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Publication Date

2016

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The assembly of plant-pollinator communities

By

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A dissertation submitted in partial satisfaction of the

requirements for the degree of

Doctor of Philosophy

in

Environmental Science, Policy and Management

in the

Graduate Division

of the

University of California, Berkeley

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Summer 2016

Abstract

The assembly of plant-pollinator communities

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Doctor of Philosophy in Environmental Science, Policy, and Management

University of California, Berkeley

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With continued degradation of ecosystems, we need to know how to restore biodiversity — both for conservation and to ensure the provision of essential services provided by nature. To manage and restore diversity in human-modified systems, however, we need to understand the mechanisms that originally maintained biodiversity. A fundamental and widely supported theory of biodiversity is the idea that diversity begets biodiversity (i.e., environmental heterogeneity, disturbance, biodiversity itself). These processes contribute to turnover of species through space and time and subsequent heterogeneity of community composition (β -diversity) — primary determinants of the total species richness supported by a landscape. Communities are being homogenized as human actions such as habitat conversion, land management practices and invasive species disrupt the processes maintaining diversity.

In this dissertation, I examine the assembly of plant-pollinator communities in a variety of landscapes through time and space to better understand how environmental, disturbance and interaction diversity sustains biodiversity. I focus on mutualistic communities because they are influential biological interactions for the generation and maintenance of biodiversity. Plant-pollinator mutualisms are also particularly important for service provision. Pollination systems, however, are under increasing anthropogenic threats. Understanding how to maintain plant-pollinator community biodiversity is this both timely and imperative.

I first investigate the capacity of environmental, disturbance and interaction diversity to sustain biodiversity in a system in Yosemite National Park where nature still drove these processes. In frequent fire forests in Yosemite National Park, California, I found that fire diversity is important for the maintenance of flowering plant and pollinator diversity, and shifts towards lower diversity fire regimes will negatively influence the long-term species richness of these communities. Changing climate and fire suppression are eroding fire diversity and thus homogenizing communities, and thus we must explore management practices that can maintain fire diversity. In these systems, fire diversity is promoted directly through prescribed fires with varied burn conditions and allowing wildfires to burn. These management strategies are already recommended, and my results affirm that their usage should continue and expand.

In Yosemite, I was able to examine the mechanisms sustaining diversity in a natural system and make recommendations for maintaining those processes. When a landscape is already degraded, however, we must determine what restoration efforts are able to reassemble functional communities of interacting organisms. This is often the case in agricultural landscapes where widespread conversion of natural ecosystems to agriculture, combined with intensification of farming practices, has led to the homogenization of biological communities. In Chapter 2, I use a long-term pollinator survey data from the intensively managed agricultural landscape of the Central Valley of California to show that on-farm habitat restoration in the form of native plant “hedgerows,” when replicated across a landscape, can re-establish community spatial turnover. I also determined that the mechanism promoting community spatial heterogeneity was the successional dynamics of hedgerow communities promoted the assembly of phenotypically diverse communities, leading to the accumulation of differences in community composition between sites over time. This work elucidates the drivers of spatial and temporal diversity while also validating the role of small-scale restorations such as floral-enhancements for conserving biodiversity and promoting ecosystem services in agricultural areas.

To fully understand the mechanisms maintaining communities we must also combine our understanding of the ecological processes enabling their persistence with the evolutionary processes that assembled those communities. Coevolution is a key process producing and maintaining complex networks of interacting species. In Chapter 3, I use a theoretical approach to determine whether the structure of interactions varied depending on the community’s evolutionary history. I found that coevolution leaves a weak signal on interaction patterns. Our

results suggest that determining whether assembly processes structure interactions within a community requires a synthetic approach, combining data about the biogeographic history of the interacting lineages and their evolution.

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Acknowledgments

First I would like to thank my adviser Claire Kremen, who has been exceptionally supportive. Beyond Claire, I have also had amazing mentors including David Ackerly, Rosemary Gillespie, Perry de Valpine, Carol Boggs, and George Roderick. I am extremely privileged to work in the Kremen lab with brilliant and remarkable people including Leithen M'Gonigle, Hillary Sardiñas, Emily Kearny, Rebecca Brunner, Aidee Guzman, David Gonthier and Amber Sciligo. The Kremen lab is filled with exceptional people from an extraordinarily broad diversity of backgrounds, united by an unfailing commitment to conservation. I have learned so much from interacting with my amazing labmates.

I also vastly appreciate the identification assistance of expert taxonomists Robbin Thorp, Terry Griswold, John Asher, Martin Hauser and Jason Gibbs. This work was only possible with the collaboration of several undergraduates at UC Berkeley including Kelly Kulhanek and Lindsay Cook.

I would like to thank my funding agencies, the National Science Foundation, the National Geographic Society, the Garden Club of America, the Berkeley Institute for Data Science, the USDA National Institute for Food and Agriculture, the Essig Museum of Entomology, the Margaret C. Walker Grant for Entomology, and the Department of Environmental Science Policy and Management at UC Berkeley. Lastly, I would like to thank the growers and land owners that allowed us to work on their properties in the Central Valley, and the National Park Service for their collaboration in Yosemite.

Introduction

With widespread degradation of landscapes and loss of biodiversity, it is important to understand how to conserve species groups that provide critical ecosystem functions (Cardinale *et al.*, 2012; Kremen, 2005). Pollinators are one such key group: 75% of all crop species depend to some extent on pollinators (Klein *et al.*, 2007), and animal-pollinated crops supply a large proportion of essential nutrients to the human diet (Eilers *et al.*, 2011). However, honey bees, managed extensively around the world to provide crop pollination, are in global decline (Neumann & Carreck, 2010; van Engelsdorp *et al.*, 2009). In addition, native pollinators, which also have the capacity to provide sufficient crop pollination (Kremen *et al.*, 2002; Winfree *et al.*, 2007; Kremen *et al.*, 2004), are threatened by land-use change, habitat fragmentation, pesticide use, and invasions of non-native plants and animals (Kearns *et al.*, 1998). Thus, we must understand how to maintain and restore native pollinator populations to both conserve biodiversity and ensure pollination service provision.

A fundamental impediment to understanding how to restore pollinators, however, is we know little about the process that originally maintained the diversity of these communities. A widely supported theory of biodiversity maintenance is the idea that diversity begets diversity. This diversity can be disturbance diversity, such as fire diversity, or in the form of environmental heterogeneity. Biodiversity can also beget further biodiversity — often through interactions across trophic levels. For example, in mutualistic systems like plant-pollinator communities where both partners benefit from an interaction, plant diversity contributes to pollinator diversity. Anthropogenic actions often degrade these processes: we suppress disturbances like fires, we destroy environmental heterogeneity through homogenizing a landscape into something like monoculture agriculture and, through causing the extinction of species, we begin to take apart the interactions that link species in a community.

In this thesis I build on our understanding of the processes that contribute to biodiversity maintenance and how we can harness these processes to manage and restore diversity in human-modified systems. Specifically I ask:

1. In a system where nature is still driving the processes that maintain biodiversity, are environmental, disturbance and interaction diversity important for sustaining plant-pollinator community biodiversity?
2. Where the processes that maintain diversity are eroded, can we restore them? Specifically can community heterogeneity (β -diversity) be reestablished?
3. Do the communities re-assembled through restoration exhibit the same patterns of interactions and thus stability dynamics as tightly coevolved communities?

I began my investigation into the processes maintaining plant-pollinator community diversity in Yosemite National Park, where a history of innovative management by the Park Service allowed natural disturbance patterns to reestablish. I then move to a highly altered system, the Central Valley of California, where widespread conversion of land to agriculture has greatly disrupted the processes maintaining diversity. There I investigated whether native plant hedgerows can restore habitat heterogeneity, and thus community diversity. Lastly, I used a theoretical approach to determine whether the structure of interactions varied depending on the community's evolutionary history.

Chapter 1

Pyrodiversity begets plant-pollinator community diversity

1.1 Abstract

Fire has a major impact on the structure and function of many ecosystems globally. Pyrodiversity, the diversity of fires within a region (where diversity is based on fire characteristics such as extent, severity and frequency), has been hypothesized to promote biodiversity, but changing climate and land management practices have eroded pyrodiversity. To assess whether changes in pyrodiversity will have impacts on ecological communities, we must first understand the mechanisms that might enable pyrodiversity to sustain biodiversity, and how such changes might interact with other disturbances such as drought. Focusing on plant-pollinator communities in mixed conifer forest with frequent fire in Yosemite National Park, California, we examine how pyrodiversity, combined with drought intensity, influences those communities. We find that pyrodiversity is positively related to the richness of the pollinators, flowering plants, and plant-pollinator interactions. On average, a 5% increase in pyrodiversity led to the gain of approximately one pollinator and one flowering plant species and nearly two interactions. We also find that a diversity of fire characteristics contributes to the spatial heterogeneity (β -diversity) of plant and pollinator communities. Lastly, we find evidence that fire diversity buffers pollinator communities against the effects of drought-induced floral resource scarcity. Fire diversity is thus important for the maintenance of flowering plant and pollinator diversity, and predicted shifts in fire regimes to include less pyrodiversity compounded with increasing drought occurrence will negatively influence the richness of these communities in this and other forested ecosystems. In addition lower heterogeneity of fire severity may act to reduce spatial turnover of plant-pollinator communities. The heterogeneity of community composition is a primary determinant of the total species diversity present in a landscape and, thus, lower pyrodiversity may negatively affect the richness of plant-pollinator communities across large spatial scales.

1.2 Introduction

Understanding the mechanisms underlying the maintenance of biodiversity in natural and human dominated systems is critical to conservation and restoration. One fundamental and widely supported theory of biodiversity in biogeography is the idea that diversity begets biodiversity (Rosenzweig, 1995; MacArthur & MacArthur, 1961; Hutchinson, 1959). The “causal” diversity here might take the form of environmental heterogeneity which could promote coexistence by facilitating resource partitioning (MacArthur & MacArthur, 1961; MacArthur & Levins, 1964), or it might correspond to some aspects of biodiversity promoting other components (Whittaker, 1972; Thompson, 2005) via interactions across trophic levels (Janz *et al.*, 2006). Disturbance diversity is also thought to promote biodiversity because shifting environmental conditions discourage dominance (i.e., the intermediate disturbance hypothesis: Martin & Sapsis, 1992; Connell, 1978; Huston, 1979). All of these mechanisms can also interact to enhance or suppress their individual effects (e.g., Collins *et al.*, 2007; Kane *et al.*, 2015; Rosenzweig, 1995).

Fire is a disturbance that has the potential to affect biodiversity patterns both directly and indirectly via interactions between biotic and environmental heterogeneity (Martin & Sapsis, 1992; Parr & Andersen, 2006; Maravalhas & Vasconcelos, 2014; Davies *et al.*, 2012; Kane *et al.*, 2015; Collins *et al.*, 2007). A fire regime

is characterized by the frequency, severity, patch size, extent, and season of fire. Fires regimes have landscape-scale consequences for fire patterns and biotic and abiotic diversity in space and time. All of these factors can be influenced by both biotic and abiotic diversity including topographic heterogeneity and forest structure (Collins *et al.*, 2007; Kane *et al.*, 2015). A landscape with a diverse fire history — high “pyrodiversity” (Martin & Sapsis, 1992) — will be characterized by significant local variation in fire history whereby adjacent patches will not have identical fire histories. This variation can generate diversity in ecological niches across space and time, thereby allowing a greater number of species to coexist (Martin & Sapsis, 1992; Parr & Brockett, 1999; Burrows, 2008). In addition, if pyrodiversity increases biodiversity, this may in turn influence subsequent fires, creating a feedback that might beget additional diversity (Parr & Brockett, 1999; Burrows, 2008). For example, pyrodiversity can create a mosaic of different successional stages, allowing flora and fauna associated with those different stages to coexist. If areas with unique fire histories support unique communities, the diversity of fire histories through space contributes to the spatial heterogeneity of communities and the turnover of species, i.e., β -diversity (Farnsworth *et al.*, 2014; Burkle *et al.*, 2015). Communities that are spatially heterogeneous in their composition support more regional diversity than areas with little species turnover (Farnsworth *et al.*, 2014).

Fire, however, also acts as an environmental filter by selecting for species that can tolerate disturbances (Cavender-Bares & Reich, 2012). Whether there is an opportunity for “pyrodiversity to beget biodiversity” has, thus, been challenged by findings that some taxa do not respond to fine-scale variation in fire histories (Andersen *et al.*, 2014; Parr & Andersen, 2006; Farnsworth *et al.*, 2014). In addition, factors associated with land management such as logging, grazing and fire suppression and their interaction with the effects of climate change such as drier summers, have acted to decrease pyrodiversity by leading to larger, homogeneous and higher severity burns (e.g., Moritz *et al.*, 2012; Noss *et al.*, 2006; Dellasala *et al.*, 2004; Miller, 2012). To assess whether changes in pyrodiversity will have impacts on ecological communities, we must first understand the mechanisms that might enable pyrodiversity to sustain biodiversity.

The preservation of species interactions is of particular concern because, through the mechanism of biodiversity begetting biodiversity, these interactions have the capacity to generate and maintain biodiversity (Thompson, 2005). Plant-pollinator interactions are particularly ubiquitous, with animal pollination positively influencing the reproduction of 87% of all flowering plant species (Ollerton *et al.*, 2011a). Pollination systems, however, are under increasing anthropogenic threats from land-use change, habitat fragmentation, pesticide use, and invasions of non-native plants and animals (Kearns *et al.*, 1998; Potts *et al.*, 2010).

Though fire directly affects resources that are critical for sustaining pollinator populations, such as floral communities, our understanding of how pollinator communities assemble in response to fire is limited (Winfree *et al.*, 2009; Thom *et al.*, 2015). Past work has shown that secondary succession after fire can increase the abundance of floral resources which can, in turn, lead to higher diversity and abundance of bees (Potts *et al.*, 2003b,a, 2001; Vulliamy *et al.*, 2006; Van Nuland *et al.*, 2013; Campbell *et al.*, 2007; Grundel *et al.*, 2010). Fire can also affect nest-site availability by increasing the abundance of key nesting resources, such as bare ground and cavities in dead wood (Potts *et al.*, 2005a). Pyrodiversity may also play an important role in sustaining pollinator diversity because pollinators differ in their degree of direct susceptibility to fire (Cane & Neff, 2011). Few studies have, however, explored the effects of fire on pollinators in forested ecosystems where altered fire regimes may have the greatest impact. This lack is likely because fire regimes are so altered by human activities (Miller, 2012) that there are few landscapes where it is possible to study the interaction between natural fire patterns and wildlife communities.

In addition to understanding the direct effects of pyrodiversity on communities, we must also examine how pyrodiversity might interact with the types of disturbances that we expect to become more frequent in the future. Future climate projections predict in some regions droughts, of both long and short duration, to double and triple, respectively (Sheffield & Wood, 2008). Drought has far-reaching effects on forested ecosystems (Dale *et al.*, 2001), and affects pollinators by diminishing availability of pollen and nectar resources (Rashad & Parker, 1958; Iserbyt & Rasmont, 2012) and may also cause shifts in the composition of pollinator communities and even extinction (Minckley *et al.*, 2013; Ehrlich *et al.*, 1980). If drought interacts with fire history such that resources are differentially affected in different areas, pyrodiversity may be important to buffer the impacts of resource scarcity.

Here, we utilize a landscape with a restored fire regime in Yosemite National Park to test whether landscape diversity, in the form of environmental diversity or pyrodiversity, contributes to the maintenance of plant-pollinator biodiversity. We first determine whether pyrodiversity or the diversity of environmental conditions (solar radiation, water availability and soil condition) affects local flowering plant and pollinator richness. In addition, to test whether landscape diversity has the potential to maintain biodiversity through promoting species interactions, we examine the relationship between landscape diversity and the richness of plant-pollinator interactions. Next, we determine whether different fire characteristics, mainly fire severity, has the potential to contribute to regional

plant-pollinator diversity through affecting community spatial heterogeneity. Lastly we examine whether fire diversity buffers pollinator communities against drought-induced resource scarcity. Our study is the first to examine the potential of fire diversity to sustain the plant-pollinator biodiversity, as well the first to examine the response of species interactions to pyrodiversity.

1.3 Methods

STUDY SITES AND COLLECTION METHODS

Our study is located in the Illilouette Creek Basin of Yosemite National Park, in the central Sierra Nevada of California. The basin is approximately 20,000 hectares, and has never been harvested or grazed. The Illilouette is in the upper elevation mixed-conifer zone and is dominated by Jeffrey pine (*Pinus jeffreyi*), white fir (*Abies concolor*), red fir (*Abies magnifica*), and lodgepole pine (*Pinus contorta* var. *murrayana*), interspersed with meadows and shrublands. Based on tree-ring reconstructions, the historic fire regime predominantly consists of frequent fires, where the alteration of vegetation and soils, known as fire severity, is low to moderate (Collins & Stephens, 2010). Fire was suppressed from the late 1800s until the early 1970s, when Yosemite National Park adopted a “let burn” management strategy. Lightning-ignited fires are allowed to run their course, restoring natural fire regimes to the basin and creating a patchwork of burns of varying severities and ages. Because of the unique fire management of the Illilouette Basin, it has a long history of research on the dynamics of frequent fires in forested ecosystems (Collins & Stephens, 2010, 2007; Collins *et al.*, 2007; van Wagtenonk *et al.*, 2012). Importantly, studies have found that after only 30 years of allowing lightning-ignited fires to burn, the historic fire regime and forest structure have been largely restored to the basin (Collins & Stephens, 2007).

In 2013, we established 18 monitoring sites, each (50 m)², across the Illilouette Basin. Monitoring sites were separated by an average of 4 km and a minimum of 500 m (greater than the foraging distance of most bees, Gathmann & Tschardt, 2002). Sites were split between two fires, one that burned in 2001, and the other in 2004.

Within each fire perimeter, sites were chosen randomly by selecting coordinates from a 100 m grid (within 2 km of a trail), but stratified to include different burn severities of the most recent fire. The severity of a burn not only influences changes to soil chemistry and vegetation, but can also affect the plant community that develops (Swanson *et al.*, 2010; Turner *et al.*, 1999; Wang & Kembell, 2005). We sampled across different fire severities so that we could explore the interaction between fire severity and plant/pollinator community assembly. Burn severity was classified according to the Relative difference Normalized Burn Ratio (RdNBR Miller & Thode, 2007) at a (30 m)² resolution and six predominantly high, five moderate, and seven low burn severity were selected (Fig. 1.1c). High severity sites had open canopies due to high rates of tree mortality following the fire and high soil disturbance from the fire. Moderate severity sites also had open canopies, but less tree mortality and soil disturbance. Low severity sites had little soil disturbance or tree mortality.

We sampled pollinator communities between June and August in 2013 and 2014. Each year, sites were sampled four times. Sampling began earlier in 2014 to account for the timing of the snow melt. In each round of sampling, the order in which sites were sampled was randomized. Surveys were conducted under sunny conditions when the temperature was above 12°C and wind speed was below 2.5 meters/second. Flower-visitors were netted for 1.5 hours of active search time (the timer was paused while handling specimens). In addition, five sets of fluorescent blue, white, and fluorescent yellow pan traps (15 total) were set 12.5m apart in two lines forming an “X” for 4.5 hours following established protocols (modified from LeBuhn *et al.*, 2003). Pans were placed in clusters of three with one pan of each color.

All insect flower visitors that touched the reproductive parts of the flower and insects that entered the pan traps were collected; however, here we focus only on bees, the most abundant and efficient pollinators in the system. Bee specimens were identified to species (or morpho-species for the genera *Hylaeus*, *Nomada* and *Sphcodes* and *Lasioglossum* subgenus *Dialictus*). Expert taxonomist Jason Gibbs aided with assigning the morpho-species classifications to males and females.

