the variability between metrics. We plotted the correlation of the functional group data with distance by the number of dimensions to select the most appropriate number of dimensions for graphical illustration. The final NMDS analyses have a minimum correlation of 0.85 with transformed data. We tested dissimilarity of sites and distances based on relative abundance of the ten most common genera collected, then on the relative abundance of the 14 functional groups. After testing the correlation of relative abundance of the groups to distances on the axes, we continued NMDS with functional groups only, as they showed more distinct patterns and higher correlation to axes. Final NMDS graphs were interpreted based on correlation between axes and relative abundance of the functional groups. We imposed ellipses over the data points based on an 80% confidence interval to better visualize clustering patterns by land use or distance class, so these ellipses are not to be interpereted as a statistical test.

Results

We collected a total of 1,753 bees representing 5 families, 47 genera, and 115 species (Table 2). Genera and morphospecies accumulation curves (Fig. 2) demonstrated that we reached asymptote for genera, but less so for morphospecies. This is evidence that our sampling was sufficient to represent those genera in the sites that are attracted to either trapping method. The most common family represented in both trapping methods was Apidae, folowed by Halictidae. Due to differences in bee taxa represented by the two trapping methods, we present all GLMM results for each method separately.

Effects from season and altitude

We observed differences in bee population metrics between wet and dry season sampling dates. Seasonal differences were most pronounced in BVT sampling, and varied among land uses. Coffee, high altitude pastures, and low altitude pastures had distinct increases in abundance from BVT sampling during the dry season, while teak plantations had less pronounced seasonal responses (Fig. 3). High altitude pastures had the highest peak in abundance in 2013, while low altitude pastures had relatively high abundance in the dry season of 2013 and early wet season of 2014. For pan traps, all sites had the highest abundance during the late dry season (Fig. 4).

GLMM tests showed that bee abundance (Table 3) was higher in the dry season for BVT sampling in all sites combined (df=36, P=0.0133). Bee abundance in pastures and low altitude sites did not differ by season in either trapping type. Among high altitude sites, bee abundance was higher during the dry season for BVT sampling only (df=16, P=0.0075).

We also found significant differences in genera and morphospecies richness between seasons. Genera richness (Table 4) was higher in the dry season for BVT results for all land uses combined (df=36, P=0.0018) and among pasture sites (df=16, P=0.0066). Genera richness was significantly affected by season in high altitude sites for BVT results (df=16, P=0.0080), and pan trap results showed statistically marginal differences due to season (df=8, P=0.0717). Morphospecies richness followed the same pattern with season as genera richness for all comparisons (Table 5).

Bee diversity (Table 6) was higher in the dry season for BVT sampling in all sites combined (df=36, P= 0.0016) and high altitude sites (df=16, P=0.0072). Evenness (Table 7) was higher in the dry season in BVT for pastures (df=16, P=0.0001), low altitude sites (df=16, P=0.0005) and high altitude sites (df=16, P=0.0005). There was an interaction between land use and season for BVT samples in low altitude sites (df=16, P=0.0004). There were no significant trends in bee abundance or richness due to altitude alone, but in some cases bee population metrics in high altitude and low altitude sites responded differently to seasonality.

We also found significant effects from season and altitude when bee metrics were examined for individual land uses among distance classes, with non-edge traps weighted for frequency (Tables 8-12). For all combined sites, season significantly influenced bee abundance (BVT: df=76, P=0.0445, PT: df=42, P=0.0261), genus richness (BVT: df=76, P=0.0003), species richness (BVT: df=76, P=0.0008, PT: df=42, P=0.0197) and evenness (PT: df=42, P=0.0261). For individual land uses, season was only significant for BVT samples. Dry season samples had higher abundance (Table 8), genus richness (Table 9), and morphospecies richness (Table 10) in teak, coffee, and high altitude pastures. Diversity (Table 11) was higher in the dry season for high altitude pastures (df=16, P=0.0088) and marginally so for coffee (df=16, P=0.0614). Evenness was higher in the wet season in low altitude pastures BVT samples only (df=16, P=0.0173). All means and standard errors for bee population metrics are presented in Appendices 4 and 5.

Effects from land use

We found significant differences in bee population metrics due to land use. There were no differences in bee abundance between coffee and high altitude pastures, but bee abundance was significantly lower in teak than in low altitude pastures in both BVTs (df=16, P=0.0433) and pan traps (df=8, P=0.0361) (Table 3). Genus richness (Table 4) and species richness (Table 5) were similar between high altitude pastures and coffee sites, but teak had lower genus (BVT: df=16, P=<0.0001, PT: df=8, P=0.0194) and species (BVT: df=16, P=<0.0001, PT: df=8, p=0.0195) richness than low altitude pastures. We illustrate means for bee abundance (Fig. 5) and richness (Fig. 6) among land uses for both trapping methods.

Bee diversity (Table 6) and evenness (Table 7) were higher in high altitude pastures than coffee in BVT sampling (df=16, P=0.0223). Bee diversity was higher in low altitude pastures than teak for both BVT (df=16, P=0.0002) and pan traps (df=8, P=0.0122). High altitude pastures also had higher evenness than coffee (df=16, P=0.0448) in BVT samples. Teak plantations had lower bee evenness in both BVT (df=16, P0.0484) and pan traps (df=8, P=0.0122). We illustrate means for bee diversity and evenness (Fig. 7) among land uses for both trapping methods. All means and standard error for bee population metrics relative to land use are presented in Appendix 6.

Visualization of functional group differences using NMDS (Fig. 8) illustrates that teak differs from other land uses most dramatically on Axis 1. Functional groups correlated with positive values on Axis 1 can therefore be considered coffee and pasture associated, and negatively correlated groups are teak associated. Based on correlations between functional group relative abundance and NMDS site ordination Axis 1 scores, these groups include moderate- to large-sized cavity-nesting bees (R^2=0.67), small to moderate-sized flower specialists (R^2=0.52), and buzz pollinating bees (R^2=0.76). Axis 3 correlated with small- to moderate-sized stem-nesting or ground-nesting solitary bees. These groups were represented similarly in space among all land use types. This pattern was most distinct during the dry season, but sustained during the wet season.

Effects from trap distance class

We did not find statistical differences in bee abundance or richness between the two distance classes across or within land uses (Tables 8-10). Bee diversity (Table 9) was related to trap distance for BVT results in teak sites (df=16, P=0.0200). There were also statistically marginal differences in bee evenness related to trap distances for BVT results in teak (df=16, P=0.0555). No other land uses showed relationships with trap distance.

Based on the NMDS procedure, we observed some differences in functional groups represented in the two distance classes within each land use. For the high altitude sites, dry season samples occupied similar spaces on the 1st and 2nd axes (Fig. 9). Wet season samples showed differences in high altitude pasture edge and non-edge traps, with edge sites differing on the 1st axis (Fig 9). This axis correlates with the moderate- to large-sized cavity-nesting bees (R^2=0.75) and buzz pollinating bees (R^2=0.75).

Functional groups in low altitude sites varied among land use but not between distance classes. Differences between teak and lowland pasture were most distinct at the forest edge, as during the dry season they diverged on Axis 1 and during the wet season they diverged on Axis 2 (Fig. 10). Correlation of NMDS ordinal distances and Axis 1 were highest for large to medium-sized flower pollinating cavity nesters (R^2=0.75), small to moderate-sized flower specialists (R^2=0.52), and buzz pollinating bees (R^2=0.75). Correlation of NMDS ordinal distances and Axis 2 were highest for moderate to small flower specialist pollinators (R^2=0.62), and small to moderate ground nesters with long tongues (R^2=-0.53), or short tongues (R^2=-0.54), ($P<0.01$).

Discussion

In this study, we sought to determine the impact of land use and distance from forest habitat on bee populations in a seasonally dry tropical region. We hypothesized that bee abundance, richness, diversity, and evenness would be highest in coffee agroforestry and lowest in teak plantations. In addition, we expected to find different relative abundances of bee functional groups among coffee, pasture, and teak. We also expected to detect lower bee richness, diversity, and evenness in non-edge traps versus traps at the edge of forest habitat, and shifts in relative abundance of functional groups with trap distance. Here we provide evidence that comparisons of bee populations need to be made with consideration of seasonal and altitudinal gradients in the seasonally dry tropics. Within these comparisons, bee populations are less abundant and bee communities have lower richness, diversity and evenness in teak plantations relative to paired pasture sites. In addition, we illustrated functional group differences among land uses, and found that differences in bee population metrics may be due to decreases in small to moderate size specialists, moderate to large-sized cavity-nesting bees, and buzz-pollinating bees.

We did not find evidence that bee population metrics change with distance from forest, except for those bees represented by BVT collections in teak plantations. Functional differences between bee populations in teak and low altitude pastures are most evident during the dry season, and this pattern is driven by the higher abundance of small to moderate-sized specialists, moderate to large-sized cavity-nesting bees, and buzz-pollinating bees in pastures relative to teak during the dry season. During the wet season, small to moderate-sized stem nesting and ground nesting bees were higher in teak, and small to moderate-sized specialists were more abundant in low-altitude pastures.

Population changes due to season and altitude

The significance of altitude and season as covariates for predicting bee populations is a new contribution to our understanding of bee populations in the seasonally dry tropics. While it is already established that bee activity is higher during the dry season (Frankie et al. 2004), our study demonstrated that the effect of season is higher for high altitude land uses. Season and altitude-related changes in bee abundance, richness, diversity, and evenness were most evident from BVT sampling. Certain bees that were more commonly observed in the BVT samples relative to pan trapping, such as anthrophorids, may therefore be the most sensitive to seasonal and altitude changes in the study region.

Population changes due to land use

Our study provides evidence that bee populations are distinct among diverse human-dominated land uses in the study region. While we expected to find the highest bee abundance, richness, diversity, and evenness in coffee sites, there were no significant differences in abundance or richness between coffee and paired high altitude pasture sites. Live fences and shade trees in both coffee and high pastures have been shown to provide resources for invertebrates (Milder et al. 2010). This would explain why, despite the temporal burst in resources from the coffee bloom in the late dry season, there was no significant difference between bee abundance and richness trapped in these two land uses. In contrast, high altitude pastures had higher diversity and evenness than coffee sites. It is possible that the shaded environment of coffee agroforestry reduces bee foraging to traps compared to the relatively open pasture sites.

We observed lower bee abundance, richness, diversity, and evenness in teak plantations compared to paired low altitude pastures. Despite potential resources for bees due to the teak bloom during the wet season, there were no seasonal differences in bee populations in teak plantations. The lower relative abundance of genera such as *Centris, Epicharis, Exomalopsis, Gaesischia, Megalopta, Ptilloglossa, Thygater,* and *Xylocopa* could be explained by their preference for large flowers in specific native trees (Frankie et al. 1983), which are not represented within the monoculture teak sites (Appendix 3). In addition, these bees require tree or nesting cavities, and since teak trees are harvested after 15-25 years, these plantations do not generally have cavity nesting resources. Stem-nesting small to moderate size bees such as *Ceratina* spp. and the ground nesting Halictids did not differ between low altitude pasture and teak in the dry season, and were relatively more abundant in teak during the wet season, suggesting that differences in functional groups represented in the two land uses were due to either availability of nesting substrates, or availability of suitable floral resources. This is particularly interesting because *Ceratina* has been observed visiting teak in its native range (Tangmitcharoen et al. 2006).

Differences due to distance from forest habitat

The similarity between bee populations at the forest edge and non-edge traps in coffee and pastures provides evidence that bees are foraging within these human-dominated land uses despite distance from forested habitat. Earlier studies have shown that bee community composition shifts with larger distances from forest in pastures (Brosi et al. 2007), so this contrasting evidence could be due to the abundance of flowering trees in our sites (Appendix 3). In teak, diversity and evenness were lower in the non-edge traps, which is further evidence that bees are not using this land use for nesting or floral resources relative to low altitude pastures.

Implications for pollination services

We selected population metrics that are proxies for pollination services. Lower abundance, richness, diversity, and evenness of bee populations in teak relative to low altitude pastures indicates that these plantations may have negative impacts on biodiversity maintenance and crop pollination, especially as they increase in the landscape. In addition, we observed that bee population metrics were driven by lower abundance of specific functional groups in teak plantations. Many native trees in seasonally dry Costa Rica depend on buzz pollination to reproduce (Frankie et al. 2004). Non-random losses of bee populations with decreased habitat due to teak reforestation could have direct implications for the biodiversity maintenance of these species.

Conclusions

Our results are applicable to current conservation policies in Costa Rica, and for other countries managing ES in low intensity, heterogeneous agroecosystems. The seasonality of flowering trees in different land uses should be considered, as resources available (i.e., teak) during seasons with low bee activity such as the wet season may not support bee diversity as well as land uses with temporal diversity of floral resources. In addition, these seasonal impacts may be different at relatively small altitude gradients. Though several studies have shown a relationship between bee richness and temporal availability of flowering resources (Kremen et al. 2007), we did not observe an increase in bee populations overall during the teak blooming period, which occurs when few native trees provide resources for bees. This may be because bees in the seasonally dry tropics are less active during the wet season, so fewer bees are foraging for resources when teak flowers are blooming.

Many functional groups of bees were represented in coffee and pasture sites relative to teak plantations. This provides evidence that the agroforestry modality of Costa Rica's PES policy, which incentivizes land owners to increase shade trees in coffee farms and pastures, may be a useful way to support pollination services. We found no evidence that teak plantations can support bee abundance, richness, or diversity to the same extent as other human-dominated land uses in the Nicoya Peninsula region. The PES scheme, which incentivizes monoculture tree plantations as reforestation, could potentially use this information to consider limiting the size or number of teak reforestation contracts, or by incentivizing management practices within teak plantations to support biodiversity. Currently, plantations do not incorporate native tree species and contain few understory flowering plants. Changes in these practices could help mitigate the potential negative impacts of teak plantations on pollinator diversity.

Large bees are particularly important for buzz pollination in the peninsula (Frankie et al. 2004). Not only do PES-incentivized teak plantations contain lower bee abundance, richness, diversity, and evenness, the loss of bee richness and diversity is not symmetrical, with relatively low numbers of crutial buzz pollinators and small to moderate bee specialists. We propose that this research can be used to inform the spatial allocation of PES in the peninsula and the use of different modalities within the scheme to better incentivize ES provided by mobile organisms such as bees in the region.

This study revealed several key findings for a relatively understudied region, including basic information about bee families captured by BVT and pan traps in seasonally dry Costa Rica. More information on trap bias in tropical regions is needed to draw consistent ecological conclusions from bee sampling. Future studies should investigate the differences in bee populations in native habitat patches considering seasonal and altitude changes in these understudied regions. In addition, more information is needed to understand the relative impact of landscape context, including the size of native habitat patches adjacent to farm sites on bee diversity. Finally, additional research is needed on landscape-level outcomes of teak plantations on biodiversity and the trade-offs for other ES due to reforestation with monoculture plantations.

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Table 1: Functional groups used for NMDS analyses. Adapted from Frankie et al. 2004.

Group #	**Description**	**Genera**
1	Large to medium flower pollinators- cavity nesters	*Xylocopa*
2	Large to medium flower pollinators- ground nesters	*Centris, Epicharis*
3	Oil flower pollinators	*Centris, Paratetrapedia*
4	Moderate to small flower specialist pollinators	*Ancyloscelis, Diadasia, Melitoma, Peponapis, Protandrena, Svastra*
5	Small flower generalists- cavity nesters	*Melipona, Freseomelitta, Cephalotrigona, Partamona, Scaptotrigona, Tetragonisca, Trigona*
6	Moderate to small flower generalists- leaf collectors	*Anthidium, Megachile*
7	Moderate to large flower specialists- fragrance collectors	*Euglossa, Eulaema, Eufreisea*
8	Nocturnal foragers	*Megalopta*
9	Small to moderate ground nesters–long tongue	*Diadasia, Floreligus, Gaesishia, Mellisodes, Mellisoptila, Peponapis, Svastra, Tetroniella*
10	Cleptoparasites	*Coelioxys, Mesoplia, Osiris*
11	Buzz pollen collectors	*Centris, Epicharis, Exomalopsis, Gaesischia, Megalopta, Ptilloglossa, Thygater, Xylocopa*
12	Moderate to large social generalist pollinators	*Apis*
13	Small to moderate solitary- stem nesters	*Ceratina*
14	Small to moderate ground nesters- short tongue	*Augochlora, Augochlorella, Augochlorini, Augochloropsis, Caenaugochlora, Halictus, Lasioglossum*

Table 2: Summary of bee taxa collected during the study. Total number of specimens divided by family, genera, and morphospecies and presented overall and by collection method.

All Traps

Family	Genera	Species or morphospecies	Abundance
Andrenidae	1	1	1
Apidae	33	82	1509
Colletidae	1	1	1
Halictidae	8	18	224
Megachilidae	4	12	17
Total	**47**	**115**	**1753**

BVT only

Family	Genera	Species or morphospecies	Abundance
Andrenidae	1	1	1
Apidae	33	78	1138
Colletidae	0	0	0
Halictidae	8	17	74
Megachilidae	4	12	17
Total	**46**	**108**	**1330**

Pan Traps only

Family	Genera	Species or morphospecies	Abundance
Andrenidae	0	0	0
Apidae	13	37	272
Colletidae	1	1	1
Halictidae	8	16	150
Megachilidae	0	0	0
Total	**22**	**54**	**423**

Table 3: Output of GLMMIX procedure for effects of season, altitude, and land use on mean bee abundance. Results are presented for both trapping methods, with significance denoted for p-values less than 0.05 (*) and 0.01 (**).

	Blue Vane Traps (2013-2014)			***Pan Traps (2014)***		
Effects	**DF**	**F Value**	**Pr>F**	**DF**	**F Value**	**Pr>F**
All sites	36			20		
altitude		0.12	0.7350		1.48	0.2383
season		6.78	0.0133**		2.20	0.1536
altitude*season		3.20	0.0872		0.52	0.4776
Pastures	16			8		
altitude		0.60	0.1981		2.95	0.1242
season		1.80	0.4083		1.23	0.2998
altitude*season		0.70	0.4083		0.20	0.6693
Low altitude sites	16			8		
land use		4.82	0.0433*		6.33	0.0361*
season		0.37	0.5538		0.32	0.5848
land use*season		0.0001	0.9619		0.04	0.8532
High altitude sites	16			8		
land use		0.0001	0.9525		0.15	0.7132
season		9.35	0.0075**		2.93	0.1253
land use*season		0.4699	0.4699		0.01	0.9402

Table 4: Output of GLMMIX procedure for effects of season, altitude, and land use on mean genus richness. Results are presented for both trapping methods, with significance denoted for p-values less than 0.05 (*) and 0.01 (**).

	Blue Vane Traps (2013-2014)			***Pan Traps (2014)***		
Effects	**DF**	**F Value**	**Pr>F**	**DF**	**F Value**	**Pr>F**
All sites	36			20		
altitude		0.09	0.0771		0.83	0.3732
season		11.41	0.0018**		1.24	0.2784
altitude*season		2.04	0.1614		1.09	0.3086
Pastures	16			8		
altitude		3.17	0.0987		2.02	0.1931
season		9.75	0.0066**		0.59	0.4632
altitude*season		0.77	0.3942		1.06	0.3335
Low altitude sites	16			8		
land use		32.61	<0.0001**		8.5	0.0194*
season		3.96	0.0639		0.0001	0.9733
land use*season		0.90	0.3569		0.12	0.7428
High altitude sites	16			8		
land use		2.11	0.1660		0.85	0.3823
season		17.13	0.0080**		4.31	0.0717
land use*season		0.07	0.7916		0.14	0.7208

Table 5: Output of GLMMIX procedure for effects of season, altitude, and land use on mean morphospecies richness. Results are presented for both trapping methods, with significance denoted for p-values less than 0.05 (*) and 0.01 (**).

	Blue Vane Traps (2013-2014)			***Pan Traps (2014)***		
Effects	**DF**	**F Value**	**Pr>F**	**DF**	**F Value**	**Pr>F**
All sites	36			20		
altitude		0.001	0.9552		6.48	0.4968
season		10.45	0.0026**		1.64	0.2143
altitude*season		2.79	0.1036		1.18	0.2908
Pastures	16			8		
altitude		1.91	0.1865		1.37	0.2748
season		7.27	0.0159*		0.73	0.4186
altitude*season		1.24	0.2825		1.27	0.2922
Low altitude sites	16			8		
land use		28.43	<0.0001**		8.48	0.0195*
season		2.50	0.1338		0.02	0.8975
land use*season		0.36	0.5588		0.21	0.6572
High altitude sites	16			8		
land use		1.68	0.2131		1.09	0.3279
season		15.13	0.0013**		4.55	0.0655
land use*season		0.05	0.8291		0.13	0.7326

Table 6: Output of GLMMIX procedure to test effect of season, altitude, and land use on mean Shannon diversity for both trapping methods. Results are presented for both trapping methods, with significance denoted for p-values less than 0.05 (*) and 0.01 (**).

	Blue Vane Traps (2013-2014)			***Pan Traps (2014)***		
Effects	**DF**	**F Value**	**Pr>F**	**DF**	**F Value**	**Pr>F**
All sites	36			20		
altitude		0.03	0.8537		0.41	0.5268
season		11.49	0.0016**		1.15	0.2969
altitude*season		0.001	0.9634		0.39	0.5390
Pastures	16			8		
altitude		3.69	0.0727		1.58	0.2437
season		2.53	0.1247		0.15	0.7058
altitude*season		0.74	0.4028		0.17	0.6871
Low altitude sites	16			8		
land use		22,97	0.0002**		10.38	0.0122**
season		1.69	0.2117		0.27	0.6151
land use*season		2.59	0.1268		0.34	0.5784
High altitude sites	16			8		
land use		6.40	0.0223*		0.08	0.7821
season		9.47	0.0072**		0.88	0.3750
land use*season		0.64	0.4362		0.02	0.9006

Table 7: Output of GLMMIX procedure to test effect of season, altitude, and land use on mean morphospecies evenness. Results are presented for both trapping methods, with significance denoted for p-values less than 0.05 (*) and 0.01 (**).

	Blue Vane Traps (2013-2014)			***Pan Traps (2014)***		
Effects	**DF**	**F Value**	**Pr>F**	**DF**	**F Value**	**Pr>F**
All sites	36			20		
altitude		0.001	0.9729		1.11	0.3046
season		8.57	0.0055**		0.02	0.8910
altitude*season		1.93	0.1724		1.17	0.6877
Pastures	16			8		
altitude		0.08	0.7862		2.02	0.1978
season		43.25	0.0001**		1.73	0.2295
altitude*season		0.001	0.9849		1.09	0.3312
Low altitude sites	16			8		
land use		4.57	0.0484*		0.52	0.4918
season		18.94	0.0005**		0.09	0.7764
land use*season		20.31	0.0004**		0.00	0.9905
High altitude sites	16			8		
land use		4.87	0.0440*		0.34	0.5785
season		18.82	0.0005**		0.01	0.9287
land use*season		3.15	0.0950		1.88	0.2124

Table 8: Output of GLMMIX procedure to test effect of season, altitude, and trap distance on mean abundance. Results are presented for both trapping methods, with significance denoted for p-values less than 0.05 (*) and 0.01 (**).

	Blue Vane Traps (2013-2014)			***Pan Traps (2014)***		
Effects	**DF**	**F Value**	**Pr>F**	**DF**	**F Value**	**Pr>F**
All sites	76			42		
trap distance		0.05	0.8193		0.03	0.8648
season		4.75	0.0445*		5.32	0.0261*
trap distance*season		0.04	0.8454		0.58	0.4524
Teak	16			8		
trap distance		4.73	0.449		1.93	0.2027
season		4.47	0.0505*		0.19	0.6716
trap distance*season		0.34	0.5625		0.14	0.7193
Coffee	16			8		
land use		0.09	0.7741		0.02	0.8992
season		6.01	0.0261*		3.45	0.1003
land use*season		0.19	0.6649		0.20	0.6683
High altitude pastures	16			6		
land use		0.23	0.6393		0.14	0.7168
season		8.96	0.0086**		7.33	0.0352*
land use*season		0.01	0.9159		0.26	0.6252
Low altitude pastures	16			8		
land use		0.17	0.6842		0.97	0.3546
season		0.05	0.8255		0.52	0.4903
land use*season		0.01	0.9308		0.15	0.7072

Table 9: Output of GLMMIX testing effects of season (wet v. dry) distance (forest edge v. non-edge traps) on mean genus richness. Results are presented for both trapping methods, with significance denoted for p-values less than 0.05 (*) and 0.01 (**).

	Blue Vane Traps (2013-2014)			***Pan Traps (2014)***		
Effects	**DF**	**F Value**	**Pr>F**	**DF**	**F Value**	**Pr>F**
All sites	76			42		
trap distance		0.02	0.8852		0.05	0.8247
season		14.20	0.0003**		2.91	0.0954
trap distance*season		0.13	0.7171		1.41	0.2560
Teak	16			8		
trap distance		1.82	0.1853		0.48	0.5060
season		4.82	0.0432*		0.03	0.8661
trap distance*season		0.57	0.4617		0.03	0.8661
Coffee	16			8		
trap distance		0.38	0.5442		0.0001	0.9880
season		11.92	0.0033**		1.92	0.2031
trap distance*season		0.28	0.6042		2.01	0.1942
High altitude pastures	16			6		
trap distance		0.0001	0.9703		4.29	0.0932
season		8.55	0.0099**		5.83	0.0605
trap distance*season		0.20	0.6603		0.12	0.7441
Low altitude	16			8		
trap distance		0.11	0.6989		0.01	0.4046
season		0.17	0.5432		0.77	0.4700
trap distance*season		0.01	0.9950		0.47	0.5131

Table 10: Output of GLMMIX testing effects of season (wet v. dry) distance (forest edge v. non-edge traps) on mean species richness. Results are presented for both trapping methods, with significance denoted for p-values less than 0.05 (*) and 0.01 (**).

	Blue Vane Traps (2013-2014)			***Pan Traps (2014)***		
Effects	**DF**	**F Value**	**Pr>F**	**DF**	**F Value**	**Pr>F**
All sites	76			42		
trap distance		0.0001	0.9873		0.02	0.8873
season		12.19	0.0008**		5.88	0.0197**
trap distance*season		0.30	0.5852		1.50	0.4524
Teak	16			8		
trap distance		2.30	0.1488		0.73	0.4186
season		5.37	0.0341*		0.18	0.6811
trap distance*season		0.80	0.3835		0.02	0.8905
Coffee	16			8		
trap distance		0.44	0.5148		0.0001	0.9480
season		10.74	0.0047**		4.36	0.0703
trap distance*season		0.35	0.5629		1.31	0.2854
High altitude pastures	16			6		
trap distance		0.02	0.8971		0.84	0.3939
season		7.06	0.0172**		4.77	0.0716
trap distance*season		0.37	0.5534		0.12	0.7395
Low altitude	16			8		
trap distance		0.11	0.7404		0.02	0.8970
season		0.17	0.6861		0.34	0.5785
trap distance*season		0.01	0.9059		0.45	0.5228

Table 11: Output of GLMMIX testing effects of season (wet v. dry) distance (forest edge v. non-edge traps) on mean Shannon diversity. Results are presented for both trapping methods, with significance denoted for p-values less than 0.05 (*) and 0.01 (**).

	Blue Vane Traps (2013-2014)			***Pan Traps (2014)***		
Effects	**DF**	**F Value**	**Pr>F**	**DF**	**F Value**	**Pr>F**
All sites	76			42		
trap distance		0.07	0.8009		0.15	0.6980
season		2.46	0.1361		0.90	0.3469
trap distance*season		0.63	0.4382		0.45	0.5045
Teak	16			8		
trap distance		6.19	0.0200*		3.55	0.0953
season		0.08	0.7757		0.50	0.4986
trap distance*season		0.0001	0.9987		0.08	0.7803
Coffee	16			8		
land use		0.01	0.9296		0.26	0.6208
season		4.05	0.0614		2.59	0.1460
land use*season		0.52	0.4852		0.60	0.4604
High altitude pastures	16			6		
land use		1.52	0.2352		0.32	0.5917
season		8.91	0.0088**		1.73	0.2361
land use*season		0.03	0.8724		0.28	0.6186
Low altitude	16			8		
land use		0.04	0.8454		1.29	0.2887
season		3.14	0.0955		0.01	0.9389
land use*season		0.02	0.9029		0.23	0.6431

Table 12: Output of GLMMIX testing effects of season (wet v. dry) distance (forest edge v. non-edge traps) on mean evenness. Results are presented for both trapping methods, with significance denoted for p-values less than 0.05 (*) and 0.01 (**).

	Blue Vane Traps (2013-2014)			***Pan Traps (2014)***		
Effects	**DF**	**F Value**	**Pr>F**	**DF**	**F Value**	**Pr>F**
All sites	76			42		
trap distance		0.27	0.6123		0.23	0.8648
season		0.33	0.5756		0.18	0.0261*
trap distance*season		1.01	0.3307		0.18	0.4524
Teak	16			8		
trap distance		4.26	0.0555		2.74	0.1362
season		1.17	0.2947		2.14	0.1821
trap distance*season		0.05	0.8307		0.43	0.5304
Coffee	16			8		
Trap distance		0.0001	0.9898		0.56	0.4772
season		2.15	0.1618		0.40	0.5441
land use*season		0.56	0.4641		0.36	0.5647
High altitude pastures	16			6		
trap distance		1.50	0.2383		0.28	0.6186
season		3.51	0.0794		0.30	0.6039
land use*season		0.02	0.8891		0.25	0.6322
Low altitude	16			8		
Trap distance		0.10	0.7604		0.97	0.3539
season		7.04	0.0173*		0.75	0.4119
land use*season		0.02	0.8850		0.15	0.7052

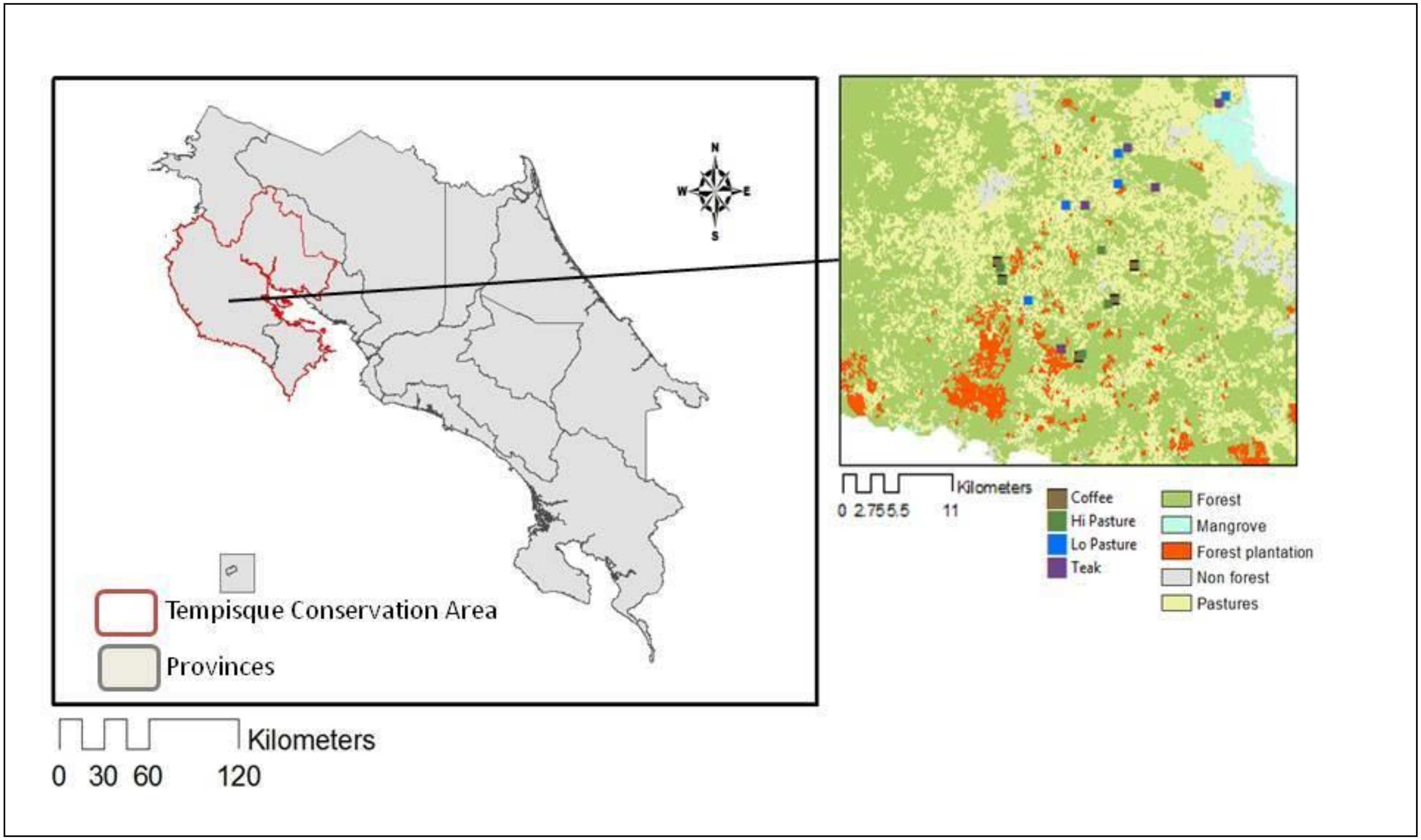

Figure 1: Map of study region and sites. Left: The 20 field sites were situated in the Tempisque Conservation area in the Nicoya Peninsula, Guanacaste, Costa Rica. Right: Teak sites (purple symbol) are paired with low pasture sites (blue symbol) and coffee sites (brown symbol) are paired with high altitude pastures (dark green symbol). Some site markers are not clearly visible because of their proximity to paired sites.