Floral resources were also surveyed each time pollinators were sampled. To do this, each blooming plant species (excluding graminoids) in the monitoring site was recorded. We did not record plants that bloomed outside of the flight season of the pollinators (e.g., early season plants like *Arctostaphylos*) or night-blooming flowers because they are not as likely to interact with the pollinator community we sampled. For each blooming species, an estimate of the number of inflorescences within the sampling area was also recorded (estimated on a log scale). To make an estimate, the site was divided into quadrants and the number of inflorescences of each species was counted, then summed for an estimate of the site.

During our collection period, the Sierra Nevada experienced a drought that began in 2012 (Griffin & Anchukaitis, 2014). In 2013 the intensity of the drought in our study area was categorized as “severe” (Griffin & Anchukaitis, 2014). In 2014, the drought conditions were upgraded to “extreme” and “exceptional” — the highest moisture deficit accumulation than any previous recorded span of years (Griffin & Anchukaitis, 2014). In the field, the difference between 2013 and 2014 was clear; water levels were lower in the streams and rivers throughout the season and there were few of the usual summer lightning storms. In addition, perennial plants like *Ceanothus cordulatus* experienced die back from exposure to freezing temperatures because of insufficient snow pack. Many plants that bloomed in 2013 did not in 2014 and many areas the blooming period was cut short. We therefore contrast the communities in 2013 and 2014 to determine the influence of drought intensity on flowering plant and pollinator communities. This test is not replicated in time and factors other than drought intensity changed. However, given the known effects of drought on plant and pollinator communities and the drastic decline in water availability between 2013 and 2014, we assume the majority of the shifts in the communities between these years were due to the increase in drought intensity.

PYRODIVERSITY

To estimate pyrodiversity, we developed a metric to quantify the diversity of the fire histories in relation to fire frequency, age, extent and severity experienced in an area. We obtained fire history data of our study area, dating back to 1984, from Yosemite National Park and the United States Forest Service (van Wagtenonk *et al.*, 2012; Miller, 2012; Yosemite National Park, 2012). Each fire digitization contains rasterized values of burn severity (Miller & Thode, 2007). Fire season, another component of fire history, was not directly considered. There was, however, little variability in fire season within any one fire, and most fires occurred in different months. Thus, season is indirectly included in the identity of each fire.

To estimate pyrodiversity, we evaluated the uniqueness of the fire history of each raster cell (30 m)² resolution, Fig. 1.1a). We first created categories of fire severity within a fire (Miller, 2012). For each raster cell, we then used the sequence of fires and the severity of each of those fires to define unique fire histories. We identified 135 unique fire histories in the basin. We then considered two different ways of characterizing pyrodiversity as the diversity of unique fire histories either unweighted or weighted by their similarity. To calculate the unweighted pyrodiversity score, raster cells received different categories if they differed in any aspect of fire history; for example, if they were burned by the same fire but at different severities, or if they were burned by different fires, even if at the same severity. Pyrodiversity was then calculated as the Simpson’s diversity of fire history categories (the compliment of the sum of the squared proportion of each fire history category) around a monitoring plot within 100 m – 250 m buffers in increments of 50 m (Fig. 1.1, Tschardt *et al.*, 2005). This allowed us to evaluate the scale at which pyrodiversity affected plant and pollinator communities most strongly.

To calculate the weighted pyrodiversity score, we transformed fire characteristics, mainly the year the fire occurred and severity, into traits for each pixel and then used a functional dispersion metric to calculate the diversity of fire “traits” (see Section 1.6.1). The fire histories of each raster cell were thus weighted based on the similarity of fire traits. For example, a low severity pixel in the same fire would be more similar to a moderate severity pixel than to a high severity pixel. Fire traits were also weighted by the number of years since the fire occurred to account for the variety of fire ages. Like the unweighted pyrodiversity, we calculated the weighted pyrodiversity score within different buffer sizes around the survey sites.

To determine the effect of pyrodiversity on flowering plant and pollinator communities and their interactions, we built generalized linear mixed models that reflected our biological hypotheses (Bates *et al.*, 2014). We included richness of bees, flowers and interactions (the unique combination of bee and floral species observed interacting in netted samples) in each sample as response variables and pyrodiversity (either weighted or unweighted) as an explanatory variable. Because fire severity can have strong effects on the plant communities that develop after fire (Swanson *et al.*, 2010; Turner *et al.*, 1999; Wang & Kembell, 2005), we included an interaction between pyrodiversity and fire severity of the most recent fire to allow the response of the flowering plant and pollinator communities to pyrodiversity to depend on the most recent fire’s severity. Because the sites were split between fires that burned only three years apart, we did not have sufficient variation in the time since the most recent fire to include it as an explanatory variable.

To test whether the effect of pyrodiversity on plant and pollinator communities is mediated by drought intensity, we also included an interaction between year, which is interpreted as primarily reflecting a shift in drought intensity, pyrodiversity and fire severity. A significant negative interaction between pyrodiversity and year would indicate that the response of flowering plants, bees and their interactions to pyrodiversity was eroded by increasing drought intensity. In addition, a significant interaction between year, pyrodiversity and the severity

of the most recent fire would indicate that the response of communities to shifts in climate varies depending on the fire severity of the area.

When considering floral species richness as our response, we included a linear and quadratic day of the year term to allow for a seasonal phenology in flower blooming. We also included a random effect of site in this and all subsequent models. We assumed negative binomial error for pollinator models, and Poisson error for floral models. To facilitate interpretation of coefficients, all continuous variables were scaled by subtracting the mean and dividing by the standard deviation.

Simulations of the null hypothesis (no effect of the explanatory variables) suggested that the models had an inflated type I error rate, approximately equal to 0.1 with a nominal P -value of 0.05 (Ives, 2015); therefore, we used parametric bootstrapping to quantify support for a model that includes pyrodiversity, an interaction between pyrodiversity and fire severity, and an interaction between pyrodiversity, fire severity and drought intensity in the models (Booth, 1995). All statistical analyses were conducted in R version 3.2 (R Core Team, 2015).

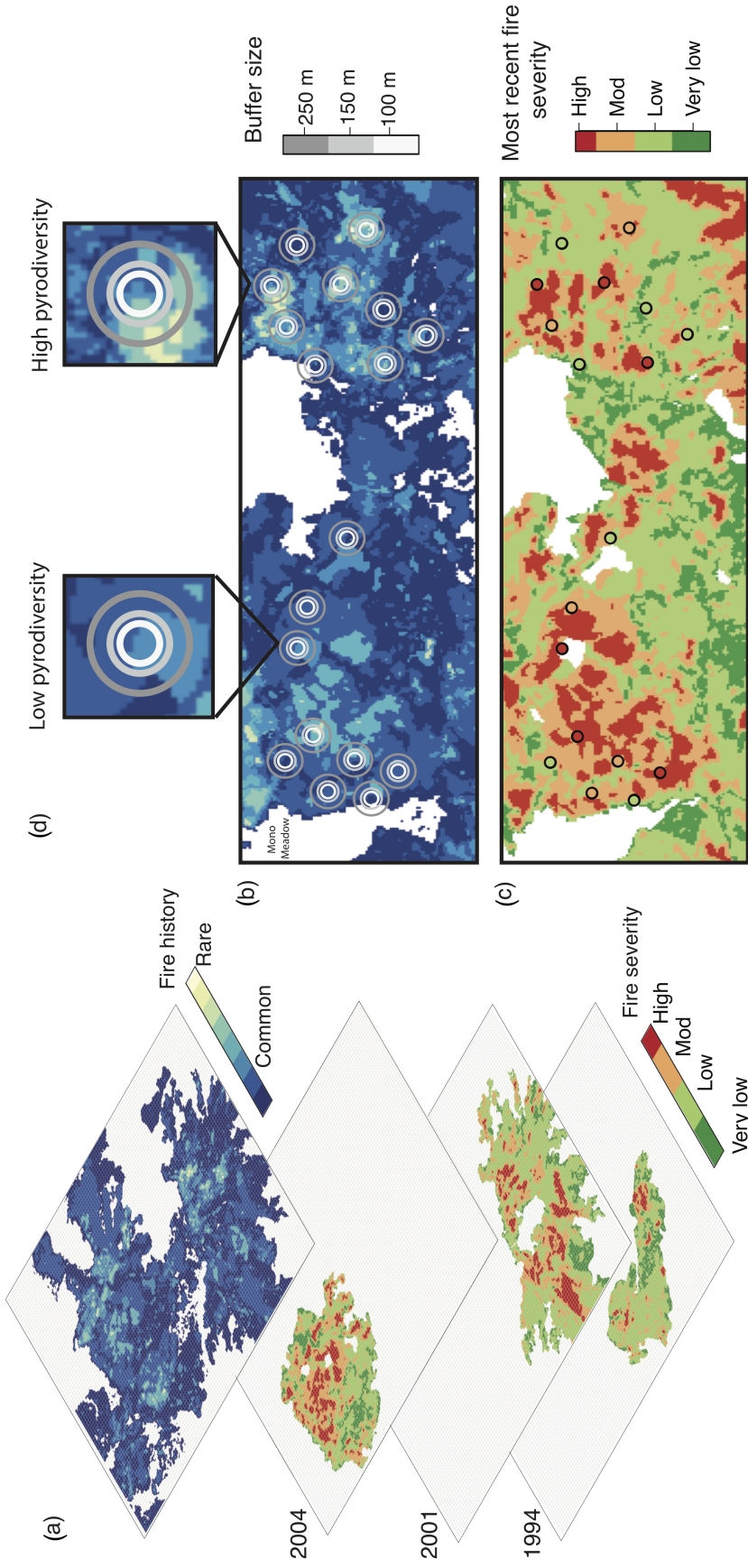


Fig. 1.1: Representation of the method used to estimate pyrodiversity. a) Each raster cell is assigned a fire history classification based on the fires and severities it experienced (three representative fires depicted). b) The diversity of fire histories, either weighted for the similarity of fire history or unweighted, is calculated within buffers 100 – 250 m around the monitoring sites. c) The severity of the most recent fire is also included as a possible interaction with pyrodiversity. d) An example of sites with relatively low and high pyrodiversity measured as the diversity of unique fire histories at different buffer sizes. In the low pyrodiversity example, the pyrodiversity was estimated as 0.2, 0.5, and 0.7 within the 100, 150, and 250 m buffers, respectively. In the high pyrodiversity example, the pyrodiversity was estimated as 0.7, 0.8, and 0.8 in buffers of increasing diameter. Within a buffer, the number of different fire history categories ranged from 1 to 23. Larger buffer sizes were not included because there was considerable overlap between buffers around different sites beyond that threshold. Smaller buffers were also not included because, at scales smaller than 100 m most buffers only contained one fire history category (i.e., a pyrodiversity score of 0). Some buffers overlapped areas that did not burn during the time period for which we have burn history data (i.e., Mono Meadow, large rocky outcrops and fires that occurred before 1984). Those areas were assigned their own fire history category.

ENVIRONMENTAL HETEROGENEITY

We hypothesized that plant-pollinator communities would likely respond to solar radiation, water availability and soil conditions. We therefore considered the effect of the following three measures of environmental heterogeneity (see Sec. 1.6.1 for details): heat load (i.e., McCune's solar radiation, an estimate of solar radiation taking latitude, slope and aspect into account, McCune & Keon, 2002) and topographic compound index (an estimate of the balance between water accumulation and drainage, Evans *et al.*, 2014).

As we did for our metric of pyrodiversity, we calculated the diversity of environmental conditions in buffers of different sizes and used this estimate as a metric of environmental heterogeneity for each variable (see Sec. 1.6.1). We considered weighted environmental heterogeneity only because the variables are not naturally categorical. We also could not create a composite metric across all environmental variables because there were too many unique combinations of variables to yield meaningful measures of diversity.

To examine the effect of environmental heterogeneity on flowering plant and pollinator communities, we followed the same approach as we did when examining the influence of pyrodiversity. With bee, floral or interaction richness as response variables, each environmental heterogeneity measure, along with terms for interactions between that environmental variable and severity of the most recent fire as well as drought intensity were included as explanatory variables. Parametric bootstraps were used to determine the support for including the environmental heterogeneity and the interaction between environmental heterogeneity, drought and fire severity in the model.

β -DIVERSITY

Pyrodiversity may also influence the regional diversity of an area by affecting the spatial heterogeneity of communities. If areas that experienced different fire characteristics support distinct communities, this will lead to species turnover (β -diversity). Similarly, communities with similar fire characteristics may share many species, leading to less spatial heterogeneity between those communities. We investigated the flowering plant, pollinator and interaction β -diversity between communities with different fire characteristics and compared that to the β -diversity between sites with similar fire characteristics. Because of its strong effects on site conditions, we focused on the severity of the most recent fire in order to group communities by fire similarity.

We first calculated the pairwise dissimilarity in plants, pollinators and interactions between site pairs across all sites and within each fire severity classification (calculated using the Jaccard index of dissimilarity, a proxy for species turnover through space. We also standardized turnover estimates to account for differences in the richness between sites (see Section 1.6.2 for details).

For the community dissimilarity across and within fire severity classifications, we regressed pairwise community dissimilarity against geographic distance using linear mixed models (Bates *et al.*, 2014; Kuznetsova *et al.*, 2014). A positive relationship between community dissimilarity and geographic distance would suggest that communities were spatially structured such that communities that are closer together share more species than communities that are farther apart.

Additionally, in the model of dissimilarities within a fire severity classification, we included an interaction between pair-wise site distances and the fire severity of the site-pair to allow the different site types to have different rates of turnover through space. A significant interaction with the severity of the most recent fire and the geographic distance between communities would indicate that the rate of species turnover was influenced by fire severity.

Lastly, if the positive relationship between geographic distance and community dissimilarity is stronger between all sites than between sites of the same fire severity, this would be evidence shared fire severity between sites increases the similarity of these communities. Thus a diversity of fire characteristics would contribute positively to the dissimilarity between sites and subsequently β -diversity.

RESOURCE AVAILABILITY AND USE

We next investigated whether fire diversity has the potential to buffer against drought-induced resource scarcity. We first asked whether the floral resources in areas with contrasting fire characteristics responded differently to drought. We again focused on severity of the most recent fire to contrast the fire characteristics of an area. We used the total number of inflorescences of each plant species as a proxy for floral resource availability.

To determine whether fire severity influenced the effect of drought on resource availability, we asked whether floral resources depended on the interaction between severity of the most recent burn and year, assuming that the resource differences between years are primarily attributable to the shift in drought intensity. We also

included a linear and quadratic term for day of the year to account for floral phenologies. The measurements of floral abundance were taken at the level of flowering plant species, so we included a random effect of plant species to account for differences in the number of inflorescences across species. We log-transformed floral abundance and assumed a Gaussian error distribution. A negative effect of year would indicate that floral resources were decreased in a more extreme drought year, and an interaction with fire severity would indicate that that magnitude of the effect of drought was influenced by fire characteristics.

Fire severity may also buffer against the effects of resource scarcity by influencing the way pollinator resource use is altered by drought. Limited floral resources might cause pollinators to visit less preferred resources or shift the pollinator community composition to favor generalists. If different fire severity areas are differentially affected by drought, however, some areas may be able to maintain a more stable level of interaction specialization through shifts in resource availability. We therefore first determined whether bee community specialization differed between years to look for an effect of drought intensity, and whether there was evidence for an interaction effect between year and the severity of the most recent fire.

To investigate this, we created plant-pollinator interaction networks for each survey day. We then calculated community-level specialization (H2, Blüthgen *et al.*, 2006). This specialization metric measures the deviation of the observed interaction frequency between plants and pollinators from a null expectation where all partners interact in proportion to their abundances (Blüthgen *et al.*, 2006). To standardize the metric across communities with different numbers of species and abundance distributions, we also corrected the specialization estimates using the expected specialization of randomly assembled communities with the same species richness, species' abundances, and interactions per species (Blüthgen *et al.*, 2006; Vázquez *et al.*, 2007). To detect changes in specialization across years, we used the community-level specialization scores as the response variable in a linear mixed model that included a term for the interaction between fire severity and year. A negative effect of year would suggest that pollinators were more generalized in a more extreme drought year, and an interaction with fire severity would indicate that the shift in foraging behavior was influenced by fire characteristics.

Fire severity might also affect pollinator resource use and its interaction with drought by influencing the spatial distribution of pollinators in relation to their floral hosts. If pollinator communities track floral resources, differences in floral community composition between sites should lead to corresponding differences in pollinator communities. Fire severity may also interact with this process if, for example, only high severity areas support plants that primarily attract the specialized pollinators that are most likely to track the distribution of their floral hosts. Thus high severity pollinator community composition would be most strongly correlated with floral host composition. Drought might enhance or diminish this pattern in areas with specific fire severities, depending on its effect on pollinator community specialization.

To investigate this hypothesis, we tested for an interaction between year and fire severity on patterns of pollinators tracking specific floral resources across space. We correlated the floral community dissimilarities to analogous dissimilarities for the pollinator communities using Mantel tests, analyzing each year separately. We did this within and across communities in different burn severities to determine whether pollinators tracked resources differently depending on the severity of the most recent fire. We used an abundance-based measure to estimate the dissimilarity of plant and pollinator communities (Chao *et al.*, 2005a).

1.4 Results

Over two years and across 18 sites, we collected 7626 bee specimens comprising 162 species or morphospecies across 32 genera. We observed pollinator visitation on 71 flowering plant species. We observed 1213 unique plant-pollinator interactions (10.5% of potential interactions). Over one thousand specimens were collected in each of the genera *Bombus*, *Lasioglossum* and *Hylaeus*. The most species rich genera were *Osmia* (36 species), *Andrena* (19 species), *Lasioglossum* (12 species or morphospecies) and *Megachile* (12 species). Approximately 20% of the bee species were observed only once, and approximately 40% of species were collected fewer than five times, rates that are consistent with what is found in other, even longer-term studies (e.g., M'Gonigle *et al.*, 2015; Petanidou *et al.*, 2008a; Olesen *et al.*, 2008). In addition, in a four-year survey across all of Yosemite National Park, T. Griswold and colleagues collected around 520 bee species and morphospecies, and in our survey we collected 30% of those species. All plant and pollinator species were native except the European honey bee, *Apis mellifera*, which was common throughout the basin. Around 800 (11%) of collected specimens were honey bees.

PYRODIVERSITY

Pyrodiversity, both weighted and unweighted by the similarity of fire histories, positively affected floral, pollinator and interaction richness, though the strength of the effect depended on the scale at which pyrodiversity was calculated (Figs. 1.2, 1.7). The effect size of both metrics of pyrodiversity peaked within 150 m of the monitoring area (Tabs. 1.1, 1.3). Within this buffer, the unweighted diversity of fire histories ranged from 0.25 to 0.85 and weighted diversity from 0.03 to 0.13 (both with hypothetical ranges from 0 – 1). In addition, unweighted pyrodiversity at a 150 m scale explained significant variation in the plant, pollinator and interaction richness. Weighted pyrodiversity interacted with the severity of the most recent fire and, for pollinators and plant-pollinator interactions, pyrodiversity also interacted with drought intensity (Table 1.1). Weighted pyrodiversity showed similar trends, though the significance was marginal (Table 1.3). Because the trends were similar but unweighted pyrodiversity showed a stronger effect, we focus on the response of communities to unweighted pyrodiversity.