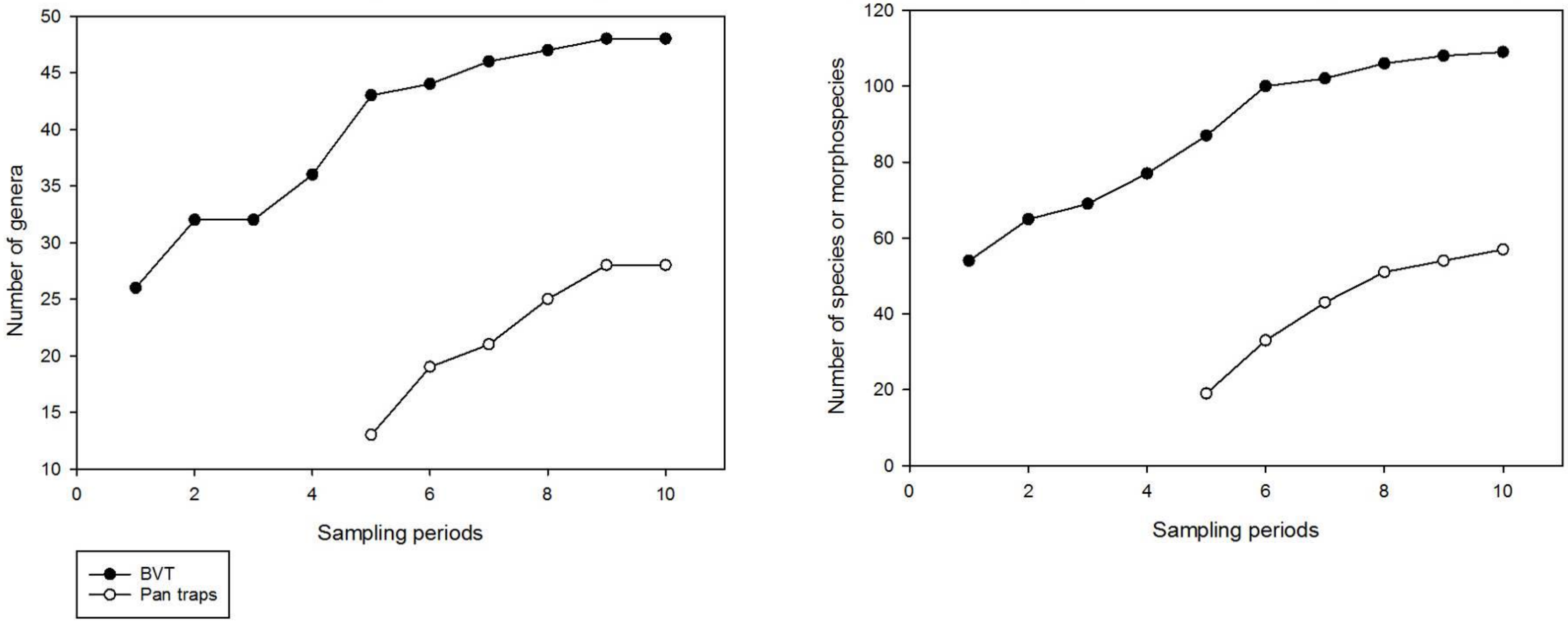

Figure 2: Genus (left) and morphospecies (right) accumulation curves by sampling period and by trapping method. See Appendix 2 for sampling period dates.

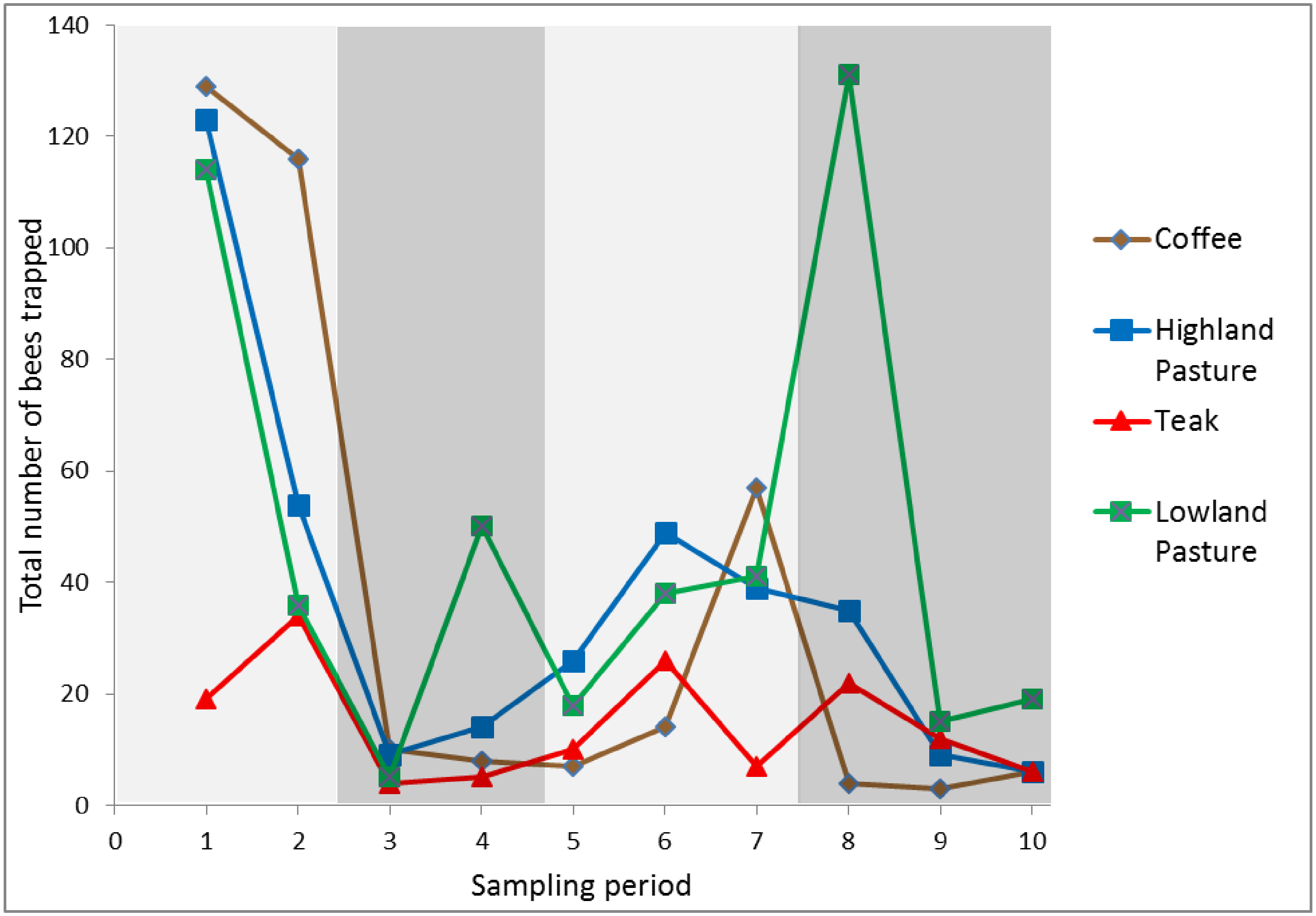

Figure 3: Total number of bees trapped in BVTs over ten sampling periods (2013-2014). Sampling varied between the dry season (light grey background) and wet season (dark grey background) and among land uses.

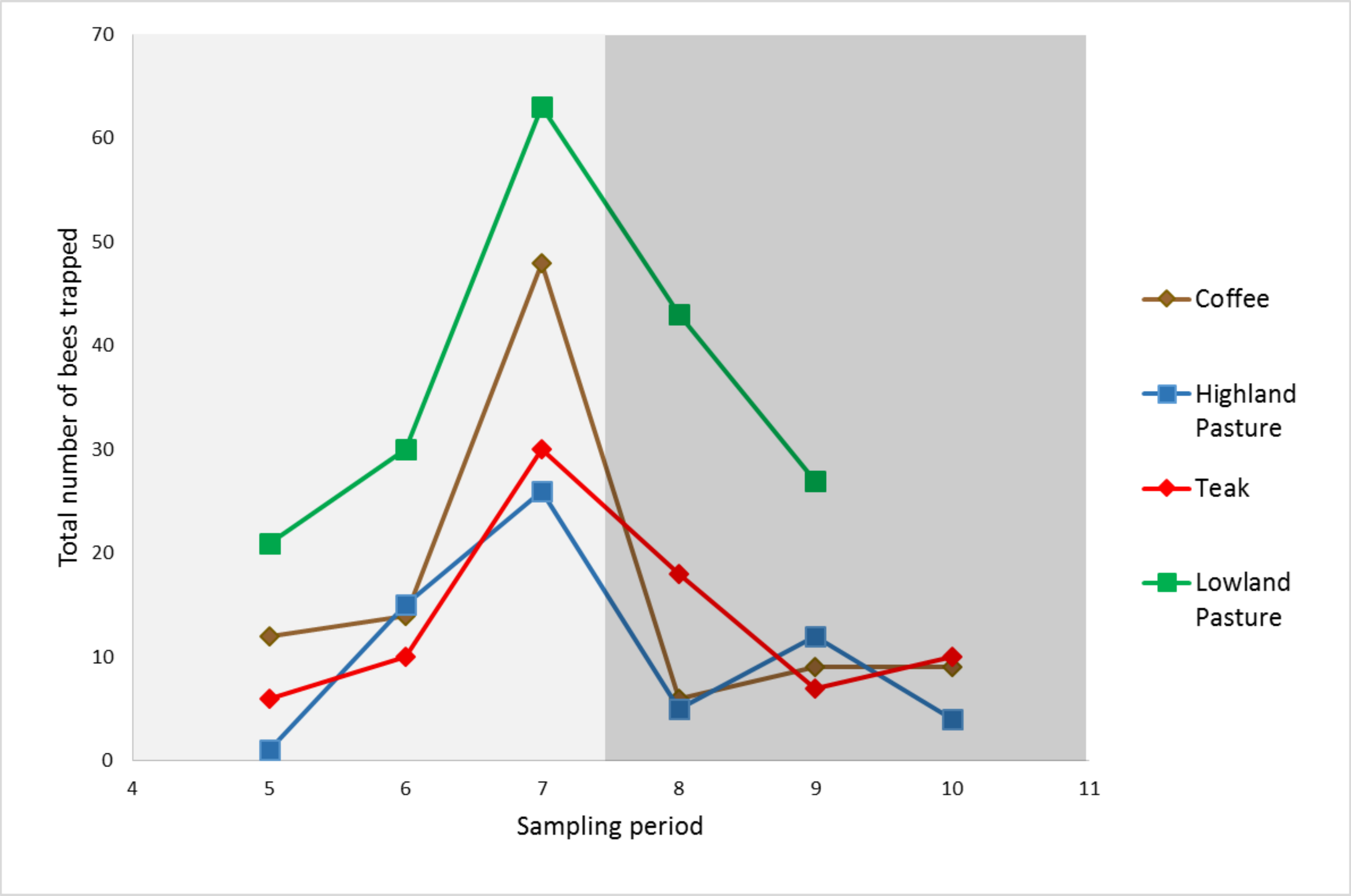

Figure 4: Total number of bees trapped in pan traps over six sampling periods (2014). In some instances traps in highland pastures were damaged, so total abundance is lower relative to other land uses. Sampling varied between the dry season (light grey background) and wet season (dark grey background) and among land uses.

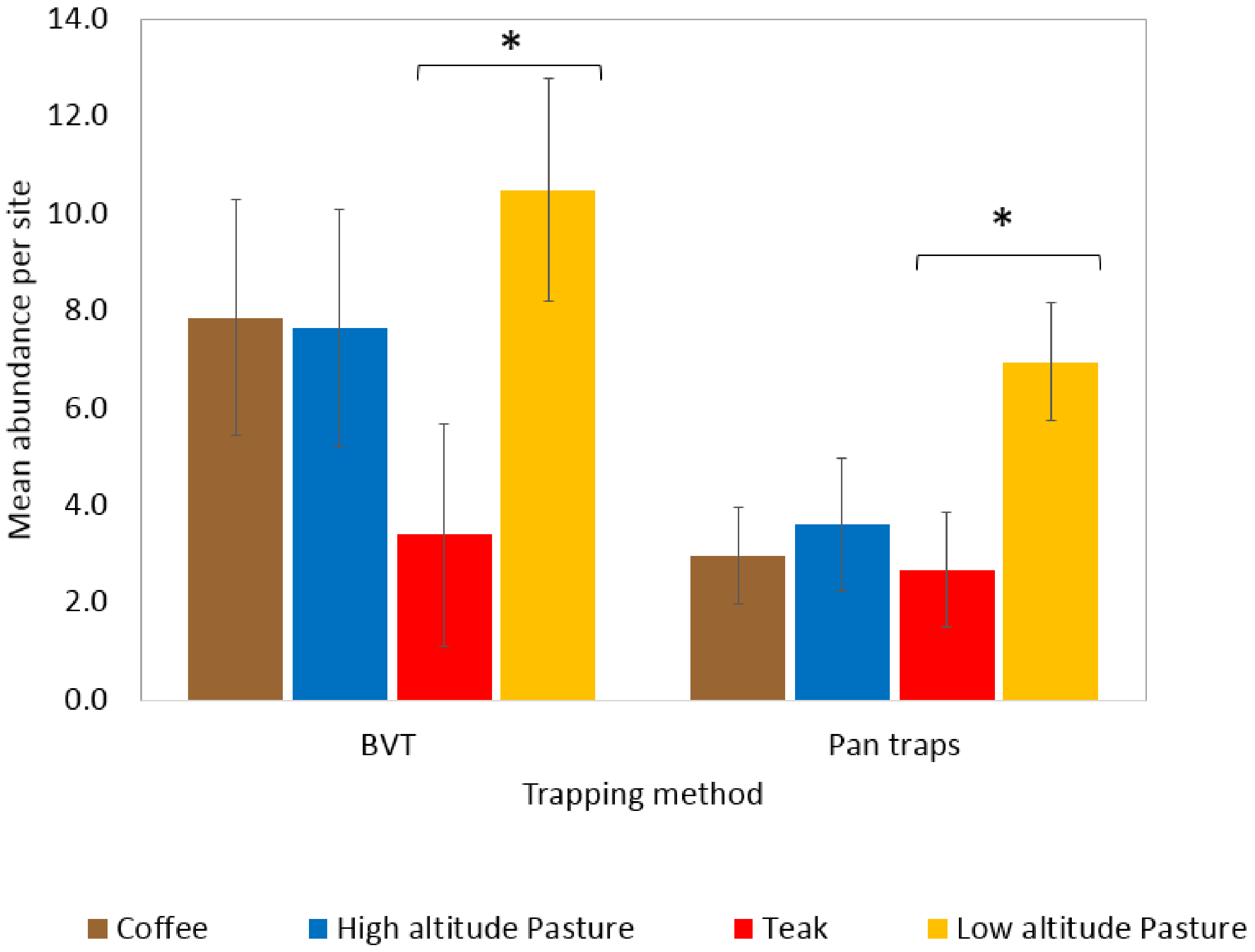

Figure 5: Mean bee abundance by land use from both trapping methods. Error bars show standard error, and asterisks denote significance at p<0.05 (*).

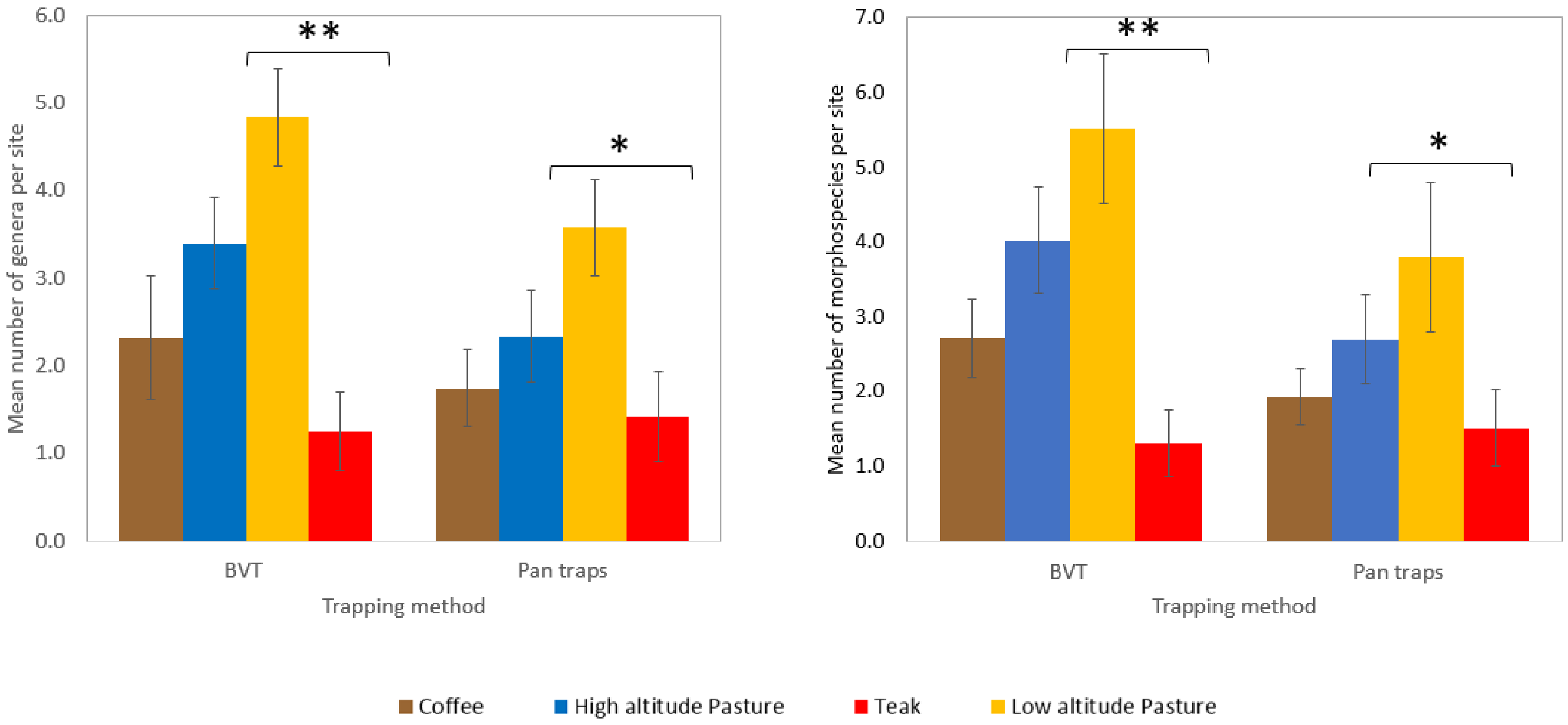

Figure 6: Mean bee genus (left) and morphospecies (right) richness by land use for both trapping methods. Error bars show standard error, and asterisks denote significance at p<0.05 (*) and p<0.01 (**).

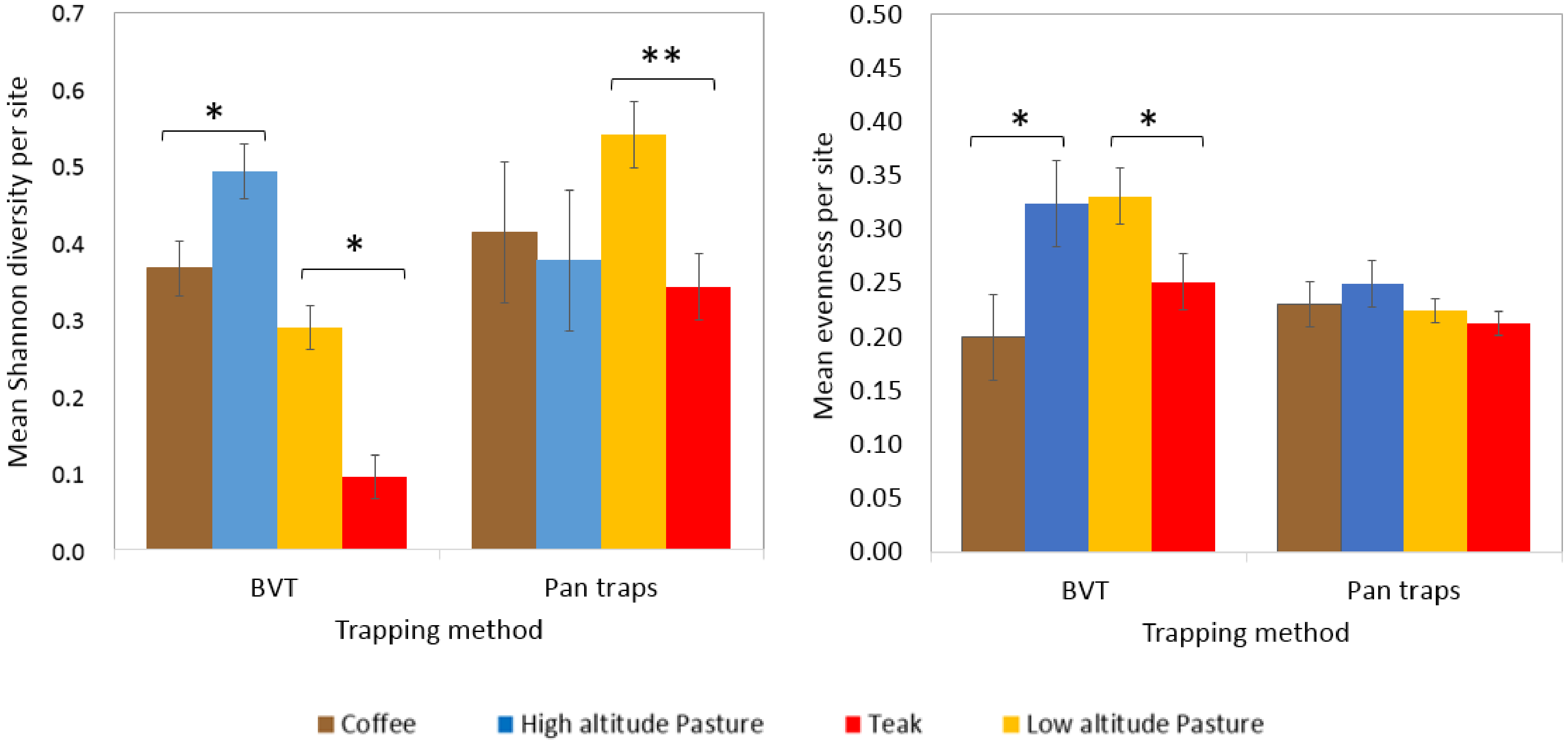

Figure 7: Mean bee diversity (left) and evenness (right) by land use for both trapping methods. Error bars show standard error, and asterisks denote significance at p<0.05 (*) and p<0.01 (**).

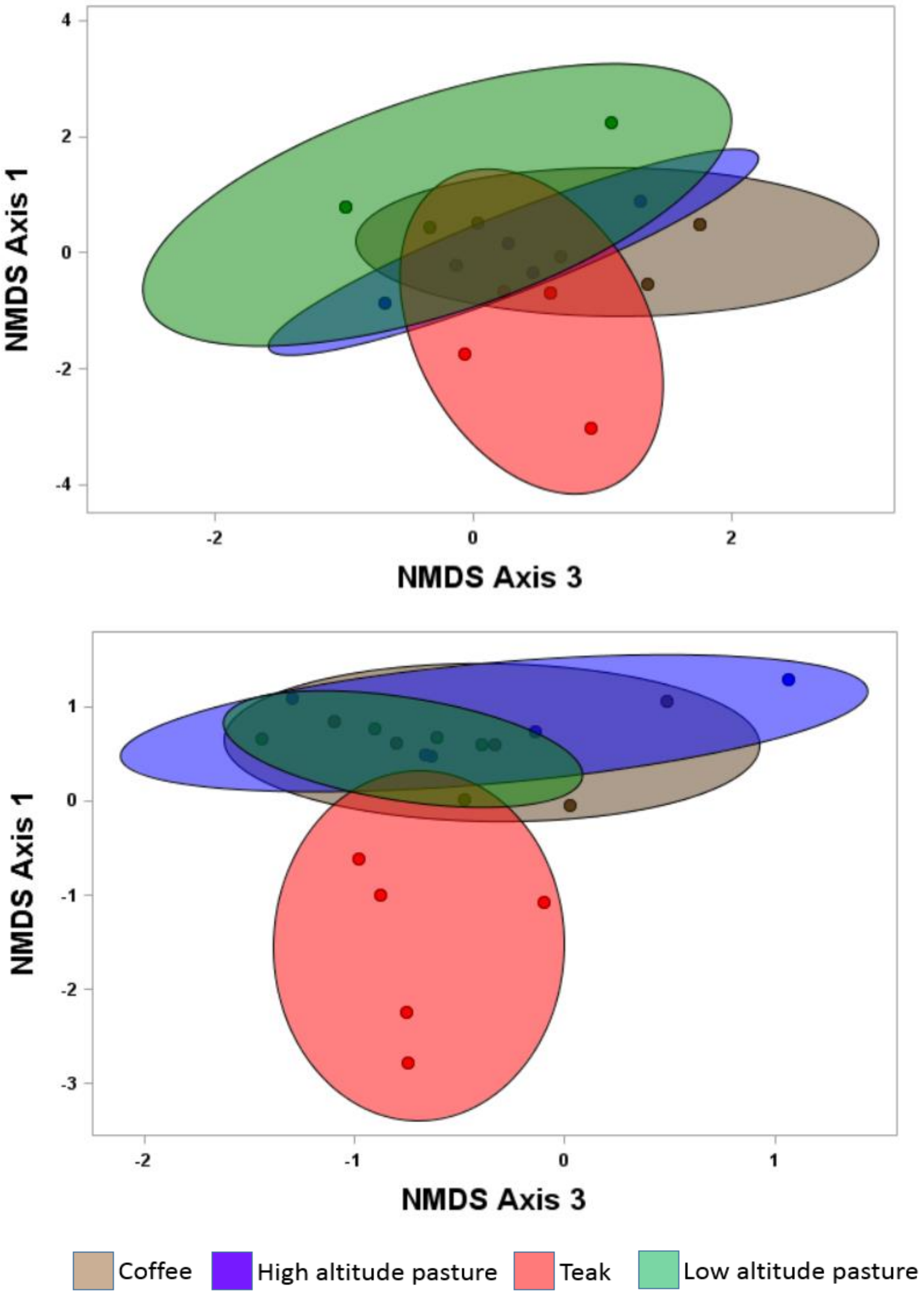

Figure 8: Nonmetric Multidemensional Scaling of functional groups by land use. Figures show divergence in functional group relative abundance during dry season (a, upper) and wet season (b, lower) for both altitude classes. Ellipses represent general grouping of points within a land use. NMDS axes correlate with functional groups, as referenced in text.

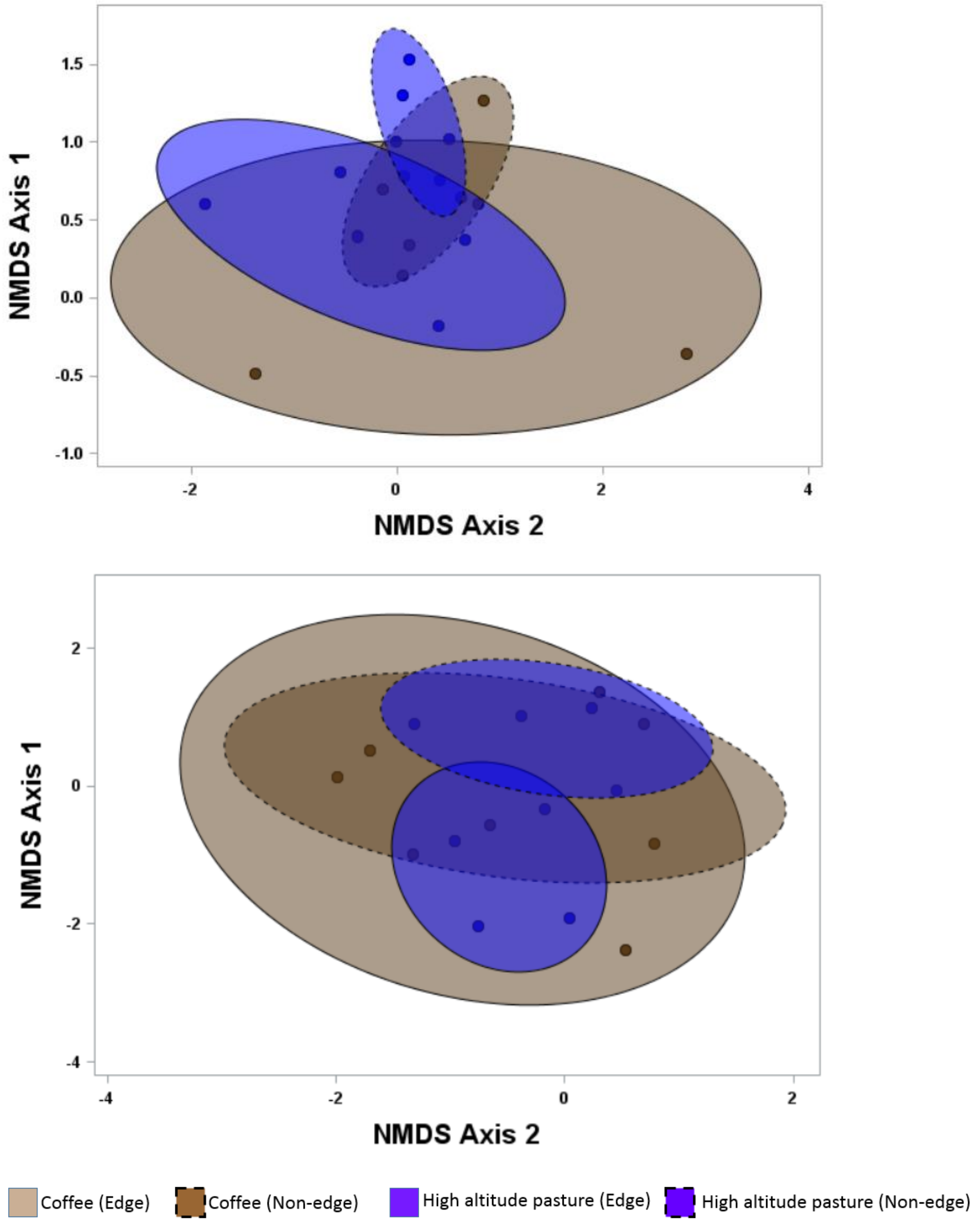

Figure 9: Nonmetric Multidimensional Scaling of functional groups by distance from forest (high altitude sites). Figures show divergence in functional group relative abundance during dry season (a, upper) and wet season (b, lower). Ellipses represent general grouping of points within a land use. NMDS axes correlate with functional groups, as referenced in text.