In areas where the most recent fire was low or moderate in severity, pyrodiversity had a positive effect on bee, floral and interaction richness (Table 1.2, Fig. 1.2). This translates into a mean gain of 54–58 bee species (~35% of the observed bees), 8–14 flowering species (~20% of flowering plants), and 24–43 interactions (~4% of interactions) between areas with the minimum and maximum observed pyrodiversity. In areas where the most recent fire was high in severity, however, floral, pollinator and interaction richness did not respond to pyrodiversity (Table 1.2, Fig. 1.2).

High severity areas, however, had higher plant, pollinator and interaction richness than low severity areas at mean levels of pyrodiversity (i.e., at pyrodiversity = 0, Fig. 1.2, estimate \pm bootstrapped standard error of the estimate of the difference between low and high severity sites bee richness, 2.171 ± 0.17 ; plant richness, 0.440 ± 0.21 ; interaction richness, 0.532 ± 0.28). This corresponds to an average of 5 more pollinator and plant species and 9 more interactions in high severity sites than in low severity sites. Moderate severity sites also had higher pollinator and floral richness than low severity sites (bee richness, 1.545 ± 0.18 ; plant richness, 0.300 ± 0.22). In moderate severity sites, there was an average of 4 more plant and pollinator species than in low severity sites.

There was a significant effect of year on bee and interaction richness, suggesting a negative effect of drought (estimate for the difference between 2013 and 2014 \pm standard error of the estimate, bee richness: -0.330 ± 0.09 ; interaction richness: -0.625 ± 0.09). This resulted in 3, 3, and 7 fewer bee species and 6, 6 and 8 fewer interactions in low, moderate, and high severity sites respectively. The decline in interaction richness in moderate severity sites was buffered in these sites where the difference between years was less pronounced (estimate for interaction between moderate site severity and year \pm standard error of the estimate, 0.315 ± 0.12).

In contrast, floral richness in low and moderate severity sites was not significantly reduced in the more extreme drought year, but it was in high severity sites (estimate of the decline in floral richness, -0.28 ± 0.14 , Fig. 1.2). Species richness in high severity areas declined by an average of 3 flowering species.

Response of bee and interaction richness to pyrodiversity was weaker in the more intense drought year, and the magnitude of the difference was higher in areas where severity of the last burn was low or moderate (Table 1.1; compare the slope of moderate and low in 2013 vs. 2014, Table 1.2; compare first and second panels, Fig. 1.2). The interaction of year and the relationship between floral richness and pyrodiversity was not significant (Table 1.1, Fig. 1.2).

Table 1.1: The support for including pyrodiversity of unique fire histories and its interaction with fire severity and drought intensity. χ^2 values represent the ratio of the likelihoods of the model with and without the variable of interest. P -values are calculated via 1000 parametric bootstrap iterations. They represent the probability of observing a χ^2 value more extreme than the observed value when data is simulated from the model without the variable of interest. Symbols denote significance, with ' and * indicating 0.1 and 0.05, respectively. Significant terms are bolded.

	Buffer radius	No interaction		Severity interaction		Severity, drought interaction	
		χ^2	P -value	χ^2	P -value	χ^2	P -value
Bee Richness	100	3.984	0.084'	6.818	0.193	12.765	0.122
	150	5.905	0.030*	10.074	0.072'	17.044	0.034*
	200	4.402	0.065'	7.517	0.163	12.467	0.140
	250	1.932	0.217	3.528	0.496	8.786	0.298
Floral Richness	100	2.06	0.222	6.91	0.186	9.341	0.280
	150	3.969	0.104	13.213	0.025*	13.84	0.064'
	200	3.101	0.123	8.269	0.132	8.442	0.318
	250	0.923	0.406	2.662	0.602	2.697	0.901
Interaction Richness	100	3.996	0.081'	6.877	0.170	15.009	0.067'
	150	5.897	0.047*	10.187	0.080	19.52	0.020*
	200	4.393	0.058'	7.563	0.161	14.427	0.078'
	250	1.940	0.248	3.582	0.487	10.903	0.179

Table 1.2: The estimate and standard error of the slope of bee , floral and interaction richness against pyrodiversity. Terms where the 95% confidence interval around the parameter estimate did not overlap zero (indicated in bold) were inferred to explain significant variation in floral, bee or interaction richness (using the parametric bootstrap). Standard errors of the parameter estimates are calculated as the standard deviation of the parametric bootstrap estimates of the coefficient of interest (Booth, 1995).

	Buffer radius	Year	Low	Mod	High
Bee Richness	100	2013	0.22 ± 0.122	0.408 ± 0.18	0.021 ± 0.105
	150	2013	0.326 ± 0.125	0.337 ± 0.148	-0.012 ± 0.115
	200	2013	0.196 ± 0.094	0.439 ± 0.188	-0.026 ± 0.141
	250	2013	0.144 ± 0.093	0.411 ± 0.219	-0.043 ± 0.138
	100	2014	0.044 ± 0.124	0.238 ± 0.176	0.076 ± 0.110
	150	2014	0.152 ± 0.127	0.16 ± 0.155	0.06 ± 0.113
	200	2014	0.086 ± 0.102	0.238 ± 0.192	0.066 ± 0.138
	250	2014	0.054 ± 0.099	0.132 ± 0.217	0.043 ± 0.141
Floral Richness	100	2013	0.095 ± 0.133	0.457 ± 0.201	-0.001 ± 0.122
	150	2013	0.317 ± 0.137	0.329 ± 0.173	-0.078 ± 0.125
	200	2013	0.161 ± 0.110	0.45 ± 0.210	-0.054 ± 0.152
	250	2013	0.102 ± 0.110	0.294 ± 0.249	-0.057 ± 0.158
Interaction Richness	100	2013	0.318 ± 0.185	0.769 ± 0.291	0.003 ± 0.183
	150	2013	0.543 ± 0.201	0.59 ± 0.245	-0.033 ± 0.174
	200	2013	0.318 ± 0.159	0.821 ± 0.3	-0.054 ± 0.216
	250	2013	0.224 ± 0.148	0.806 ± 0.357	-0.076 ± 0.239
	100	2014	0.272 ± 0.207	0.444 ± 0.296	0.084 ± 0.174
	150	2014	0.485 ± 0.209	0.325 ± 0.235	0.045 ± 0.179
	200	2014	0.307 ± 0.164	0.406 ± 0.309	0.059 ± 0.218
	250	2014	0.229 ± 0.155	0.18 ± 0.357	0.038 ± 0.226

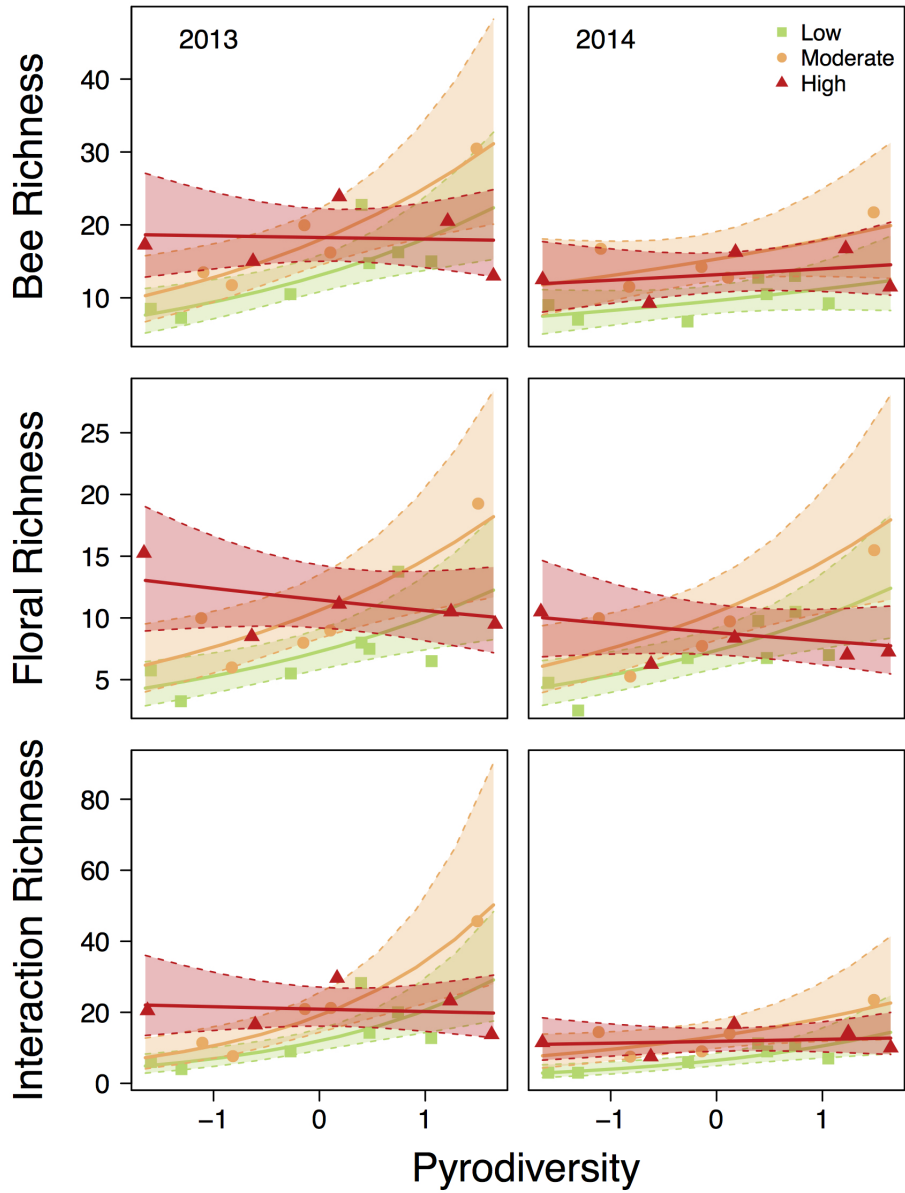


Fig. 1.2: The response of bee, floral and interaction richness to pyrodiversity. The color of the curves and points correspond to low, moderate, and high severity of the most recent fire classifications. The columns depict trends in 2013 and 2014, severe and extreme/exceptional drought years, respectively. The solid line indicates the mean slope estimate and the dashed lines are the 95% confidence intervals around the estimate. Points represent the richness of plants, pollinators or interactions averaged across the study season. The pyrodiversity axis is scaled so that zero represents the mean pyrodiversity.

ENVIRONMENTAL HETEROGENEITY

Plant and pollinator communities did not respond to the measures of environmental heterogeneity we considered at any scale, except there was a negative relationship between bee and interaction richness and heat load diversity at a buffer size of 200m and 250m (Tabs. 1.4, 1.5, Fig. 1.8).

β -DIVERSITY

The dissimilarity between flowering plant communities across the landscape was positively related to the distance between sites (estimate of the slope of dissimilarity with distance across all sites, 0.06 ± 0.026 , p -value = 0.02, Fig. 1.3). In addition, the rate of turnover of floral communities depended on the severity of the fire they experienced (Fig. 1.3). The dissimilarity between floral communities in high severity sites did not respond to the distance between sites, whereas the dissimilarity between communities in low and moderate burn sites increased with distance at the same rate (estimate of the slope of dissimilarity with distance in low and moderate severity areas: 0.18 ± 0.055 , P -value=0.002, Fig. 1.3). The floral community dissimilarity at the mean geographic distance between sites was not significantly affected by burn severity, though the dissimilarity of higher severity sites was higher at the smaller geographic distance between sites.

The relationship between floral community dissimilarity and distance was weaker across all sites than the relationship within moderate and low severity sites. In addition, at the mean distance between sites, the dissimilarity of floral communities between all sites was similar to the dissimilarity between sites that experienced the same fire severity (estimate of the dissimilarity across all sites vs. within the same fire severity, 0.47 ± 0.026 vs. 0.470 ± 0.054). Therefore, floral species turnover between sites across different fire severities is not stronger, on average, than the turnover between sites that experience similar fire histories.

In contrast to the floral communities, bees and interactions were only structured geographically across all sites (estimate of the slope of distance and bee community dissimilarity: 0.046 ± 0.020 , P -value=0.03; interaction dissimilarity 0.053 ± 0.026 , P -value=0.03; Fig. 1.3).

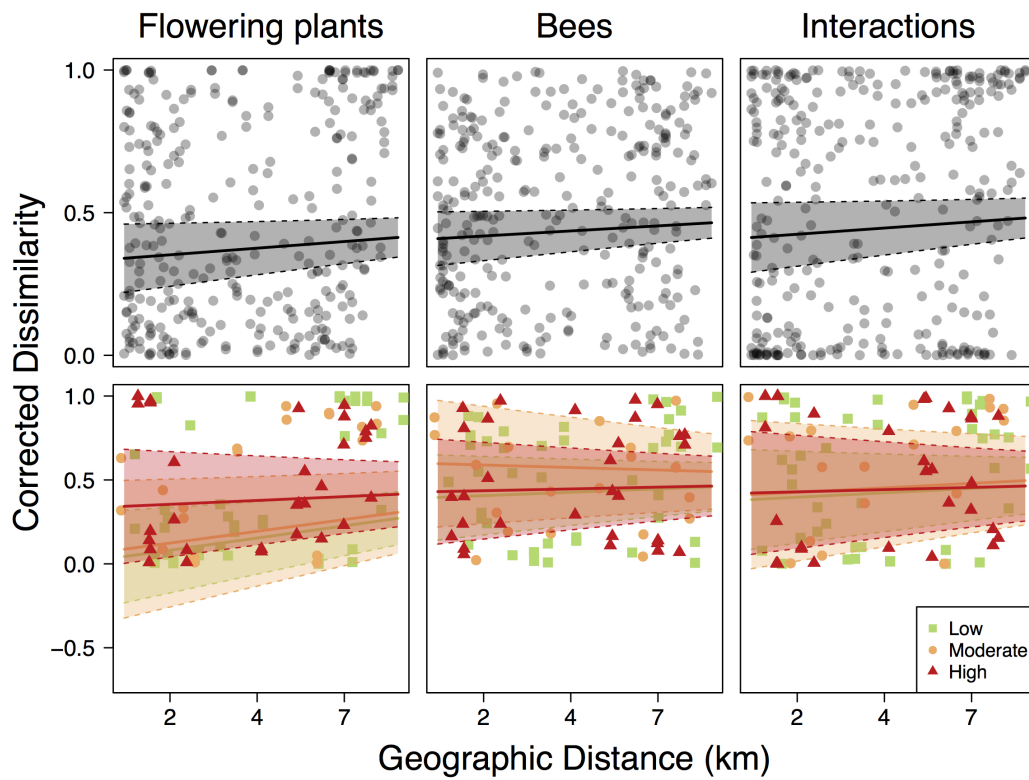


Fig. 1.3: The floral, bee and interaction composition turnover across all sites (top panels) and within a fire severity classification (bottom panels). Points represent the pair-wise dissimilarity of communities (corrected for differences in species richness). The solid line indicates the mean slope estimate and the dashed lines are the 95% confidence intervals around the estimate.

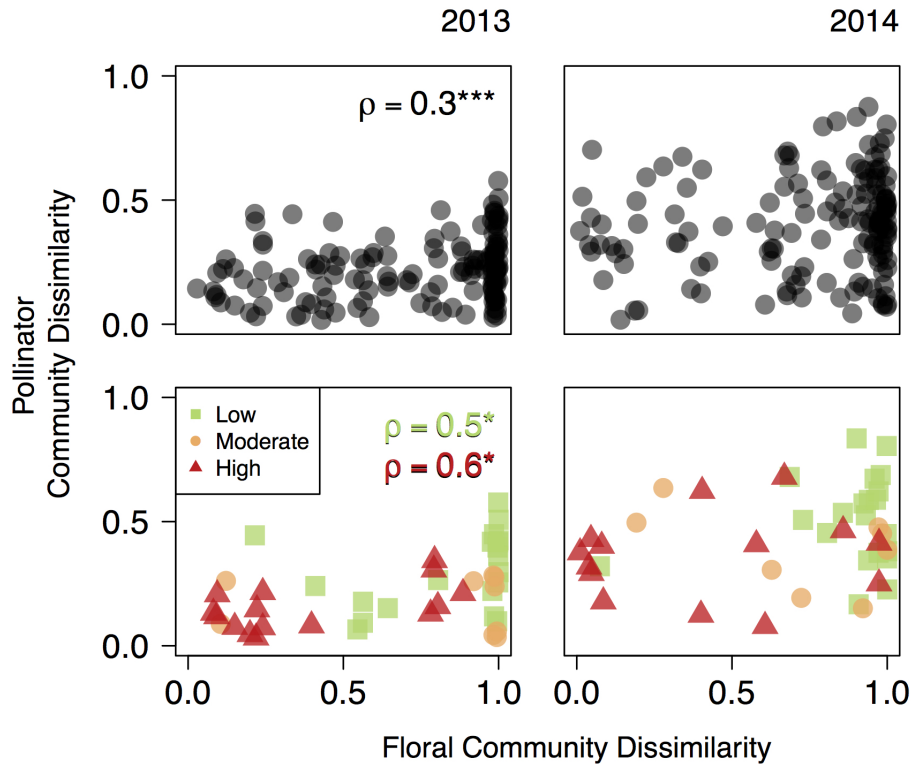


Fig. 1.4: The effect of the more recent fire severity an area experienced and drought intensity on resource use of pollinators across different fire severities (top panels) and between plant and pollinator communities at sites with similar fire histories (bottom panel). ρ corresponds to the Mantel statistic.

RESOURCE AVAILABILITY AND USE

Fire severity affected both availability of floral resources and their diminishment in response to increasing drought intensity. High severity burn areas had higher floral abundance than low severity areas (estimate \pm standard error of the difference between high and low severity sites in log floral abundance, 2.920 ± 1.42 , p -value = 0.05, Fig. 1.9), but flower abundance declined more strongly than in low and moderate severity sites in the extreme drought year (estimate of the decline in floral abundance, -7.60 ± 0.90 , p -value = 10^{-16} , Fig. 1.9). Moderate and low severity sites also declined in flower abundance between years (-3.74 ± 0.96 , p -value = 10^{-5} , Fig. 1.9). Pollinators were significantly more generalized in the more extreme drought year (estimate of the difference in specialization between 2013 and 2014, -0.45 ± 0.21 , p -value = 0.004, Fig. 1.10), though fire severity did not influence this shift.

In addition, drought also disrupted the spatial correspondence between the composition of pollinator and floral communities. Like specialization, however, fire severity did not influence this change. In 2013, across the study landscape, the dissimilarity of pollinator communities was significantly correlated with the plant community ($\rho = 0.3$, p -value = 0.009, Fig. 1.4), suggesting that pollinators track their floral hosts. Additionally, in high and low severity sites, the dissimilarity of plant and pollinator communities were significantly correlated (high: $\rho = 0.6$, p -value = 0.02, low: $\rho = 0.5$, p -value = 0.05, Fig. 1.4). These relationships disappeared in 2014. The dissimilarity of bee communities in areas with moderate severity burns was not significantly correlated with the dissimilarity of flowering plants in either year.