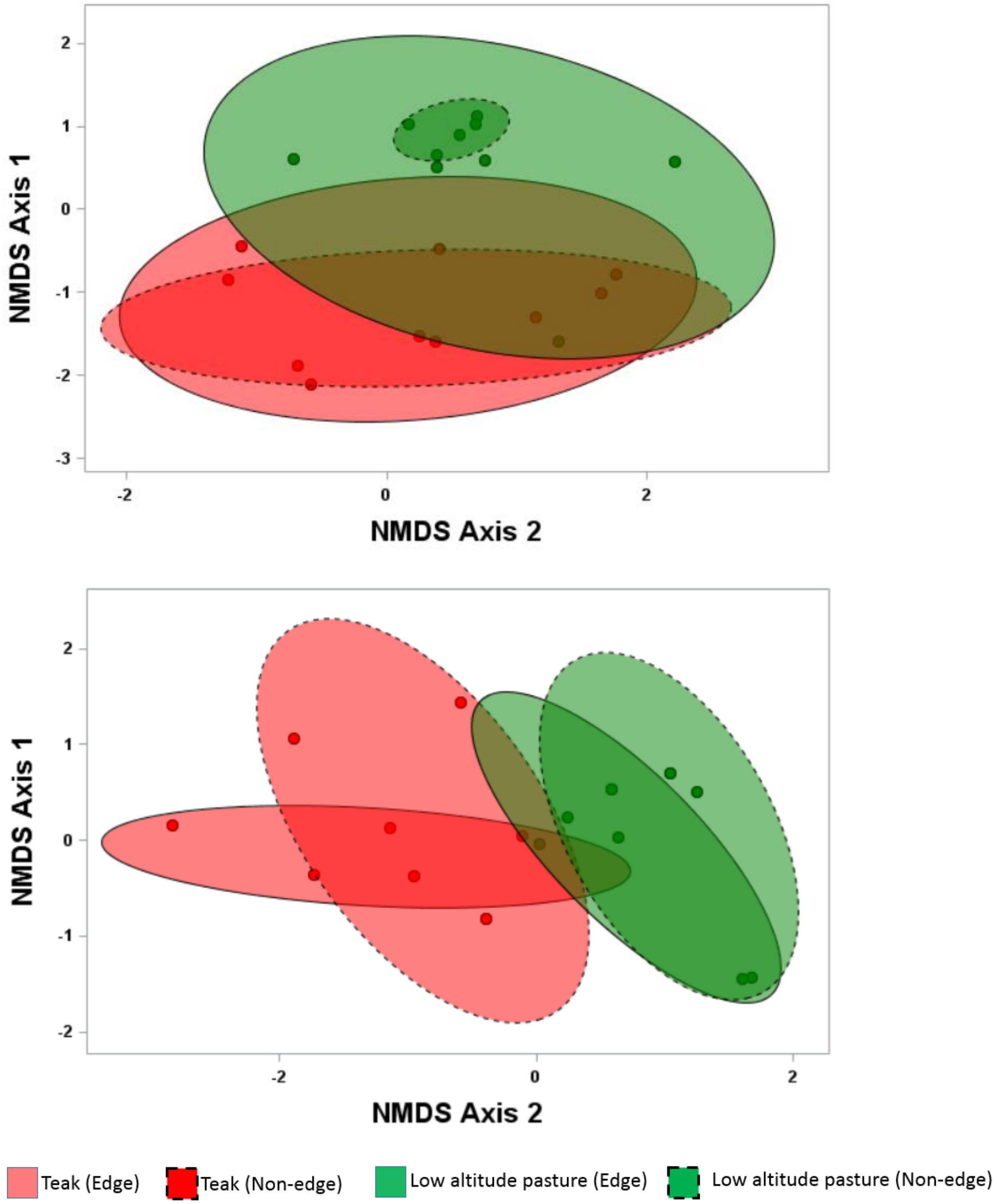

Figure 10: Nonmetric Multidimensional Scaling of functional groups by distance from forest (low altitude sites). Figures show divergence in functional group relative abundance during dry season (a, upper) and wet season (b, lower). Ellipses represent general grouping of points within a land use. NMDS axes correlate with functional groups, as referenced in text.

Chapter 3: A Mixed-Methods Approach for Applying Local Ecological Knowledge to Ecosystem Service Valuation

Submitted to *Ecosystem Services*

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Abstract

Attempts to measure the impact of land use change on ecosystem services (ES) typically focus only on landowners or aggregate the social impacts among diverse groups. There is a need for new approaches that focus on the value of ES change, especially for marginalized groups of non-landowners. We illustrate a mixed-methods approach for using local ecological knowledge to generate practical information for the valuation of ES. Our approach included mapping apiary locations (n=215) on a high-resolution land use map of the Nicoya Peninsula of Costa Rica to measure land cover used by beekeepers, then using a questionnaire (n=50) and follow-up interview (n=21) to understand beekeepers' land use preferences and perceptions of how land use change has impacted their provisioning services of honey and other income-generating products. Apiary maps revealed that hives are significantly more likely to be placed in pastures than in other land uses. However, questionnaire results demonstrated that beekeepers would prefer to place apiaries in secondary forest, native tree plantations, or primary forest for access to floral resources from native tree species. In the interviews, beekeepers reported increased challenges to honey production due to the spatial and temporal change of floral resources, often as a result of land use change incentivized by national conservation policies. They also described adverse changes such as the loss of shade trees in pastures and interactions between land use and climate change. Beekeepers' long-term observations provided information on resource changes from species to landscape scale and specific recommendations for improving ES management and conservation policies. Our method can be combined with approaches from other disciplines to contribute to more comprehensive ES valuation that includes spatially-explicit non-landowner perspectives.

Highlights

- Non-landowning groups may value ES differently than land owners
- Mapping, questionnaires and interviews can generate useful data on ES valuation
- The approach was tested with beekeepers in the Nicoya Peninsula, Costa Rica
- Participants prefer native forests and crops with floral diversity
- Some land uses that garner payments for landowners are not valued by beekeepers
- Participants do not perceive reforestation with plantations as viable for beekeeping
- Some conservation policies constrain beekeeper access to ES
- Local ecological knowledge is helpful to inform conservation policy

Keywords

Payments for ecosystem services, land use change, participatory mapping

Introduction

Ecosystem services and valuation

Since the publication of the Millennium Ecosystem Assessment (MEA 2005), scientists have been increasingly interested in understanding how changes in the environment impact the provision of ecosystem services (ES) (Fisher et al. 2009). Ecosystem services, the benefits humans derive from nature, include provisioning services, such as the production of lumber or food; regulating services, such as pollination or pest control; supporting services, such as carbon storage and nutrient cycling; and cultural services, such as recreational or spiritual use (MEA 2005). Many ES that are critical for human well-being are being degraded or used unsustainably worldwide, largely because of land use and cover change and land use intensification to produce food and energy for a growing population (MEA 2005). Growing concern for the negative outcomes from ES loss has resulted in development of diverse methods for the valuation of ES from ecological, economic, and social perspectives.

In this paper, we define valuation as the act of assessing, appraising or measuring the worth or importance of something, in this case ES from different land use and cover types (Gomez-Baggethun et al. 2014). Several ES-related challenges call for interdisciplinary mixed-methods approaches to consider, compare, or combine different valuation perspectives (Fontaine et al. 2014; Gomez-Baggethun et al. 2014). Examples of interdisciplinary ES challenges include ES trade-offs, where one service is increased at the cost of another (Jackson et al. 2005), intangible outcomes due to spatial and temporal mismatch of service production and reception (Brauman et al. 2007; Fremier et al. 2013), and unequal benefits to different stakeholders (Daw et al. 2011; Muradian et al. 2013).

Several conservation strategies worldwide incentivize "favorable" land uses and management for maximizing ES (Milder et al. 2010). These policies are often described as win-win solutions because they are designed to support human livelihoods while protecting ES (Muradian et al. 2013). Various approaches exist for valuation of different types of ES (Martin-Lopez et al. 2014). In terms of social valuation, the most well developed approaches are based in economics. However, some economic valuation methods have been criticized for providing biased estimates of value and not being consistent with economic theory (Hausman 2012; Kling et al. 2012). Furthermore, they often focus on landowners or aggregate values from different social groups, thereby underestimating the impact of small net economic changes for low-income groups (Daw et al. 2011). This can lead to policies that exacerbate inequality for already marginalized groups such as non-landowners.

To improve ES-related strategies, particularly for low-income, rural residents for whom small shifts in income could have the most impact (Milder et al. 2010), we must improve our ability to assess the impacts of land use and cover change from diverse stakeholder perspectives (Gomez-Baggethun et al. 2014; Martin-Lopez et al. 2014). Here, we use a combination of data collection methods (mapping, questionnaire, and interview) and analytical approaches (i.e., GIS analysis and assessment of local ecological knowledge) in a study of beekeepers in the Nicoya Peninsula of Costa Rica to determine how they perceive the value of different land use and cover types to sustain bee populations. Results provide useful insights for improving ES management practices and conservation policies at relatively low cost. These mixed-methods can be combined with other methods, such as economic valuation of non-market goods, for integrated ES valuation.

Local ecological knowledge (LEK) for valuation of ES among land use and cover types

Because of the scope, complexity, and uncertainty of global environmental problems, various types of knowledge are needed to better understand ES changes and associated impacts on human well-being (Raymond et al. 2010; Fagerholm et al. 2012). LEK is knowledge held by a specific group of people about their local ecosystems (Barber and Jackson 2015). LEK from geographically distant and ethnically different locations but with a similar agroecological context show strong similarities (Sinclair & Joshi 2000). Traditional Ecological Knowledge (TEK) is a subset of LEK, but while TEK is embedded in long-term culture and practices, LEK comes from more recent, site-specific, contextualized observations and experiments generated by local users over the last few generations (Gadgil et al. 2003). We drew from literature on both LEK and TEK for this study.

Research that considers TEK or LEK has identified different priorities and concerns among local communities than those perceived by external institutions and has shown that LEK can be used to identify gaps in scientific inquiry. Thus, including LEK is important for studies that seek to respond to environmental problems in a way that is both scientifically sound and considers local value systems and priorities (Gómez-Baggethun et al. 2013; Barber & Jackson 2015). There is increasing recognition of the role that LEK can play to inform environmental policy (MEA 2005; Turnhout et al. 2012; Gomez-Baggethun et al. 2013). Some examples include incorporating LEK into wildlife population monitoring (Moller et al. 2004) and marine conservation (Huntington 2000; Drew 2005). It has also been used to improve technical interventions and land management for livestock (Thapa et al. 1995), coffee (Albertin & Nair 2004; Cerdán et al. 2012), plantain (Polidoro et al. 2008) and cocoa agroforestry systems (Dahlquist et al. 2008; Anglaaere et al. 2011).

While Costa Rica has become well known for novel conservation strategies, including payments for ecosystem services (PES), there is still significant potential for research focused on the impacts of land use changes that occurred over the last half century, particularly for local residents who are not receiving payments but are otherwise impacted by land use and cover change. Efforts of ES valuation in Costa Rica have often measured the direct economic outcomes for landowners who have converted land into protected forest or protected existing forest patches, but have failed to consider implications for other stakeholders. For example, Milder et al. (2010) assessed the current status and future potential for PES to alleviate poverty in developing countries, but only suggested solutions for landowners or stewards, who would receive payments and make decisions about land use and management. Similarly, McLennan and Garvin (2012) investigated the impacts of land use and cover change on landowner livelihoods in Northwestern Costa Rica. Their study focused on sustainable rural livelihoods, but did not look at any groups who may utilize ES without receiving payments or making land use decisions. In contrast to these studies, Caceres et al. (2015) conducted a more integrated study of the ES values in a region of Argentina and compared diverse stakeholder perspectives. Their approach showed that diverse stakeholders perceived different ES from the same land uses, and demonstrated the need for methods to capture this diversity as part of ES valuation.

Study objectives

Our objectives were: 1) to illustrate a mixed-methods approach using mapping and LEK to generate practical information applicable to ES valuation; 2) to use this approach to assess and explain changes in ES provision, as perceived by beekeepers in the Nicoya Peninsula, examining how this has been influenced by conservation policies; and 3) to contribute to the discussion of the impact of land use and cover change on ES for non-landowners so as to achieve more integrated valuation of ES by including diverse social groups and perspectives.

Study region

The study was part of an interdisciplinary effort to understand the impact of conservation incentives in the Nicoya Peninsula (Fig. 1). The peninsula, bordered by the Pacific Ocean to the west and the Gulf of Nicoya to the east, is a mix of seasonally dry and moist tropical ecological life zones (Calvo-Alvarado et al. 2009). Currently, the peninsula is dominated by secondary forest regrowth, pasture, tree plantations, and agricultural crops (Serrano 2005), but in recent history, the region has undergone dramatic changes in land cover. Due to high beef prices and a growing cattle industry, extensive dry tropical forest in the peninsula was converted to pasture from the 1950s to mid-1970s (McLennan & Garvin 2012). However, a drop in the international beef market combined with a severe El Niño-induced drought in the late 1970s resulted in land abandonment and migration from the region. Over subsequent years, supported by landscape stewardship led by local institutions and policy reforms that focused on forest protection, much of the pasture regenerated into secondary forest (Vallejo et al. 2006), and in some counties forest cover increased from 14% to 52% between 1970 and 2005 (Serrano 2005).

Nationally protected areas, regulation of extraction of products from natural forests, forestry incentives, and a national PES scheme were created to incentivize reforestation and protection on private lands (Vallejo et al. 2006). Though PES may have had a role in reforestation of the Nicoya Peninsula, some of the PES-sponsored reforestation has occurred in the form of monoculture plantations of introduced species like teak (*Tectona grandis*) and melina (*Gmelina arborea*). The ownership of these plantations is common among landowners who receive PES in the peninsula (Cárdenas et al. 2014). While the Costa Rican PES plan states goals for decreasing poverty, participation in the program is more common among landowners with larger properties, higher education levels, and absenteeism (Zbinden & Lee 2005) and may in some instances exclude traditional uses and users (Pagiola et al. 2005).

Case study: Beekeeper LEK

Beekeeping is an important rural livelihood strategy in many countries worldwide (Bradbear 2009), with some of the highest honey-producing countries located in Latin America (Vandame & Palacio 2010). There are an estimated 400-500 beekeepers in Costa Rica, and many of the hives are located in the province of Guanacaste (Dr. Johan W. van Veen, personal communication), where the Nicoya Peninsula is located. The global demand for honeybee (*Apis mellifera)* pollination services is outpacing the honeybee stock, with implications for crop production and biodiversity maintenance (Aizen & Harder 2009). With pollinator populations decreasing and increasing rates of colony collapse among honeybees (Potts et al. 2010), it is of pressing importance to understand how human activities influence bee populations (Vanbergen 2013). Therefore, we focused on the perspectives of commercial beekeepers.

Beekeeping occupies a unique niche because it does not require landownership, provides an essential ES for agriculture and biodiversity maintenance and relies on other ES in the form of pollen and nectar resources from flowering plants. Beekeeping takes advantage of existing floral resources without requiring deforestation or competing with other livelihood strategies or conservation efforts in the landscape (Brown 2001; Brown 2009; Ingram & Njikeu 2011). Beekeepers generally have an extensive knowledge of the quantity, quality, and location of floral resources for honeybees based on the production of their colonies and location of successful hives. The potential of using this type of LEK to understand and interpret observations of land use and cover change has been historically underappreciated and largely untapped (Kleinman & Suryanarayanan 2012).

Methods

Data collection

Our mixed-methods approach included a mapping exercise, questionnaire, and semi-structured interview, which were applied to beekeepers in the Nicoya, Hojancha, Nandayure, and peninsular Puntarenas Counties. Data were collected from March to

November of 2014. The questionnaire was given to 50 beekeepers whom we located using beekeeping association records (Jicaral Beekeeping Association, n=21; Chorotega Beekeeping Association, n=17), or, in the case of non-members, through chain referrals (n=12). The Jicaral and Chorotega Beekeeping Associations are the only two beekeeping associations within the study region, thus our survey was conducted with the majority of working beekeepers in this area.

The primary purpose of the questionnaire was to collect information on beekeepers' preferences for different land use and cover types. In addition to providing socio-demographic information and information about their business practices, respondents were asked to rate the importance of 12 land use and cover types for beekeeping on a five-point Likert-type scale from one (not important) to five (extremely important). To guide the mapping exercise, we asked respondents to rank the factors used when choosing apiary locations on a five-point Likert-type scale from zero (not important) to four (extremely important). They also listed the five most important floral resources in the region for beekeeping.

For the mapping portion, we obtained hive locations from beekeeping associations and several other participants who had GPS locations in their records. Beekeepers who did not have GPS locations identified the location of their apiaries on a physical map of the region. We used color printed cartographic maps (scale 1:50,000), which included roads, homes, and topography to maximize accuracy in identifying hive locations. Beekeepers also provided information on the number of hives kept at each apiary. In total, we mapped 215 apiaries representing 4,332 hives managed by the 50 beekeepers that responded to the questionnaire.

The semi-structured interview was focused on the Chorotega Beekeeping Association members and non-members within the northern portion of the study region. We restricted this sample to beekeepers with at least five years of experience beekeeping in the region (n=21), because the questions focused on participants' perspectives of land use and cover change over time. There were no interview refusals. We started each interview with the question: "How has land use and cover changed since you began beekeeping in the peninsula, and how has this affected your business?" We then allowed the conversation to continue, focusing on explanations for their questionnaire responses and topics such as characteristics of preferred land use and cover types and the impact of conservation policies on the resources available to beekeepers. We recorded the interviews to be transcribed verbatim and translated them from Spanish to English for later analysis.

Data analysis

We summarized and graphed questionnaire data using R version 3.2.1. Recorded conversations during the questionnaire portion and semi-structured interviews were transcribed and translated, and co-authors discussed material to find sections that were pertinent to our research questions. We then developed a codebook for identifying themes and relationships among themes in the interviews (Weston et al. 2001). Two of the researchers independently applied the codebook to the interviews across five iterations, calculating an inter-rater reliability agreement coefficient after each iteration, until reaching an acceptable reliability coefficient (Cohen's Kappa >0.80; Krippendorff 2004). Then all interviews were uploaded to NVivo, coded using the codebook, and analyzed for overall patterns related to the research objectives. Interviews were semi-structured, so that not every participant was asked the same questions in the same way. Therefore, it is inappropriate to interpret the importance of different themes based solely on the number of participants who included those topics. However, the questionnaires generated mean rankings of land use and hive selection variables and standard error of responses, which provided a quantitative measurement of agreement among participants to use in conjunction with interview data. In presenting results, we included interview excerpts that provide the most insight into the questionnaire results.

We used responses from the questionnaire to inform the mapping analysis, both to determine buffer zone distances for land cover analyses and to understand which variables were possible predictors of hive location. Hive mapping was performed on the Sistema Nacional de Áreas de Conservación (National System of Conservation Areas) land cover classification made through the National Forestry Inventory program, which has a spatial resolution of 10 meters (Ortiz 2013). We overlaid hive points as a feature class in ArcGIS 10, and added buffers of 500-meters and 2-kilometer radii from each point. We then calculated the total area of land cover types within each buffer zone. We chose the 500-meter buffer because studies have shown that this is a typical honeybee foraging range when resources are available (Schneider & Hall 1997). This radius was used to assess the land uses immediately surrounding apiaries. The 2-kilometer buffer was selected because honeybees will also forage at these larger distances (Beekman & Ratnieks 2000).

We recorded the land cover output of area within the 500-meter and 2-kilometer hive buffers to assess the total area of each cover type per apiary. In addition, we combined all apiary buffer zones into a single polygon. We calculated the mean proportion of hive buffer zone overlap by dividing the summed areas for individual hive buffer zone from the combined polygon. We generated a convex hull feature around the two primary regions of usage and generated random points (n=215) within each of these features to compare beekeeper land use to land uses surrounding randomly selected locations.

We compared actual to random hive placement using logistic regression, which is an established method for assessing wildlife resource selection (Keating & Cherry 2004; Baash et al. 2010). This method allows researchers to assess habitat usage of animals by comparing presence-only data to habitat availability within a constrained region. In this case, we determined habitat selection for bees by beekeepers using the standard logistic regression equation:

$$P(i) = \frac{\exp(\beta_0 + \beta_1 x_{i1} + \beta_2 x_{i2} + \beta_3 x_{i3})}{1 + \exp(\beta_0 + \beta_1 x_{i1} + \beta_2 x_{i2} + \beta_3 x_{i3})}$$

Where β values are coefficents that relate the probability of use [i.e., P(i), or in this case probability of hive placement] to the habitat covariates x_{i1} (the proportion of forest), x_{i2} (the proportion of pasture) and x_{i3} (the proportion of forest plantations) for sample *i*. The results show the odds of finding a hive in a particular set of land uses. We exponentiated the output to determine the odds that a point would be an actual hive versus a “random hive” based on land use proportions.

Results

Socio-demographic information about respondents

Ninety percent of beekeepers who completed the questionnaire were male, and approximately half of the participants had a primary school education only. Participants ranged from 21 to 77 years of age (mean=51). The average beekeeper had 17.4 years of experience beekeeping in the Nicoya Peninsula (range of 1 to more than 50 years of experience). The average participant had 4 to 5 apiaries and about 126 hives. Approximately half (n=24) of the beekeepers made less than $5,000 U.S. dollars gross income annually from beekeeping, and one third of participants (n=15) made over $8,000 annually from beekeeping.

Apiary site selection

When asked the distance they considered around potential apiary sites, the mean response by beekeepers was 2.1 kilometers (SE= 1.3 kilometers) with a range from 100m to 6 -kilometers, bracketing the 500m and 2-kilometer buffers used in our landscape analysis. Output from the mapping exercise showed that: 1) at a 500-meter range from the hives, the mean area around the apiaries is mostly pasture, followed by forest (Fig. 2); 2) at a 2-kilometer range from the hive, the mean area around the apiaries is mostly forested, followed by pasture lands (Fig. 2); and 3) there is a substantial overlap of buffer zones, particularly at the 2 kilometer range (38.8%). The overlap of buffer zones is important because questionnaires revealed that beekeepers generally seek to avoid other beekeepers' apiaries, which was indicated in questionnaire results (Fig. 3).

Results from the logistic regression of land use for actual and random hives revealed that at the 500-meter buffer zone, only the coefficient for pasture was significant, indicating beekeepers actively select apiary locations based on the amount of pasture within 500-

meters (Table 1). Based on the odds ratios, which is the exponentiated probability function, for each percent increase in pasture within the buffer zone, points are 1.2 percent more likely to be an actual apiary versus a randomly placed apiary (p=0.002). At the 2-kilometer range, the complete coverage of apiary buffer zones within the constrained region prevented statistical analysis because hives could not be randomly located with a different land cover distribution than the existing hives, so results would underestimate beekeeper land use selection.

Beekeeper land use and cover preferences

Questionnaire results demonstrated that beekeepers consider land use and other biophysical factors when choosing where to place their hives (Fig. 3). On average, the most important variables for determining hive location were proximity to water (3.5/4), surrounding land uses (3.2/4), tree diversity in the region (3.1/4), and distance from other beekeepers' apiaries (3.1/4). During the interviews, respondents explained that proximity to water is important because it decreases the number of trips they have to make to tend the hives, and because high quality water resources improve bee health and production. Water was also related to land use and cover. For example, one beekeeper said, "*The melon farms have another problem: there is no water there. The bees have to spend a certain amount of time searching for water... they die of thirst in the melons because they don't put water there. There are no rivers, no streams, nothing. Just melon farms*." Another beekeeper noted a connection between water resources and floral resources: "*We prefer to put the hives close to rivers because the water is there, but also a higher diversity of plant species*."

The land use types ranked as most preferred for beekeeping were secondary forest (4.5/5), native tree plantations (4.3/5), primary forest (4.2/5), and shade coffee (3.9/5) (Fig. 4). These were notably different from the locations where hives are actually placed, namely pastures. Native tree plantations are not currently a significant land use in the region, but several beekeepers take their hives to laurel (*Cordia alliodora)* plantations in Upala, which is north of the study region. Shaded native pasture was ranked significantly higher than improved pasture with shade trees (2.4/5), improved pasture species with no shade trees (2.2/5), and native pasture with no shade trees (2.1/5). Beekeepers explained that improved pastures, where new species of grasses have been introduced to improve productivity for livestock, will eventually compete for water with shade trees. One beekeeper noted that "*they removed all of the natural pastures of the region, like the jaraguá and the brama, and put all these improved grasses; brisanta, tanzania, guinea... there used to be some trees in the natural pastures, but those grasses are killing them, and the trees won't survive.*"

Beekeepers were also asked in the questionnaire to list the five most important plants needed for beekeeping in the region. Of the 231 plants listed, 79% were native trees, including the five most common plants mentioned (Table 2). In the interviews, 10 beekeepers emphasized the temporal availability of floral resources as the main reason why they value certain plants over others. For example, a common weed in pastures, florecilla, helps beekeepers sustain the harvest during the rainy season: "*The florecilla... it flowers in the rainy months, when no one harvests the honey. It is just for the bees. It is one of the most important flowers because it helps you in the wet season so the hive survives*." The high value of native trees also explains why beekeepers ranked shade coffee (3.9/5) significantly higher than sun coffee (3.1/5) in the questionnaire.

Melina (1.9/5) and teak (1.3/5) had the lowest preference values among the land use types. Several explanations for this trend were revealed during follow-up interviews, all related to the availability of flowers: "*Reforestation with plantations does affect [beekeeping] because teak just flowers once, in the wet season. I have never found it flowering in the dry season. On the other hand, with native species, as there are many types, there are always flowers, and everything does not flower at the same time*." Several beekeepers perceived that teak, in particular, does not serve as a floral resource for bees: *"A long time ago, there was more pasture than lumber, but the pasture had trees, shade. So, the pastures had a lot of different trees that gave shade. Now there are no pastures, but there is melina and teak, that doesn’t give anything to the bees, nor to the animals... Not* *even the birds like it*." When comparing plantations to the improved pastures, one beekeeper explained that, "*In the case of Hojancha, when it's October, there is nothing that produces pollen and some farms are empty, so the improved pasture flowers and produces pollen... It's not as if we aren't going to produce without it, but in this season it is useful*."

The questionnaire results, combined with explanation from interviews, support our analysis of hive location trends with regard to land use and cover, as several of the most important factors considered for hive placement are connected to the current land use and cover types in the surrounding area. Although beekeepers prefer forested land uses, they routinely locate their hives around pastures as a strategy to access forested regions that are either logistically difficult to enter or prohibited by law due to their protected status. This is confirmed by the high proportion of pasture at the small buffer distance and high proportion of forest at the large buffer distance.

Perceived changes in location, abundance, and quality of floral resources for honeybees

In the interviews, respondents described trends in land use change and the resulting impact on floral resources for beekeeping. Reforestation with tree plantations was described by seven of the beekeepers as "deforestation," as they lose valuable resources when teak replaces the natural plant succession that might otherwise occur in abandoned pastures. One beekeeper noted that "*the teak and melina plantations affect us a lot because* [prior to planting] *those were young secondary forests and they chopped everything down."* Another beekeeper said*, "everybody cuts when they are going to 'reforest.' They remove everything that is native, which is what gives honey, let's say, flowers, vines, and young forest growth*." Beekeepers also had a long-term perspective on reforestation: "*The thing is that they 'reforested' a bunch of farms here, and when they are 15 years old, they cut everything down and leave things worse off, because they had to cut native trees to plant them*."

Eleven of the beekeepers raised concerns about the loss of preferred tree species due to the introduction of improved pastures in the region. During the interviews, three of the nine most important tree species for beekeeping listed in Table 2 were referred to as decreasing due to wood harvest or competition with improved pastures. One beekeeper said, "*People, when they cut trees, go to search for an economic harvest… they cut gallinazo, yes they have cut the pochote, yes they have cut the guanacaste, yes they have cut the cenizaro.... I am mentioning four, but we are talking about cachimbo, laurel... there are many.*" Another beekeeper said, "*Now we are seeing that the improved grasses are having problems like, they are drying the trees that are near the grass. So if there was a tree in the middle, a pochote for example, or gallinazo -- which was very good -- now they are dry.*"

There were also several neutral or positive comments about land use change over time in the region. For example, one beekeeper said, "*Before, there was a lot more deforestation...We are talking about 30 years ago... But, many people who have livestock now are leaving a protected area to grow... in this sense, the people have more conscience about leaving natural forest to grow; the changes have been magnificent*."

Impact of conservation policies on beekeeper livelihoods

Beekeepers are prohibited by law from keeping hives within national parks. Of the six beekeepers who explicitly mentioned national parks or reserves in the interviews, four were concerned with the lack of access and two explained that they can easily access the parks by placing hives at the forest edge. Two of the beekeepers in the interviews explicitly mentioned Monte Alto, a reserve in Hojancha County. One beekeeper said, "*There's plenty of forest right now. More forest--Because Monte Alto was protected. It was once a livestock farm and now has become a protected forest*." Another beekeeper mentioned that, "*yes, here [near Monte Alto] there have been good changes for beekeepers. Reforestation. Before, all of this was deforested. Now it is different.*"

PES also have impacted beekeeper livelihoods by encouraging forest conservation, secondary forest regeneration, and the establishment of teak and melina plantations. PES lands contracted for natural forest types are seen favorably by beekeepers, but plantations are seen as poor resources because they are established in place of secondary forest regrowth, they are planted as monocultures, the understory is managed intensively, and they are ultimately harvested completely.

Restrictions on native tree removal protect floral resources for beekeepers, but six participants mentioned the lack of enforcement locally. One beekeeper noted that, "*When you have a family and your family has to eat and you don't have a means to generate resources to get this food and you have property -- you have farms -- what you are going to do is cut a tree, sell it, and eat. That's how it works*." Another beekeeper stated, "*Wood production is a big problem for the bees. The wood harvesters take trees from everywhere. MINAE [a government agency] sometimes prohibits harvesting wood but... the more they try, the more wood people harvest*."

Discussion

Overall, mapping, interview, and questionnaire data combined demonstrate that non-plantation forests, followed by agricultural land uses containing native trees, are preferred for beekeeping. Given that pastures occupy such large portions of the landscape, native trees within pastures are perceived as important floral resources for beekeepers. In addition, pastures provide access to forested areas. Land uses that are mostly monocultures, such as teak and melina plantations, melon, and pastures without shade trees, are less preferred for beekeeping activities.

Methodological insights

Our study demonstrated the importance of mixed methods approaches to properly integrate LEK into ES valuation. Hive mapping was helpful to identify land cover types currently in use by beekeepers, showing that beekeepers mostly place their hives in or near pasture and native forest, and that there is considerable overlap between hive foraging ranges at a 2-kilometer buffer distance. In the questionnaire, beekeepers indicated that they prioritize avoiding other beekeepers' hives, so the overlap suggests that preferred locations are insufficient in the region. By combining map data with the questionnaire and interview results, policymakers could target certain regions of the peninsula, specifically by increasing floral resources in heavily utilized pastures, to increase provisioning services for beekeepers. Mapping, in the right context, also makes findings more appealing for policy applications than questionnaire and interview data alone (Hauck et al. 2012), and we demonstrate here that spatially-explicit descriptions of land use can provide insights into resource availability and use by non-landowners.

Reliance on mapping alone would have given a misleading picture, however. Specifically, questionnaires suggested that pastures are not valued as much as forest. Likewise, hives are sometimes placed near teak or melina, even though these were not highly valued in the questionnaire and interviews. The questionnaires lead us to interpret these mapping results as an effect of lack of access to preferred land uses (agricultural land uses and plantations being more accessible than natural forests). Given the diverse matrix in the landscape, apparently beekeepers still have indirect access to forest resources within 2-kilometer of their hives. The questionnaire also permitted us to explore the level of agreement among beekeepers. Because of the small variation in beekeeper preferences for different land use types, we can say with confidence that the group has relatively homogenous views. The questionnaire also provided the novel opportunity to apply participant-derived feedback towards map analyses, such as specifying the relevant buffer zone distances.

In addition to describing actual behavior (mapping) and explaining the basis for preferences (questionnaire), our study used interviews to reveal LEK related to impacts of land use and cover changes that occurred on multiple spatial and temporal scales. For example, interviews highlighted the use of different floral resources throughout the year, as well as changes in plant species that are valuable for beekeeping. This was particularly important, as there are limited data on the impact of introduced species beyond their economic value for plantation owners and employees. Beekeepers also stressed the adverse impact of teak management on valued ES, including the removal of early successional forests from pastures to establish plantations and the lack of understory plants that would otherwise provide resources for bees and other organisms.

Beekeeper LEK may also be useful in guiding biophysical research for better ES valuation. Biophysical studies of teak farms have found low biodiversity of plants and animals when compared to secondary forest, though some researchers argue that it is more justified to compare biodiversity in plantations with the biodiversity in land use and cover types such as pasture, which the plantations typically replace (Hallet et al. 2011). Beekeeper LEK provides evidence that, in some cases, it is reasonable to make ES comparisons between teak plantations and non-managed regional forests, as early successional secondary forest growth is sometimes removed to establish teak plantations. In addition, beekeepers knowledge demonstrated the value of regional pasture systems that include flowering native tree species.

Actionable insights for policymakers

This study provides practical LEK that can be used by policymakers, particularly because of beekeepers' detailed, long-term observations from the species to landscape scale. The main themes from beekeeper LEK include an emphasis on heterogeneity: they are most concerned about the diversity of flowering native plants both spatially and temporally in the peninsula. Several beekeepers explained that pastures, coffee, and other land use and cover types can be viable for beekeeping if there are shade trees, live fences, or small patches of forest, such as riparian areas. In addition, all of the plants listed by 15 or more of the participants are common trees used for shade or live fences in coffee (Albertin & Nair 2004) and pastures (Esquivel 2007) in the Nicoya Peninsula. This reinforces findings from previous work showing that live fences provide habitat, resources, and connectivity for wildlife in Central America (Harvey et al. 2005). The most valuable forms of reforestation for beekeepers, therefore, may be the PES modalities within the Costa Rica program that incentivize the use of shade trees in certain land uses (FONAFIFO 2013).

In addition, this study identified that access to preferred land use types is a major limitation for beekeepers, despite reforestation trends in the Nicoya Peninsula. At the 500-meter buffer distance, beekeepers are more likely to choose pastures than the random sample of points, although they utilize high proportions of forest at the 2-kilometer buffer zone. Based on questionnaire data, beekeepers clearly prefer native forests and native trees, so the placement of hives in pastures highlights the lack of preferred land uses. Since they are unable to use national forest or reserve areas in the region, some reforestation efforts have not benefitted them, except insofar as they can place hives in other land use and cover types at the periphery of parks and reserves. Policymakers could increase park utility by providing edges around parks and reserves that are accessible for local users.

Since many of the beekeepers rent the land where they place their hives, they are not necessarily eligible to receive PES or make choices about land use, cover, or management practices. Like other rural user groups, beekeepers are heavily impacted by land use change and often by conservation policies that are meant to guide land use and cover change in the region. Some of the PES go to landowners as compensation for adopting practices that adversely affect ES valued by beekeepers.

Conclusions

LEK from beekeepers can be useful for policymakers, as beekeepers hold practical information on the impact of land use, land cover and management change on floral resources over long periods of time and across broad landscapes. Beekeeper TEK also provided information on the trade-offs of different conservation policies, such as harvesting regulations, protected national parks, and conservation incentives on private land. Such combination of methods can contribute to integrated valuation in cases where different stakeholder groups depend in different ways on natural resources; certain groups -- like beekeepers -- are impacted by land use and cover change or other policy outcomes but not in power to influence decision-making processes. Actively seeking out and including LEK as part of ES valuation would empower groups of stakeholders that are often marginalized, while providing useful information from species to landscape scales, and over long, sometimes multi-generational, time scales.

Our study revealed several opportunities for novel interdisciplinary study. Beekeeper LEK provided information on the decline of specific tree species due to the use of improved pasture. Additional studies are needed to understand the influence of land management practices on tree species distribution, particularly in improved pastures, and the impact on the biodiversity of organisms that depend on shade trees for landscape connectivity. Furthermore, future research could look at the impact these management changes have on rural livelihoods or cultural practices that depend on native trees, some of which provide additional resources such as edible fruits and seeds.

Beekeeper LEK revealed the need to study the impact of climate change on flowering phenology and distribution of native trees in Costa Rica. Nine of the 21 beekeepers interviewed mentioned seeing shifts in phenology, temperature, and precipitation, consistent with projections in scientific models for the region (Delgado et al. 2012). Such changes compound the impact of land use and cover change to make beekeeping more difficult. For example, one beekeeper said, "*The rain in the wet season prepares the honey harvest for the next year. Land use and the climate are both changing. Under normal conditions the harvest would be low, [and] land use accentuates the problem of the changing climate*." Several beekeepers mentioned the climate becoming drier and hotter. Another beekeeper explained that the timing of the rain is also an issue: "*the thing that is changing lately is the climate -- the rain. It rains [in the dry season] when the trees are already flowering and the flowers are ruined*." Though honeybees are non-native pollinators, they have served worldwide as an indicator species for changes happening in the environment. If climate shifts are impacting beekeepers and their livelihoods, there is a need to understand these patterns and their impacts on floral phenology and related processes, particularly in under-studied regions of the tropics.

Finally, future studies should combine methods such as those we present here with ES valuation from different disciplinary perspectives. For example, combining ecological data from monoculture tree plantations versus silvopastoral systems with LEK and valuation of various services of these land uses to different stakeholders will improve our understanding of potential trade-offs, as illustrated by this study. Economic valuation could quantify the extent to which land use and cover change have impacted groups such as beekeepers relative to the landowners who are receiving PES and who also depend on these land uses for their livelihoods. By combining social valuation methods with established ecological and economic methods, researchers can produce more integrated analyses to inform policymakers and improve conservation strategies for diverse stakeholder groups.

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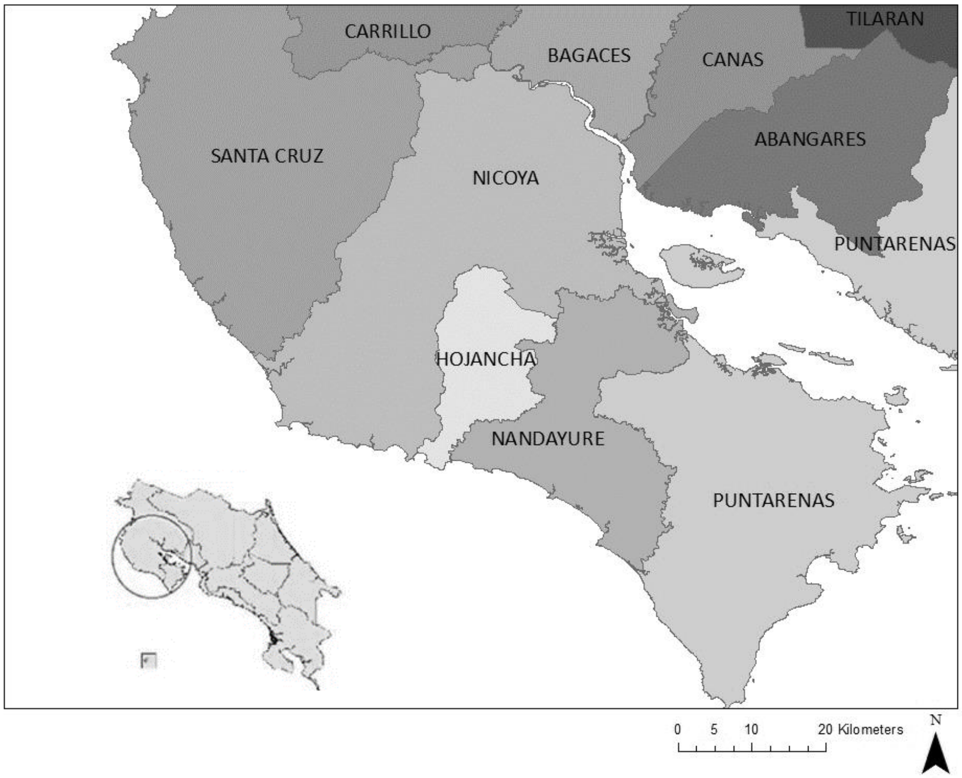

Figure 1. Map of the study region. The Nicoya Peninsula is located in the province of Guanacaste, and we included four counties within the peninsula: Nicoya, Hojancha, Nandayure and Puntarenas.

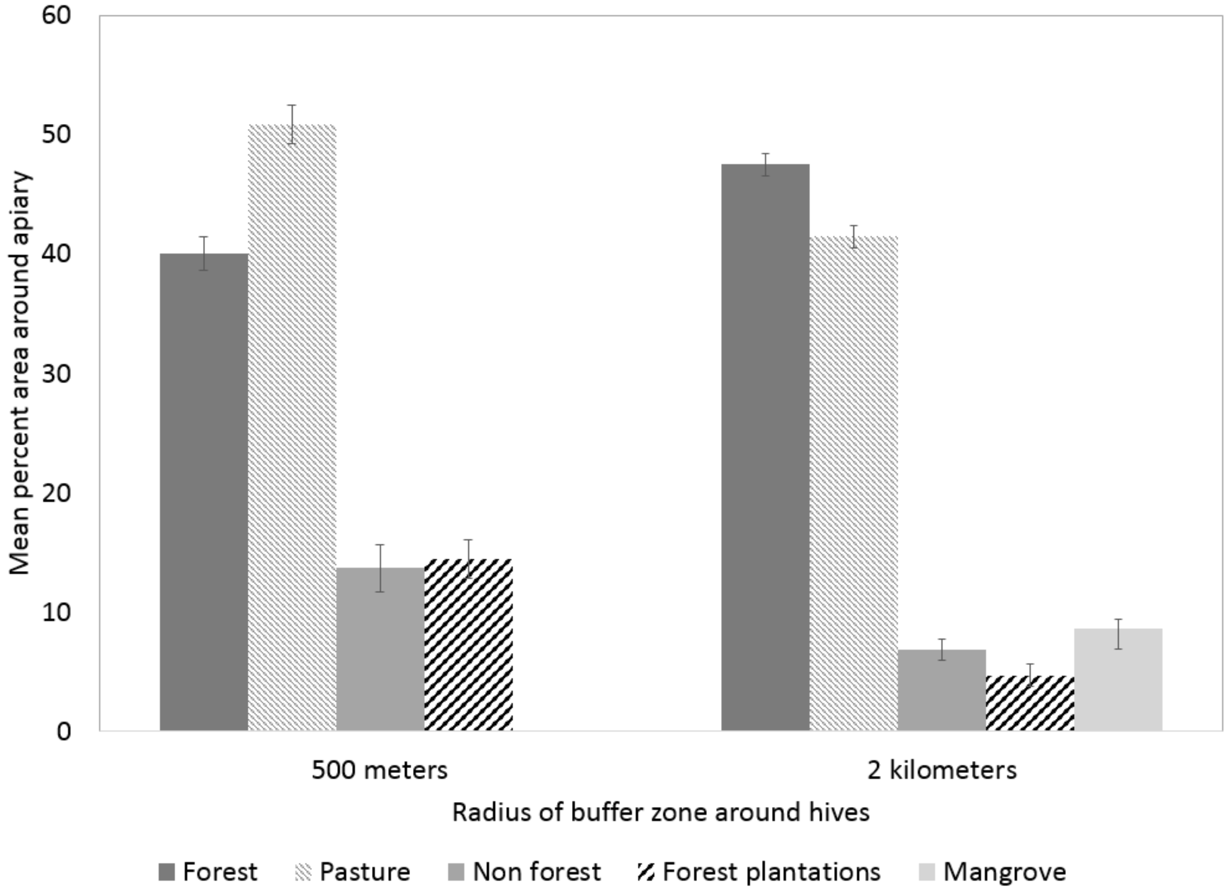

Figure 2. Proportion of land cover types surrounding apiary locations. Columns represent mean proportion of land uses for the 215 hives, sampled at 500-meter and 2 kilometer radii. Bars represent standard error.

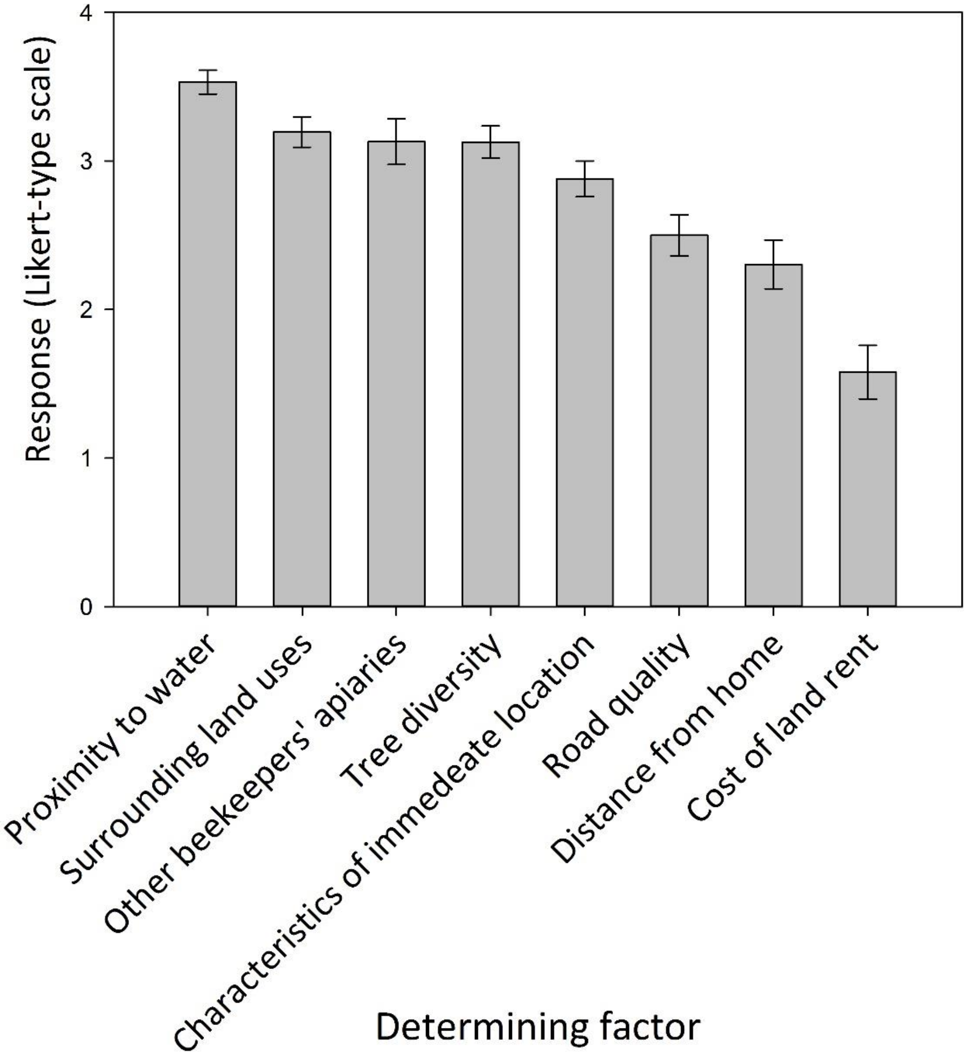

Figure 3. Importance of factors for selecting apiary locations. Columns represent mean responses based on 5-point Likert scale from 0 (not important) to 4 (extremely important). Error bars represent standard error.

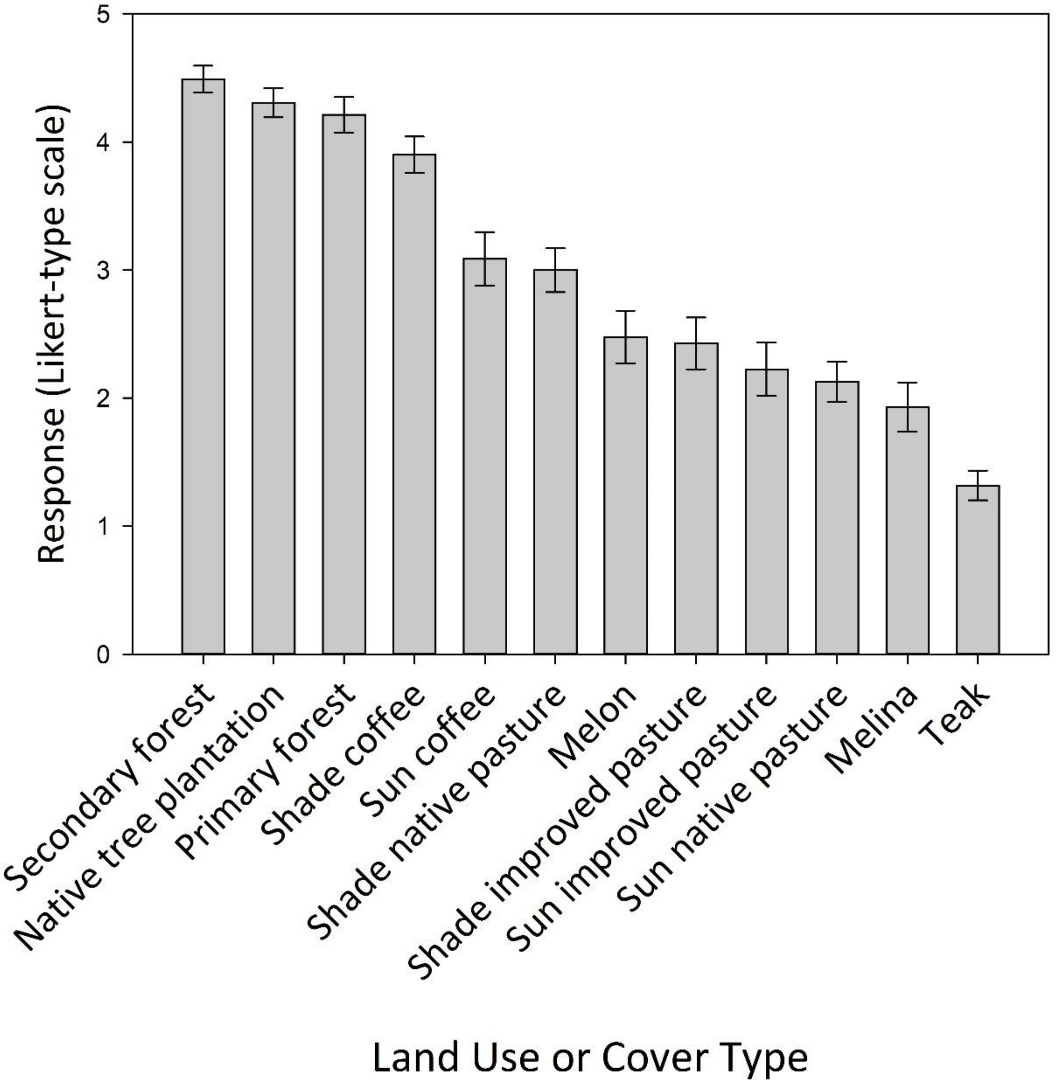

Figure 4. Land use and cover preferences for beekeeping activities. Columns represent mean response from 1 (bad for beekeeping) to 5 (excellent for beekeeping). Error bars represent the mean with standard error bars.

Table 1. Output of logistic regression procedure comparing land cover around apiaries. Significance at $P<0.01$ denoted with (**).

Coefficient	**Estimate**	**SE**	**Z value**	**Pr(>|z|)**	**Odds ratio**	**95% confidence interval**
Intercept	-0.6957	0.477	-1.460	-0.144	0.499	0.188, 1.243
Forest	-0.001	0.006	-0.157	0.875	0.999	0.099, 1.010
Pasture	0.017	0.006	3.046	0.002**	1.017	1.006, 1.028
Tree plantation	-0.004	0.009	-0.413	0.680	0.996	0.978, 1.014

Table 2. Plants reported as most valuable for beekeeping. Plants are listed in order from most to least mentioned. Data include the proportion of participants who listed the plant as one of the top five most important for beekeeping (Proportion of participants) and proportion that the given plant comprises of the total list of plants mentioned, including those not displayed in the table (Proportion of mentions). Plant categories are: native tree (NT; any tree considered native by the local population), vine, or herbaceous plant (herb). We include all responses that were mentioned by at least 5 beekeepers (10% of participants).

Common name	**Scientific name**	**Number of mentions**	**Proportion of participants**	**Proportion of mentions**	**Plant category**
Carao	*Cassia grandis*	22	0.46	0.10	NT
Madroño/Salamo	*Calycophyllum candidissimum*	21	0.44	0.09	NT
Saino	*Caesalpinia eriostachys*	21	0.44	0.09	NT
Gallinazo	*Schizolobium parahyba*	18	0.38	0.08	NT
Laurel	*Cordia alliodora*	15	0.31	0.06	NT
Pochote	*Pachira quinata*	15	0.31	0.06	NT
Bejuco	NA: vines	10	0.21	0.04	Vine
Espavel	*Anacardium excelsum*	9	0.19	0.04	NT
Florecilla	Asterácea: eg., *Melampodium sp.*	9	0.19	0.04	Herb
Palo de agua	*Bravaisia integerrima*	9	0.19	0.04	NT
Guacimo	*Guazuma ulmifolia*	5	0.10	0.02	NT

Chapter 4: Remote Sensing and Ecosystem Services: Current Status and Future Opportunities for the Study of Bees and Pollination-Related Services

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Abstract

An unprecedented array of observing systems, coupled with ever increasing computing capacity, makes this a golden era for ecologists to study and quantify ecosystem services using remote sensing technology. Here, we review recent studies that utilize remote sensing to understand the supply and demand of ecosystem services, with a specific focus on pollination services by bees in forested and agroforestry contexts. Pollination by bees is a globally threatened ecosystem service that supports the production of food crops and maintains plant biodiversity. We explore how studies that use remote sensing to characterize landscapes, monitor individual organisms, measure biodiversity proxies or species habitat, and describe ecosystem processes may improve modeling of pollination services on spatial scales that match large-scale management efforts, such as forest conservation policy. We then discuss future research opportunities, such as exploring LiDAR and radar for 3-D habitat measurements, mapping phenology in space and time, and direct measurement of pollination events and outcomes.

Keywords: Ecosystem services; remote sensing; pollination; bees

Introduction

Steady advances in technological capacity have created new avenues for using remote sensing techniques to study complex ecological questions. Ecologists have used remotely sensed data to quantify landscape characteristics [1,2], observe physical and biological processes [3,4], and gauge human-ecosystem feedbacks [5]. In many cases, remotely sensed data enable these phenomena to be scaled across time and space, resulting in the development of predictive models useful for mapping and managing the benefits that humans derive from nature, known collectively as ecosystem services [6,7].

Ecosystem services include provisioning services, such as the production of lumber or food; regulating services, such as pollination or pest control; supporting services, such as carbon storage and nutrient cycling; and cultural services, such as recreational or spiritual use [8,9]. The Millennium Ecosystem Assessment has spurred a great deal of work over the past decade to understand spatiotemporal patterns of ecosystem service provisioning. Because remote sensing can provide time- and cost- efficient observations at varying spatial and temporal resolutions, it has been adopted as an important tool to study ecosystem services [7]. The widespread adoption of remote sensing tools for this research can be challenged by the rapid pace of remote sensing technology development, leaving many opportunities for collaborative research among specialists in various disciplines to integrate the two fields of study [10,11].

Arthropods influence the provisioning of several important ecosystem services. However, despite their significant role in many ecosystem services such as pest suppression, decomposition, and pollination, arthropods are disproportionately underrepresented among studies that utilize remote sensing techniques [12-14]. To date, application of remotely sensed data to study arthropods have predominantly concerned insect pests. Examples include studies to detect insect damage on forests or croplands [3,15], follow pest migration [15,16], and examine the movement of insect vectors of pathogens that cause human or plant disease [17,18]. Few studies have applied these tools to the study of insects that provide ecosystem services [10].

Pollination, the transfer of genetic material via pollen, is perhaps the most studied ecosystem service that derives from insect activity. Eighty-seven percent of all flowering plant species depend on animals to transfer pollen [19]. Humans directly depend on pollination for food production and economic activities, as 35% of crop species worldwide depend on pollinators [20]. Bees (Superfamily Apoidea) are the most important animal pollinators in the majority of geographic regions [20,21]. Unfortunately, their services are threatened by disturbances such as habitat loss, pesticide use, and the spread of pathogens and invasive species [22,23]. Thus, bees have become a model organism for studying how environmental disturbances impact the provisioning of ecosystem services [24].

Recognizing the contributions that remote sensing approaches can make to the study of pollination, the objectives of this paper are to: 1) review key remote sensing concepts and tools that have been applied to studying ecosystem services, particularly those with potential applications for pollination in agroforestry contexts, and 2) identify opportunities and challenges for new research on bees and pollination services. The review is aimed at improving how ecologists adapt existing and new remote sensing technology to the study of pollination services. Though we focus on bees, many of the concepts and approaches presented here are generalizable to other organisms and interactions, including other pollinators (e.g., other insects, birds, and bats), and other mobile ecosystem service providers.

Remote sensing and pollination services: A brief primer

Remote sensing in this review is defined as the science of acquiring, processing, and interpreting data obtained from detection of energy by radiometric sensors [16,25,26]. While many applications rely on sensors placed on satellites and aircraft, ground-based sensors [27] and telemetry [28] are also rapidly increasing in use and scientific value. Sensors can be passive or active in nature. Passive sensors measure energy that is reflected by or emitted from matter. Passive approaches include aerial photography and many classes of satellite image data, and have produced long-term records for ecosystem monitoring in the shortwave and thermal portions of the electromagnetic spectrum [29,30]. In contrast, active remote sensing instruments (e.g., radar and LiDAR; Light detection and ranging) emit pulses of radiation, then measure the amount and timing of the returned energy. Because the timing electronics of active sensors are highly sophisticated and can therefore resolve returns on the order of nanoseconds, the returns measured by these systems can often estimate the physical characteristics of multiple vertical layers of surfaces (e.g., canopy layers) within ecosystems [31,32].

Remote sensing is a rapidly developing science that spans many disciplines. The number of related tools has grown in both quantity and quality, and as the technology matures, these tools are also becoming more affordable and accessible. Remotely sensed data can be categorized based on spatial, temporal, and spectral resolution and data sources (terrestrial, aerial, or satellite sensors; Table 1). Several resources are available to guide ecologists in selecting data sources and applications [26,33,34].

Biotic pollination is provided by organisms like insects, birds, and mammals [21]. Because animal pollinators are so diverse, one critical step for applying remote sensing tools to the study of pollination is defining the appropriate proxies of the service supply, and/or demand of interest for each case (Fig. 1). Good proxies should be quantifiable, sensitive to landscape composition and configuration, temporally and spatially explicit, and scalable [35].

Remotely sensed measures of landscape composition and configuration are commonly used proxies for pollination supply. For example, proximity to forest and other natural areas is positively related to bee abundance and diversity and the provision of pollination services in many crop systems [36-38]. Land use intensity is another possible proxy of pollination service provision. The functional diversity of pollinators (defined as the differences in morphological or behavioral characteristics that determine how pollinators interact with the environment) decreases with increased land use intensity [39], and is correlated with crop yield and biodiversity maintenance [40-43]. In addition, habitat fragmentation can lead to changes at the genetic level [21] even in mobile organisms such as bees [44] and bats [45]. Landscape-mediated genetic effects could therefore impact the ability of a population to respond to disturbance, with associated feedbacks on community composition and pollination outcomes.

Ecosystem services by definition cannot exist outside of human demand [8], so proxies are used to identify where pollination is needed. Two example proxies are the spatial location and pollinator dependency of crops. In this case, the resultant human benefit is a function of biological pollinator dependence of the crop and the total yield or value of crops produced [46]. The presence of a diverse pollinator community may provide additional benefits to farmers, because a more diverse community of pollinators can service changes in farming practices due to market shifts or climate change [8].

Pollination service demand is also determined by the need for biodiversity maintenance, which sustains a wide range of ecosystem services [47]. Pollinator loss in turn triggers the loss of native pollinator-dependent plants [40], while increased bee functional diversity is correlated with plant persistence [41]. Plant genetic diversity may also increase with pollinator abundance [41]. In turn, biodiversity maintenance has implications for service feedbacks to food crops. Native forest, agroforestry, and silvopastoral systems can all contain high pollinator biodiversity that increase ecosystem service provision within farms [49,50].

Remote sensing applications related to the study of pollination services by bees

The use of remote sensing in ecology and entomology has been reviewed periodically [10,11,12,16,33], necessitated by the rapid progress in remote sensing technology and its applications. Here we focus on recent remote sensing developments and discuss their contributions to understanding the composition of bee populations and the outcome for pollination services.

Landscape characterization

One of the most common applications of remote sensing methods in ecology is to characterize 2-dimensional spatial patterns of land cover and land use at scales ranging from the field, to the landscape, to entire regions (Fig.2) [10,33]. This process typically involves assessing aerial photography or passive satellite imagery for temporal and spatial trends. Spatial scales of analysis range from the fine-grained (stand size and structure), to intermediate (habitat corridors and edges) and landscape levels (habitat or land use types and distributions within a preponderant type or matrix). Aerial photography, which has been available in the United States since the 1930s, is one of the most spatially and temporally complete records of landscape change [51]. It has played a critical role in quantifying human impacts on the landscape such as deforestation, reforestation, or afforestation [52,53], changing agricultural practices and land use [54], and urban encroachment [55]. Complementing these data is the ever growing suite of satellite data (e.g., those sensors listed in Table 1), enabling analyses of landscape change using a record of multispectral data reaching back to the early 1970's.

Landscape characterization is often central to studies of bees and pollination. Aerial photography and passive satellite imagery have been used to test hypotheses of the relationship between native habitat and bee population metrics. The broad spatial coverage of remotely sensed datasets also allows researchers to compare multiple spatial scales and identify the scale of bee response to habitat loss. This is critical for bee research because of the varying foraging ranges and dispersal abilities among bee species [56]. For example, one study used aerial photography and Landsat images to determine that small-scale isolation from forest fragments was not correlated with overall bee species richness and abundance in a tropical system [57]. Interestingly, however, the abundance of Meliponines (stingless bees), which have relatively small foraging ranges, did increase with higher proportion of forest cover at short distances (200-600 meters) from the sampling points [57].