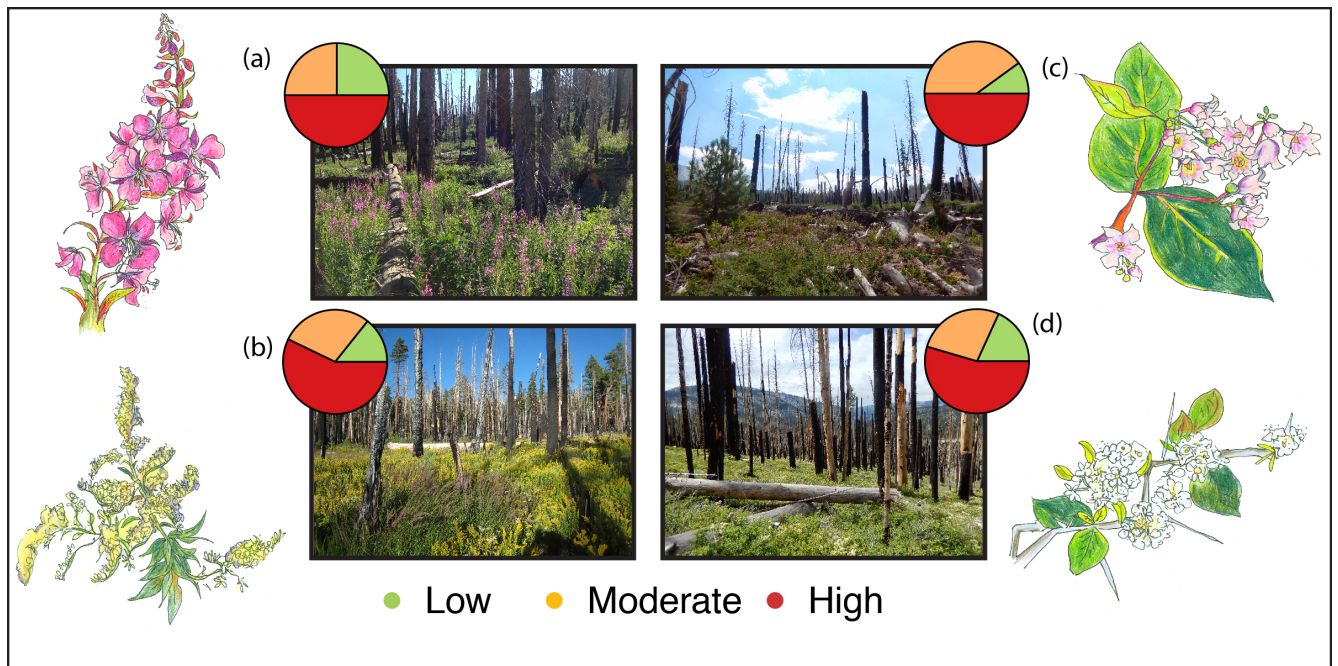


Fig. 1.5: The proportion of sites with disturbance specialists a) *Epilobium angustifloium circumvagum* (fireweed), b) *Solidago canadensis elongata* (goldenrod), c) *Apocynum androsaemifolium* (dogbane), and d) *Ceanothus cordulatus* (mountain whitethorn). *C. cordulatus* is a nitrogen fixer. Photos a),b),d) by L. Ponisio, c) by S. Stephens. Botanical illustrations by T. Norwood.

1.5 Discussion

We have shown that fire diversity contributes to the maintenance of flowering plant and pollinator biodiversity. Plant-pollinator communities in low and moderate severity burn areas with the maximum observed pyrodiversity (as measured by the diversity of fire histories around a site) had 34% more pollinator species, 33% more flowering plant species, and 14% more interactions, on average, than areas with the minimum pyrodiversity. The turnover of pollinators and species interactions between areas with different fire characteristics was also greater than within areas that experienced the same most recent fire severity, suggesting fire characteristic diversity is important for maintaining the spatial heterogeneity of pollinator community composition and plant-pollinator interactions. Lastly, fire severity interacted with drought such that floral resources were differentially affected depending on the severity of the most recent fire, suggesting that the diversity of fire characteristics may buffer the impacts of resource scarcity.

Importantly, however, the severity of the most recent fire interacted with the response of plant-pollinator communities to fire diversity. Flowering plants, pollinators, and their interactions in low and moderate severity burns responded positively to pyrodiversity, whereas communities in high severity burns did not. Similarly, flowering plant communities in low and moderate severity sites were spatially structured (i.e., species turnover between sites increased with the geographic distance between them) while the floral communities at high severity sites were not. High severity fires, by definition, strongly affect biotic and abiotic soil conditions and, importantly, often volatilize soil nitrogen (Hamman *et al.*, 2008; Hart *et al.*, 2005; Johnson *et al.*, 2008). This may act as a biotic filter, limiting which plant species can establish and persist after a high severity fire. If only a subset of plant species are able to colonize or germinate after a high severity fire, the community that forms will be depend less sensitively on landscape context and, hence, will be less affected by the surrounding pyrodiversity. A limited successful species pool would also constrain the spatial turnover of species. For example, in our study, the communities that characterize high severity patches are often early successional species such as nitrogen fixers and other disturbance specialists (Alekssoff, 1999; Groen, 2005; Coladonato, 1993, Fig. 1.5).

In contrast to high severity sites, low severity sites were characterized by a greater number of late succession species, while moderate severity sites were characterized by a mix of early and late colonizers (Fig. 1.5). By altering the biotic and abiotic soil and canopy structure around these sites (Hamman *et al.*, 2008; Hart *et al.*, 2005; Johnson *et al.*, 2008), a mosaic of fire histories may create a diversity of ecological niches at local and

landscape scales. Unlike in high severity sites, after a fire, a diversity of source populations could subsequently colonize and persist. Together, these mechanisms would allow species of different successional stages to coexist, thus facilitating the establishment of species rich floral communities. The response of the bee communities to pyrodiversity mirrored the response of the flowers. This is likely a result of plant-pollinator interactions and suggests that pyrodiversity has the capacity to generate and maintain biodiversity via interactions across trophic levels (Potts *et al.*, 2003b; Janz *et al.*, 2006; Thompson, 2005).

Bees may also benefit from the greater diversity of nesting resources that may be found in sites with greater pyrodiversity. In low and moderate severity sites, the strongest responses to pyrodiversity were in genera of species with diverse nesting habits, particularly *Osmia* and *Bombus* (Fig. 1.11, Cane *et al.*, 2007). A diverse fire history may thus increase heterogeneity among nesting resources and thus allow species with different preferences to co-exist. In addition, in some genera there is evidence that floral preferences mediate the response of species to pyrodiversity. For example, *Andrena* species richness was generally positively related to pyrodiversity, though with some variability (Fig. 1.11). Nine of the 19 *Andrena* species were collected visiting primarily *Ceanothus cordulatus* (Fig. 1.5), and the sites with high pyrodiversity but low *Andrena* species richness did not have blooming *C. cordulatus*. Thus though bee richness may respond to diversity of fire histories in an area, the reaction of specialized species will be depend the presence of their floral hosts.

Interestingly, at a local scale, high severity burn areas had higher richness and abundance of flowers, which translated into more species rich pollinator communities and interactions. Canopies opened by fire will often support more floral resources which in turn attract more pollinators (Van Nuland *et al.*, 2013; Grundel *et al.*, 2010; Campbell *et al.*, 2007). Focusing only on a local scale, therefore, would overlook the potential for high severity fires to homogenize communities over larger scales by decreasing the spatial structure of floral communities. It is thus important to consider the effect of pyrodiversity at multiple spatial scales (Farnsworth *et al.*, 2014).

Drought also interacted with the effect of pyrodiversity on plant-pollinator communities by weakening the response of bees and plant-pollinator interactions to pyrodiversity. This is possibly because a lower level of overall resource availability across the landscape caused pollinators to shift their resource use. Specifically, the increase in drought intensity led to changes in pollinator community composition and foraging behavior such that interaction networks were less specialized and pollinators no longer tracked plant communities. The effect of pyrodiversity on pollinator communities is, therefore, context dependent, and the capacity for pyrodiversity to maintain diverse pollinator communities may diminish with increasing drought occurrence.

In contrast to pollinators, the effect of pyrodiversity on floral community richness did not depend on drought intensity. Floral species richness was most negatively affected by drought in the high severity sites and, prior to the shift in drought intensity, floral richness at those sites was not related to pyrodiversity. Thus there is no expectation that increasing drought intensity would alter the response of floral richness to pyrodiversity. It is unclear, however, whether drought might, over longer time scales, mediate pyrodiversity's ability to sustain floral diversity.

We found limited evidence that environmental heterogeneity directly affected plant and pollinator communities and, in fact, the only significant relationship we observed (that between bee and interaction richness and heat load) was negative. This may be because pollinators might respond positively to certain levels of solar radiation and negatively to others such that a diversity of conditions could negatively affect bees and subsequently interaction richness. Environmental heterogeneity is known to contribute to pyrodiversity (Kane *et al.*, 2015; Collins *et al.*, 2007) and, thus, fire may provide a link between the diversity of abiotic conditions and the maintenance of biodiversity.

In the future, fires in this region are predicted to shift from primarily low/moderate to high severity. Historically in the Sierra Nevada, high severity patches comprised less than 5% of fires and high severity patches were also smaller (Collins *et al.*, 2007). In the 2013 Rim Fire, over 20% of a nearly 260,000 acre burn was classified as high severity (Lydersen *et al.*, 2014). Based on our findings, lower heterogeneity of fire severity may act to reduce spatial turnover in plant-pollinator communities. The heterogeneity of community composition is a primary determinant of the total species diversity present in a landscape and, thus, lower pyrodiversity may negatively affect the richness of plant-pollinator communities across large spatial scales (Burkle *et al.*, 2015).

On average, every 5% increase in pyrodiversity within 150 m of a site (a 0.05 unit increase in Simpson's diversity) gained approximately one pollinator and flowering plant species and almost two interactions. Thus predicted shifts in fire regimes to include less pyrodiversity compounded with increasing drought occurrence will negatively influence the richness of plant and pollinator communities in this and other forested ecosystems. Some managers only allow fires to burn under mild (prescribed fire) or extreme (wildfire) conditions. We provide further evidence that pyrodiversity contributes to biodiversity and therefore managers should place more significance on burning under a wider-range of fire conditions. Wildland Fire Use programs that restore fire regimes, such as those implemented in the Illilouette Basin, are integral for promoting both pyrodiversity and biodiversity. Additionally,

the combination of Wildland Fire Use and prescribed fires with varied burn conditions will prevent homogenizing mega-fires such as the Rim Fire. These management strategies are already recommended, and our results affirm that their usage should continue and hopefully also expand.

1.6 Supplemental methods

PYRODIVERSITY AND ENVIRONMENTAL HETEROGENEITY WEIGHTED METRICS

Pyrodiversity

To calculate the weighted pyrodiversity metric we used a functional diversity framework (Villéger *et al.*, 2008; Schleuter *et al.*, 2010; Laliberté & Legendre, 2010). We treated fires like traits and the different fire severity values as trait values. Within a fire, the severities are treated as ranked traits (so low severity fire is more similar to a moderate severity fire than a high). Pixels are species categorized by different combinations of fire traits. We also weighted the importance of different fires in determining the uniqueness of fire histories by the number of years ago they occurred. Within each buffer around the monitoring site, we calculated the number of pixels of each combination of fire traits. We then used the metric of functional dispersion to calculate the diversity of fire histories weighted by similarity (Laliberté & Legendre, 2010).

Environmental heterogeneity

Spatial data were prepared in ArcGIS 10.2. Environmental variables originated with a USGS 10 meter Digital Elevation Model and projected using bilinear interpolation into NAD 83 UTM 11N (Gesch *et al.*, 2002). Heat load and topographic compound index were generated with an ArcScript (Fig. 1.6, McCune & Keon, 2002; Dilts, 2010; Evans *et al.*, 2014). We rounded the values of the environmental variables to the hundredth decimal place.

We used a similar procedure to calculate environmental heterogeneity as we did for pyrodiversity. We treated environmental variables like traits and the different values of those variables as trait values. Pixels are species categorized by different values of each environmental variable. Unlike pyrodiversity, however, the weighted diversity of each environmental variable was calculated separately because treating the different variables as different “traits” of pixels lead to too many unique combinations of traits values to estimate a meaningful metric of heterogeneity.

DISSIMILARITY STANDARDIZATION

Dissimilarity estimates can be affected by the total number of species sampled at a site (e.g., Chase *et al.*, 2011a). We use null models to estimate the deviation of the observed β -diversity from that which would be expected under a completely random community assembly process Chase *et al.* (2011a).

Randomly assembled communities were generated by constraining the species richness so that they were the same as those in the observed communities. The algorithm randomizes a binary matrix while maintaining the same row sums (species richness at a site) and column sums (number of sites at which a species was observed) using the quasiswap method in the R function `commsimulator` (Oksanen *et al.*, 2013b). We then calculated the fraction of randomly assembled communities with dissimilarity values less than (and half of those equal to) that of the observed community. We used this fraction as a “corrected dissimilarity score” for our observed data. Corrected dissimilarity values near one indicate that our observed communities exhibit more species turnover between sites than expected under a random assembly process while values near 0.5 indicate that our observed communities exhibit levels of turnover more in line with the null expectation.

To account for the fact that the same pair-wise comparisons were included in each year (i.e., the dissimilarity between site 1 and site 2), we included a random effect of each site-site combination. This helps account for the non-independence of pair-wise dissimilarities but does not account for spatial non-independence (i.e., the dissimilarity of site 1 and site 2 is not independent from the dissimilarity of site 2 and site 3, Anderson *et al.*, 2011). *P*-values for linear mixed models were obtained using Satterthwaite’s approximations (Kuznetsova *et al.*, 2014).

Table 1.3: The support for including pyrodiversity weighted by fire history similarity and its interaction with fire severity and drought intensity. χ^2 values represent the ratio of the likelihoods of the model with and without the variable of interest. P -values are calculated via 1000 parametric bootstrap iterations. They represent the probability of observing a χ^2 value more extreme than the observed value when data is simulated from the model without the variable of interest. Symbols denote significance, with ', * and ** indicating 0.1, 0.05 and 0.01, respectively. Significant terms are bolded.

	Buffer radius	χ^2	P -value	χ^2	P -value	χ^2	P -value
Bee Richness	100	2.821	0.133	4.487	0.383	8.345	0.369
	150	0.1	0.764	10.683	0.057'	14.051	0.08'
	200	0.364	0.576	9.085	0.109	10.653	0.184
	250	0.191	0.713	3.454	0.481	6.182	0.562
Floral Richness	100	1.745	0.257	5.901	0.246	8.943	0.309
	150	1.592	0.259	9.682	0.088'	10.808	0.177
	200	2.361	0.2	5.356	0.303	5.916	0.563
	250	0.572	0.511	4.409	0.385	4.608	0.678
Interaction Richness	100	2.835	0.175	4.483	0.352	10.316	0.190
	150	0.11	0.762	10.698	0.057'	15.236	0.063'
	200	0.376	0.577	8.973	0.097'	11.219	0.175
	250	0.21	0.726	3.406	0.511	7.169	0.439

Table 1.4: The support for including heat load diversity and interaction with fire severity and drought intensity.

	Buffer radius	χ^2	<i>P</i> -value	χ^2	<i>P</i> -value	χ^2	<i>P</i> -value
Bee Richness	100	2.131	0.205	6.124	0.243	11.7	0.177
	150	2.749	0.153	6.643	0.227	10.115	0.228
	200	5.596	0.043*	6.911	0.199	9.651	0.235
	250	6.275	0.027*	7.627	0.148	11.165	0.185
Floral Richness	100	0.968	0.415	5.803	0.280	7.173	0.452
	150	1.58	0.268	5.47	0.274	5.881	0.588
	200	2.196	0.205	2.986	0.566	3.48	0.817
	250	1.99	0.236	3.051	0.535	4.278	0.737
Interaction Richness	100	2.164	0.210	6.158	0.244	14.162	0.070
	150	2.75	0.149	6.644	0.217	11.8	0.136
	200	5.561	0.030*	6.865	0.221	11.033	0.175
	250	6.219	0.034*	7.584	0.171	12.852	0.103

Table 1.5: The support for including topographic compound index diversity and interaction with fire severity and drought intensity. Including this variable in the model was not supported by the data.

	Buffer radius	χ^2	<i>P</i> -value	χ^2	<i>P</i> -value	χ^2	<i>P</i> -value
Bee Richness	100	1.058	0.363	1.062	0.852	3.565	0.828
	150	1.479	0.288	1.564	0.782	5.361	0.619
	200	0.914	0.414	1.345	0.823	3.635	0.798
	250	0.247	0.653	1.714	0.761	3.318	0.845
Floral Richness	100	0.384	0.594	0.741	0.902	2.771	0.881
	150	0.736	0.458	0.856	0.904	1.858	0.960
	200	1.213	0.336	1.305	0.824	2.766	0.903
	250	0.861	0.432	1.453	0.808	2.829	0.854
Interaction Richness	100	1.033	0.371	1.037	0.893	4.726	0.723
	150	1.466	0.278	1.557	0.775	7.102	0.449
	200	0.904	0.432	1.334	0.838	4.698	0.706
	250	0.243	0.659	1.686	0.775	4.003	0.777

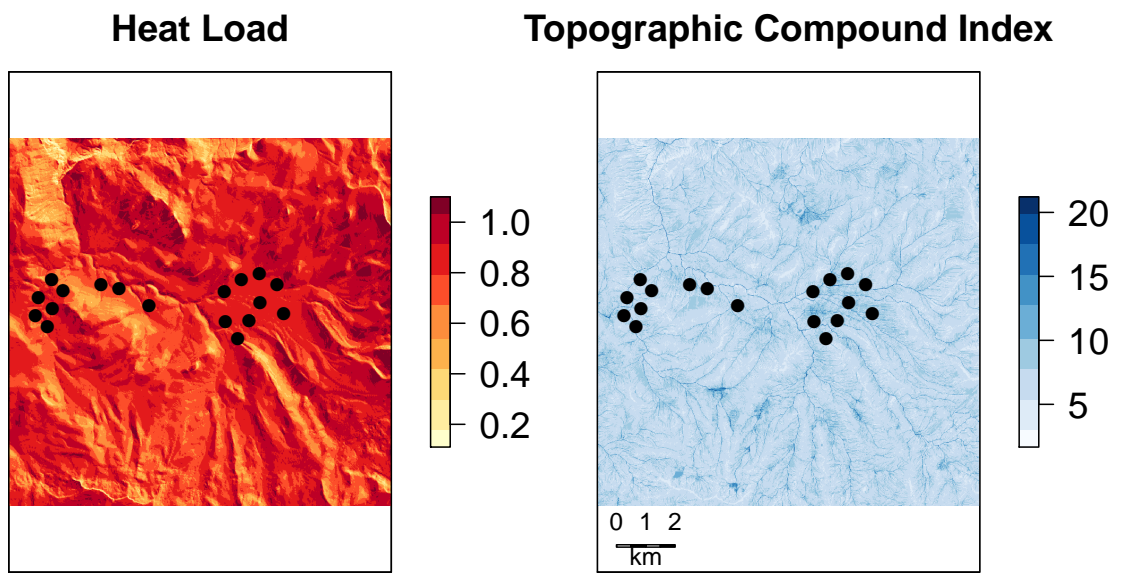


Fig. 1.6: The distribution of heat load estimates, topographic compound index estimates in the Illilouette Basin. Monitoring sites are indicated by points.