Detection of individuals

For decades, ecologists have employed remotely sensed data to identify individual organisms or groups of individuals, especially plants. Aerial photography can be used to quantify the size classes and distributions of individual trees [58] and in some cases to identify trees to species based on color, size, shape, and texture [51]. Using more sophisticated imaging spectrometers capable of measuring hundreds of spectral bands, relationships may be established between individual tree spectral diversity and chemical properties, and as a result, the spectral tools to identify plants even within dense canopies are constantly improving [59].

One specific application to pollinators is the remote monitoring of non-native plant invasions [11,60]. Invasive plants can have positive, negative, or neutral impacts on native bee populations [61]. Non-native plant invasions are of particular interest to pollination research because they can affect the timing and type of floral resources available in an area. If invasive plants do not provide resources for bees, a positive feedback loop can result where the invasive plants increase competition with native plants and reduce the total floral resources available in a landscape. As the feedback continues, the abundance of native plant pollinators, particularly specialists, can be severely affected [62]. Therefore, remote sensing techniques for monitoring plant invasions can be of particular importance to understanding native pollination dynamics and trends.

Remote sensing applications for animals are more limited because of their smaller size and greater agility [25]. This is particularly true for mobile ecosystem service providers, which move within or between habitats [21]. Though rare, there have been studies using remote sensing to directly sense these organisms. Radar has been used for almost a century to locate individual organisms such as birds [63]. This tool can now also be used to identify characteristics of movement such as organism flight speed and height. Vertical-Looking Radar (VLR), which measures echoes sent back from a stationary vertical beam, can convey information about individuals such as size, shape, and wing-beat frequency [15].

Harmonic radar, which identifies the frequency of a diode, can be used for tagging and tracking of animals [16]. Tags can be light enough for use with medium-sized bees such as honey bees (*Apis mellifera)*. This has contributed to our understanding of how honey bees seek out resources, communicate resource locations, and navigate flight. For example, harmonic radar provided evidence for the "waggle dance": researchers tracked the movements of bees that performed the dance and subsequent foragers, finding that the direction and distance of floral resources were communicated using the dance [15]. Harmonic radar has also been used on beetles [16,64] and additional bee species [65]. Original limitations of this method, such as high cost, large size of the sensor, and difficulty of use, are rapidly subsiding as the technology improves.

Individuals are also tracked using radio telemetry, which is similar to harmonic radar but does not require a stationary radar unit or have a fixed detection distance [28]. Radio telemetry requires a battery-powered tag, so it has only recently been successfully employed for the study of insects, and can only be used on large bees such as bumble bees [66] and orchid bees [67]. These studies provide information on foraging distance, habitat use, and time of activity of the tagged individual, but are likely still influenced by the increased energy requirements of the individual due to tag weight.

In contrast, LiDAR has been used for population counts and information about movement of individuals without introducing observer bias. Bees can be trained to locate land mines for removal via odor detection, and LiDAR has been used as an effective off-site monitoring method to measure bee location and dwell time over potential mines. LiDAR can be used to detect bee density over time and space, and using a continuous-wave diode laser, can detect the unique wing-beat of the bees [68,69].

LiDAR data is also useful for directly sensing other pollinating organisms, such as bats. This tool has been used to make exact counts of stationary individuals, like brooding bats in a cave [70], and to measure movement of active individuals. By combining thermal imaging and ground-based LiDAR, Yang and colleagues [71] determined the flight path, velocity, and altitude of big grown bats in a forest plot. Improved methodology will expand the spatial and temporal scale of these experiments, and improve their applicability to understanding service provisioning by similar mobile organisms.

Biodiversity proxies and species habitat

Various aspects of biodiversity relate closely to ecosystem function [72], resilience [73], and ecosystem services [47]. Remote sensing methods can be used for detecting variables that serve as a proxy for biodiversity [25,26,74]. Proxies include biogeographic patterns, land cover, topography, vegetation indices, vertical and horizontal vegetation structure, weather events, plant functional traits, and plant chemistry [34].

Remotely sensed biodiversity proxies have improved significantly in recent years. LiDAR can be used to bridge the gap between grain and extent because it has a high spatial resolution and can measure variables from the individual to landscape level [32,75]. It can also complement the spectral variation hypothesis, which states that spectral heterogeneity of remotely sensed images can reveal landscape structure and complexity, and will signify more niches and therefore greater diversity [76,77]. Variables measured with LiDAR reveal vertical vegetation heterogeneity, including metrics such as the standard deviation of vegetation height [14]. This can be linked to biodiversity of animals within the vegetation, and has been tested on several animals, including arthropods such as spiders [14] and beetles [13,78].

Other studies link remote sensing to relevant ecological data to identify the current or potential habitat of a specific taxon [examples in 10,75,76,79]. Vierling *et al.* [75] outline a five-step process for incorporating remote sensing with habitat characteristics to predict population distributions. Common habitat characteristics derived using LiDAR and radar include vegetation height and canopy density described in 3-D. These variables can also predict certain details about the populations themselves. Hill *et al.* [80] demonstrated that avian habitat can be determined by remotely sensed vegetation structure, and that the body mass of one species in this study could be predicted to an accuracy of 2.1% based on the habitat data. LiDAR variables were also equally or more useful than variables gathered via fieldwork to predict body size of beetles [13] and occurrence of spider species [14].

Habitat suitability models predict potential habitat for organisms based on habitat requirements [81]. These models have been particularly important for predicting the movement of invasive species, like the invasive Africanized honey bee, which may compete for resources and disrupt specialist plant-pollinator mutualisms [82]. A model using 40 data layers, including MODIS (Moderate Resolution Imaging Spectroradiometer) land cover and phenology products, was used to show current Africanized honey bee distribution and predict northward movement in the future [83].

Ecological processes

The temporal and spectral properties of remote sensing data are increasingly useful for deriving information on ecological processes (such as photosynthesis, phenology, and plant stress) that occur within a landscape. Derivations of primary productivity can be applied to the study of invertebrates, particularly to understand the distribution of insect herbivores on crops and disease vectors [12]. These data are now available at high spatial and temporal scales [84].

Some studies have focused on estimating invertebrate diversity. For example, Levanoni *et al.* [85] used the normalized difference vegetation index (NDVI) to predict butterfly diversity in a mountainous Mediterranean climate. It is interesting to note that it was not the net primary productivity, but the spatial heterogeneity of productivity, that predicted butterfly richness along the elevation gradient. Because butterflies, like bees, are highly mobile insects and important pollinators and biodiversity indicators, this study demonstrates potential for the use of these variables for other pollinator studies.

Other work has related remotely sensed vegetation phenological assessments to arthropod ecology. For example, remotely-sensed phenology data from MODIS was used to measure the impact of climate change and urbanization on the equilibrium range of Africanized and European honey bees [83,86]. The greening and browning of leaves (as quantified using MODIS NDVI, enhanced vegetation index, leaf area index, and fraction of photosynthetically active radiation products) have been found to coincide with a critical blooming period for the honeybee life cycle. These variables, compared with hive weight, showed resources available in the environment for Africanized bees and enabled researchers to make current and future range maps [86]. Multitemporal remote sensing data can also be highly useful for tracking plant fruiting and flowering phases [see 26,87], which could help quantify temporal and spatial availability of resources for pollinators. As multitemporal remote sensing datasets and analysis procedures are becoming increasingly available and affordable [2], they will be more valuable to ecologists interested in pollination services.

The future of remote sensing and bees: new frontiers for pollination service research

Remote sensing tools have potential for new applications to research of bees and pollination services (Table 1). We highlight opportunities for improved landscape characterization, detection of individuals, invasive species detection, habitat quality and heterogeneity, phenology, and pollination events. In addition, we discuss prospective improvements in the study of pollination demand and outcomes, such as biodiversity maintenance and crop production.

Landscape characterization

Although landscape characterization has produced useful hypotheses about bee populations and pollination services, there are several ways that remote sensing techniques may further improve our understanding of these topics across landscapes. New studies could expand the analysis of bee response to landscape change by including different study regions, thematic resolution, and measurements of bee response.

Remotely sensed data hold great potential for expanding bee research geographically.

The majority of bee research has taken place in few geographic regions, and mostly limited to land uses that are heavily altered by humans [24]. Future research should focus on how bee populations respond to moderate land use changes and in disproportionately understudied areas, such as the tropics [88]. Though remotely sensed data may be more abundant in developed regions of the world, it also allows for cost-efficient research in areas that have historically been understudied or difficult to access.

Remote sensing also allows researchers to match scales of grain and extent with field data. Mismatched scale can mask interesting relationships, particularly in the case of insect habitat [56,89]. Previous bee research has demonstrated non-intuitive multi-scale responses of bee populations to landscape change [56,57]. New studies should focus on how pressures from the patch to regional scales can impact bee populations, and if and how these variables interact.

Increased temporal, spatial, and spectral resolution of sensors are allowing for greater thematic resolution in land cover characterization while maintaining acceptable levels of mapping accuracy. Maps based on coarse imagery often cannot resolve characteristics critical to bee habitat, such as patchy floral resources and nesting areas. Improved distinction of land uses may improve predictions of bee populations [46]. In existing work, there is little distinction given between types of habitat bees may utilize. Distinguishing among types of forest based on forest age, species composition, or structure may change our understanding of bee response to landscape change. Among human-dominated land uses, separating crop areas from hedgerows, weedy, or fallow areas may better demonstrate resources available to bees.

One of the most important advancements for improving the mapping of pollination services will be understanding how functional traits determine organism response to landscape change. Some ecosystem service work is moving from species-level measurements to emphasizing guild traits that are critical to ecosystem function (Abelleira *et al.*, in review). Plant functional traits are poor predictors of bee abundance, yet good predictors of bee assemblage and structure [90]. While different species are correlated to different plant trait predictors, there is still a paucity of research on which traits are important and why. Bee functional traits such as body size, sociality, nest construction, feeding strategy, and habitat specialization can determine the response to landscape change, as well as the effect on pollination services [42].

Detection of individuals

Recent work has emphasized how certain bee behaviors are functional traits that can influence pollination services. For example, bee communication can impact their foraging range and resource selection. Though we have evidence linking bee size to foraging distance [91], estimates still vary, even among well-studied species. Harmonic radar or radio tracking tags on large to medium-sized bees (other than the well-studied honey bee) could help improve records of foraging range and improve our understanding of the relationship between flight distances and easily measured morphological traits. In addition, harmonic radar might be used to monitor behaviors such as habitat preference and nesting location, particularly for rare species where little data is currently available. This could contribute to our understanding of how bees perceive landscapes, and in turn affected by habitat changes.

Invasive species

One of the biggest threats to bee conservation is the introduction of invasive species [22,82,92]. The spread of exotic honey bees may disrupt mutualistic networks and have implications for the persistence and stability of pollination services in the future [82]. Studies have recorded negative impacts on native bee species, but have also observed an increase in pollination services in areas invaded by feral honey bees [62,92]. In contrast, native bees are more effective pollinators than honey bees in many agricultural crops globally [93]. While past studies have focused on potential habitat of Africanized bees [83,86], future work should combine local data on bee fauna with datasets on the spatial distribution of domestic honeybees.

Remote sensing methods present researchers with the opportunity to follow the spread of invasive plant species through time across a wide range of spatial scales, and should be used to understand the impact of invasive plant dispersal on bee populations and pollination of native plants or crops. Negative impacts of plant invasion on native bees and plants can be direct, such as competition for floral resources, or indirect, though the introduction of parasites and disease. Tracking of invasive plants holds significant promise for comparing to changes in native bee populations, particularly rare or highly specialized species.

Habitat quality and heterogeneity

Active remote sensing tools such as LiDAR and radar hold potential for measuring canopy architecture and associating these data with variation in faunal diversity of pollinators [32,75,89]. Few studies to date use LiDAR to understand arthropod populations, and these datasets are underutilized for assessing habitat quality for bees. The connection between vertical diversity of canopy height and biodiversity has been demonstrated in some taxa. The resource heterogeneity hypothesis, which states that ecosystems with more varied structure provide more niches and therefore higher species richness [89,94], could help to predict bee richness. More data is becoming available to study habitat heterogeneity variables in tropical and temperate latitudes using vertical forest structure metrics [95]. Despite connections between bee diversity and metrics of habitat structure such as plant height [96], no studies have yet attempted to test hypotheses such as these with bee population metrics over multiple ecosystems.

Active sensing methods can also be used to predict bee foraging and nesting. The radiation penetration rate at different stages of forest canopy openness, combined with collections of various arthropod indicator taxa, show that open canopies can have more indicator species than transition or closed forest, including species of bees and wasps [97]. LiDAR can be used to derive temporal variation in insolation values across the full continuum of 3-D canopy locations. Because bee foraging rates respond to changes in temperature and insolation, such 3-D maps may help predict bee foraging activity. New studies should focus on how the spatial distribution of solar radiation in forest, agroforestry or agricultural land uses impact pollination services by bees.

Bees nest in various substrates, including soil, pithy stems, and wood cavities (Fig. 2). In the tropics, increased tree diameter is positively related to the presence of stingless bee nests [98]. LiDAR-derived maps of tree basal area and tree height may help predict tree age and the presence of habitat for cavity-nesting bees. Prediction of tree snags and cavities using LiDAR [as in 99] may also provide avenues for assessing the availability of nesting habitat for bees and other pollinators.

Ecological processes

Time series of remotely sensed data may provide new insights on how plant phenology affects bee diversity and foraging activity. The spatial and temporal availability of flowering plants is related to availability of resources for bees in a number of habitats. Multitemporal remote sensing data of land surface phenology and productivity proxies can be linked to phenological events such as budbreak, full leaf expansion, flowering, and onset of senescence (Fig. 3) [100]. However, no models have used remotely sensed phenology to predict native bee distributions [83]. The improved spatiotemporal resolution of orbiting and ground-based sensors [101] as well as improved methods for analyzing these data [102] will improve knowledge about the relationship between phenology and bee species distribution and activity.

Terrestrial laser scanners and other ground-based radiometers also hold potential for future advances in pollination service research. Functional trait research can be combined with remotely sensed data to study the relationship between plant structure and function [100,103]. Terrestrial LiDAR shows promise for deriving of plant physiological parameters such as foliar chlorophyll [103], nitrogen content [104], water status [105], and photoprotection [4]. Terrestrial lasers and passive narrow-band radiometers may be deployed to detect signs of plant stress [4,106], pointing to opportunities for exploring potential impacts of plant stressors via changes in floral rewards for pollinators and pollinator visitation.

Pollination events

While studies have shown a direct link between the composition and behavior of bee populations to the provisioning of pollination services, it can be tedious to measure the outcome in terms of plant reproduction. A promising future application of remotely sensed data is thus the measurement of visitation and crop production to better quantify the efficiency of pollination. While several field-level methods exist to quantify yield quantity and quality, remote sensing provides opportunities for broad-scale data to be collected that are fine-grained and spatially explicit. For example, data from high resolution passive commercial sensors can be used to remotely quantify crop production variables within farms [107], which could be compared to variables such as bee visitation, solar radiation and landscape context.

Bee visitation does not always result in pollination, but pollination biologists often use visitation as a proxy for service provision. There are several issues with visitation observations: the observer's movement or physical presence could influence bee visitation, researchers may cause disturbances in systems where flowers are easily damaged, and observations are limited spatially and temporally. Automated imaging and classification may provide an alternative method for observing bee visitation, and therefore hold great potential for understanding pollination services (Fig. 4). The fine (mm- to cm-scale) scale of observation enabled by TLS can detect the 3-D presence of aerial insects, such as mosquitoes, in the environment (Vierling et al., unpublished data). TLS also holds opportunities for comparing bee visitation with environmental variables such as microclimate and landscape context, particularly as automated scanning approaches become more common [see 108].

Remote sensing can also improve our ability to map pollination service demand. Mapping crop production via land use has been done for systems where there is sufficient information on plant-pollinator relationships and crop dependence. For example, GIS-based models are designed with cells that can be given attributes such as potential habitat or pollination dependence [46,109]. Understanding the importance of bee pollination for biodiversity has historically been more challenging. Remote sensing offers tools for approximating biodiversity in a region, scaling-up local measurements of dependence on pollination services, and quantifying the spatial demand for biodiversity services.

Challenges for future research

Data Selection

Choosing the appropriate remotely sensing tool or data is one of the biggest challenges for researchers who are not experts in the field. Data widely vary in availability. For example, Landsat data from multiple decades are easily downloadable at little to no cost [11]. On the other hand, the spatial and temporal resolution of Landsat data may be too coarse to capture the variables of interest to pollination. More advanced data such as those derived from LiDAR have only recently become available, and are especially challenging to obtain in less developed regions of the world [11,12].

Tradeoffs also exist among the spectral, spatial, and temporal resolution of data [100]. In some cases, high resolution does not equate to better data. For example, it can be more difficult to assess spectral heterogeneity as a proxy for species diversity using hyperspatial data because of the noise created due to shadows [74,100]. Higher resolution may also result in higher cost or lower availability relative to the benefit to the study. Collaboration between ecologists and remote sensing experts must advance with the technology in order to ensure that studies take full advantage of these new tools.

Data analysis and interpretation

Analytical challenges may also impede ecologists who are not experienced with the large datasets or corresponding software involved in remote sensing work. Many ecological studies lack explanation on the method used to integrate these data. This includes omission of metadata, data processing methods, description of statistical analysis, and uncertainty [10]. These issues can be exacerbated by lack of training and integration within ecological studies that utilize remote sensing, and could be improved by better collaboration among disciplinary experts [11].

It is also critical to distinguish correlating variables in the analysis of habitat suitability models [81]. For example, NDVI and land cover are related to climate at regional scales. Remote sensing data have the greatest benefit when information is generated that is distinct from climate or other codependent variables. To avoid issues due to codependent variables, researchers must clarify terminology, define the roles of variables a priori, and be specific about model goals in order [81].

Scaling challenges

One of the greatest challenges for researchers concerned with ecosystem services is potential scale mismatches among service supply, demand, and human decision-making, such as policy implementation [35]. This is one of the core issues that has given rise to the development of ecosystem service mapping and modeling. Spatially explicit models such as the Natural Capital Project's InVEST Crop Pollination Model have been used to map services based on what is known about bee habitat and foraging, with variable success [46,109].

There are various challenges that limit generalizability of these models. First, pollination services are locally provided, but the service providers (i.e., bees) are impacted by variables from the local and patch up to the landscape and regional scales [24,36,37]. These variables may not be independent, and may thus interact across scales. The scaling-up of services provision also depends on clear definition and understanding of variables being measured. This is made more difficult in the case of pollination services because there is a lack of basic ecological data on bee behaviors that are critical to their service, such as foraging, nesting, and seasonality of behavior [46]. The temporal mismatch between ecological field study and availability of new remote sensing images can also present challenges [11]. Flowering phenology and visitation rates can vary on scales of days to weeks, so time lags might hide important ecological relationships.

Lack of ecological data

More ecological data about plant-pollinator relationships will improve remote sensing-based approaches to understand the location and timing of pollination services. This barrier is greatest in understudied regions of the world, such as the Neotropics [88]. It is estimated that only one-third of bee species in the Neotropics have been named [92]. The lack of data on species richness and diversity, taxonomy, distribution, and ecology of bees in these regions limits our ability to understand pollination services. Furthermore, pollination relationships are often poorly understood, even for some common wild plants and crops [22]. Researchers need to expand the range of organisms, landscapes, and ecosystems of pollination studies to better understand local to global impacts of changes in bee populations. Doing so will assist in understanding the varying impacts of remotely sensed estimates of habitat loss due to deforestation, agricultural intensification, and the spread of exotic species on pollination services in understudied regions of the planet.

Conclusion

There are burgeoning opportunities for ecologists interested in using remote sensing methods to improve our understanding of bee (and other pollinator) populations, floral resources, and the resultant effects on pollination service provision. The most important step towards applying new remote sensing technology to these studies is improved collaboration of experts from both fields. With cooperation at every step of the research process, from question-formulation to analysis and interpretation of results, remote sensing approaches stand to improve our understanding of pollination service provisioning. Resultant maps will in turn allow for better interpretation at multiple scales to support improved pollination service management.

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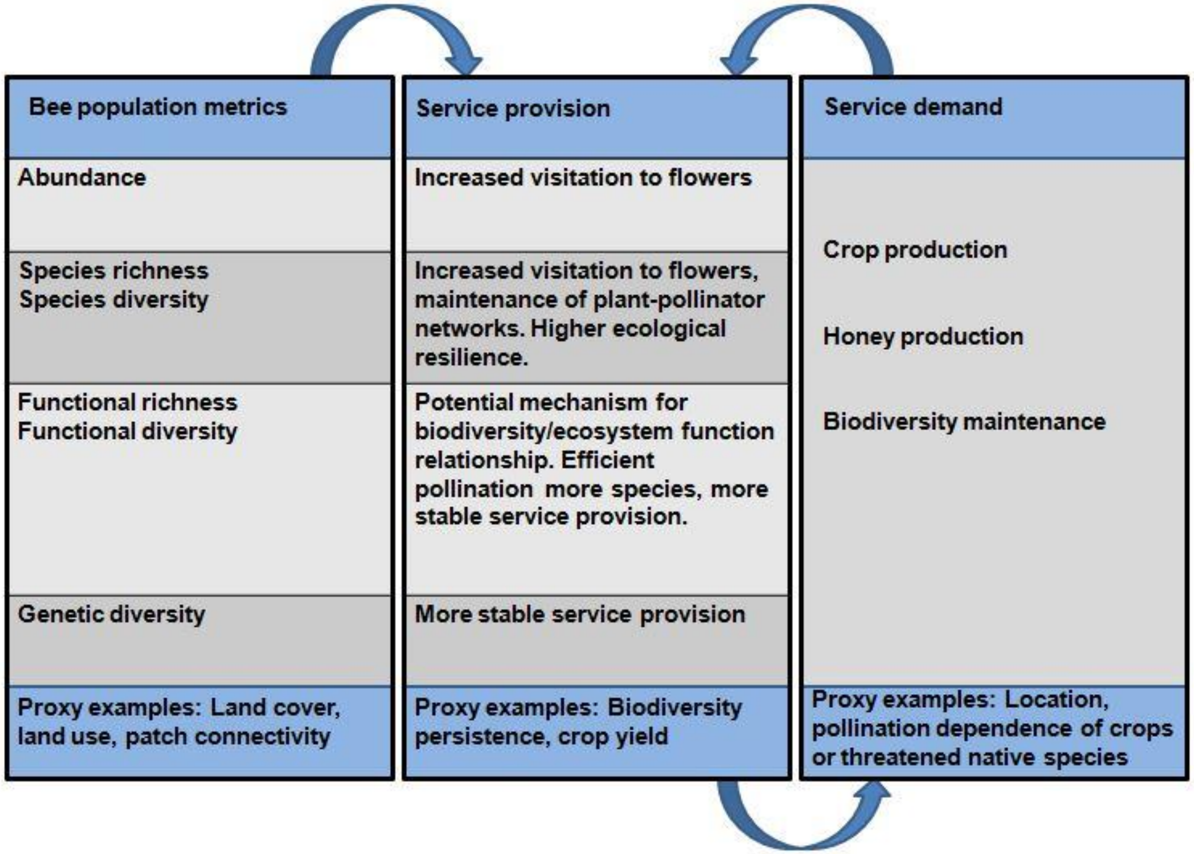
Table 1. Remote sensing tools and potential use for bee studies. Abbreviations: a. Satellite Pour l'Observation de la Terre, b. Advanced Spaceborne Thermal Emission and Reflection Radiometer, c. Moderate Imaging Spectroradiometer, d. Compact High Resolution Imaging Spectrometer, e. Advanced Very-High Resolution Radiometer, f. Scanning LiDAR Imager of Canopies by Echo Recovery, g. Laser Vegetation Imaging Sensor, h. Vertical Looking Radar, i. Side Looking Radar

RS Category	RS Method	Data types	Potential sensors	Established variables	Potential uses in bee studies
Passive Sensors	Aerial photography	2-Dimensional	Photo cameras	Landscape characterization Change over time	More thematically resolute land uses Phenology (if high temporal resolution)
	Satellite imagery	Multi spectral	Landsat TM (7 bands), ETM + (8 bands) SPOT[a] (4-5 bands) ASTER[b] (4-6 bands) MODIS[c]	Meteorological observations Landscape characterization Phenology (esp. high temporal resolution) Plant productivity Plant biochemistry	Model current or potential bee species habitat Map phenology, phenological diversity of a region
		Hyper spectral	CHRIS[d] (up to 63 bands) Hyperion (220 bands)	Meteorological observations Landscape characterization Phenology (esp. high temporal resolution) Species composition Plant productivity and biochemistry	Model current or potential bee species habitat Map phenology, phenological diversity of a region
		High spatial resolution	RapidEye (5m) IKONOS (<1m) Quickbird (<1m) Worldview (<1m)	Fine-scale landscape characteristics Identifying individuals	Certain plant species may be linked to bee species or guilds
		High temporal resolution	SPOT (4-5 days) MODIS (1-2 days) AVHRR[f]e(daily)	Demonstrating change over time	Map phenology, phenological diversity of a region
Active sensors	Airborne lidar and radar	Multi-level, high spatial resolution	SLICER[f], LVIS[g] (1-10m) VLR[h] radar, SLR[i] radar	Landscape characterization 3D structure characterization Crop production Identifying individuals	More thematically resolute land uses Map nesting habitat, small resource patches Map canopy openness (lightscape) for foraging activity Map pollination services via crop yield
	Harmonic radar			Tracking individuals Determining characteristics of movement 3D Vegetation structure	Radar tags on diverse bee guilds for FT such as foraging, communication, and nesting. Understand bee perception of habitat (connectivity)
	Terrestrial lasers	High spatial, temporal resolution	Mobile Static	Physical and biophysical characteristics of vegetation Identifying individuals	Monitor bee visitation Quality/quantity of crop production



Bee population metrics	Service provision	Service demand
Abundance	Increased visitation to flowers	Crop production Honey production Biodiversity maintenance
Species richness Species diversity	Increased visitation to flowers, maintenance of plant-pollinator networks. Higher ecological resilience.	
Functional richness Functional diversity	Potential mechanism for biodiversity/ecosystem function relationship. Efficient pollination more species, more stable service provision.	
Genetic diversity	More stable service provision	
Proxy examples: Land cover, land use, patch connectivity	Proxy examples: Biodiversity persistence, crop yield	Proxy examples: Location, pollination dependence of crops or threatened native species

Figure 1. Conceptual model of pollination service flow that includes supply (measured via bee population metrics), service, and demand. Several bee population measurements are predictors of pollination, but must be matched to a demand to represent a service. See [35] for a more general model of service supply and demand. Evidence for link between bee population metrics and service provision in [40-43,110-112].

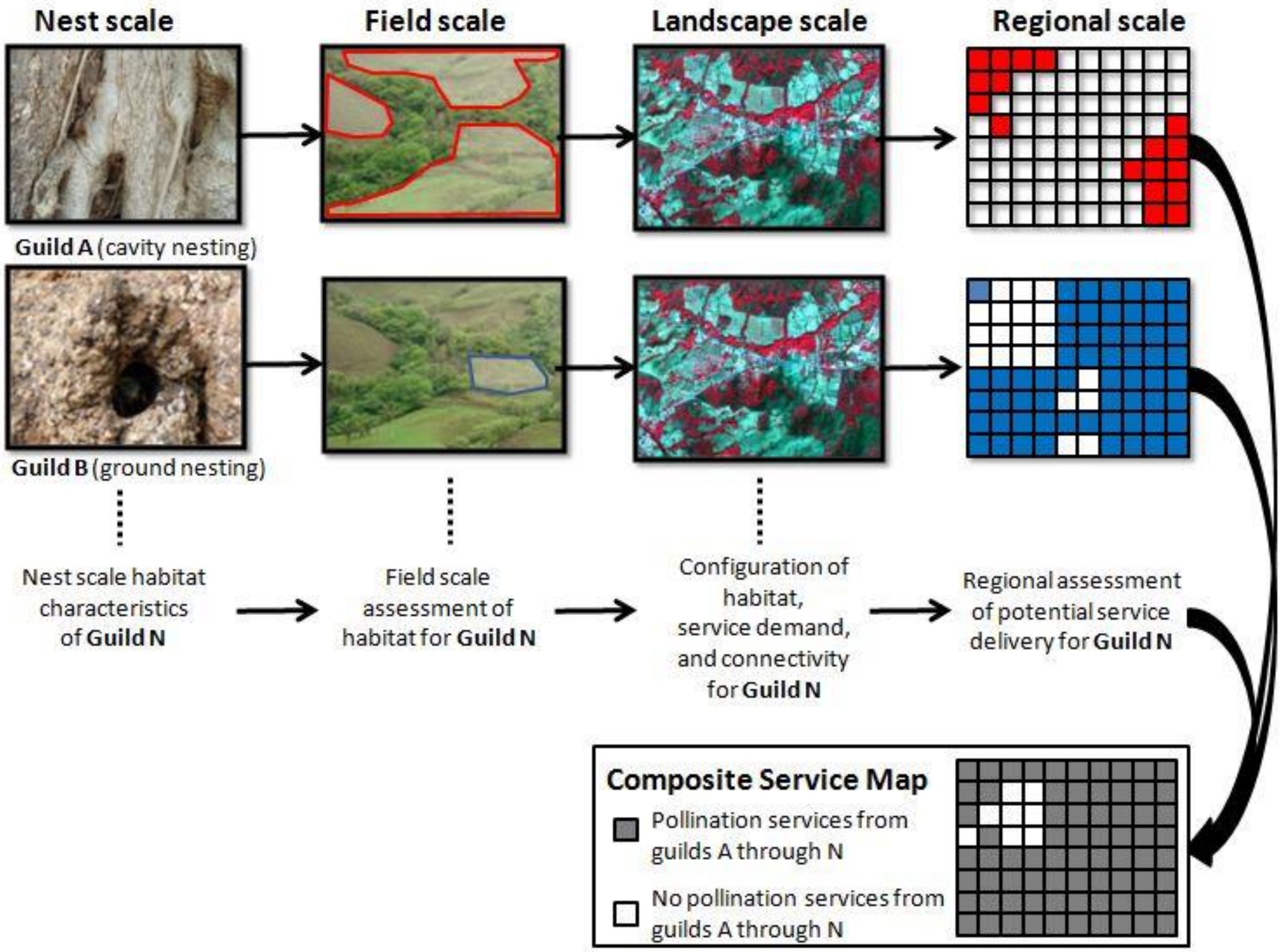


Figure 2. Example of scales of data used to understand ecosystem services. Pollination services from bees are used as an example. The final product in this case is a regional map of areas with pollination service provision based on service demand in the landscape and habitat availability from guilds A through N. The final map shows areas of service (grey) and paucity (white) when all maps are layered together.

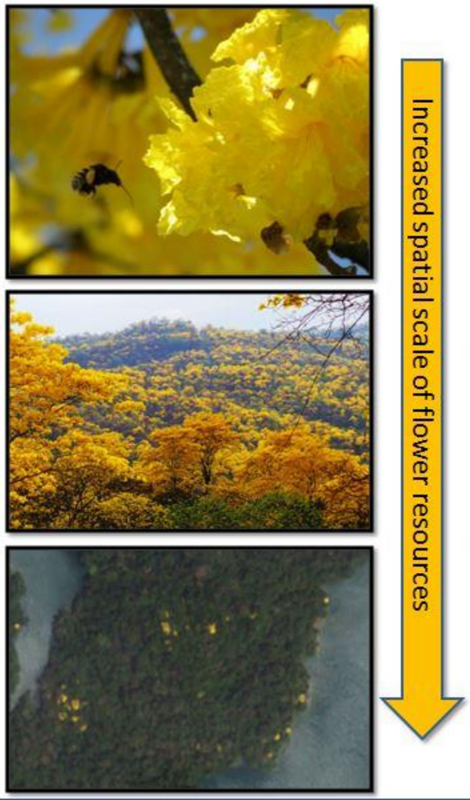


Figure 3. Remotely sensed data can be used to map flowering events across landscapes that sustain pollinators. This example shows the mass flowering phenology of the tropical tree *Tabebuia guayacan* at (top) the flower scale, visited by a bee, (center) the landscape scale using oblique digital photography, and (bottom) broader scales using high spatial resolution satellite imagery [see also 87]. This species is pollinated by medium to large bees [113]. *Top photo credit: Olga Berrio. Bottom image credit: Digital Globe and NASA*

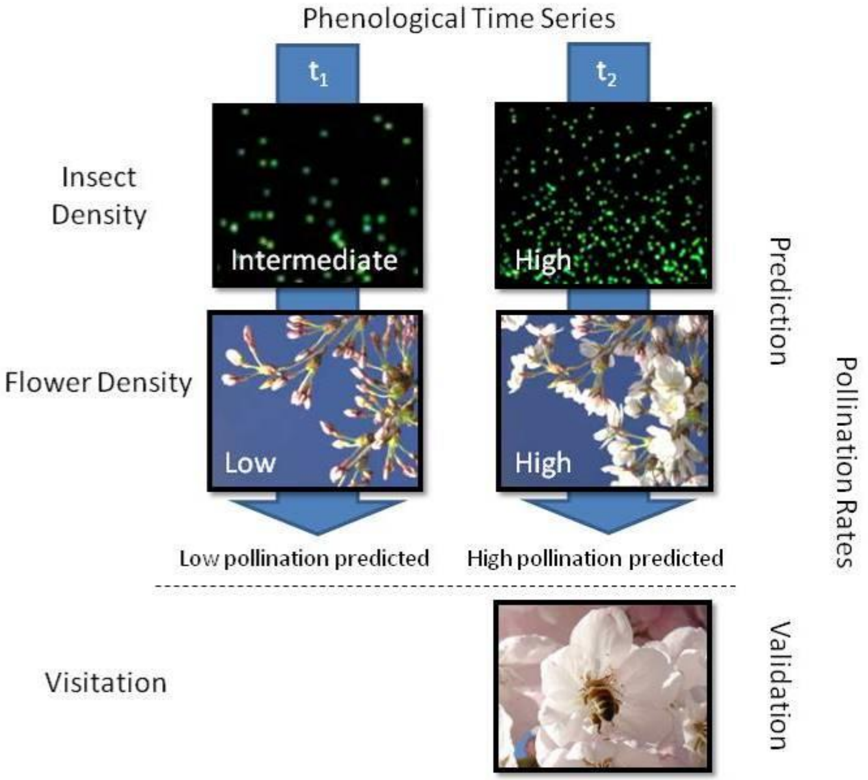


Figure 4. Fine-scale, multitemporal remote sensing approaches to capture details of pollinator density, flowering density, and pollination events through time. Remotely sensed data of pollinator density near plants (top panel) using automated imaging and classification methodologies may be combined with imagery on flowering phenology (middle panel) to predict visitation rates. Predicted visitation rates can be validated at individual flowers using digital cameras (bottom panel) [114].

Chapter 5: Spatial Scaling-Up of Functional Traits for Ecosystem Services: Concepts and Methods

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Summary

1. Ecosystem service based approaches to land management need an accurate understanding of how land cover change influences biota and ecosystem processes. Current understanding posits that these relationships are best understood through functional traits rather than land cover alone or taxonomic classifications.
2. Functional trait research occurs at many spatial scales, applying multiple methods to quantify patterns in trait variation in order to link traits to ecosystem services provisioning. In this paper, we review concepts and methods to scale-up plant and animal functional trait composition across spatial scales that cover the range of individuals, species, communities, and landscapes with the goal of assessing biotic influences on ecosystem processes and services.
3. First, we synthesize current knowledge on the sources of variability that need be considered for capturing effect functional traits from local to regional spatial scales. Second, we discuss three methodological approaches that can be used to scale-up local functional trait composition to regional scales – those are, biophysical gradients, remote sensing, and hybrid methods.
4. Remote sensing approaches are emphasized, as recent technological developments have significantly improved their capacity to map functional trait variation at the regional scale. We illustrate their application using a case study to examine functional links of land cover change, ecosystem fluxes, and ecosystem service policy in an intensely human-modified tropical region.
5. We end our review by providing a brief outlook for further application and development of these methods. This review narrows the gap between ecological knowledge and ecosystem service assessments with the development of tools for planning and improving ecosystem service management.

Keywords Costa Rica, effect functional traits, ecosystem processes, human-modified regions, land cover change, remote sensing.

Introduction

The functional traits of organisms, such as morphology and behavior, can vary substantially across time and space in response to climatic variation and environmental gradients (McGill et al. 2006; Suding et al. 2008). The resulting communities modulate ecosystem processes through functional traits that occur at the individual organism level, termed effect functional traits (Lavorel & Garnier 2002; Violle et al. 2007). The effect trait composition of communities is altered by anthropogenic land cover change and this can impact the provision of ecosystem services to humans (Díaz et al. 2007; Laliberté et al. 2010). Evaluation of ecosystem service policy and management requires understanding the consequences of land cover change on ecosystem processes and dependent ecosystem services at regional scales (*sensu* Forman & Godron 1986; Chazdon 2008; Daily et al. 2009). To this end, functional trait approaches have the potential to be more accurate than species based approaches due to the continuous nature of functional traits and the more direct link between traits and processes (McGill et al. 2006; Westoby & Wright 2006). Nevertheless, we currently lack consensus on how to estimate functional trait variation at broad spatial scales relevant to land use planning and policymaking. In this paper, our main goal is to review concepts and methods for scaling local plot-scale effect functional trait composition to regional scales relevant to ecosystem service management (Fig. 1).

Traditionally, methods for assessing the impact of land cover change on ecosystem services rely on correlating vegetation type with ecosystem processes (Daily et al. 2009). For example, in the Amazon basin change from forest to pasture vegetation affects local water fluxes by modifying interception and transpiration (Foley et al. 2003). These local changes can be scaled-up to basin-wide scale vis-à-vis vegetation structure to assess effects on ecosystem services such as flood control (Foley et al. 2007). However, this approach is limited because it does not incorporate the fine-scale functional trait variation that occurs within vegetation types, which can constitute up to 75% of the variation in trait values (Kattge et al. 2011). For instance, individual level variation in effect traits, such as tree size and leaf area, can significantly affect interception and transpiration water fluxes in forest vegetation (Meinzer et al. 2005; Park & Cameron 2008). Coarse classifications like these that lump heterogeneous forest communities into broad vegetation types potentially miss important fine-resolution trait variation and could result in inaccuracies when inferring changes at broad spatial scales. In addition, species composition may change but functional trait composition may not, or vice-versa, within a given vegetation type due to trait variation at the individual, species, and community levels (Albert et al. 2010; Messier, McGill & Lechowicz 2010). Consequently, vegetation classifications that are based on pure taxonomic or structural composition may miss the effect trait variation that drives ecosystem processes. Furthermore, vegetation classifications may be of limited utility when the ecosystem processes of interest are dependent on highly mobile organisms that are influenced by landscape structure.

Current methods aim to resolve these issues by focusing on metrics of effect functional traits, such as the community-weighted mean (CWM) or functional diversity indices, rather than vegetation types or species compositions (Lavorel & Garnier 2002; Díaz et al. 2007). These metrics can be related to the ecosystem processes of interest based on experimental data gathered at local plot scale, and subsequently to dependent ecosystem services according to the values placed on ecosystem properties or fluxes by stakeholders. For example, the CWM of vegetative height and leaf nitrogen content are related to biomass production, which has high agronomic value for residents of the Alpine prairies (Lavorel et al. 2011). However, it may be unclear how functional trait and ecosystem process relationships behave as spatial scale is broadened (Violle et al. 2007). Moreover, it is questionable whether it is even possible to collect high-resolution functional trait data over broad areas with currently available methods (Van Bodegom et al. 2012). These concerns limit the adoption of functional trait approaches to quantify ecosystem processes at regional scales where ecosystem services are typically managed (Fig. 1; Daily et al. 2009; Fremier et al. 2013). A promising approach is the fine-resolution mapping of functional trait composition by the remote sensing of vegetation properties. Currently available remote sensing methods can offer a direct link between local functional trait variation and regional ecosystem service management because they are repeatable across time and space, and are capable of producing high-resolution data across broad areas (Fig. 1; Asner et al. 2011a). Although technological advances have improved the available array of remote sensing methods and their capabilities, their application to functional trait mapping at regional scales has not become widespread (Ustin & Gamon 2010).

To better understand how functional traits can be used to determine effects on ecosystem processes with the goal of assessing impacts on dependent ecosystem services, we review the current conceptual understanding of trait-based approaches and the existing methods to capture trait variation at broad spatial scales. Our objectives were to: 1) describe current assumptions for scaling-up effect functional traits, with emphasis on capturing the necessary sources of effect trait variation across spatial scales; and 2) review current approaches for scaling-up effect functional trait composition across space from plot to regional scales, with emphasis on remote sensing methods. We illustrate the applicability of some of these methods by utilizing a case study on how effect functional traits of organisms in two trophic levels (e.g., forest trees and bee pollinators) affect relevant ecosystem processes and services in a human-modified tropical region. We use our case study to highlight the methodological challenges to scaling-up functional traits from plot to regional scales, and discuss on-going developments with the ultimate goal of using functional traits to inform ecosystem service policy and management.

Capturing functional effect traits

Trait effects on ecosystem services

Current approaches that quantify the relationship between effect functional traits and ecosystem processes recognize three aspects of traits that affect ecosystem processes and thereby ecosystem services (*sensu* Díaz et al. 2007). The first aspect is based on the *biomass ratio hypothesis* and states that the CWM value of effect traits is the main driver of ecosystem properties or fluxes (Grime 1998; Lavorel & Garnier 2002). For both plants and animals, CWM values are estimated by plot-scale species abundance or biomass

(Lavorel et al. 2013). For plants, the CWM is usually the most relevant proxy for assessing trait effects on ecosystem processes (Díaz et al. 2007; Violle et al. 2007).

The second aspect is that the *functional trait diversity* of the community is representative of the complementarity effects of traits on ecosystem processes (Petchey & Gaston 2006; Cadotte, Carscadden & Mirotchnick 2011). Functional diversity is captured by indices of trait variation, such as evenness, divergence, and similarity (Hillebrand & Mathiessen 2009). Complementarity occurs when functional trait combinations enhance or modify ecosystem properties or fluxes. In plant communities, complementarity effects on ecosystem processes are context-dependent (e.g., varying by forest type or successional status; Paquette & Messier 2011; Lasky et al. 2014) and secondary to the effects of the CWM of traits (Díaz & Cabido 2001; Balvanera et al. 2006; Díaz et al. 2007). Functional trait diversity is potentially more important for ecosystem processes driven by higher trophic levels (Chapin et al. 2000; Cardinale et al. 2012). For example, a high diversity of pollinator traits is needed to satisfy all plant pollination mechanisms, and therefore trait diversity is a better indicator of pollination than a CWM (Fründ et al. 2013; Winfree 2013).

The third aspect applies in a few special context-dependent situations where one or very few species possess a special suite of traits, making them *biological engineers*. These unique species overwhelmingly drive ecosystem processes in spite of contributing little to the community species abundance or biomass (Jones, Lawton & Shachak 1994). For example, beaver construct dams that affect stream geomorphology and nutrient cycling (Naiman et al. 1994). In such cases, CWM or diversity indices can be poor indicators of ecosystem processes and a functional trait approach may not be as helpful as a more detailed study on an individual species (Díaz et al. 2007).

Sources of trait variation

Functional traits can vary across individuals, species, communities, and landscapes. A better understanding of the spatial scales at which most of the effect trait variation in these sources is found will improve the application of functional trait approaches to ecosystem services by allowing for more efficient allocation of sampling effort. Current approaches to scaling-up functional trait variation across spatial scales may rely on sampling species composition across land cover types and assigning effect trait values to each species according to published databases (Lavorel et al. 2008; Kattge et al. 2011; Kazakou et al. 2014). This approach may miss sources of trait variation that can affect ecosystem processes, such as variation across individuals of the same species and across species within the same communities (Baraloto et al. 2010; Messier et al. 2010). Although we cannot logistically measure all trait values across all ecological levels, some understanding of the magnitude of trait variation sources will reduce uncertainty when scaling from local plot-scale estimates of trait values to broader spatial scales.

Individuals and species

Within-species or intraspecific variation in functional trait values arises from microsite environmental variability and environmental gradients occurring across the geographical range of plant and animal populations (Albert et al. 2010; Bolnick et al. 2011; Violle et al. 2012). Intraspecific trait variation can rival that observed between species, or interspecific variation (Elias & Potvin 2003; Hulshoff & Swenson 2010; Messier et al. 2010; Ruiz & Potvin 2011). The degree of plant trait variation attributable to intra- versus interspecific sources can be species (Elias & Potvin 2003), system (e.g., plantation vs. natural forest; Ruiz & Potvin 2011), or trait dependent (Albert et al. 2010; Kattge et al. 2011; Kazakou et al. 2014).

Intraspecific variation in traits such as individual body size affects home or foraging range and resource use of mobile animals (Haskell, Ritchie & Olff 2002; Kuhn-Neto et al. 2009). For example, between colonies of the same species, climate and resource availability influence bee size and morphology, which determine floral resource use (Peat et al. 2005a; Peat, Tucker & Goulson 2005b). However, measuring the degree of variation attributable to intra- versus interspecific sources for mobile organisms is hampered by the inability to obtain a fully random sample using trapping methods (de Bello et al. 2011).

Communities and landscapes

Environmental gradients produced by soil properties, topography and climate drive functional trait variation across and within natural plant communities (Díaz, Cabido & Casanoves 1998; Cornwell & Ackerly 2009; Baraloto et al. 2012). This structuring has been shown to be less evident at small spatial scales within communities (≤100 m^2) due to founder effects and successional processes (Ackerly & Cornwell 2007; Swenson et al. 2007; Yang et al. 2014). Land cover change can disrupt the natural trait variation found within and across plant communities by altering land use history, successional status, landscape structure, and by species introductions (Fig. 2; Díaz et al. 1999; Adler et al. 2004; Leishman et al. 2007; Giraõ et al. 2007). For example, the functional trait composition and diversity of tropical secondary forests is strongly dependent on successional stage and previous land use intensity (Lebrija-Trejos et al. 2010; Lasky et al. 2014). When accounting for this effect, patterns can still emerge across environmental gradients constrained by similar land use history and successional stage. For example, the trait composition of tropical secondary forests in Mexico varies across successional stages according to climatic regime (dry vs. wet; Lohbeck et al. 2013). Similarly, the trait composition and diversity of early successional and mature tropical plant communities differ from each other yet vary predictably across landscapes of similar environment and land use history in Costa Rica (Mayfield et al. 2005; Mayfield, Ackerly & Daily 2006). However, there are no consistent patterns in the plant trait composition of secondary forests across landscapes of varying regional environmental conditions and land use history, and this is more so for trees than for understory plants (Mayfield et al. 2013).

Overlaying environmental gradients and land use history is the confounding effect of animals on plant trait composition, and vice versa. Multiple studies have shown that the functional trait composition of plants can be mediated by the functional diversity of organisms at higher trophic levels, and in turn, this can modulate the trait composition of plant and animal communities across the landscape (Naeem & Wright 2002; Suding et al. 2008; Cardinale et al. 2012). Pollinators and seed dispersers, which include a wide array of animal groups from insects (e.g., bees and beetles) to vertebrates (e.g., bats and birds), affect the trait composition of plant communities in ways that are beginning to be understood (Chazdon et al. 2003; Girañ et al. 2007). For example, given that trait composition of pollinators and seed dispersers is mostly determined by habitat suitability and landscape structure variables such as patch size and isolation (Lindenmayer et al. 2002; Liira et al. 2008; Tscharntke et al. 2008; Bommarco et al. 2010), landscape structure can eventually become an important driver of functional trait variation in sessile plants. Although the effects of landscape structure on tree species composition are not as evident as those of previous land use history (Chinea & Helmer 2003), landscape fragmentation that results in the loss of pollinator functional groups may eventually modify the functional trait composition and diversity of plant communities through species extirpations (Fig. 2; Girañ et al. 2007; Sutton & Morgan 2009).

Trait variation across scales

Although much research has quantified trait variation within specific ecological levels, less research has focused on how this variation is partitioned across multiple levels. Knowledge of how trait variation is partitioned across spatial scales and ecological levels of organization is important for the design of trait sampling schemes. For example, if 90% of the variation in traits occurs at the species level, then accounting for intraspecific variation across communities may not be necessary. Although variance partitioning across levels remains mostly unstudied in animals, natural trait variation appears to be partitioned similarly across intraspecific and interspecific sources in plants (Fig. 2; Albert et al. 2010; Hulshof & Swenson 2010; Messier et al. 2010). Accordingly, a higher degree of trait variation exists within natural communities (alpha diversity) than across communities (beta diversity) within a region because within community variation includes both intra- and interspecific sources (Ackerly & Cornwell 2007; De Bello et al. 2009; Messier et al. 2010; Kattge et al. 2011; Freschet et al. 2012).

Relatively less is known about how functional trait variation is partitioned across regions. This may be due to the method of using global database values that include unequal sampling schemes and sources of variation across sites to determine how trait variation is partitioned across fine to broad ecological levels (Freschet et al. 2012). Recently, Freschet et al. (2012) conducted balanced sampling to quantify the variation in selected traits (specific leaf area and leaf N content) nested at the level of communities, regions, and biomes. They found that most trait variation occurred within communities (~50%) and across biomes (~35%), whereas variation across communities within a biome was relatively low (~15%; Fig. 2). On the other hand, they found higher divergence (i.e., bimodality in trait value distribution) in traits across and within communities than across biomes, which was attributed to higher environmental heterogeneity and disturbances at the regional scale. This agrees with the findings of Willis et al. (2010) that show the steepness of environmental gradients within the spatial extent of interest, rather than the spatial scale itself, drives functional trait variation (Freschet et al. 2012). Thus, environmental gradients drive functional trait variation across all ecological levels and spatial scales, and natural or anthropogenic disturbances can act on any level or scale to counteract convergence in trait composition due to these gradients.

Influence of land cover change and introduced species on traits and implications for sampling

Whereas climate change affects the distribution of organisms at long time scales via trait responses to the environment (Suding et al. 2008), changes on effect traits are largely driven by land cover change that occurs at shorter time scales (Fig. 1; Foley et al. 2005; Daily et al. 2009). Across regions, increasing land use change and intensification have negative impacts on the functional trait diversity of plant and animal communities (Flynn et al. 2009; Laliberté et al. 2010). This can result in human-modified regions that have (1) high species dominance and high cross-community trait variation, and (2) heterogeneous landscape structure.

Species dominance and cross community trait variation

Species dominance within and across communities due to land cover change can result in high variation in trait composition across regions with contrasting levels of land cover change within a biome (Hillebrand, Bennet & Cadotte 2008). Land cover change can also result in the introduction of species possessing novel suites of traits for which there is no native analog (Leishman et al. 2007; Drenovsky et al. 2012). Some introduced species may become dominant under certain conditions (e.g., land use history or landscape fragmentation), which may lead to the emergence of novel community types (Hobbs et al. 2006; Abelleira 2010). Within the novel communities they dominate, introduced species may increase the magnitude of intra- vs. interspecific trait variation (Fig. 2; Hillebrand et al. 2008). In addition, managed systems, such as plantations, agriculture, and agroforestry, may perpetuate the dominance of introduced species, which can lead to higher trait variation sources across community types (natural versus managed systems) within a region. Thus, novel and managed communities introduced by land cover change may differ in functional trait composition from the original communities they replaced and increase the source of trait variation across communities relative to other sources within a region (Fig. 2; *see* Case Study *below*). Additionally, functional trait homogenization may occur in regions that have suffered extensive land conversion, and high rates of native species extirpations and species introductions (Olden et al. 2004). This homogenization can bring the mean trait values of heavily human-modified regions closer to the global mean for a given biome (Fig. 2). Thus, land cover change can potentially act to increase the variation in functional trait composition within a biome by increasing trait divergence across relatively natural and human-modified regions.

For the design of sampling schemes, quantifying intra-specific variation may be unnecessary for capturing trait effects on ecosystem processes. However, this variation can be of importance when one or few species dominate certain community types across environmental gradients (Hillebrand et al. 2008; Albert et al. 2011). In such cases, capturing the in-situ CWM is an appropriate integrator of the relevant intra-specific trait variation (Albert et al. 2011). The use of database values for dominant species may miss important intra-specific trait variation effects on ecosystem processes in regions where environmental gradients are steep and where few species dominate common and widespread community or land cover types (Hillebrand et al. 2008). In addition, since species that become dominants as the result of land cover change are usually introduced, database values from regions with different environmental conditions may assign inaccurate trait values (Drenovsky et al. 2012).

To account for variation across communities, sampling stratification by community types of varying successional status, land use history, or management intensity is necessary to capture the modification of effect functional traits by land cover change (Garnier et al. 2007). Considering the magnitude of other sources of variation (Fig. 2), sampling needs to be efficient at capturing cross-community variation without compromising other sources. One plot (e.g., ~500m^2 for forest tree communities) per site per community type (≥3 sites per community type) at selected points across the environmental gradient of interest can be enough to capture the necessary effect trait variation into CWM or trait diversity indices (Ackerly & Cornwell 2007; Lavorel et al. 2008; Messier et al. 2010). Dominant species (i.e., those contributing >80% of the CWM) should be adequately sampled as outlined by protocols (e.g., Cornelissen et al. 2003). For subordinate species (i.e., those contributing <20% of the CWM; Grime 1998; Pakeman & Quested 2007; Freschet et al. 2012) occurring in species-rich communities, such as old-growth or mature tropical secondary forests, sampling of one individual per species per plot per site is enough to capture the necessary effect trait variation (Baraloto et al. 2010). In plant communities exhibiting high species dominance and low species richness, database values may be appropriate to estimate effect traits of subordinate species but not of dominant ones (Pakeman & Quested 2007; Lavorel et al. 2008).

In the case of mobile animals, CWM and trait diversity indices are typically based on in-situ species abundance estimates across community types (Vandewalle et al. 2010). Measuring traits directly among the community being studied is often not possible due to logistical constraints. In such cases, traits can be inferred from phylogeny or published keys (Moretti et al. 2009; Vandewalle et al. 2010; Wray, Naeme & Elle 2014). This is more acceptable when trait diversity indices are used to infer ecosystem services, as the mean trait values in a community may differ from database values depending on variables such as climate and resource availability (Peat et al. 2005a).

Heterogeneous landscape structure

Landscape structure (i.e., the size, shape, arrangement, and distribution of different types of patches across the landscape) can modulate the functional trait effects on ecosystem processes captured at the plot scale. Increasing regional spatial extent adds landscape heterogeneity that may result in non-linear trait effects emerging across space (Fig. 3; Violle et al. 2007). For example, forest fragmentation increases canopy surface roughness and evaporative demand near forest edges, which can result in transpiration water fluxes deviating from predictions based on CWM values of tree traits, such as sapwood area or crown diameter (*see* Case Study *below*), in continuous forest environments (*purple line in* Fig. 3). However, since edge effects on transpiration fluxes penetrate into fragments as large as 100 ha and as far as 3 km from forest edges, these effects can be constrained at the regional scale by the degree of land use intensity and landscape fragmentation occurring within the study region (Herbst et al. 2007; Briant, Gond & Laurance 2010). In addition, as spatial extent increases, other regions with contrasting environmental conditions, land use histories, or landscape structures are included. This can also result in non-linear effect trait to spatial extent relationships since the effect of trait values on ecosystem processes in one region is not necessarily translated to another (De Deyn, Cornelissen & Bardgett 2008). These examples illustrate that plant trait effects on ecosystem processes may not be directly transferable or equivalent across regions with varying degrees of human modification.

At higher trophic levels, landscape structure can have greater influence on trait effects by affecting dispersal capacity of highly mobile organisms (Keitt, Urban & Milne 1997; Keitt 2009; Bommarco et al. 2010). In the case of plant pollinators and seed dispersers, local plot-scale effect trait composition may not matter as much as that of broader spatial scales because animals may visit unfavorable patches but not utilize them. Instead, the spatial scale of relevant effect trait composition for such processes is determined by the organism's mobility and foraging range (Fig. 3). For example, bee trait composition can display exponential effects on pollination as spatial extent increases up to their foraging distance because the proportion of native habitat within the foraging range is the main factor driving pollinator trait effects (Fig. 3; *see* Case Study *below*; Kremen et al. 2004; Kremen et al. 2007). Similarly, the effect of trait composition and diversity of birds and other vertebrates on seed dispersal may exhibit a sigmoidal relationship with increasing spatial extent because there may be a range of distances between patches at which dispersal is optimized (Fig. 3; Keitt et al. 1997). Whereas much research has shown that stratification for sampling plant traits is mainly determined by local scales of community types, which are constrained by regional land use history, more research is needed to clarify appropriate sampling methods for animal traits that need to explicitly consider stratification at spatial scales that cover landscape structure (*see* Case Study *below*; Lavorel et al. 2013). In both cases, changes in effect trait composition due to human modification can be better assessed by sampling methods that can directly account for trait variation across new community types and heterogeneous landscape structure, such as methods that rely on remote sensing technology.

Scaling-up trait composition

Trait-based ecosystem service assessments can be improved if the relevant local effect trait variation can be captured and appropriately scaled-up to regional scales (Daily et al. 2009; Lavorel et al. 2011). Eventually, dynamic vegetation models may be able to reproduce the distribution of effect traits after their response to climatic and environmental variation at a fine-resolution, but this is currently not a viable option (Suding et al. 2008; Van Bodegom et al. 2012). However, changes on effect traits due to land cover change need not be modeled after complex feedback dynamics that are designed to account for climate change if tools such as scenario modeling are used to assess how changes in traits affect ecosystem processes and dependent services (Fig. 1; Daily et al. 2009). If the goal is to observe the relative effect of having one land cover scenario versus another on ecosystem fluxes of interest in short time scales, the fine-resolution mapping of the current “snapshot” distribution of effect trait composition can suffice. Therefore, instead of using response trait-mediated maps of effect trait distribution, the mapping of effect trait composition by alternate approaches is a viable option. These involve (1) static statistical modeling based on trait to biophysical gradient relationships; (2) spatially explicit remote sensing of traits; and (3) a hybrid combination of these methods. Capturing regional trait variation by local plot sampling as previously discussed is required to varying degrees by all three alternatives. We review these three approaches but give emphasis to remote sensing methods because technological developments in this field offer a promising bridge to directly scale-up plot scale effect trait variation to regional spatial scales with high resolution (Fig. 1).

Biophysical gradients

Environmental conditions regulate functional trait assembly at local to regional scales in such a way that robust statistical relationships can be used to link local trait variation to regional biophysical gradients that modulate the environment (e.g., elevation and precipitation, topography and soil moisture; Cornwell & Ackerly 2009). For example, Swenson et al. (2011) produced maps of variation in maximum height, leaf N and P content, specific leaf area, seed mass, and wood density for the woody vegetation of the Americas. Their method consisted on the spatial interpolation of mean trait values collected from sampling points corresponding to grid cells distributed across biophysical gradients. At a grid cell resolution of 1° to 5°, they found that latitude, elevation, temperature, and precipitation were related to each trait with varying strength. These maps are unprecedented in their portrayal of trait variation at broad spatial extents.

However, this method is potentially limited in reproducing the variation needed for regional ecosystem service assessments because it does not incorporate variation in land cover type (e.g., stand age and land use history) and landscape structure. Remote sensing methods are particularly well suited at mapping variation in both land cover or vegetation types and, more recently, functional traits.

Remote sensing

Remote sensing methods offer opportunities for mapping functional trait variation at broad spatial extents with the advantage of being spatially explicit, extensive, and repeatable over time (Figs 1 and 4; Ustin & Gamon 2010; Homolová et al. 2013). Current limitations of remote sensing methods for mapping traits are (1) mostly restricted to sensing plant canopy traits, (2) low agreement in many cases between fine resolution in-situ measurements of functional traits and coarser remote sensing data, and (3) confounding factors that affect plant spectral properties such as vegetation architecture and soil background (Ollinger 2011; Homolová et al. 2013). Fusion of remotely-sensed data types, such as passive-optical (e.g., Landsat) with active (e.g., LiDAR) remote sensing, and technological developments of sensor spectral, directional, spatial, and temporal resolutions, can improve the detection of leaf to canopy spectral properties for the mapping of plant functional traits (Ustin & Gamon 2010; Ollinger 2011). Passive, optically-based remote sensing can be used to infer a wide range of vegetation spectral and biochemical properties while active remote sensing approaches are particularly useful for retrieving canopy and understory structural information. Here, we describe the passive optically-based remote sensing methods that may be used for mapping plant canopy functional traits and landscape structure, and the potential of active remote sensing methods to capture individual to plot-scale traits related to vegetation structure. In the case of animals, we show how the trait composition of animals can be inferred from remote sensing of landscape and vegetation structure.

Passive remote sensing

Passive optical remote sensing methods can be used for mapping discrete land cover classes, landscape structure, and plant functional types (Fig. 4; Ustin & Gamon 2010). Land cover or vegetation class delineations are derived from relatively low spatial resolution (e.g., 30 m) and broad extent digital imagery acquired by satellites by using a set of decision rules where each pixel is assigned to a class based on spectral reflectance properties and ancillary data such as topography. For example, some optical satellite sensors such as IKONOS and Worldview-2 have high enough spatial resolution to resolve forest successional status. Others, such as AVHRR and MODIS, are characterized by high temporal sampling, offering the temporal resolution to quantify leaf and flowering phenology (Fig. 4; Vieira et al. 2003; Kalacksa et al. 2007; White et al. 2009). Landsat data can be used for both successional and phenological studies because of its spatial and temporal resolution (e.g., Kennedy et al. 2012; Melaas, Friedl & Zhu 2013).

Aerial photography has been used at fine resolution to map tree species based on flowering events or on individual tree crown traits (Fig. 4; Valerie & Marie 2006). Tree crown diameter has been mapped with some success using multispectral aerial photography (Strand et al. 2006). Phenological variation and lack of contrast between over- and understory can prevent crown detection with this method, and needs further development for use in closed canopy conditions (Garrity et al. 2008). High-resolution aerial photography has been combined with satellite imagery (e.g., Quickbird) to estimate fruit crop size based on its relationship to palm crown diameter, which was mapped by individually delineating polygons (Jansen et al. 2008). The use of aerial photography for regional trait mapping is limited by its high cost and tradeoff with covered extent, and by the dearth of automated methods for image processing, interpretation, and analysis due to differing radiometric properties of each aerial remote sensing platform and image-to-image variation in illumination conditions (Morgan, Gergel & Coops 2010).