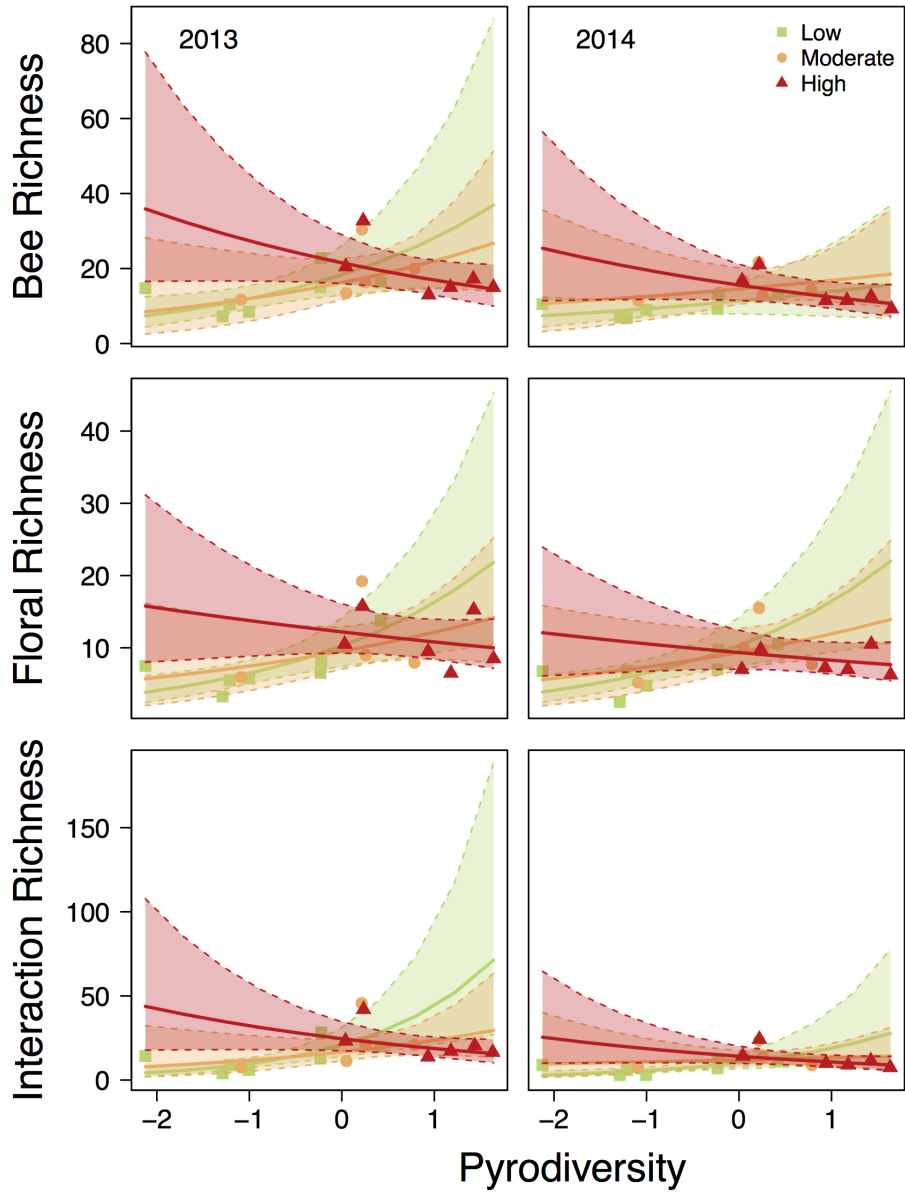


Fig. 1.7: The response of floral, bee and interaction richness to pyrodiversity weighted by the similarity of fire history. The color of the curves and points correspond to low, moderate and high severity fires classifications. The columns depict trends in 2013 and 2014, severe and extreme/exceptional drought years, respectively. The solid line indicates the mean slope estimate and the dashed lines are the 95% confidence intervals around the estimate. Points represent the richness of plants, pollinators and interactions averaged across the study season. Pyrodiversity axis is scaled so zero represents the mean pyrodiversity.

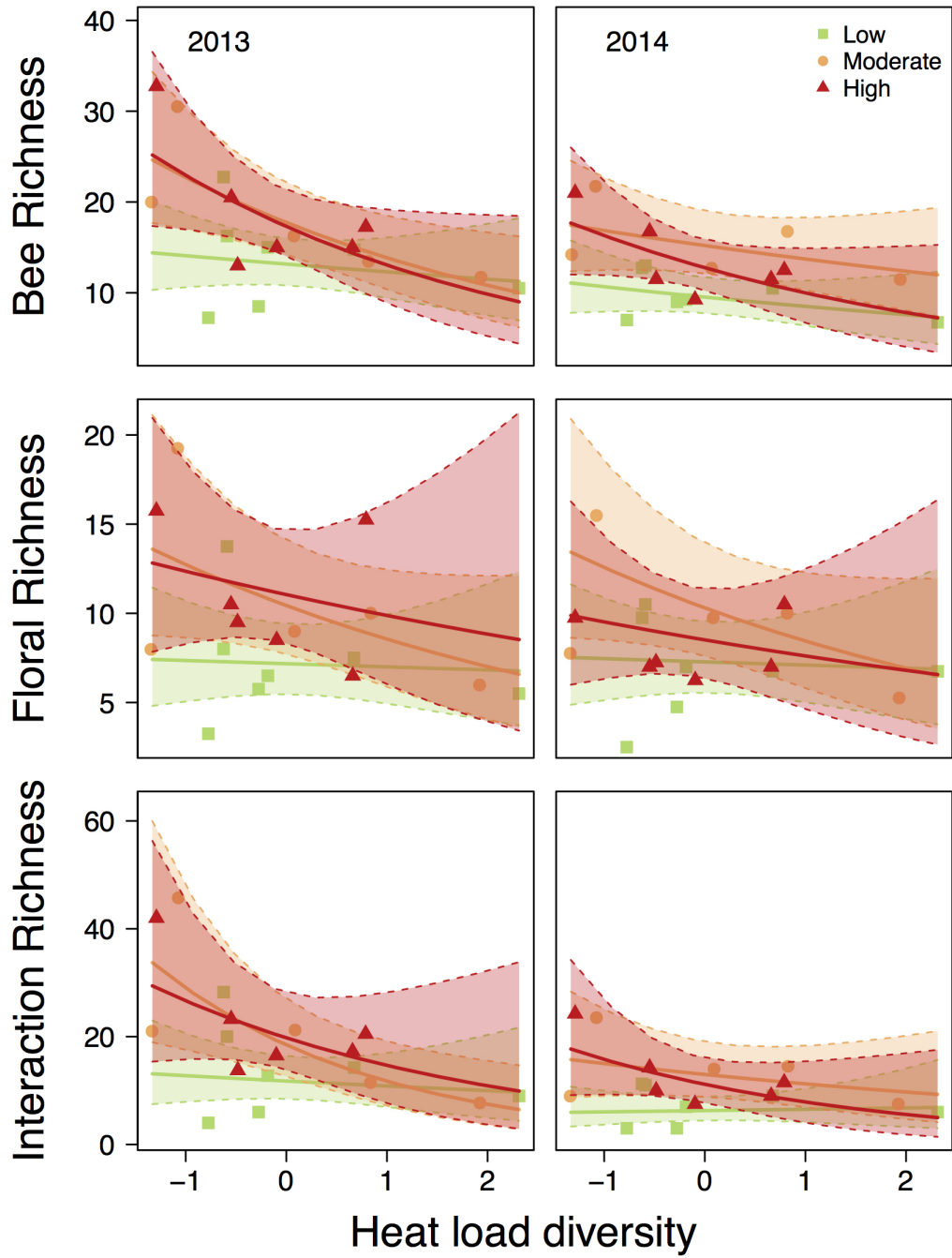


Fig. 1.8: The response bee, floral and interaction richness to heat load diversity.

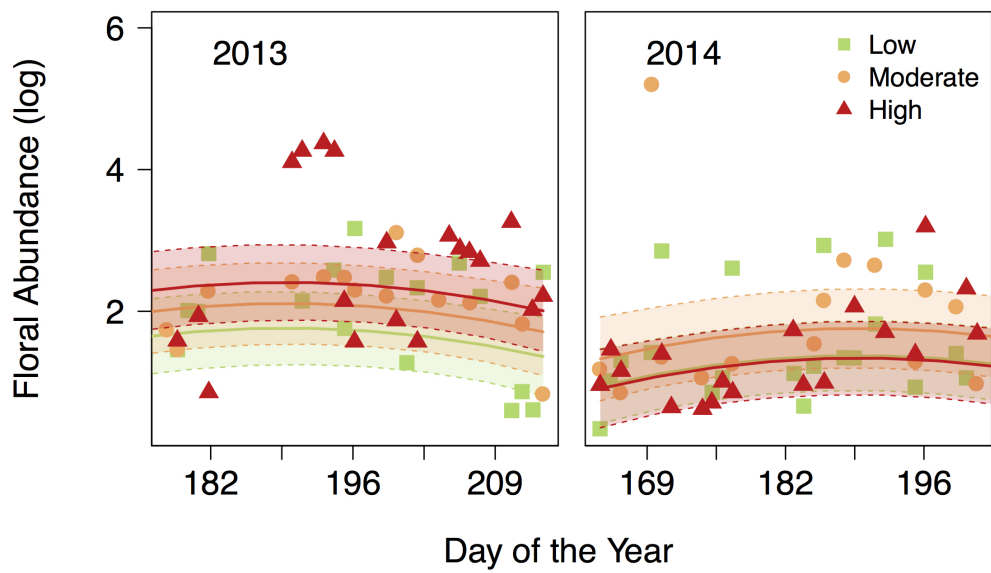


Fig. 1.9: The effect of fire severity on the abundance of floral resources throughout the study season. Points represent the mean species abundance of floral resources at each site.

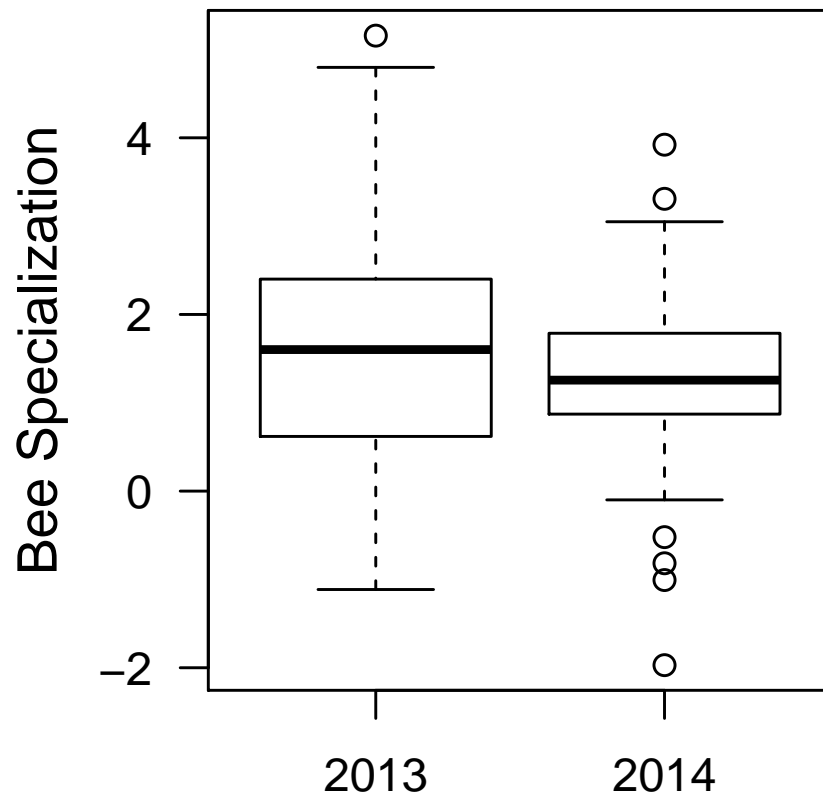


Fig. 1.10: The specialization of pollinator communities across the study landscape in severe (2013) and extreme (2014) drought years. To account for the differences in the abundance distributions and species richness between years, we generated an ensemble of 9999 randomly assembled communities and calculated z-scores of specialization by subtracting the mean of the specialization estimator of the randomly assembled communities from the observed specialization estimator and dividing by the standard deviation of the specialization estimators.

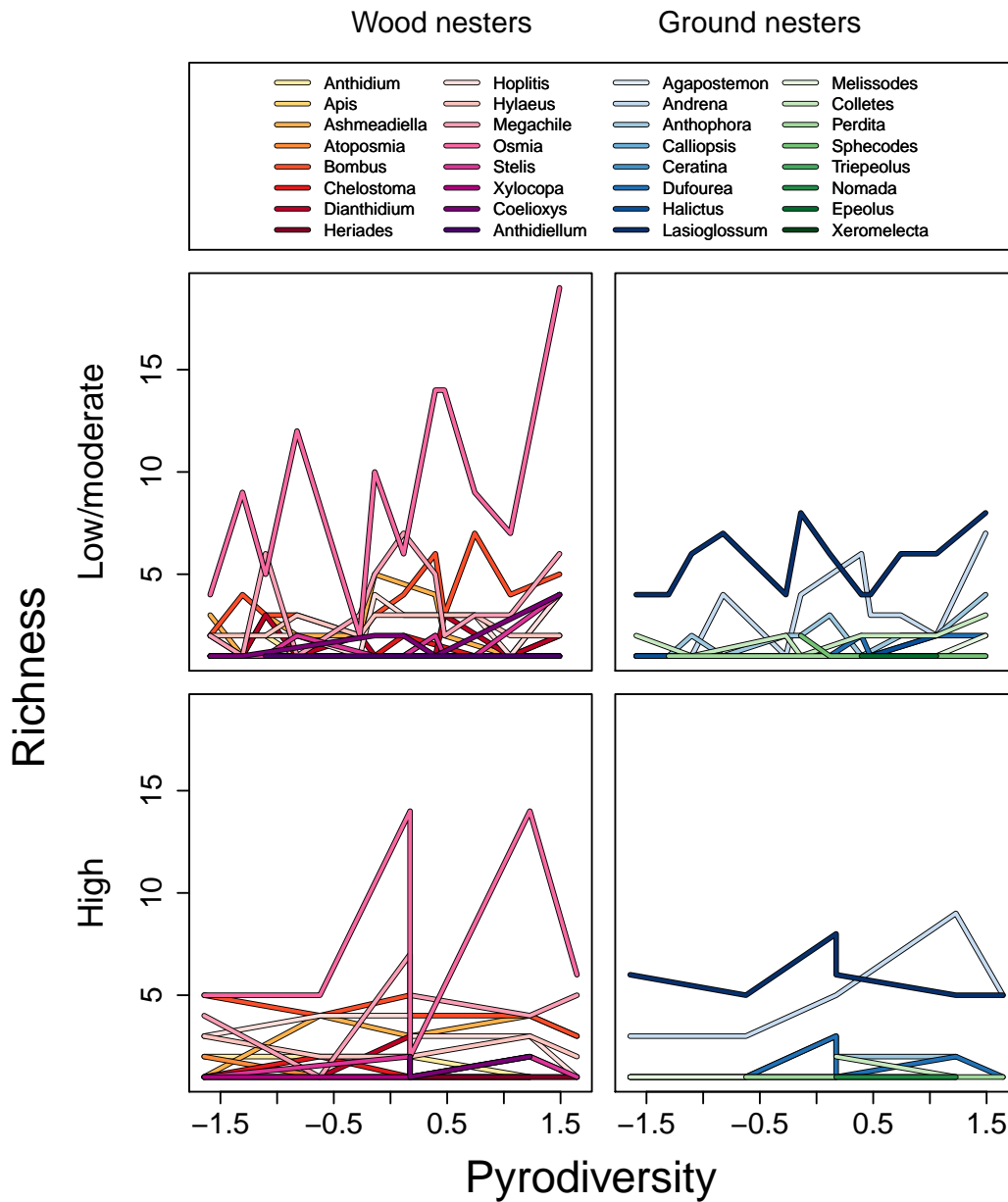


Fig. 1.11: The response of richness of species within the 32 genera collected to pyrodiversity. The top panels are the patterns found in sites where the most recent fire was of low or moderate severity, and the bottom panels are high severity sites. The left panels are the genera where the majority of species use wood to nest, and primarily ground-nesting genera are on the right panel. Multiple genera of both wood- and ground- nesters responded positively to pyrodiversity in the low and moderate severity sites. Few genera responded to pyrodiversity in high severity sites.

Chapter 2

On-farm habitat restoration counters biotic homogenization in intensively-managed agriculture

2.1 Transition

In Yosemite I was able to determine the mechanisms sustaining diversity in a relatively natural system and make recommendations for maintaining those processes. Often, however, a landscape has already been degraded and we must determine what restoration efforts are able to reassemble functional communities of interacting organisms. This is often the case in agricultural landscapes where widespread conversion of natural ecosystems to agriculture, combined with intensification of farming practices, has led to the homogenization of biological communities.

2.2 Abstract

To slow the rate of global species loss, it is imperative to understand how to restore and maintain native biodiversity in agricultural landscapes. Currently, agriculture is associated with lower spatial heterogeneity and turnover in community composition (β -diversity). While some techniques are known to enhance α -diversity, it is unclear whether habitat restoration can re-establish β -diversity. Using a long-term pollinator data-set, comprising ~9,800 specimens collected from the intensively managed agricultural landscape of the Central Valley of California, we show that on-farm habitat restoration in the form of native plant “hedgerows”, when replicated across a landscape, can boost β -diversity by approximately 14% relative to unrestored field margins, to levels similar to some natural communities. Hedgerows restore β -diversity by promoting the assembly of phenotypically diverse communities. Intensively managed agriculture imposes a strong ecological filter that negatively affects several important dimensions of community trait diversity, distribution, and uniqueness. However, by helping to restore phenotypically diverse pollinator communities, small-scale restorations such as hedgerows provide a valuable tool for conserving biodiversity and promoting ecosystem services.

2.3 Introduction

Widespread conversion of natural ecosystems to agriculture, combined with intensification of farming practices, is causing major declines in biodiversity globally (Green *et al.*, 2005; Tscharntke *et al.*, 2005; Tilman *et al.*, 2001). Agriculture is particularly associated with the homogenization of biological communities (Flohre *et al.*, 2011; Gabriel *et al.*, 2006; Hendrickx *et al.*, 2007; Vellend *et al.*, 2007; Clough *et al.*, 2007; Ekroos *et al.*, 2010). The turnover of species through space and subsequent heterogeneity of community composition (β -diversity) is a primary determinant of the total species diversity present in a landscape (Flohre *et al.*, 2011). Thus, by homogenizing communities, agriculture can act to reduce biodiversity on both local and regional scales (Flohre *et al.*, 2011; Hendrickx *et al.*, 2007; Ekroos *et al.*, 2010).

Spatial heterogeneity in community composition can be influenced by a variety of deterministic (niche-based) and stochastic (neutral) processes. Species are thought to “deterministically” track the biotic and abiotic

conditions to which they are adapted and, in a heterogeneous environment, this will contribute to the spatial structuring of communities (e.g., Whittaker, 1960; Püttker *et al.*, 2014; Chase, 2007; Condit *et al.*, 2002). Stochastic processes, such as priority effects or rare long distance dispersal events, can then amplify or weaken these signals (Püttker *et al.*, 2014; Condit *et al.*, 2002; Chase, 2003).

Ecological filters are one deterministic process that can shape community assembly because only species with particular sets of physical, functional, and life-history traits are able to persist (Chase, 2007; Püttker *et al.*, 2014). The diversity and distribution of ecological filters in a landscape contributes to spatial heterogeneity. By reducing the diversity of filters, habitat homogenization (e.g., the conversion of complex landscapes into simplified landscapes such as monocultures) can reduce β -diversity and species' trait diversity (Chase, 2007; Püttker *et al.*, 2014).

The loss of species and/or species trait diversity that can result from conventional monoculture agriculture may also compromise the provisioning of important ecosystem services such as pollination, pest control, and nutrient cycling (Tschardt *et al.*, 2005; Kremen & Miles, 2012). Currently, our agricultural system compensates for these lost ecosystem services by increasing external inputs (Kremen *et al.*, 2012), which can have unwanted negative consequences on both humans and wildlife (e.g., Gill *et al.*, 2012; Eskenazi *et al.*, 2007). The negative ramifications of high input agricultural systems have fostered the development and refinement of agricultural techniques that minimize external inputs by utilizing and regenerating ecosystem services (Kremen & Miles, 2012; Kremen *et al.*, 2012). Through local and landscape-scale diversification of crops and habitat, these techniques seek to promote biological interactions that lead to better provisioning of ecosystem services. Such systems also support higher local biodiversity (Gonthier *et al.*, 2014; Tuck *et al.*, 2014; Hole *et al.*, 2005; Gabriel *et al.*, 2013) and spatial heterogeneity in community composition (Gabriel *et al.*, 2006; Clough *et al.*, 2007) than conventional monoculture agriculture. Particularly, techniques that foster landscape-level diversification by maintaining or restoring fragments of natural habitat have been shown to be effective in supporting greater numbers of species and the ecosystem services that they provide (e.g., Kennedy *et al.*, 2013; Garibaldi *et al.*, 2011; Ricketts *et al.*, 2008) while also increasing community level β -diversity (Kehinde & Samways, 2014). However, if landscape diversification reduces yields, it may lead to further extensification, harming biodiversity (land-sparing argument Phalan *et al.*, 2011). Recent work suggests that land-sparing arguments promoting intensive, simplified agriculture are over-simplified (Kremen, 2015), since such forms of agriculture often also lead to extensification (Meyfroidt *et al.*, 2014).

In the most simplified agricultural areas, natural habitat is nearly non-existent. In some cases farmers have adopted the habitat restoration technique by planting strips of native plants along farm edges (hedgerows) to help diversify the landscape, without removing arable land from production. Hedgerows have been shown to support higher diversity and abundance of various ecosystem service providers, including beneficial insects, and birds (Morandin & Kremen, 2013; Hinsley & Bellamy, 2000; Bianchi *et al.*, 2006; Morandin *et al.*, 2014; Hannon & Sisk, 2009). It remains unclear, however, whether they mimic natural habitat by re-creating spatially structured communities, by leading to higher β -diversity. In addition, communities with diverse traits can provide higher quality and more stable ecosystem services (Klein *et al.*, 2009). Thus if hedgerows maintain the spatial heterogeneity of communities at different hedgerows by supporting species with a diversity of traits, they may promote the provisioning of ecosystem services such as pollination in agricultural areas (Klein *et al.*, 2009). Understanding whether simple restoration interventions such as hedgerows can counter biotic homogenization when replicated across a landscape will be critical in assessing their value for ecosystem service provision and biodiversity conservation.

Focusing on pollinators, key ecosystem service providers (Klein *et al.*, 2007), here we ask whether hedgerows support more spatially rich communities with more diverse suites of species traits. We do so using a long-term data-set from the highly simplified and intensively managed agricultural landscape of California's Central Valley. We also identify which mechanisms are likely responsible for driving the spatial trends we find. Specifically we uncover the processes leading to the observed patterns in pollinator β -diversity and, further, investigate whether there is evidence that pollinator species track biotic and abiotic resources. Lastly, we test whether simplified agriculture imposes an ecological filter on insect pollinators by favoring species with particular set of traits. In our study landscape, hedgerows augment the richness and abundance of pollinators (Morandin & Kremen, 2013) and the occurrence, persistence and colonization of both resource generalists and specialists (M'Gonigle *et al.*, 2015; Kremen & M'Gonigle, 2015), while also exporting pollinators into agricultural fields (Morandin & Kremen, 2013). Understanding whether hedgerows support spatial heterogeneity of communities is the next step towards understanding whether they can conserve biodiversity and promote the provisioning of ecosystem services in agricultural areas.

2.4 Materials & Methods

STUDY SITES AND COLLECTION METHODS

We surveyed pollinators from 21 hedgerow sites and 24 unrestored control sites, located in the Central Valley of California in Yolo, Colusa and, Solano Counties (Fig. 2.1). This is an intensively managed agricultural area dominated by monocultures of conventional row crops, vineyards and orchards. The monitoring sites represent a sample of field margin conditions across the northern Central Valley. Hedgerows, which consist of native, perennial, shrub and tree plantings (Morandin & Kremen, 2013), are ca. 3–6m wide and approximately 350m long and border large (ca. 30–hectare) crop fields. They are typically planted along field margins where they do not remove valuable land from production. Hedgerows differ in age from newly established, “maturing” (1–10 years post-planting) to “mature” (established greater than 10 years ago). By investigating hedgerows at different stages of maturity, we can determine whether the effects of hedgerows on β -diversity accumulate with hedgerow maturation. We also monitored unrestored control sites which are weedy edges that represent a variety of relatively unmanaged field edges found in the region. Control sites were selected to match conditions surrounding the hedgerow sites. For each hedgerow, we selected 1-2 unrestored controls adjacent to the same crop type (row, orchard, pasture, or vineyard), within the same landscape context. The crop fields adjacent to hedgerows and controls were similarly managed as intensive, high-input monocultures. The mean distance between monitoring sites was 15 km, and the minimum distance between sites of the same type sampled in the same year was 2 km. The entire area surveyed spanned almost 300 km².

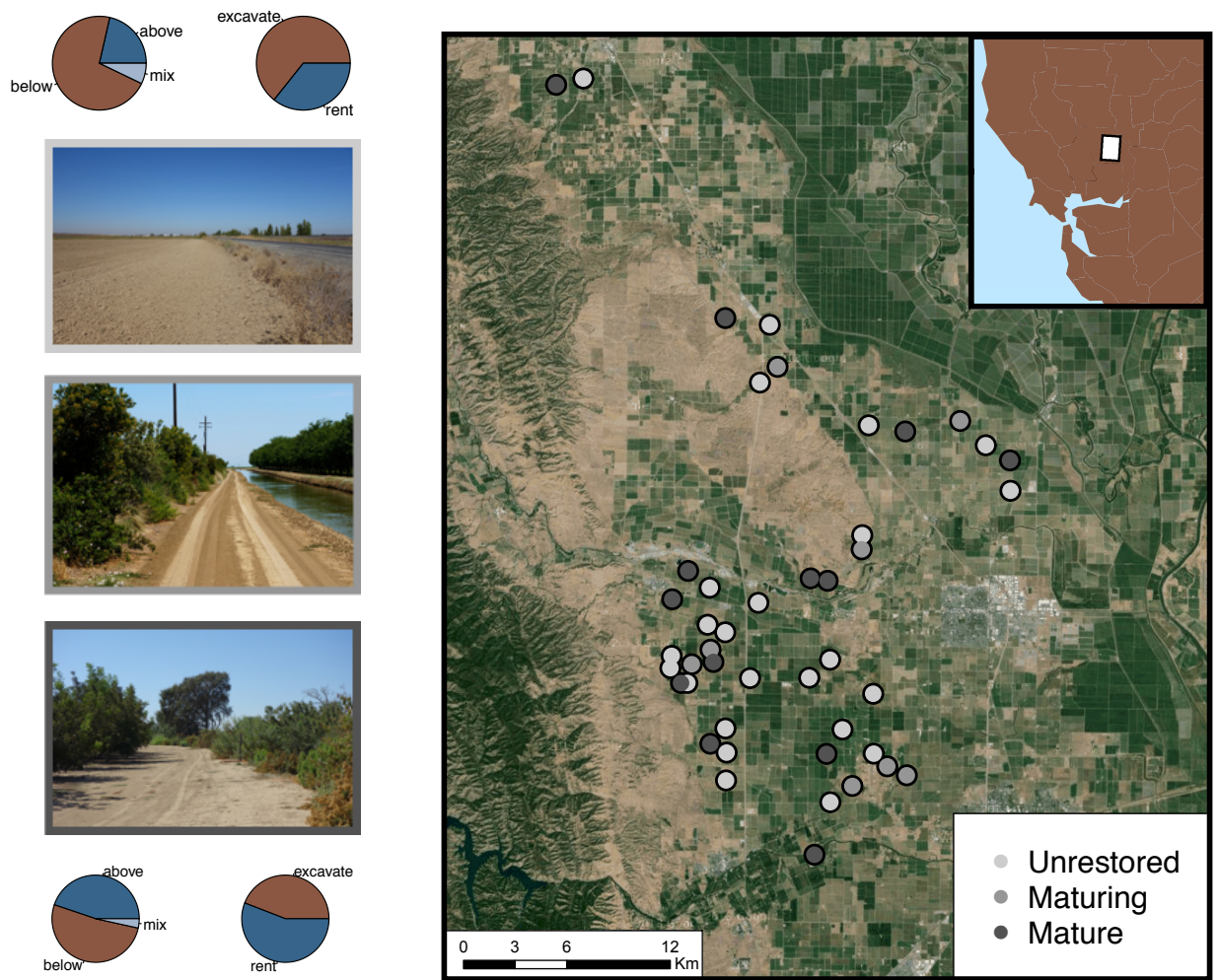


Fig. 2.1: Location of hedgerow and unrestored control sites in California (inset) and surrounding landcover. Pie charts represent the selected trait make-up of species found only at controls (top) or hedgerows (bottom). The left pie charts represent the nest location of the species, and the right charts depict the nest construction behavior.

We sampled pollinator communities between April and August each year from 2007 through 2013 (Table 2.3 & 2.4). Sites were sampled between two and five times per year (Table 2.3 & 2.4).

In each round of sampling, the order in which sites were sampled was randomized. Surveys were conducted under sunny conditions when the temperature was above 21°C and wind speed was below 2.5 meters/second. Flower-visitors to plants in hedgerows and unrestored controls were netted for one hour of active search time (the timer was paused when handling specimens). All insect flower visitors that touched the reproductive parts of the flower were collected; however, here we focus only on wild bees, the most abundant and effective pollinators in the system (C. Kremen, A. Klein and L. Morandin, unpublished data). Bee specimens were identified to species (or morpho-species for some bee specimens in the genera *Nomada* and *Sphecodes*) by expert taxonomists.

Surveys of the biotic and abiotic conditions were also conducted at each site throughout the flight seasons of the pollinators. At each site, each flowering plant in 50 one meter quadrats along the length of the hedgerow or control site was identified to species or morpho-species. The abundance of each plant species was estimated as the mean number of quadrats a species was present in, each year. In addition, in 2011 and 2012, we used the same quadrats to evaluate the physical characteristics of the site including the amount of vegetative cover and uncultivated, bare ground.

DIVERSITY ESTIMATES AND STATISTICAL ANALYSIS

To estimate the species turnover between sites of the same type (i.e., unrestored controls, maturing hedgerows, or mature hedgerows), we used the variance in community composition as a measure of β -diversity (i.e., multivariate dispersion, see Section 2.7.1 for details, Anderson *et al.*, 2011, 2006). To calculate this metric, we first calculated the pairwise dissimilarity between sites within each year of the dataset using a dissimilarity estimator that incorporates species abundances, while also accounting for unobserved species (Chao *et al.*, 2005b).

Dissimilarity estimates can be affected by the total number of species and individuals sampled at a site (e.g., Chase *et al.*, 2011b; Kraft *et al.*, 2011). For example, sampling from a fixed species pool, the probability that two sites do not share any species is higher when there are few individuals at those sites. Confounding sampling effects and species turnover can yield misleading results (e.g., Chase *et al.*, 2011b; Kraft *et al.*, 2011). By extending the method described by Chase *et al.* (2011b) to include estimates of species' abundances, we used null models to estimate the deviation of the observed dissimilarity from that which would be expected under a completely random community assembly process (see Section 2.7.1 for details). With the corrected dissimilarity values, we then calculated the multivariate dispersion of communities as the variability in species composition within a site type (see Section 2.7.1 for details, Anderson *et al.*, 2011).

In order to investigate effects of site type, the β -diversity estimates were used as the response variable in a linear mixed model with site type (unrestored control, maturing hedgerow, mature hedgerow) as an explanatory variable along with random effects for both year and site (Bates *et al.*, 2014; Kuznetsova *et al.*, 2014). All analyses were conducted in R, version 3.1.1 (R Core Team, 2015).

SOURCES OF β -DIVERSITY

We next assessed which spatial pattern was most responsible for maintaining β -diversity within each site type in our landscape. Communities that turnover in species composition across space (i.e., those that exhibit β -diversity) are thought to arise via two processes: 1) species replacement and 2) predictable species loss/gain (Baselga, 2012; Gaston & Blackburn, 2008). In the latter case, species-poor sites will often be subsets of species-rich sites and thus communities should exhibit some degree of nestedness. Such a pattern might occur when, for example, species assemble along a resource gradient (Baselga, 2012). In contrast, species replacement should lead to communities that turnover in composition via substitution of species. This pattern could result when species track their preferred resource or, somewhat randomly *via* colonization and priority effects. Unlike species loss/gain, these communities would not be expected to exhibit any patterns in nestedness. Thus, to identify which of these two scenarios best describes the patterns in the landscape within each year, we determined whether our communities were significantly nested (Almeida-Neto *et al.*, 2012). We used the index NODF to measure nestedness (Almeida-Neto *et al.*, 2012; Ulrich & Gotelli, 2007).

To further uncover the processes contributing to spatial heterogeneity, we asked whether the dissimilarity between pollinator communities within and between site types was related to the geographic distance between sites. To do this, we compared the pollinator community dissimilarity matrix to the geographic distance between sites using Mantel tests. To assess the significance of the correlation, we permuted dissimilarity values among sites within each year to maintain the hierarchy of the data.

We also looked for evidence that pollinator communities track resources across the landscape. One important such resource is floral hosts; if the majority of the pollinators track specific floral resources, differences in floral community composition between sites should generate corresponding differences in pollinator communities. To test this, we used Mantel tests to compare the pollinator community dissimilarity matrix to an analogous dissimilarity matrix for flowering plant species within and between site types. As we did for the bee community, we used an abundance-based measure to estimate the dissimilarity of the floral communities (Chao *et al.*, 2005b).

Rather than tracking particular flowering plant species, bees may track floral resources generally. Therefore, we also characterized floral communities according to their species richness, diversity, and total floral abundance, all proxies for floral resource availability. We then used a Gower dissimilarity measure to characterize the changes in the floral resources between sites and then compared that to the pollinator community, again using Mantel tests to look for associations between and within site types.

Lastly, both abiotic conditions and resources may affect which pollinator species are present. Bee species vary considerably in their nesting habits and, therefore, the availability of specific nesting materials may influence which species are able to occupy an area (e.g., Potts *et al.*, 2005b; Sardinias & Kremen, 2014). To examine this, we characterized the nesting resources at each site. Specifically, we measured the mean and variability of the amount bare ground, dead wood, hollow stems, cracks in the soil, and vegetation cover (Potts *et al.*, 2005b). We used Mantel tests to correlate pollinator community turnover with differences in the physical characteristics of sites, between and within site types, estimated using Gower dissimilarity.

COMMUNITY TRAITS

We determined whether agricultural areas act as an ecological filter on pollinator groups by comparing the trait distributions of pollinators found at unrestored controls to those found at hedgerows. Our unrestored control sites comprise a variety of unmanaged crop field edges and, therefore, represent the dominant conditions in our landscape. Consequently, the species visiting these sites are those that are likely present in the landscape prior to any restoration.

To characterize the trait diversity of the bee communities, we computed three metrics that capture diversity, uniqueness, and distribution of trait values in the community: trait dispersion, divergence, and evenness (Villéger *et al.*, 2008; Schleuter *et al.*, 2010). Trait dispersion is a measure of trait diversity, corrected for species richness (Schleuter *et al.*, 2010); trait divergence measures how species abundances are distributed within the trait space (i.e., a measure of trait uniqueness, Villéger *et al.*, 2008); trait evenness measures the regularity with which traits are distributed across trait space, accounting for abundance (Villéger *et al.*, 2008). In combination, these metrics provide a relatively complete overview of the different aspects of species trait diversity (Villéger *et al.*, 2008; Schleuter *et al.*, 2010).

Selection of appropriate characters is essential to the characterization of the community's distribution and diversity of traits (Villéger *et al.*, 2008). We selected resource capture and use traits that collectively influence the distribution of bee species as pollinators over space and time (Kremen & M'Gonigle, 2015) including resource specialization (quantitative, d' ; Blüthgen *et al.*, 2006), body size (quantitative, inter-tegular span, mm, Cane, 1987), sociality (categorical: eusocial, solitary, cleptoparasitic), nest location (categorical: above ground, below ground or mix), and nest construction (categorical: excavate or rent; Williams *et al.*, 2010) as described in more detail in Kremen & M'Gonigle (2015). Each trait has the same weight in trait diversity metric estimation (Villéger *et al.*, 2008; Schleuter *et al.*, 2010). Pollinator specialization was calculated using plant-pollinator interaction observations from a more extensive data-set from Yolo County (18000 interaction records) that included both the data included in this study and additional data from sites where we collected flower visitors using the same methods (M'Gonigle *et al.*, 2015). The specialization metric measures the deviation of the observed interaction frequency between a plant and pollinator from a null expectation where all partners interact in proportion to their abundances (Blüthgen *et al.*, 2006). It ranges from 0 for generalist species to 1 for specialist species. To determine whether trait evenness, dispersion, and divergence differed between controls and hedgerows at different stages of maturation, we used the trait diversity metrics as response variables in linear mixed models with site type as a fixed effect and year and site as random effects (Bates *et al.*, 2014; Kuznetsova *et al.*, 2014).

If agriculture creates an ecological filter, the trait composition of agricultural bee communities should differ from that of a community that was randomly assembled from a shared meta-community. To test whether agriculture constitutes an ecological filter, we compared the observed trait values with the distribution of traits of randomly assembled communities. Because species richness differs between hedgerow and control sites (Morandin & Kremen, 2013) and, furthermore, because differences in species richness may constrain the observed trait values and trait diversity (for example, if only one species was observed, the trait diversity will always be zero), we

randomly assembled communities of the same species richness as the observed communities. For quantitative traits, we focused on the mean trait value at a site weighted by abundance and for categorical traits we calculated the mean Simpson's diversity of traits (finite sample formulation). To generate the randomized communities, we shuffled the species between sites while maintaining the species richness and the number of occurrences of a species within each year. We then re-calculated the mean trait value and Simpson's diversity of traits for 9999 randomly assembled communities (Schleuter *et al.*, 2010). Lastly, to calculate the probability of the observed trait value given a random assembly process, we computed the fraction of randomly assembled communities that had trait values greater than or equal to that of our observed community. For a given trait, if that probability was less than 0.025% (two-tailed test), we concluded that site type exerted an ecological filter on that trait.

To complement the previous analysis, we also asked whether the trait diversity and Simpson's diversity of traits was significantly different between hedgerows and unrestored controls. We compared the mean trait value or Simpson's diversity across site types using linear mixed models, with site status as an explanatory variable and site and year as random effects, as before (Bates *et al.*, 2014; Kuznetsova *et al.*, 2014).

Lastly, we asked whether the pollinator composition of communities supported by between hedgerows and unrestored controls differed using a Permutational Multivariate Analysis of Variance (PERMANOVA) (Anderson & Walsh, 2013). When comparing community composition, PERMANOVAs can be too liberal when the experimental design is unbalanced and the multivariate dispersions are heterogeneous because it is testing multiple hypotheses simultaneously (Anderson & Walsh, 2013). Since the number of sites was nearly equal for hedgerows and controls within but not between years, we compared the community composition within each year.

2.5 Results

Over seven years and 545 samples, we collected and identified 9898 wild bees comprising 114 species. The species came from five families and 30 bee genera. Most species occurred infrequently in the landscape: nearly 20% of species were observed two or fewer times.