Most passive remote sensing methods can be divided by their use of empirical and physical approaches for the retrieval of plant functional traits (Homolová et al. 2013). Generally, plant traits cannot be directly retrieved from passive remotely sensed data but may be inferred by their relationship to canopy spectral properties using empirical or physical models based on statistical relationships or spectral processes, respectively (Gray & Song 2012; Homolová et al. 2013). Empirical and physical models may be used to estimate the spatial variation of similar traits, and may be used in tandem to facilitate or improve estimation of other traits. For example, leaf mass per area (LMA), which is related to phenology and drought resistance, has been estimated from remote sensing data using empirical and physical models, and may be used to estimate leaf dry matter content based on its relationship with other remotely sensed traits such as leaf area index (LAI) and canopy water content (Fig. 4; Colombo et al. 2008; Asner & Martin 2009).

Empirical remote sensing approaches use regression analysis to quantify functional relationships between field observations of traits and remotely sensed data. The statistical models are then used to predict trait values across broader spatial extents. Spectral vegetation indices (e.g.; normalized difference vegetation index or NDVI) are commonly used in these regressions to enhance sensitivity to canopy traits or properties. One of the most important limitations of empirical methods is that the regression relationships between remotely sensed data and field observations of traits can be time, site, and species specific, lack causality, and consequently often lack robustness and transferability across regions (Homolová et al. 2013). However, concurrent ground-based measurements of canopy properties, such as LAI, canopy height, and vegetation water content, coupled with sensors that capture information at different spatial resolution and extents (e.g., 1 m and >10 km^2 for airborne LiDAR, and 30 m and >10^4 km^2 for Landsat, respectively) can improve the scaling of local measurements to broader extents (Fig. 4; Anderson et al. 2004; Williams et al. 2008). For example, Gray and Song (2012) developed a model to map effective LAI using information of multiple sensors to address limitations related to both the tendency of spectral vegetation indices to saturate at moderate levels of LAI (~ 3) and the tradeoff between spatial and temporal resolutions in remotely sensed images. They generated daily maps of effective LAI at Landsat spatial resolution by combining spatial, spectral, and temporal information from IKONOS, Landsat, and MODIS satellite sensors, respectively (Fig. 4).

One of the main limitations of empirical approaches is that most widely available multispectral sensors sample only a few portions of the electromagnetic spectrum at bandwidths too wide to capture subtle spectral features that are important for the discrimination of plant functional traits (Ollinger 2011). This limitation may be addressed by the use of hyperspectral data, which contain a high number of contiguous, narrow spectral bands and can be used to derive leaf and canopy chemical properties (Fig. 4; Townsend et al. 2003; Malenovský et al. 2007). When hyperspectral data are used, the effects of soil background, illumination, albedo, or leaf water content may be reduced with spectral transformations to enhance absorption features in vegetation spectra (Schlerf et al. 2010). Also, the effects of canopy structure on leaf chemical data retrieval are difficult to quantify with regression analysis, yet a solution may be to combine empirical and physical modeling approaches. For example, Asner & Martin (2008) developed partial least squares regression (PLSR) models between leaf chemical properties and species leaf spectral data for the tropical forests of Australia. Subsequently, leaf spectral measurements were used in a radiative transfer model to simulate top-of-canopy reflectance (*see below*). Asner and Martin (2009) repeated the PLSR analysis at the canopy level in the forests of Hawaii using the simulated canopy reflectance to estimate leaf chemical traits (N, P, chlorophyll, carotenoid, & water content) and LMA.

Physical remote sensing approaches are based on radiative transfer models at the leaf and canopy levels (Malenovský et al. 2007). Radiative transfer models account for absorption and scattering processes based on leaf and canopy structure, and biochemistry to simulate leaf to canopy reflected or emitted optical spectral properties (Fig. 4; Baret & Buis 2008; Jacquemoud et al. 2009; Ollinger 2011). The coupling of leaf and canopy radiative transfer models allows the spectral and directional variation of canopy reflectance to be described as a function of leaf biochemistry and canopy structure. This inverse modeling potentially allows for the retrieval of fine-resolution plant functional traits from plot-scale to broader spatial extents (Colombo et al. 2008; Croft et al. 2013; Homolová et al. 2013). Coupling canopy, leaf, and soil models further improves the retrieval performance by imposing a strong spectral constraint on the inversion process, decreasing greatly the number of unknown variables while providing enhanced spectral consistency (Baret & Buis 2008; Jacquemoud et al. 2009). The main drawback of this approach is that inverse modeling has high uncertainty because model solutions are not unique. This is so because several combinations of canopy traits could lead to similar remotely sensed signals (Koetz et al. 2005). Using field data to help constrain the distribution and limits of the variables could improve the stability and reliability of solutions (Baret & Buis 2008).

Since radiative transfer models do not incorporate all known sources of variability in leaf spectra (Asner et al. 2011b), the retrieval by inversion is limited to those functional traits or structural properties that are directly involved in the modeled process, such as leaf or canopy chlorophyll and water content, and LMA (Baret & Buis 2008; Asner et al. 2011c; Homolová et al. 2013). To address this limitation, Asner and Martin (2008) developed leaf-to-canopy scaling of multiple leaf chemical properties and specific leaf area (SLA; inverse of LMA) of 162 humid tropical forest tree species by combining field-based leaf spectra and chemical data with PLSR analysis and radiative transfer models. In a subsequent study, Asner et al. (2011c) developed a scaling method of multiple leaf chemical components and LMA for the entire humid tropical forest biome, using a combination of a globally-distributed, consistently measured leaf spectral and chemical databases, along with canopy radiative transfer models, PLSR and high-frequency noise modeling. They showed that under conditions of varying canopy structure and spectral noise, the method consistently and accurately predicted chemical components and LMA using visible-to-shortwave infrared spectroscopy although improvements in sensing shortwave infrared (1300-2500 nm) bands could increase the accuracy of LMA estimates.

Active remote sensing

Active remote sensing methods, such as airborne LiDAR, are revolutionizing the study of vegetation structure from plot- to regional scales. For example, LiDAR has been used in conjunction with passive remote sensing satellite images to scale plot-estimated aboveground carbon stocks in forests to regional and global scale with high accuracy (Asner et al. 2011a; Baccini et al. 2012). Besides estimating aboveground biomass, LiDAR has also been used to map individual tree functional traits such as height and crown diameter (Fig. 4; Popescu, Wynne & Nelson 2003; Popescu & Wynne 2004; Koch, Hyder & Weinacker 2006; Falkowski et al. 2006; Popescu & Zhao 2008), and stand traits such as LAI and understory vegetation density (Riaño et al. 2004; Martinuzzi et al. 2009; Zhao & Popescu 2009). LiDAR typically underestimates tree height due to the possibility of returns missing the highest point of tree crowns, although the error remains constant (~0.15 m) and is mostly negligible for tall forest canopies (Asner et al. 2012). As with aerial photography, the sensing of tree crowns with LiDAR remains limited in closed canopy conditions (>50% cover), yet finer post-spacing of LiDAR returns (<1 m) may improve the sensing of this trait (Garrity et al. 2008; Falkowski et al. 2008). Coupled with passive sensors that can map leaf chemistry and phenology, LiDAR's potential to relate plot-scale structural properties, such as canopy height, crown diameter, and aboveground biomass, could facilitate the spatial scaling-up of multiple plant traits (Fig. 4; Zhao & Popescu 2009; Asner et al. 2011a; Gray & Song 2012).

Due to its accuracy in sensing forest structure across heterogeneous terrain, LiDAR can be used to map forest type, successional status, and potentially tree species diversity (Asner & Martin 2009; Castillo et al. 2012; Martinuzzi et al. 2013; Hernández et al. 2014). Recent analyses show promising links between plant structure and function that can be derived directly from combining the 3-dimensional location data of returned LiDAR pulses with return intensity, which can open new opportunities for fine-resolution mapping of leaf chlorophyll and N content, and photosynthetic performance (Eitel, Vierling & Long 2010, Eitel et al. 2011; Magney et al. 2014). Improvements in airborne and terrestrial LiDAR technology have increased the utility of these measurements in characterizing structural traits of low-stature ecosystems such as shrublands and tundra (Streutker & Glenn 2006; Vierling et al. 2012; Greaves et al. 2015). Other active remote sensing methods, such as satellite-based LiDAR (Lefsky et al. 2005), high-density laser scanning (Maltamo et al. 2004), and synthetic aperture radar (Santos et al. 2003) can be used to map forest canopy height yet their development lags behind compared to airborne LiDAR.

Remote sensing of animal traits

Remote sensing is useful for mapping the functional traits of animals because they move within and across landscapes depending on traits such as foraging range and dispersal abilities, which are related to landscape and vegetation structure (Leyequien et al. 2007; Pettorelli et al. 2014). High-resolution aerial photography and passive multispectral imagery are the most common tools used to determine variables related to horizontal landscape structure (Fig. 4; Bergen et al. 2009). For example, landscape structure variables such as matrix type, habitat area, and heterogeneity correlate with response traits measured in mobile organisms such as bee body size, foraging range, dispersal ability, sociality, and trophic level (Steffan-Dewenter et al. 2002; Jauker et al. 2014; Wray et al. 2014), beetle morphological trait diversity (Vandewalle et al. 2010), and bird and butterfly life history traits (Barbaro & van Halder 2009).

At more local spatial scales, leaf and flower phenology, and habitat vegetation structure are related to the distribution of animal functional traits across broad spatial extents. Remotely sensed phenological variables can be used to predict the spatial and temporal distribution of resources for functional groups of mobile organisms (Fig. 4). For example, the impact of climate change and urbanization on the range of Africanized honeybees was determined using leaf phenology from vegetation indices (e.g., NDVI) and LAI derived from the MODIS sensor (Nightingale et al. 2008; Jarnevich et al. 2014). When compared to hive weight, these variables correlated with the availability of resources for Africanized bees, effectively estimating their distribution (Nightengale et al. 2008).

Vegetation structure variables derived from airborne LiDAR are applicable to studies of animal trait diversity and distribution by being useful in describing horizontal and vertical (3-dimensional) habitat structure across landscapes. LiDAR-derived structural variables include understory vegetation density, canopy architecture, snag size and density, and tree biomass and basal area (Fig. 4; Turner et al. 2003; Vierling et al. 2008; Bergen et al. 2009). In-situ field data on the abundance of animal functional groups can be combined with structural variables to scale-up functional group distributions based on field-validated models (Martinuzzi et al. 2009; Newton et al. 2009). To illustrate, Hinsley et al. (2002) used LiDAR to estimate vegetation height and compared it to chick mass and foraging behavior of blue and great tits. Chick mass of blue tits, which forage in upper areas of the canopy, had a positive relationship with vegetation height while the chick mass of great tits, which forage in lower branches or understory, had a negative relationship with the same variable (Hinsley et al. 2002). In another example, Müller and Brandl (2009) linked local and regional scale functional trait composition of beetles by relating beetle activity, abundance, and composition to structural variables derived from LiDAR. They found that beetle body size was negatively related to the standard deviation of vegetation height. Both studies demonstrate that functional traits and trait diversity are connected to remotely sensed habitat structure variables. As ecologists apply these rapidly developing tools, there will be more opportunities for scaling-up animal trait diversity predictions to broader spatial scales.

Hybrid methods

Hybrid methods that rely on biophysical gradients to integrate functional trait variation into land cover or vegetation types, which can be classified using remote sensing, can be used to scale-up trait variation to regional scales (akin to *hybrid models*; Van Bodegom et al. 2012). For example, Lavorel et al. (2011) mapped vegetation types based on land use trajectories using aerial photography and conducted plot-sampling to estimate functional trait CWM and diversity indices across the biophysical gradients covered by each vegetation type. Linear models relating trait values to abiotic variables were developed for each vegetation type and used to spatially portray the regional variation in traits relevant to ecosystem services. To our knowledge, this remains the only example where functional trait variation has been spatially scaled-up to inform ecosystem services management. Clearly, there is ample space to further integrate plot-based functional trait approaches with remote sensing methods, especially to fully capitalize on current developments in the latter.

Case study: Traits and ecosystem services in the Nicoya Peninsula

Our case study in the Nicoya Peninsula, northwestern Costa Rica, illustrates how remote sensing of functional trait variation and land cover change can be applied to ecosystem service assessments. The Nicoya Peninsula, where mean annual precipitation varies from 1400 to 2900 mm along elevations of 0 to 800 m, is located within the Mesoamerican dry tropical forest biodiversity hotspot (Miles et al. 2006) and the Mesoamerican drought corridor (Vega-García 2005). Up until the 1970's, the region experienced extensive land cover change from mostly old-growth forest cover to near-complete deforestation driven by conversion to grassland for cattle ranching. During this time, two events occurred that changed government policy and land use practices in the region: a severe drought coupled with a drop in price of beef for export (Vega-García 2005; Calvo-Alvarado et al. 2009). Reduction of ranching combined with new government policies to incentivize reforestation, such as payments for ecosystem services (PES), resulted in the reforestation of nearly 40% of the region by 2000 into secondary forests and commercial tree plantations (Serrano 2005; Calvo-Alvarado et al. 2009). Plantations are dominated by the introduced tree species *Gmelina arborea* (melina) and *Tectona grandis* (teak). Melina has naturalized and grows in secondary forests of the region, which may be considered novel ecosystems (Hobbs et al. 2006). The current landscape is a heterogeneous mosaic of old-growth, mature and early secondary forest, novel forests, commercial plantations, pastures, and agricultural land that have likely impacted the functional trait composition of the region (Fig. 2). The question facing the region is to what extent the new trait composition found across the landscape provides a resilient set of ecosystems services.

The Nicoya Peninsula case study highlights how land cover change influences the provision of ecosystem services through functional traits. We illustrate how variation in key functional traits can be measured and scaled-up from local to regional scales, focusing on functional traits that affect water use in trees and pollination traits of bees. The functional traits of these organisms influence water provision and pollination services, which have social-economic significance in the region (Step 1 in Fig. 5; Frankie et al. 2004; Vega-García 2005). Land cover and forest type can influence water availability in the dry season (Jackson et al. 2005; Abelleira 2015) and agricultural production (i.e., coffee and melon) is dependent on diverse bee pollination services (Garibaldi et al. 2013).

Scaling-up traits of tree water use using remote sensing

Variation in traits such as tree trunk diameter and sapwood area affect the amount of water used in tree transpiration (Step 2 in Fig. 5; Meinzer et al. 2005; Reyes-García et al. 2012). At the plot scale, researchers are able to measure these traits in the field. However, at broader spatial scales, such as a watershed, field measures are logistically difficult, particularly in regions that are highly diverse in land cover, forest type, and tree age structure, resulting in high trait variability (Fig. 2; Fig. 6a). Remote sensing methods able to capture the spatial heterogeneity of these functional traits, or their proxies, may be used to facilitate the scaling-up of ecosystem processes, such as forest water use, to spatial scales relevant to ecosystem service management (Daily et al. 2009). For example, tree trunk diameter at breast height (DBH) and sapwood area are related to tree crown diameter (Fig. 6b-c; Kunert et al. 2012; Verma et al. 2014). Tree crown diameter can be mapped at a fine resolution (<1.5 m) over broad areas (>10 km^2) using airborne LiDAR (Fig. 4; Popescu et al. 2003; Falkowski et al. 2006). Therefore, tree crown diameter would be a useful trait and proxy for scaling-up variation in tree water use to broad spatial scales, facilitating coverage across the biophysical gradients of elevation and precipitation in the study region (Steps 3 and 4 in Fig. 5).

A number of issues remain to be resolved to utilize this approach. First, plot-based measures that relate water use to traits such as tree crown diameter often rely on integrated measures such as the CWM of the trait (Step 3 in Fig. 5; Abelleira 2015). Relationships of individual-level tree water use to crown diameter would be better suited to make this approach operational. Fortunately, individual tree trait to water use relationships are more robust than stand trait CWM to water use relationships (Abelleira 2015). Secondly, although tree trunk DBH, sapwood area, and crown diameter are all related to tree water use, these relationships vary among tree functional types (e.g.; N-fixers vs. non-fixers; Fig. 6a-c). Remote sensing technologies that map N-fixation capacity using airborne hyperspectral sensors, could resolve this issue (Fig. 4; Step 4 in Fig. 5; Asner & Martin 2009). In addition to spatial variation, tree water use changes with seasons, such as leaf drop during seasonal dry periods. In such cases, tree phenology can be remotely sensed using multispectral satellite imaging to quantify water use changes through the seasons (Fig. 4; Kunert, Schwendemann & Hölscher 2010; Gray & Song 2012).

Scaling-up traits of pollination: Habitat quality and landscape structure

Pollination services in plant communities are driven by trait diversity among pollinators (Step 2 in Fig. 5; Gagic et al. 2015). Functional diversity of bee communities has been shown to increase the persistence of diverse plant communities (Biesmeijer et al. 2006; Fontaine et al. 2006), increase crop yield (Hoehn et al. 2008; Tsharntke et al. 2008; Martins, Gonzalez & Lechowicz 2015), and buffer pollination services from environmental changes (Brittain, Kremen & Klein 2013; *but see* Winfree & Kremen 2009). Studies have identified morphological (Larsen, Williams & Kremen 2005; Fontaine et al. 2006) and behavioral (Biesmeijer et al. 2006; Klein et al. 2008; Hoehn et al. 2008; Williams et al. 2010; Frund et al. 2013) bee traits where trait diversity is related to pollination services. For example, long-tongued bees are able to access resources in flowers with a long corolla, but short-tongued bees or flies may be more efficient at accessing resources in flowers with a short corolla. If there are insects with different mouthpart lengths within a community, pollination services will be sustained for flowering plants of diverse morphologies (Fontaine et al. 2006).

Though bee pollinator traits are not remotely measureable, trait diversity of bee populations is related to proxies in the landscape that can be measured at broad spatial scales (Step 3 in Fig. 5). Landscape structure variables, such as proportion of native habitat, patch isolation, and land use intensity, influence bee trait diversity at different spatial scales trough traits such as dispersal ability and foraging range (Fig. 3; Step 4 in Fig. 5; Steffan-Dewenter et al. 2002; Kremen et al. 2004; Winfree, Bartomeus & Cariveau 2011). Habitat structural data from field surveys or fine-resolution remote sensing, such as airborne LiDAR, can be used to test additional variables that may impact bee trait diversity at local scales (Step 4 in Fig. 5). For example, understory plant height (Hoehn et al. 2008), tree height and DBH (Eltz & Bruhl 2002; Samejima et al. 2004), canopy openness (Lehnert et al. 2013), and plant species richness (Grass, Berens & Farwig 2014) have significant effects on the composition and trait diversity of bee pollinators. However, there are limitations to associating these local-scale relationships to regional-scale landscape structure because the relative magnitude of their impacts on bee trait diversity depends on the traits of interest (Step 4 in Fig. 5; Kremen et al. 2004; Ricketts et al. 2008; Winfree 2013). This remains a problem to be solved by identifying the relevant traits and scales of trait variation on a regional scale case-by-case basis (Rollin et al. 2015).

Scaled-up traits and ecosystem services

To evaluate the effectiveness of policies, such as PES, it is necessary to assess simultaneously the impact of land use change on multiple services. For example, reforestation with teak may result in similar water balance as secondary forest, but provide less bee nesting and foraging habitat to support bee pollination of nearby crops. Understanding the relative impacts of traits that impact water and pollination services requires the integration of multiple disciplines and datasets. Spatially explicit evaluation tools are particularly helpful in integrating ideas and data across subject matter (Daily et al.

2009; Mulligan et al. 2010). Such tools use spatially explicit models where pixels are characterized by values that correspond to service provision. For example, current ecosystem service evaluation tools, such as InVEST and Co$ting Nature, use process-based models to estimate water yield under different land cover scenarios (Mulligan et al. 2010; Tallis et al. 2012). Remotely sensed metrics of functional traits that are related to water fluxes, such as tree crown diameter, could be integrated into these tools to improve estimates of water use across communities within a watershed to estimate water yield. Similarly, the InVEST crop pollination module, which predicts relative pollination value of pixels based on bee habitat, foraging quality, and crop location, has been tested on a number of regions, including coffee producing regions in Costa Rica (Lonsdorf et al. 2009). Regional estimates of bee trait diversity across land cover types and landscape structure can be used to improve the predictive capacity of the pollination module.

Ecosystem service evaluation tools that link land cover change to ecosystem fluxes typically incorporate the social-economic impacts of biophysical change. However, given the context dependent nature of social-economic systems, regionally specific data may be needed to better assess the social-economic impacts of land use change. For example, we have conducted interviews and economic choice experiments where residents outline how they would be impacted by changes in the provision of pollination and water in the Nicoya Peninsula (Sara M. Galbraith, unpublished data; Hector S. Tavárez, unpublished data). A next step would be to incorporate these types of data into the ecosystem service evaluation tools so that land cover impacts on ecosystem fluxes can be translated into impacts on ecosystem services with higher accuracy for the better implementation of policy and management.

Conclusion: Looking forward

Much work remains to achieve accurate and cost-efficient representations of local functional trait variation at the spatial extent and resolution needed for regional ecosystem service assessments. One of the main barriers is the regional context dependency of the relationships that are needed for this achievement: between trait variation and degree of human modification, between traits and ecosystem properties and fluxes, and between traits and proxies that may be related to trait variation via remote sensing (De Deyn et al. 2008; Mayfield et al. 2013; Müller et al. 2014). At this point in time, in-situ sampling of trait variation is still needed at the regional scale, and more so in human-modified regions for which ecosystem service assessments are relevant. In particular, this needs to take into account the regional modification of natural trait variation due to dominant introduced species, managed and novel community types, and ever-changing land use history and landscape structure. Remote sensing methods are particularly useful to capture all of this variation in traits at multiple spatial scales and, to improve their accuracy, ecosystem service assessments should take advantage of functional traits that can be remotely sensed. Incorporating higher resolution of trait variation into the mapping of land cover and vegetation types coupled with the sampling of trait variation across biophysical gradients using remote sensing holds great promise for improving the use of functional traits to inform ecosystem service assessments in human-modified regions. Linking functional trait metrics used in most local assessments of trait and ecosystem process relationships (i.e., CWM and diversity indices) with remotely sensed imagery remains a next step to improve the utility of functional traits for ecosystem service policy and management. We foresee that ongoing and future research in this area will promptly allow for scaling-up functional traits for regional ecosystem service management.

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Data Accessibility

All data are included in the manuscript.

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Figure 1. Temporal and spatial scale of functional traits and ecosystem services. The use of functional traits to inform ecosystem service policy and management requires the scaling-up of fine-scale plot-scale data from local to regional scales. In this review, we outline (1; *purple dashed arrow*) the sampling considerations for capturing the necessary variation in effect functional trait composition from individual to community levels so that these proxies can be used for (2; *brown dashed arrow*) the high-resolution scaling-up of effect functional trait composition from local to regional scales. Remote sensing methods offer the most promising bridge between these spatial scales.

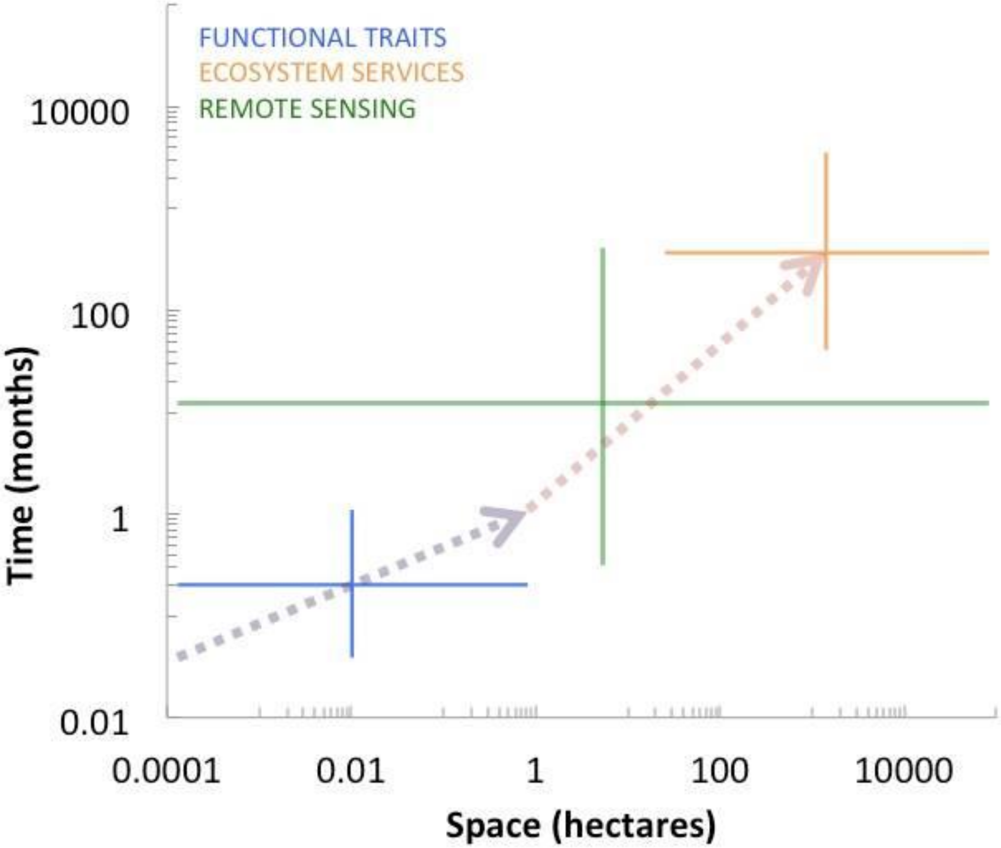


Figure 2. Global trait values by ecological level. Range of hypothetical deviation from a global mean functional trait value of a given biome corresponding to individual, species, community, and landscape ecological levels under natural conditions and under conditions modified by land cover change and species introductions. Black empty bars represent the range of trait variation as a percentage of the total (100%) found across ecological levels in natural undisturbed conditions (after Freschet et al. 2012) for two given regions within a biome. Green colored bars represent a region (case A) where land cover change and species introductions have resulted in a relative decrease of trait variation found across the species level due to localized extirpation of species (e.g., due to the loss of pollinators or seed dispersers), coupled with a relative increase in trait variation found across the individual, community, and landscape levels due to the dominance of introduced species, new community types (e.g., secondary forests, managed systems, and novel ecosystems), and various degrees of land use intensification affecting landscape structure, respectively. Red colored bars represent another region (case B) where land cover change, and species introductions and extirpations have acted to homogenize trait variation by increasing trait values that deviate less from the global mean trait value for the biome at each ecological level. Divergence in trait values between natural and human-modified conditions is higher within the region in case B.

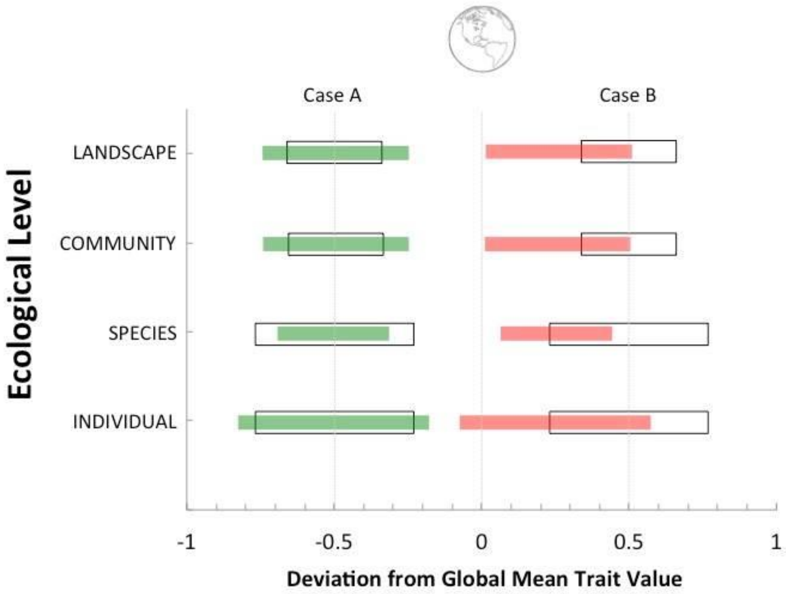


Figure 3. Examples of possible relationships of functional trait effects on ecosystem processes across space. A process whose dependency on functional trait variation does not change across space (*blue*); a process that is dependent on functional traits at local spatial scales but mostly modulated by other factors at broader spatial scales (*purple*); a process that is driven by functional traits at relatively broad spatial scales (*green*); and a process that is highly driven by functional traits at intermediate spatial scales (*orange*).

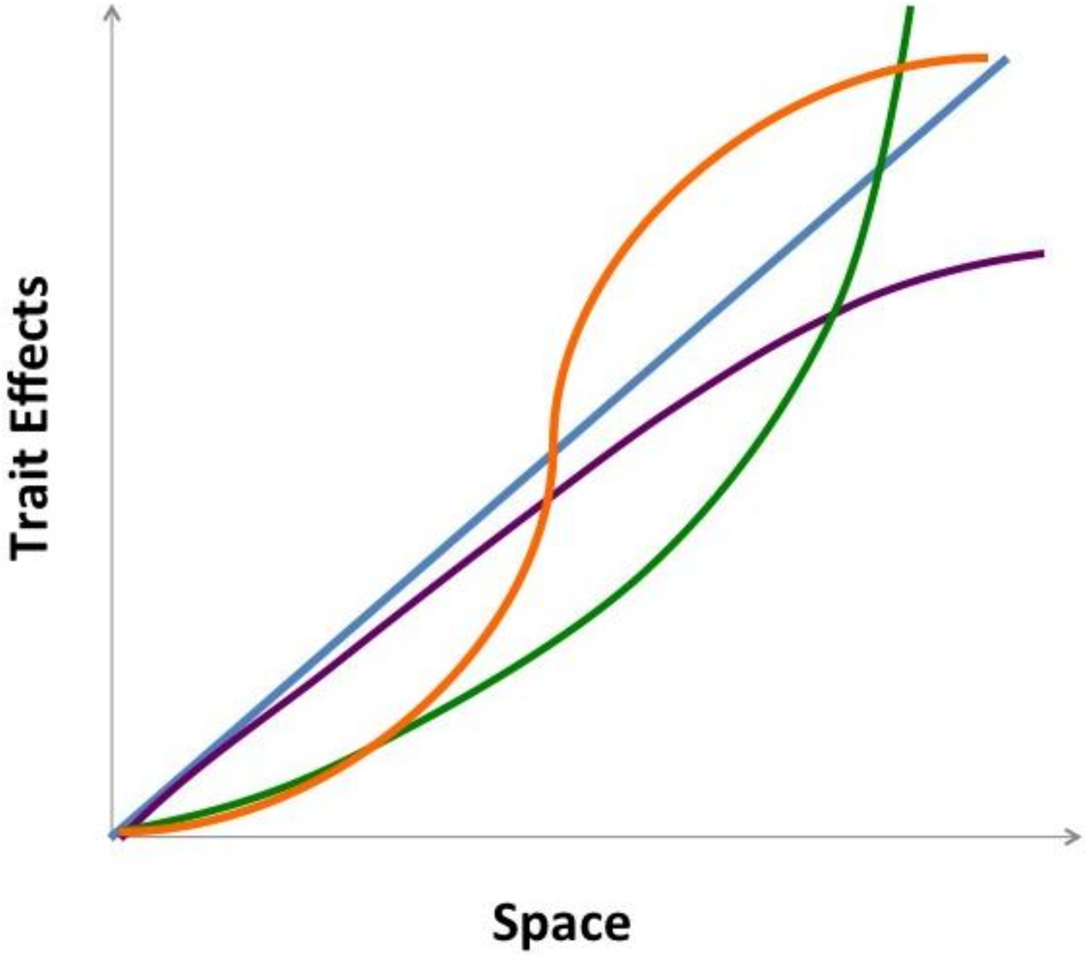


Figure 4. Ecological levels of operation of remote sensing methods available for mapping plant functional traits and animal functional trait proxies. The area of the solid boxes cover the ecological levels where remote sensing methods coupled with field sampling and validation allow for the mapping of the following plant functional traits: tree crown diameter (blue), tree height (orange), specific leaf area and leaf chemistry (green), and phenology (brown). Dashed boxes cover the ecological levels where remote sensing methods allow for the mapping of the following proxies that relate to animal functional trait diversity: habitat and vegetation structure (e.g., tree density and biomass; yellow), leaf area index (purple), and landscape structure (e.g., patch size, isolation, and perimeter to area ratio; red).