We found that β -diversity was higher in mature hedgerows than unrestored controls (estimate for the difference between mature hedgerows and controls, \pm standard error of the estimate, 0.134 ± 0.045 , p -value=0.005, Fig. 2.2). β -diversity across maturing hedgerow sites was not, however, significantly different from that for control sites. These findings were robust to our use of different methods when generating the randomly assembled communities that we used to account for the expected β -diversity given the observed differences in the number of individuals and species (compare Fig. 2.2 and Fig. 2.7).

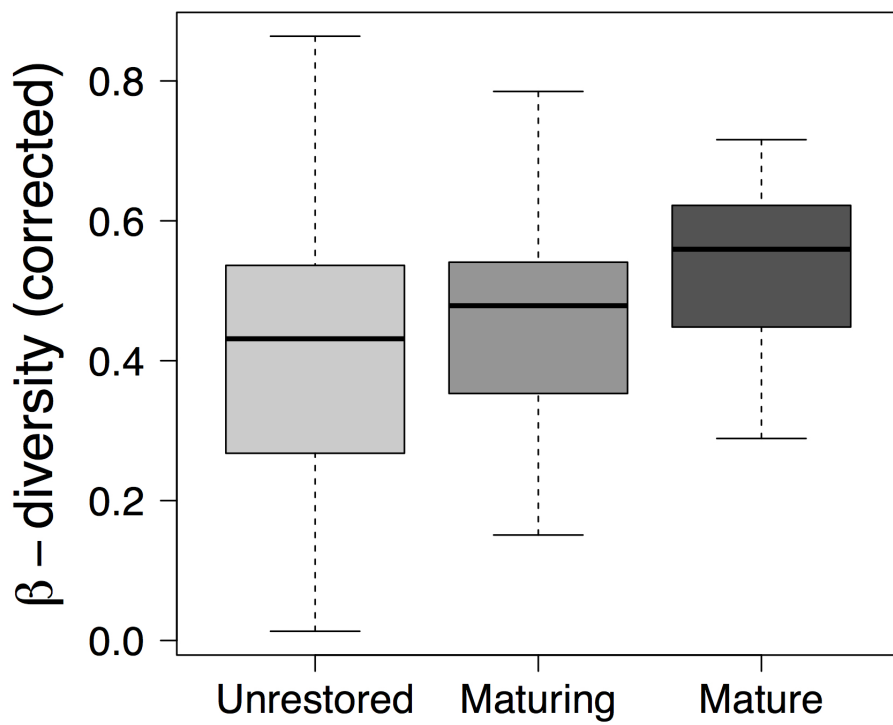


Fig. 2.2: Mature hedgerows support significantly higher corrected β -diversity than maturing hedgerows and un-restored controls. Corrected β -diversity values represent the dispersion of site community composition to the centroid of each site type. Boxplots represent medians (black horizontal line) first and third quartiles (box perimeter) and extremes (whiskers).

	Year	z-score	<i>p</i> -value
Unrestored control	2007	-2.357	0.971
	2008	0.403	0.369
	2009	0.766	0.23
	2010	2.864	0.019
	2011	-0.787	0.78
	2012	-0.314	0.607
	2013	3.634	0.001 * **
Maturing hedgerow	2009	-0.391	0.644
	2011	1.617	0.059
	2012	1.062	0.153
	2013	-1.55	0.957
Mature hedgerow	2009	-1.15	0.892
	2010	-0.788	0.769
	2011	-0.785	0.781
	2012	0.524	0.287
	2013	-0.786	0.79

Table 2.1: The nestedness of pollinator communities, by year, for each site type. The z-scores were calculated by generating 9999 null communities, subtracting the mean of the calculated nestedness from the observed nestedness, and dividing by the standard deviation of the nestedness (Ulrich & Gotelli, 2007). Empirical *p*-values were calculated as the probability that the nestedness of the null communities was equal to or greater than the observed community nestedness. Pollinator communities were significantly nested only in 2013 for the unrestored site type. Symbols denote significance, with *, **, and *** indicating 0.05, 0.01 and 0.001, respectively.

We found that pollinator communities were not significantly nested, except for a single year and site type (Table 2.1), suggesting that species replacement, rather than species loss/gain, was the primary determinant of spatial heterogeneity in species composition for each site type.

Dissimilarity of pollinator communities at unrestored sites and between all site types was significantly correlated with the geographic distance (Fig. 2.5, Table 2.2). In addition, we found that the bee community dissimilarity was significantly correlated with the floral community dissimilarity between site types (Fig. 2.5, Table 2.2). The bee community was also significantly correlated with the floral community at mature hedgerows and controls, though the strength of the association at controls was weak (Table 2.2). Thus, the dissimilarity of floral communities between sites predicts the dissimilarity of the pollinator communities within mature hedgerows, while geographic distance more strongly structures the compositional turnover in controls. Maturing hedgerows may still be undergoing community assembly and therefore pollinator communities do not significantly respond to floral communities. The bee community was not correlated with floral or nesting resources, however (Fig. 2.5, Table 2.2).

	Geographic distance			Floral Community			Floral resources			Nesting resources		
	Mantel statistic r	p -value	Mantel statistic r	p -value	Mantel statistic r	p -value	Mantel statistic r	p -value	Mantel statistic r	p -value	Mantel statistic r	p -value
Across all site types	0.029	0.02*	0.134	0.0003***	-0.002	0.588	0.139	0.159	0.139	0.159	0.139	0.159
Unrestored controls	0.076	0.003**	0.085	0.019*	0.024	0.156	0.063	0.286	0.063	0.286	0.063	0.286
Maturing hedgerows	0.03	0.205	0.011	0.373	-0.061	0.697	-0.042	0.517	-0.042	0.517	-0.042	0.517
Mature hedgerows	-0.011	0.298	0.187	0.004**	-0.035	0.738	-0.619	0.979	-0.619	0.979	-0.619	0.979

Table 2.2: The correlation between the dissimilarity of pollinators communities and floral communities, nesting and floral resources, and geographic distance within and between site types.

Mature hedgerows positively affected each of the three trait diversity metrics compared to unrestored controls (estimate for the difference between mature hedgerows and controls, evenness: 0.100 ± 0.0366 , $p = 0.009$; dispersion: 0.0759 ± 0.023 , $p = 0.002$; divergence: 0.100 ± 0.0367 , $p = 0.009$, Fig. 2.3). Compared to control sites, mature hedgerows therefore better support individuals with unique traits, as well as a greater diversity of trait values that are more evenly distributed across trait space. The trait diversity supported by maturing hedgerows, however, was not significantly different from controls.

Examining each trait individually, we also found evidence that only species characterized by particular trait values are found in unrestored, agricultural areas. We found that, compared to randomly assembled communities, control sites exhibited significantly lower trait values for floral specialization and body size, and lower diversity than expected for each categorical trait except sociality (Fig. 2.4) suggesting that the species that visit or inhabit unrestored controls comprise only a subset of the available species pool. Mature and maturing sites had trait values expected by randomly assembled communities. Similarly, the linear mixed models indicated that, compared to bee communities occupying unrestored controls, bee communities at both mature and maturing hedgerow sites were comprised of species that are significantly larger (estimate for the difference between controls and mature 0.278 ± 0.080 , $p = 0.001$; controls and maturing: 0.223 ± 0.092 , $p = 0.02$) and more specialized (controls and mature: 0.048 ± 0.013 , $p = 0.0004$; controls and maturing: 0.058 ± 0.015 , $p = 0.0003$, Fig. 2.4 & 2.8). Bees at hedgerows also exhibited more diversity in nesting locations and nest construction behaviors (nest location diversity, estimate for the difference between controls and mature: 0.137 ± 0.057 , $p = 0.022$, controls and maturing: 0.172 ± 0.067 , $p = 0.014$; nest construction trait diversity, controls and mature: 0.121 ± 0.051 , $p = 0.02$, controls and maturing: 0.158 ± 0.060 , $p = 0.012$, Fig. 2.4 & 2.8). Sociality diversity was not significantly different between site types.

Though the trait diversity at hedgerows and unrestored controls differed significantly, the composition of communities did not significantly differ between controls and hedgerows (Tab. 2.6, Fig. 2.6).

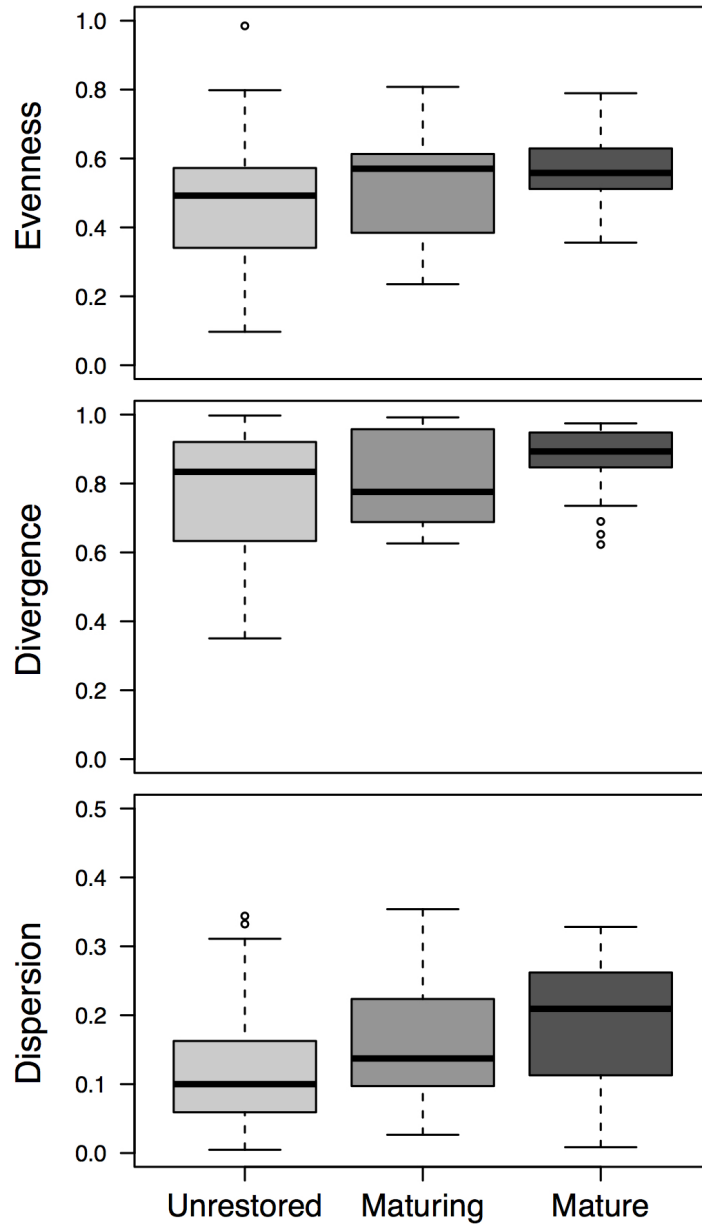


Fig. 2.3: The evenness, divergence and dispersion of the pollinator traits for communities at control sites, maturing hedgerows, and mature hedgerows. Pollinator communities at mature hedgerows had significantly higher values for all metrics. Relative to the range of trait values in the landscape, mature hedgerows had 12% higher evenness, 15% higher divergence, and 21% higher dispersion than unrestored controls.

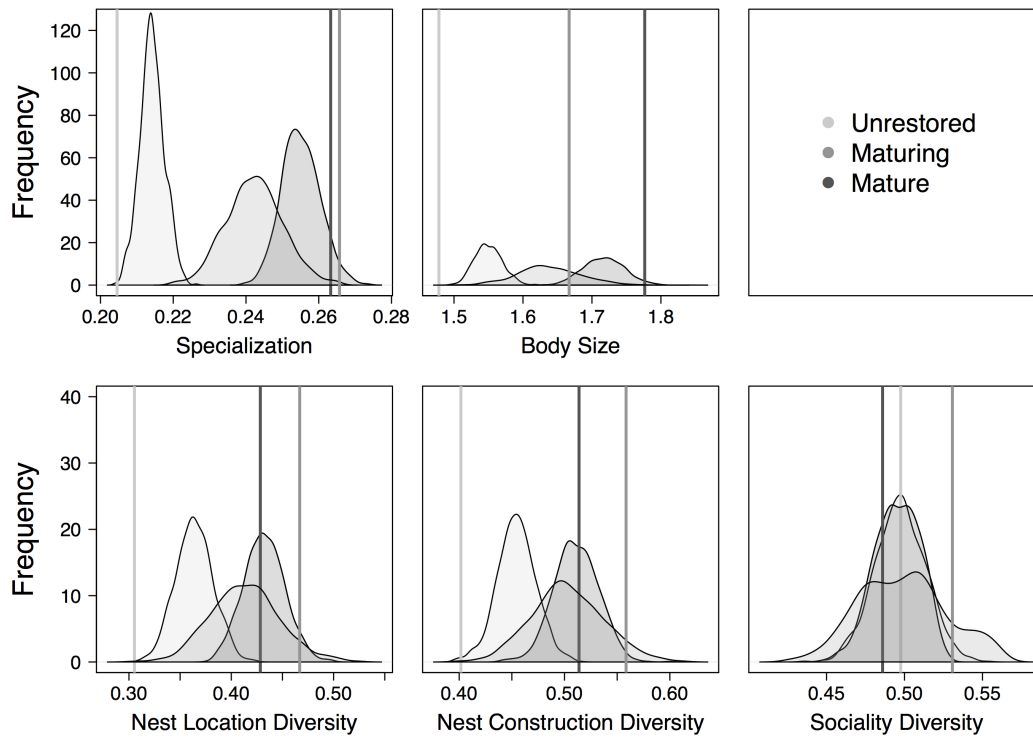


Fig. 2.4: The mean trait value (top panel) and trait diversity (bottom panel) of pollinator communities at different site types. The solid lines are the observed trait values, and the shaded curves are trait distributions for randomly assembled communities with the same species richness as the observed communities for each site type. The unrestored controls had significantly lower ($p < 0.025$) trait values and diversity than expected for a randomly assembled community for all trait groups except sociality diversity. In the context of the range of trait values observed in the study landscape, mature hedgerows had 21% higher specialization than controls, 16% larger bees, 12% more nest location diversity, and 11% more nest construction diversity.

2.6 Discussion

We have shown that on-farm restorations in the form of hedgerows, when replicated across a landscape, can promote the assembly of spatially heterogeneous and phenotypically diverse pollinator communities in intensively managed and simplified agriculture. Such restorations may thus help to slow or even reverse the biotic homogenization that is characteristic of such landscapes. Without hedgerows, intensive and simplified agriculture imposed a strong ecological filter that eroded patterns of spatial structuring between communities and diminished almost every aspect of community trait diversity and distribution that we investigated. This ecological filter affected a variety of phenotypic traits including nesting habits and also selected for smaller, less specialized bees. In concordance with a number of other studies conducted across a wide variety of taxa, we found that, by homogenizing communities, agriculture has the potential to affect the distribution of species over large scales (Flohre *et al.*, 2011; Gabriel *et al.*, 2006; Hendrickx *et al.*, 2007; Ekroos *et al.*, 2010).

Loss of such diversity may impact the functioning and resilience of natural systems which could have profound implications for humans and wildlife. The provisioning of ecosystem services, such as pollination, requires a stable and diverse community of wild bees (Kremen, 2005; Klein *et al.*, 2009). These pollination services are critical both in natural communities and economically: 87% of all flowering plant species and 75% of crop species depend to some extent on animal pollinators in order to produce fruits or seeds (Klein *et al.*, 2007; Ollerton *et al.*, 2011b). Animal-pollinated crops also supply a large proportion of essential nutrients to the human diet (Eilers *et al.*, 2011; Smith *et al.*, 2015).

Based on findings in other cropping systems, lower functional diversity, combined with the loss of key service providers, will likely negatively affect levels of pollination in both crops and wild plant populations (Klein *et al.*, 2009; Hoehn *et al.*, 2008; Brittain *et al.*, 2013). In addition, by reducing the size of the species pool, simplified agriculture may impact the stability of services (Winfrey & Kremen, 2009) and thus the reliability and predictability of plant reproduction and crop yields (Garibaldi *et al.*, 2011, 2013). Encouragingly, however, relatively small-scale restorations such as hedgerows can mitigate the homogenization caused by simplified agriculture, when replicated across landscapes. Hedgerows have also been shown to support other ecosystem services (Hinsley & Bellamy, 2000; Bianchi *et al.*, 2006; Hannon & Sisk, 2009), so these small-scale, on-farm restoration measures may also provide an economic benefit to growers (Blaauw & Isaacs, 2014), though this is likely to be context dependent (Sardiñas & Kremen, 2015).

We have shown that, in addition to supporting a higher diversity and abundance of pollinators (Morandin & Kremen, 2013), hedgerows also support approximately 14% higher β -diversity and approximately 10% more trait diversity, uniqueness, and evenness than unrestored field margins. In addition, because the trait diversity of the communities differed significantly between hedgerows and unrestored controls but community composition did not, the communities at controls are likely a subset of those at hedgerows. For example, 28% of the total species pool was found only at hedgerows, whereas only 13% of species were unique to unrestored controls (Tab. 2.5). Of the species only at controls, 80% were represented by a single individual. The species only at hedgerows tended to have more specialized nesting requirements (above-ground renters), whereas those only at controls were primarily generalists (below-ground excavators, Fig. 2.1). Also, though the majority of the species (68%) were found at both hedgerows and unrestored controls (Tab. 2.5), species ranging from relatively rare (less than 10 individuals) to common (between 10 and 100 individuals) were infrequent at controls and more abundant in hedgerows (Fig. 2.9). Interestingly, the three species observed over 100 times, *Lasioglossum incompletum*, *Halictus tripartitus* and *Halictus ligatus*, all small-bodied floral and nesting resource generalists, were at similar abundances in hedgerows and unrestored controls, if not slightly more abundant in controls (Fig. 2.9).

Though hedgerows may help counter homogenization of pollinator communities in simplified agricultural landscapes, comparing the spatial heterogeneity they support to that which is observed in natural communities is important in assessing their overall conservation value. In remnant chaparral/oak woodland communities in the same ecoregion and adjacent to our study landscapes (Forrest *et al.*, 2015), an average of 30% of species were not shared across sites located within 3.5–50 km of each other. The Central Valley, which was once described as “one vast, level, even flower-bed” (Muir, 1998), has been extensively converted to agriculture, likely limiting the species pool due to local extinctions. Even so, at hedgerows an average of 15 km apart, we found between 36% and 67% of species were not shared between sites, depending on the year. Both the spatial scale and biota of our study and that of Forrest *et al.* (2015) are comparable, suggesting that hedgerows are, in fact, restoring spatial heterogeneity to approximately the same range as might occur in adjacent natural systems. In addition, in the disparate landscape of the southwestern U.S., a diversity hotspot for bees (Minckley *et al.*, 1999), 61% of species were not shared across sites within 1–5 km of each other (Minckley *et al.*, 1999). Though the species pool is richer in the southwest, the amount of species turnover at hedgerows is not unlike what is observed in that

highly heterogeneous region (Minckley *et al.*, 1999). Thus, across many aspects of biodiversity, hedgerows might provide a valuable measure for conserving biodiversity (Klein *et al.*, 2009; Hinsley & Bellamy, 2000; Bianchi *et al.*, 2006; Morandin & Kremen, 2013; Garibaldi *et al.*, 2014; Kremen & M'Gonigle, 2015).