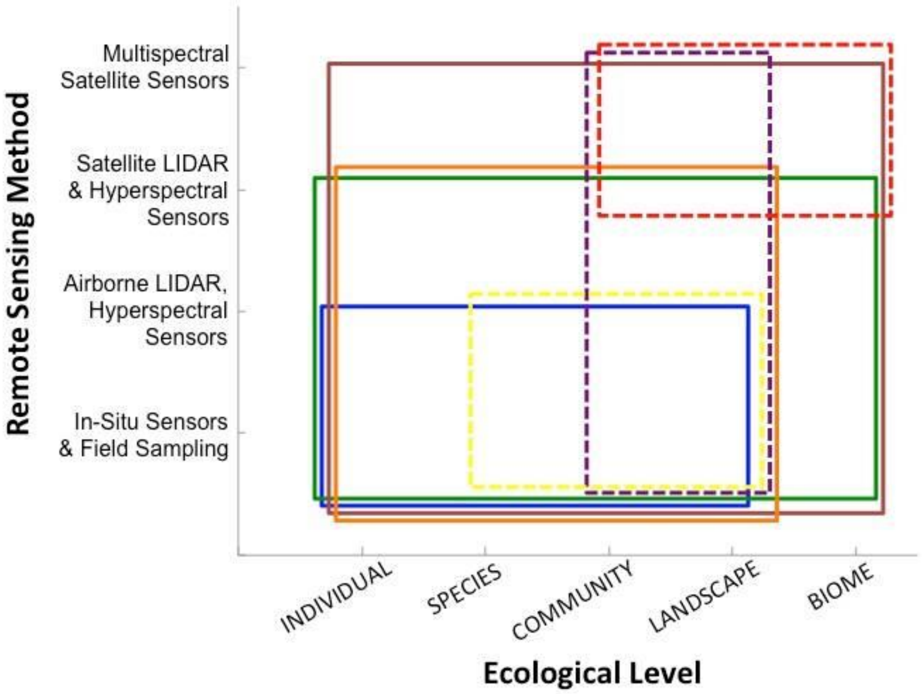


Figure 5. Stepwise process for scaling-up functional trait metrics using remote sensing for ecosystem service assessments.

Step 1: Identify the ecosystem service of interest

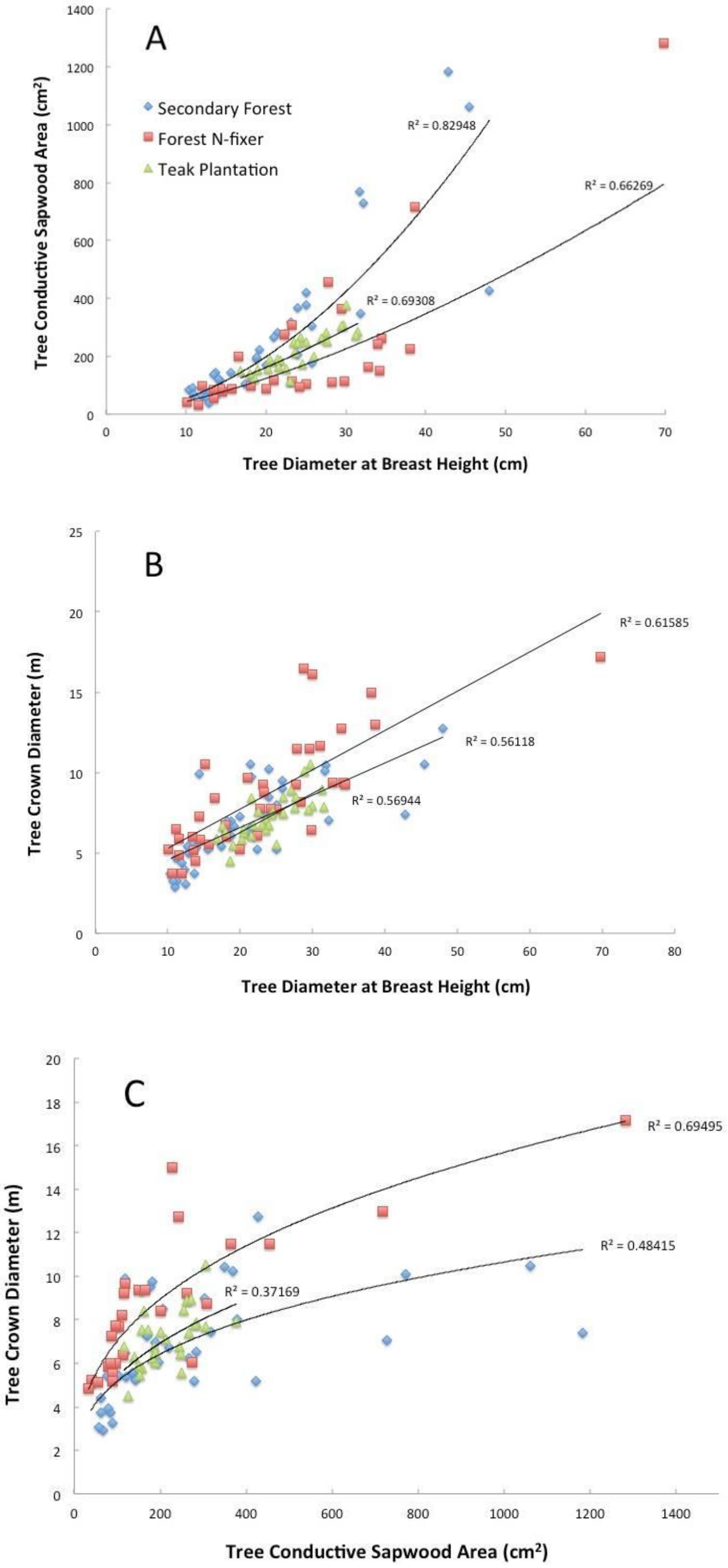
Step 2: Determine the trait metric that best predicts the service

Step 3: Identify remotely sensed proxies for the trait metric

Step 4: Map heterogeneity in the trait metric proxy

Step 5: Incorporate socio-economic values to model service

Figure 6. Relationships of tree functional traits. Figures show trunk diameter (DBH), sapwood area, and crown diameter for secondary forest trees (non N-fixers), N-fixing trees in secondary forests, and introduced teak trees in plantations in the Nicoya Peninsula.



Appendix 1. Description of field sites. Includes each of the five replicates per land use, their location, altitude, area (in square hectares) and perimeter (in meters).

Site	Land Use	Location	Altitude (MASL)	Area (Ha^2)	Perimeter (m)
1	Coffee	N 10 01' 06.8" W 085 28' 27.7"	624	8.37	1219.36
2	Coffee	N 10 00' 58.6" W 85 20' 55.4"	543	2.41	739.37
3	Coffee	N 09 59' 19.7" W 085' 21' 56.0"	680	6.96	1062.73
4	Coffee	N 09 56' 25.5" W 85 23' 56.5"	573	21.11	2202.91
5	Coffee	N 10 00' 14.1" W 085 28' 14.1"	778	1.58	510.76
	Mean			**8.09**	**1147.03**
7	High pasture	10 00' 53.8" W 085 28' 18.0"	714	2.00	554.46
8	High pasture	N 09 59' 05.2" W 085 22' 22.0"	622	20.25	1957.72
9	High Pasture	N 09 56' 35.9" W 085 23' 44.6"	587	8.20	1194.86
10	High Pasture	N 010 00' 50.9" W 085 28' 18.9"	748	28.51	3035.21
6	High Pasture	N 10 01' 44.7" W 085 22' 44.6"	634	7.88	1620.36
	Mean			**13.37**	**1672.52**
11	Low Pasture	N 10 09' 26.8" W 085 15' 55.6"	35	4.50	1138.83
12	Low pasture	N 10 05' 06.2" W 085 21' 54.0"	93	4.28	918.44
13	Low pasture	N 10 06' 38.4" W 085 21' 52.5"	124	12.58	1563.78
14	Low Pasture	N 9 59' 18.7" W 085 26' 47.1"	254	32.23	3063.41
15	Low Pasture	N 10 04' 00.8" W 085 24' 45.2"	346	5.22	1099.72
	Mean			**11.76**	**1556.84**
16	Teak	N 10 03' 57.4" W 085 23' 40.6"	153	12.75	1748.74
17	Teak	N 10 09' 02.3" W 085 16' 21.8"	45	3.25	863.48
18	Teak	N 10 06' 48.1" W 085 21' 23.8"	67	12.96	1387.78

19	Teak	N 10 05' 03.5" W 085 19' 46.3"	130	11.67	1458.79
20	Teak	N 09 56' 51.2" W 085 24' 53.3"	172	21.08	2054.23
	Mean			**12.34**	**1502.61**

Appendix 2. Dates and seasons of the ten sampling periods. Dry season in the Nicoya Peninsula lasts from approximately December to April, which encompasses the first rainfall event and coffee blooming period. DS=dry season, WS=wet season.

Sampling period	Season	Trapping dates
1	Mid DS	April 2013
2	Late DS	May 2013
3	Early WS	Late June-Mid July 2013
4	Mid WS	Mid September-Mid October 2013
5	Early DS	Mid December 2013- Mid January 2014
6	Mid DS	Late February-Late March 2014
7	Late DS	Mid April- Mid May 2014
8	Early WS	Mid July- Early August 2014
9	Mid WS	Late August-Mid September 2014
10	Late WS	Late October-Mid November 2014

Appendix 3. Plants observed blooming within sites, categorized by land use. Includes common name (in Spanish), family, and scientific name.

Land use	**Common name**	**Family**	**Scientific name**
Coffee	Aguacate	Lauraceae	*Persea americana*
	Banano	Musa	*Musa acuminata*
	Cacao	Malvaceae	*Theobroma angustifolium*
	Churristate	Convolvulaceae	*Ipomoea violacea*
	Carao	Leguminosae	*Cassia grandis*
	Cedro	Meliaceae	*Cedrela odorata L.*
	Cenizaro	Leguminosae	*Albizia saman*
	Coffee	Rubiaceae	*Coffea arabica*
	Cortez Amarillo	Bignoniaceae	*Handroanthus ochraceus*
	Cortez Negro	Bignoniaceae	*Handroanthus impetiginosus*
	Florecilla	Asteraceae	*Melampodium sp.*
	Guaba	Leguminosae	*Inga punctata*
	Guachapelin	Leguminosae	*Diphysa americana*
	Guacimo	Malvaceae	*Guazuma ulmifolia*
	Guanacaste	Leguminosae	*Enterolobium Cyclocarpum*
	Guapinol	Leguminosae	*Hymenaea courbaril*
	Guayaba	Myrtaceae	*Psidium guajava*
	Guayaquil	Malvaceae	*Ceiba trichistandra*
	Jiñocuabe	Burseraceae	*Bursera simaruba*
	Laurel	Boraginaceae	*Cordia alliodora*
	Llama de Bosque	Bignoniaceae	*Spathodea camponulata*
	Mango	Anacardiaceae	*Mangifera indica*
	Nance	Malpighiaceae	*Byrsonima crassifolia*
	Naranja	Rutaceae	*Citrus sinensis*
	Ojoche	Moraceae	*Brosimum alicastrum*
	Poro	Leguminosae	*Erythrina fusca*
	Quizarra	Lauraceae	*Ocotea floribunda*
	Roble	Bignoniaceae	*Tabebuia rosea*
	Ronron	Anacardiaceae	*Astronium graveolens*
	Saino	Leguminosae	*Caesalpinia eriostachys*
	Santa Maria	Callophilaceae	*Calophyllum brasiliense*
	Tallo	Malvaceae	*Bernoullia flammea*
	Teak	Lamiaceae	*Tectona grandis*
High altitude pasture	Aguacatillo	Lauraceae	*Ocotea tenera*
	Aguacate	Lauraceae	*Persea sp.*
	Carao	Leguminosae	*Cassia grandis*

	Chuirristate	Convolvulaceae	*Ipomoea violacea*
	Cortez amarillo	Bignoniaceae	*Handroanthus ochraceus*
	Durmilona	Fabeaceae	*Mimosa pudica*
	Espavel	Anacardiaceae	*Anacardium excelsum*
	Florecilla	Asteraceae	*Melampodium sp.*
	Flor blanco	Apocynaceae	*Plumeria rubra L.*
	Gallinazo	Leguminosae	*Schizolobium parahyba*
	Guaba	Leguminosae	*Inga punctata*
	Guacimo	Malvaceae	*Guazuma ulmifolia*
	Guanacaste	Leguminosae	*Enterolobium Cyclocarpum*
	Guayaba	Myrtaceae	*Psidium guajava*
	Jiñocuabe	Burseraceae	*Bursera simaruba*
	Jobo	Anacardaceae	*Spondias mombin*
	Laurel	Boraginaceae	*Cordia alliodora*
	Lengua de vaca	Melastomataceae	*Meconia sp.*
	Limon	Rutaceae	*Citrus aurantifolia*
	Madera negra	Leguminosae	*Gliricidia sepium*
	Malinche	Fabeaceae	*Delonix regia*
	Mango	Anacardiaceae	*Mangifera indica*
	Nance	Malpighiaceae	*Byrsonima crassifolia*
	Papa miel	Combretaceae	*Combretum farinosum*
	Pasto	Poaceae	*Brachiaria brizantha*
	Pasto	Poaceae	*Hyparrhenia rufa*
	Pasto	Poaceae	*Dischantium aristatum*
	Pochote	Malvaceae	*Pachira quinata*
	Roble	Bignoniaceae	*Tabebuia rosea*
	Santa maria	Callophilaceae	*Calophyllum brasiliense*
	Tallo	Malvaceae	*Bernoullia flammea*
	Targua	Euphorbaceae	*Croton draco*
	Tuete	Asteraceae	*Vernonia sp.*
Teak	Churristate	Convolvulaceae	*Ipomoea violacea*
	Durmilona	Fabeaceae	*Mimosa pudica*
	Florecilla	Asteraceae	*Melampodium sp.*
	Gallinazo	Leguminosae	*Schizolobium parahyba*
	Pochote	Malvaceae	*Pachira quinata*
	Papaya	Caricaceae	*Carica papaya*
	Teca	Lamiaceae	*Tectona grandis*
Low altitude pasture	Aguacatillo	Lauraceae	*Ocotea tenera*
	Carao	Leguminosae	*Cassia grandis*
	Cenizaro	Mimosoideae	*Samanea saman*

	Churristate	Convolvulaceae	*Ipomoea violacea*
	Cocobolo	Leguminosae	*Dalbergia retusa*
	Cortez Amarillo	Bignoniaceae	*Handroanthus ochraceus*
	Coyol	Arecaceae	*Acrocomia aculeata*
	Durmilona	Fabeaceae	*Mimosa pudica*
	Malba de escoba	Malvaceae	*Sida rhombifolia*
	Florecilla	Asteraceae	*Melampodium sp.*
	Gallinazo	Leguminosae	*Schizolobium parahyba*
	Guaba	Leguminosae	*Inga punctata*
	Guacimo	Malvaceae	*Guazuma ulmifolia*
	Guanacaste	Leguminosae	*Enterolobium Cyclocarpum*
	Guapinol	Leguminosae	*Hymenaea courbaril*
	Laurel	Boraginaceae	*Cordia alliodora*
	Lengua de vaca	Melastomataceae	*Meconia sp.*
	Madroño	Rubiaceae	*Calycophyllum candidissimum*
	Malva	Malvaceae	*Malva sp.*
	Melina	Lamiaceae	*Gmelina arborea*
	Mango	Anacardiaceae	*Mangifera indica*
	Nance	Malpighiaceae	*Byrsonima crassifolia*
	Palma real	Arecaceae	*Attalea butyracea*
	Pasto	Poaceae	*Brachiaria brizantha*
	Pasto	Poaceae	*Hyparrhenia rufa*
	Pasto	Poaceae	*Dischantium aristatum*
	Roble	Bignoniaceae	*Tabebuia rosea*
	Saino	Leguminosae	*Caesalpinia eriostachys*
	Teca	Lamiaceae	*Tectona grandis*
	Tuete	Asteraceae	*Vernonia sp.*

Appendix 4: Means and standard error from GLMMIX procedure, by season, for BVT sampling. DS=dry season, WS=wet season.

BVT

			Abundance		Genera richness		Species richness		Diversity		Evenness	
Land use		Season	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
All	High altitude	DS	13.018	2.396	4.400	0.641	5.320	0.796	0.508	0.035	0.139	0.040
		WS	2.490	2.396	1.320	0.641	1.420	0.796	0.353	0.035	0.385	0.040
	Low altitude	DS	7.913	2.396	3.672	0.641	4.037	0.796	0.495	0.029	0.210	0.026
		WS	5.960	2.396	2.423	0.641	2.793	0.796	0.408	0.029	0.373	0.026
All high altitude	Coffee	DS	14.397	3.443	3.760	0.744	4.560	1.003	0.464	0.051	0.128	0.057
		WS	1.320	3.443	0.880	0.744	0.880	1.003	0.270	0.051	0.273	0.057
	Pasture	DS	11.640	3.443	5.040	0.744	6.080	1.003	0.551	0.051	0.151	0.057
		WS	3.667	3.443	1.760	0.744	1.960	1.003	0.437	0.051	0.498	0.057
All low altitude	Teak	DS	4.447	2.230	1.583	0.627	1.703	0.787	0.390	0.041	0.254	0.037
		WS	2.337	2.230	0.930	0.627	4.657	0.787	0.251	0.041	0.249	0.037
	Pasture	DS	11.380	2.230	5.760	0.627	6.370	0.787	0.600	0.041	0.166	0.037
		WS	9.583	2.230	3.917	0.627	0.930	0.787	0.565	0.041	0.497	0.037

Appendix 5: Means and standard error from GLMMIX procedure, by season, for pan trap sampling. DS=dry season, WS=wet season.

			Abundance		Genera richness		Species richness		Diversity		Evenness	
Land use		Season	Mean	SE	Est	SE	Est	SE	Est	SE	Est	SE
All	High altitude	DS	4.600	1.310	2.560	0.585	2.667	0.600	0.457	0.072	0.232	0.017
		WS	1.792	1.337	1.333	0.597	1.250	0.588	0.335	0.072	0.242	0.017
	Low altitude	DS	5.226	1.176	2.484	0.525	2.857	0.588	0.458	0.072	0.221	0.017
		WS	4.259	1.260	2.444	0.563	2.483	0.578	0.426	0.072	0.217	0.017
High altitude	Coffee	DS	4.353	1.359	2.294	0.518	2.588	0.599	0.484	0.130	0.207	0.030
		WS	1.600	1.446	1.200	0.551	1.267	0.638	0.345	0.130	0.254	0.030
	Pasture	DS	5.125	1.980	3.125	0.755	3.625	0.873	0.430	0.130	0.270	0.030
		WS	2.111	1.867	1.556	0.711	1.778	0.823	0.325	0.130	0.229	0.030
Low altitude	Teak	DS	3.000	1.613	1.563	0.702	1.750	0.742	0.377	0.061	0.216	0.016
		WS	2.357	1.725	1.286	0.750	1.286	0.793	0.309	0.061	0.211	0.016
	Pasture	DS	7.600	1.666	3.467	0.725	3.667	0.767	0.540	0.061	0.227	0.016
		WS	6.308	1.790	3.692	0.779	3.923	0.823	0.543	0.061	0.222	0.016

Appendix 6: Means and standard error from GLMMIX procedure, by land use, for both sampling methods.

BVT

	Abundance		Genera richness		Species richness		Diversity		Evenness	
Land Use	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Coffee	7.858	2.434	2.32	0.526	2.72	0.709	0.148	0.024	0.044	0.007
High altitude Pasture	7.650	2.434	3.4	0.5262	4.02	0.709	0.203	0.024	0.061	0.007
Teak	3.392	2.284	1.257	0.444	1.317	0.557	0.095	0.028	0.030	0.008
Low altitude Pasture	10.482	2.284	4.838	0.444	5.513	0.557	0.288	0.028	0.089	0.008

Pan traps

	Abundance		Genera richness		Species richness		Diversity		Evenness	
Land Use	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Coffee	2.977	0.992	1.747	0.378	1.928	0.438	0.162	0.032	0.053	0.010
High altitude Pasture	3.618	1.361	2.340	0.519	2.701	0.600	0.122	0.035	0.040	0.011
Teak	2.679	1.181	1.424	0.514	1.518	0.543	0.133	0.025	0.044	0.009
Low altitude Pasture	6.954	1.223	3.580	0.532	3.795	0.563	0.326	0.026	0.109	0.009

Appendix 7: Beekeeper questionnaire.

Parte 1: *Esta sección está diseñada para obtener información socio-económica y demográfica, así como prácticas de negocio.*

Información socio-económica y demográfica

1. ¿Cuál es su género? Masculino _____ Femenino _____
2. ¿Donde usted vive? (cantón, distrito y región)

   ____
3. Por favor, marque el nivel más alto de educación que ha completado:

   _____ Primaria

   _____ Colegio (secundaria)

   _____ Créditos universitarios

   _____ Grado de bachillerato universitario o más alto
4. Número de dependientes (niños o adultos que dependen de usted un 50% o más para cubrir sus necesidades): _____
5. Porciento del ingreso del hogar que viene de la apicultura: _____

Prácticas del negocio

6. ¿Donde coloca sus colmenas?

a. Temporada:_______________ Cantón, Distrito, Región:______________número de colmenas_________

b. Temporada:_______________ Cantón, Distrito, Región:______________número de colmenas_________

c. Temporada:_______________ Cantón, Distrito, Región:______________número de colmenas_________

d. Temporada:_______________ Cantón, Distrito, Región:______________número de colmenas_________

e. Temporada:________________ Cantón, Distrito, Región:_______________número de colmenas__________

7. ¿Por cuantos años ha estado practicando la apicultura? _____ años
8. De esos años, ¿cuantos han sido en la Península de Nicoya? _____ años
9. ¿Cuál es el valor promedio en colones que paga de renta en los lugares donde coloca sus colmenas?

   __________ colones al mes por __________ meses al año
10. ¿Cuántos barriles de miel produjo el año pasado? _____ barriles

    a. ¿Es esto lo que normalmente produce todos los años?

    _____ Si

    _____ No, representa mas de lo usual

    _____ No, representa menos de lo usual
11. ¿A qué precio vende la miel? __________ colones por __________ (¿barril o kilogramo?)
12. ¿Produce miel derivada de alguna flor específica?

    _____No (vaya a la pregunta 13)

    _____ Si

    a. ¿Qué tipo de flores prefiere? Provea el nombre de las flores abajo:

    _________________________________ _________________________________

    _________________________________ _________________________________

    b. ¿Cuáles son los factores que influyen la preferencia por la miel proveniente de ciertas flores? (Marque con una "X" todos los factores que apliquen):

    _____ Color de la miel

    _____ Sabor de la miel

    _____ Cantidad de miel producida

    _____ Confiabilidad de las flores

    _____ Duración de la floración

    _____ Tiempo de la floración

_____ Otros (mencione todos los factores):____

13. ¿Genera ingreso por la venta de polen?

_____ No (vaya a la pregunta 15)

_____ Si

14. ¿Produce polen derivado específicamente de un tipo de flor?

_____ No (vaya a la pregunta 15)

_____ Si

a. ¿Qué tipo de flores prefiere para la producción de polen? Indique abajo:

_________________________________ _____________________________

_________________________________ _____________________________

b. ¿Cuáles son los factores que influyen la preferencia por polen de ciertas flores? (Marque con una "X" todas las que apliquen):

_____ Color del polen

_____ Sabor del polen

_____ Cantidad de polen

_____ Confiabilidad de las flores

_____ Duración de la floración

_____ Tiempo de floración

_____ Otros (mencione todos los factores):______________________________________

15. ¿Genera ingreso por servicios de polinización a los agricultores?

_____ No (vaya a la pregunta 16)

_____ Si

a. ¿Cuánto dinero recauda por los servicios de polinización?

__________ colones por __________ (¿colmena o hectárea?)

b. ¿Cuántas colmenas alquila al año? ________colmenas

c. ¿A cuantas hectáreas le provee servicio al año? _____ hectárea

d. ¿Para cuales cultivos ha sido contratado para proveer los servicios de polinización?

_________________________________ _____________________________

_________________________________ _____________________________

16. ¿Genera ingreso por cualquier otro producto relacionado a las abejas de miel (e.g., sera, reinas, etc.)?

_____ No (vaya a la pregunta 17)

_____ Si

a. Por favor, marque con una "X" el tipo de producto (puede seleccionar más de uno):

_____ Propóleos

_____ Cera

_____ Reinas

_____ Colmenas

_____ Otros (por favor, describa): ____

b. ¿Cuánto dinero genera anualmente por esos productos? ________ colones al año

17. Aproximadamente, ¿cuál es el costo total anual relacionado al negocio de apicultura? Estos costos incluyen mantenimiento de colmenas, proveer comida o agua, medicamentos, procesamiento de sus productos, y cualquier otro costo que usted incurra. __________________ colones al año

18. ¿Cuáles son las cinco flores más importantes para la apicultura?

_________________________________ _____________________________

_________________________________ _____________________________

____

Impacto de el uso de terrenos

19. ¿Qué tan importante es cada uno de los factores siguientes cuando escoge donde ubicar sus colmenas? (marque un número para cada factor)

Factor	No es importante	Un poco importante	Importante	Muy importante	Extremadamente importante
a. Distancia desde su hogar	0	1	2	3	4
b. Pago mensual al dueño del terreno	0	1	2	3	4
c. Calidad del camino	0	1	2	3	4
d. Uso de terreno en el punto donde coloca las colmenas	0	1	2	3	4
e. Diversidad de los arboles en la región	0	1	2	3	4
f. Distancia a una fuente de agua	0	1	2	3	4
g. El lugar donde otros apicultores colocan sus colmenas	0	1	2	3	4
h. Uso de terreno alrededor de los apiarios	0	1	2	3	4
i. Otro factor (especifique): _____________________________	0	1	2	3	4

De esta lista, ¿cual factor es el más importante? _____________________

De esta lista, ¿cual factor es el segundo más importante? _____________________

20. Por favor, califique la calidad de cada uno de los siguientes usos de terrenos para la apicultura. En otras palabras, si cada uso de terreno estuviese presente cerca de donde

usted ubica sus colmenas, ¿qué tan bueno sería para su negocio? (marque un número para cada uso de terreno)

Uso de terreno	Mal o	Ligeramente malo	Ligeramente bueno	Bueno	Excelente	No se
Bosque primario	1	2	3	4	5	NS
Bosque secundario	1	2	3	4	5	NS
Plantación de melina	1	2	3	4	5	NS
Plantación de teca	1	2	3	4	5	NS
Plantación de árboles nativos	1	2	3	4	5	NS
Café con sombra	1	2	3	4	5	NS
Café sin sombra	1	2	3	4	5	NS
Pasto de zacate nativo con sombra	1	2	3	4	5	NS
Pasto de zacate nativo sin sombra	1	2	3	4	5	NS
Pasto mejorado con sombra	1	2	3	4	5	NS
Pasto mejorado sin sombra	1	2	3	4	5	NS
Fincas de melón	1	2	3	4	5	NS
Áreas residenciales	1	2	3	4	5	NS
Otro tipo: ________________	1	2	3	4	5	NS

21. Es importante considerar usos de terrenos a _____ km de distancia de donde se ubican las colmenas.

22. ¿Mueve las colmenas a través del año?

_____ No (vaya a la pregunta 23)

_____ Si

a. ¿Qué tan seguido mueve sus colmenas? (marque una):

_____ una vez al año

_____ dos veces al año

_____ más de dos veces al año

b. ¿Por qué mueve sus colmenas? (marque todas las que apliquen):

_____ por cambios en recursos florales durante las temporadas lluviosa y seca

_____ para aprovechar las especies de flores específicas que están floreciendo

_____ debido a cambios en el acceso en la carretera o camino

_____ para encontrar un mejor lugar

23. ¿Brinda comida a sus abejas?

_____ No (vaya a la pregunta 24)

_____ Si

a. ¿Por cuantos meses al año usualmente le brinda comida a sus abejas?

_____ meses al año

b. Durante este tiempo, ¿qué tan frecuente les brinda comida?

_____ veces a la semana

24. ¿Brinda agua a sus abejas?

_____ No (vaya a la pregunta 25)

_____ Si

a. ¿Por cuantos meses al año le brinda agua a sus abejas?

_____ meses al año

b. Durante este tiempo, ¿qué tan frecuente les brinda agua?

_____ veces a la semana

25. ¿Qué tipo de vehículo usa para tener acceso a sus colmenas? (Marque todas las que apliquen):

_____ Vehículo 4x4
_____ Vehículo que no es 4x4
_____ Motocicleta (moto)
_____ Otro (especifique): ______________________________

26. ¿Mantiene colmenas de abejas nativas?

_____ No (vaya a la pregunta 27)
_____ Si

a. ¿Cuales especies de abejas nativas mantiene? (indique todas las especies que mantiene):

_________________________ _________________________
_________________________ _________________________

b. ¿Qué productos derivados de abejas nativas vende? (marque todas las que apliquen):

_____ Miel
_____ Otros (especifique): ________________________________

c. ¿Cuánta miel de especies nativas produce anualmente? (especifique la unidad): _____

d. ¿Cuál es el precio de venta de la miel? (especifique la unidad): _____ colones por ________

Retos mayores de la apicultura

27. ¿Hasta qué punto es afectado por los siguientes problemas? (marque un número por cada problema):

	No es un problema	Es un problema menor	Es un problema mediano	Es un problema grande

Ácaro varroa	0	1	2	3
Colapso de la colonia	0	1	2	3
Africanización de las abejas	0	1	2	3
Acceso a equipo o medicinas para las abejas	0	1	2	3
Acceso a mercados para vender los productos	0	1	2	3
Entrenamiento o información	0	1	2	3
Acceso a reinas de buena genética	0	1	2	3
Habilidad para procesar los productos de sus abejas	0	1	2	3
Falta de recursos florales para las abejas	0	1	2	3
Uso de plaguicidas por otras personas	0	1	2	3
Falta de ayuda de agencias de gobierno	0	1	2	3
Otro (mencione): ________________	0	1	2	3

28. ¿Es miembro de alguna asociación de apicultores?

_____ No

¿Por qué no es miembro de alguna asociación? (Marque con una "X" todas las que apliquen):

_____ Costo de la inscripción (o mensualidad)

_____ Distancia desde el hogar al lugar de reuniones

_____ Inconveniente

_____ En desacuerdo con el liderazgo actual

_____ Estoy considerando participar en una asociación

_____ Otra (especifique): ____

_____ Si

Nombre de la asociación ____________________________

Antes de que conteste las preguntas siguientes, recuerde que este cuestionario es confidencial y que no le hemos preguntado o anotado su nombre.

29. ¿Cuál es su edad? __________ años
30. ¿Cuánto dinero genera **anualmente** por actividades relacionadas a la apicultura?

_____ Menos de ₡250,000

_____ Entre ₡250,005 y ₡ 1,000,000

_____ Entre ₡1,000,005 y ₡2,500,000

_____ Entre ₡2,500,005 y ₡4,000,000

_____ Más de ₡ 4,000,005

31. ¿Qué porciento de su ingreso personal anual esto representa? __________ %