Only mature hedgerows (and not young, recently planted hedgerows) in this study supported higher trait and β -diversity when compared to non-restored farm edges. Thus, the processes that lead to a build-up of spatial turnover in pollinator communities are slow and may take considerable time before observably affecting pollinator communities. However, we have recently shown that hedgerow restoration leads to increased rates of colonization and persistence of pollinators in maturing hedgerows and that this effect becomes stronger over time (M'Gonigle *et al.*, 2015). Further, we found that maturing hedgerows differentially support more specialized species over time (Kremen & M'Gonigle, 2015). These two temporal studies on the early phases of hedgerow maturation (0 – 8 years post restoration) show that hedgerows begin to impact pollinator communities much earlier than 10 years. Combined, these findings suggest a possible mechanism whereby restoration might lead to increases in species turnover; as a hedgerow matures, species with a wider variety of life history traits are better able to colonize and persist there, thus leading to the accumulation of differences in community composition between sites over time. This then leads to greater spatial heterogeneity in pollinator communities at hedgerows. Conversely, in unrestored areas, the rate of colonization and persistence is lower, particularly for species with more specialized habitat requirements, thereby creating an ecological filter that limits the total diversity and, thus, turnover that is possible.

This above described process can be, in part, deterministic; restored and non-restored farm edges differ fundamentally in which pollinator species are able to colonize and/or persist in them (M'Gonigle *et al.*, 2015; Kremen & M'Gonigle, 2015). Thus pollinators respond to the differences in the plant communities between hedgerows and controls, and the pollinator community at mature hedgerows tracks floral hosts. Interestingly, however, the pollinator communities at hedgerows that were closer to one another were not necessarily more similar than sites that were further apart. In addition, hedgerows maintain β -diversity in the landscape by supporting unique combinations of species, and we did not find evidence that communities at hedgerows were nested subsets of one another (Baselga, 2012). Because hedgerows are planted, the floral communities the pollinators are tracking will not necessarily be spatially structured like natural communities. In addition, bees are known to be highly spatially and temporally variable (Minckley *et al.*, 1999; Williams *et al.*, 2001) and, thus, stochastic processes that do not result in spatial structuring are likely operating as communities assemble.

In contrast to within hedgerows, the dissimilarity of pollinators at unrestored controls responded positively to geographic distance. Because the conditions at controls are relatively uniform across space, this suggests a role for dispersal limitation in determining pollinator community composition at unrestored controls (i.e., Chase *et al.*, 2005). In addition, the number of shared species between hedgerows and controls was also positively related to distance (Tab. 2.2), suggesting the communities at controls may be influenced by landscape context such as the presence of nearby hedgerows. Hedgerows may therefore represent a source of bee diversity in the landscape.

Here we focus on the effects of hedgerows on β -diversity, but there are likely other contributions to spatial heterogeneity in our landscape. There are a number of crops that provide floral resources to pollinators in our area, including mass-flowering sunflower, melons and almonds (Klein *et al.*, 2012; Greenleaf & Kremen, 2006; Kremen *et al.*, 2002). Different crops attract different pollinators (e.g., Winfree *et al.*, 2008) and thus may affect the spatial heterogeneity of communities. In addition, some crops might also pull resident species from the hedgerows (Sardiñas & Kremen, 2015), while others may attract species that may subsequently colonize hedgerows (Kovács-Hostyánszki *et al.*, 2013). Differences in adjacent crops between hedgerows or unrestored controls thus may add noise to the underlying signal of β -diversity. However, because hedgerows and controls are matched for crop type, while there may be a contribution of crop type on β -diversity, it should be a random one affecting hedgerows and controls simultaneously.

To achieve sustainable food production while protecting biodiversity, we need to grow food in a manner that protects, utilizes and regenerates ecosystem services, rather than replacing them (Kremen & Miles, 2012; Kremen *et al.*, 2012; Kremen, 2015). Diversification practices such as installing hedgerows, when replicated across a landscape, may provide a promising mechanism for conserving and restoring ecosystem services and biodiversity in working landscapes while potentially improving pollination and crop yields (Blaauw & Isaacs, 2014; Garibaldi *et al.*, 2014).

2.7 Supplemental methods

β -DIVERSITY CALCULATION

Following (Chase *et al.*, 2011b), we corrected our estimates of β -diversity using null models. We first calculated the pairwise dissimilarity between sites within each year of the dataset using a dissimilarity estimator that incorporates species abundances, while also accounting for unobserved species (Chao *et al.*, 2005b).

We next created an expected distribution by generating randomized communities and calculating the dissimilarity of these communities. To do this, we defined the species pool within each year as the species and number of individuals present across all samples from that year. We then generated 9999 random communities by constraining either 1) the total number of individuals caught at each site or 2) the species richness at each site (for details on the community generation algorithms, see Section 2.7.2). For each of these communities, we calculated the pair-wise dissimilarity between sites. We then used these dissimilarities to calculate the expected β -diversity when communities are randomly assembled but constrained so that they have either the same 1) number of individuals or 2) species richness as the observed communities and with species drawn from a meta-community with the same species abundance distributions. In order to do this, we followed Chase *et al.* (2011b). Specifically, we calculated the fraction of randomly assembled communities with dissimilarity values less than (and half of those equal to) that of the observed community. We used this fraction as a “corrected dissimilarity score” for our observed data. Corrected dissimilarity values near one indicate that our observed communities exhibit more species turnover between sites than expected under a random assembly process while values near 0.5 indicate that our observed communities exhibit levels of turnover more in line with the null expectation. We calculated the corrected dissimilarities for each type of randomized community.

We also corrected dissimilarity values by calculating z-scores (subtracting the mean of the nulls from the observed dissimilarity and dividing by the standard deviation of the nulls (Trøjelsgaard *et al.*, 2015) to confirm that the method of calculating the corrected dissimilarity score did not qualitatively affect results.

We then generated principle coordinate axes (PCoA) based on the corrected pair-wise dissimilarities (Oksanen *et al.*, 2013b; Anderson *et al.*, 2006, 2011; Anderson, 2006). We calculated dispersion for each site type by finding the centroid in PCoA space for that site type and then calculating the distances from sites of that type to that centroid. The centroid is the point that minimizes the sum of these distances. We calculated dispersion scores separately for each year in order to account for possible changes in the total species pool that can occur between years (e.g., Petanidou *et al.*, 2008b). The dispersion values were then used in linear mixed-effect models to investigate the effect of different site types on β -diversity.

Though commonly used (e.g., Karp *et al.*, 2012), average pairwise dissimilarity may be misleading if spatial heterogeneity in community composition is due to nestedness and not species replacement (Baselga, 2012, 2013). However, in our case, because dissimilarity is due to species replacement, pair-wise measures of β -diversity are comparable to multi-site measures (Baselga, 2013).

COMMUNITY RANDOMIZATION ALGORITHMS

Randomly assembled communities were generated by either constraining 1) the species richness at a site or 2) the number of individuals at a site so that they were the same as those in the observed communities. In 1) we begin by randomizing a binary matrix while maintaining the same row sums (species richness at a site) and column sums (number of sites at which a species was observed) using the quasi-swap method in the R function `commsimulator` (Oksanen *et al.*, 2013b). Next, we fill the matrix by drawing species with probabilities proportional to their relative abundances until the total number of individuals in the randomly assembled community is the same as that in the observed community (Vázquez *et al.*, 2007). To constrain the total number of individuals at a site but not the species richness at that site, we used a swap-algorithm (Gotelli & Graves, 1996).

	Year						
	2007	2008	2009	2010	2011	2012	2013
Control-1	0	0	3	4	0	4	5
Control-2	3	3	0	0	0	0	0
Control-3	3	3	3	0	2	4	5
Control-4	0	0	0	0	0	4	5
Control-5	3	3	3	0	2	4	5
Control-6	0	0	3	0	0	4	5
Control-7	0	0	0	0	0	0	5
Control-8	3	3	3	0	2	4	5
Control-9	3	3	3	0	2	4	5
Control-10	3	3	3	0	2	4	5
Control-11	0	0	3	0	0	4	5
Control-12	0	0	0	0	0	4	0
Control-13	3	3	3	0	2	0	0
Control-14	0	0	3	4	0	4	5
Control-15	0	0	0	0	0	0	5
Control-16	0	0	0	0	0	0	5
Control-17	0	0	0	0	0	4	0
Control-18	3	3	3	0	2	4	5
Control-19	0	0	0	0	0	4	5
Control-20	3	3	3	0	2	4	5
Control-21	3	3	3	0	2	4	5
Control-22	3	3	3	0	2	4	5
Control-23	0	0	0	0	0	4	5
Control-24	0	0	0	4	0	4	5

Table 2.3: The number of sampling rounds conducted at each control site in each year of the study.

	Year						
	2007	2008	2009	2010	2011	2012	2013
Hedgerow-1	0	0	0	0	0	4	5
Hedgerow-2	0	0	0	0	0	0	5
Hedgerow-3	0	0	0	0	0	4	5
Hedgerow-4	0	0	3	4	2	4	5
Hedgerow-5	0	0	0	0	0	4	5
Hedgerow-6	0	0	3	0	2	4	5
Hedgerow-7	0	0	0	0	0	4	5
Hedgerow-8	0	0	0	4	2	4	5
Hedgerow-9	0	0	0	0	0	4	5
Hedgerow-10	0	0	0	0	0	4	5
Hedgerow-11	0	0	3	4	2	4	5
Hedgerow-12	0	0	3	0	2	4	5
Hedgerow-13	0	0	0	0	0	4	0
Hedgerow-14	0	0	0	0	2	4	5
Hedgerow-15	0	0	3	0	2	4	5
Hedgerow-16	0	0	0	0	0	4	5
Hedgerow-17	0	0	3	0	2	4	5
Hedgerow-18	0	0	0	0	0	0	5
Hedgerow-19	0	0	3	0	2	4	5
Hedgerow-20	0	0	0	0	0	4	5
Hedgerow-21	0	0	0	0	2	4	5

Table 2.4: The number of sampling rounds conducted at each hedgerow site in each year of the study.

Only Hedgerows	Both Hedgerows & Controls	Only Controls
Andrena angustitarsata	Agapostemon texanus	Andrena nigrocaerulea
Andrena subaustralis	Andrena auricoma	Andrena subchalybea
Andrena w-scripta	Andrena candida	Ceratina timberlakei
Anthidium manicatum	Andrena cerasifolii	Colletes hyalinus
Ashmeadiella cactorum basalis	Andrena chlorogaster	Diadasia consociata
Bombus vandykei	Andrena cressonii infasciata	Diadasia diminuta
Calliopsis hesperia equina	Andrena knuthiana	Diadasia ochracea
Calliopsis scitula	Andrena piperi	Eucera actuosa
Coelioxys apacheiorum	Andrena scurra	Eucera frater albopilosa
Coelioxys gilensis	Anthidiellum notatum robertsoni	Hylaeus leptocephalus
Coelioxys novomexicana	Anthophora urbana	Lasioglossum (Evylaeus) diatretum
Dianthidium ulkei	Ashmeadiella aridula astragali	Lasioglossum mellipes
Heriades occidentalis	Ashmeadiella buconis denticulata	Megachile brevis
Hylaeus calvus	Bombus californicus	Nomada sp. A
Hylaeus episcopalis	Bombus crotchii	Osmia nemoris
Lasioglossum (Evylaeus) granosum	Bombus melanopygus	
Lasioglossum (Evylaeus) nigrescens	Bombus vosnesenskii	
Megachile coquilletti	Ceratina acantha	
Megachile occidentalis	Ceratina arizonensis	
Melissodes communis alopex	Ceratina dallatorreana	
Osmia aglaia	Ceratina nanula	
Osmia coloradensis	Coelioxys octodentata	
Osmia granulosa	Diadasia enavata	
Osmia laeta	Halictus ligatus	
Osmia texana	Halictus tripartitus	
Peponapis pruinosa	Hoplitis producta gracilis	
Stelis laticincta	Hylaeus bisinuatus	
Stelis montana	Hylaeus conspicuus	
Triepeolus sp. A	Hylaeus mesillae	
Xeromelecta californica	Hylaeus rudbeckiae	
Xylocopa tabaniformis orpifex	Lasioglossum (Dialictus) brunneiiventre	
Xylocopa varipuncta	Lasioglossum (Dialictus) diversopunctatum	
	Lasioglossum (Dialictus) impavidum	
	Lasioglossum (Dialictus) incompletum	
	Lasioglossum (Dialictus) megastictum	
	Lasioglossum (Dialictus) punctatotentre	
	Lasioglossum (Dialictus) tegulare group	
	Lasioglossum (Evylaeus) kincaidii	
	Lasioglossum sisymbrii	
	Lasioglossum titusi	
	Megachile angularum	
	Megachile apicalis	
	Megachile fidelis	
	Megachile frugalis	
	Megachile gentilis	
	Megachile lippiae	
	Megachile montivaga	
	Megachile onobrychidis	
	Megachile parallela	
	Megachile rotundata	
	Melissodes agilis	
	Melissodes lupina	
	Melissodes robustior	
	Melissodes stearnsi	
	Melissodes tepida timberlakei	
	Nomada sp. 3	
	Osmia atrocyanea	
	Osmia gaudiosa	
	Osmia lignaria propinqua	
	Osmia regulina	
	Sphecodes sp. B	
	Svastra obliqua expurgata	
	Triepeolus concavus	
	Triepeolus heterurus	
	Triepeolus melanarius	
	Triepeolus subnitens	
	Triepeolus timberlakei	

Table 2.5: Bee species found at hedgerows and controls.

Year	F-statistic	<i>p</i> -value
2009	1.44 _{2,18}	0.18
2010	0.18 _{1,4}	1.00
2011	0.99 _{2,17}	0.48
2012	1.71 _{2,35}	0.17
2013	1.08 _{2,37}	0.40

Table 2.6: The test statistics for the permutation anovas comparing pollinator community composition between mature hedgerows, maturing hedgerows and unrestored controls within each year. The community composition did not vary significantly between site statuses in any year.

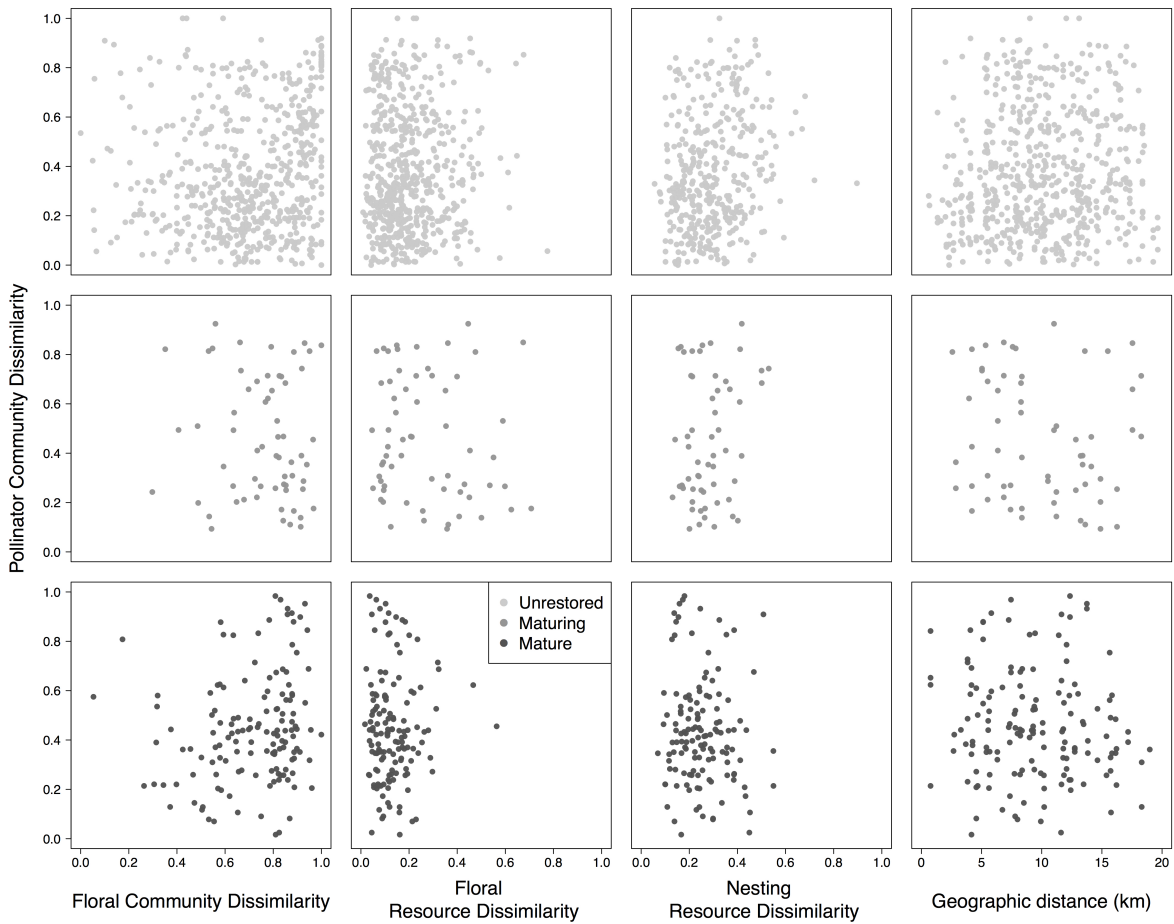


Fig. 2.5: The dissimilarity of pollinator communities as a function of the dissimilarity of the floral communities, floral resources, nesting resources, and geographic distance at each site type across all years of the study. Pollinator community dissimilarity is not correlated with any of the variables investigated.

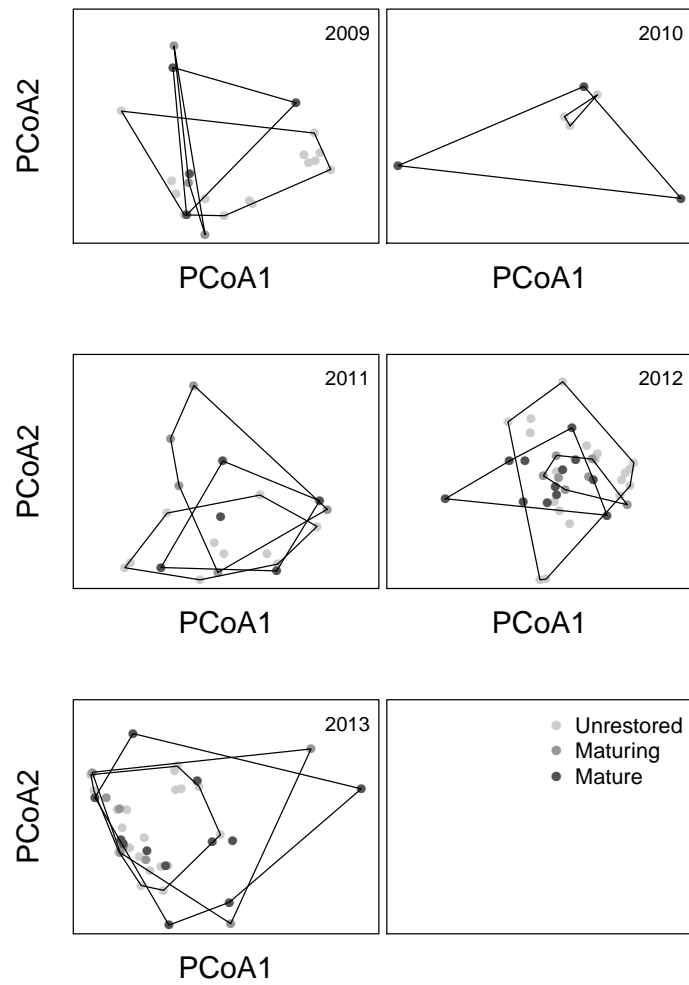


Fig. 2.6: The dissimilarity of communities in multivariate space using a principal coordinate analysis. The axis represent the first two principal coordinate axes. There is substantial overlap in the community composition of the different site types.

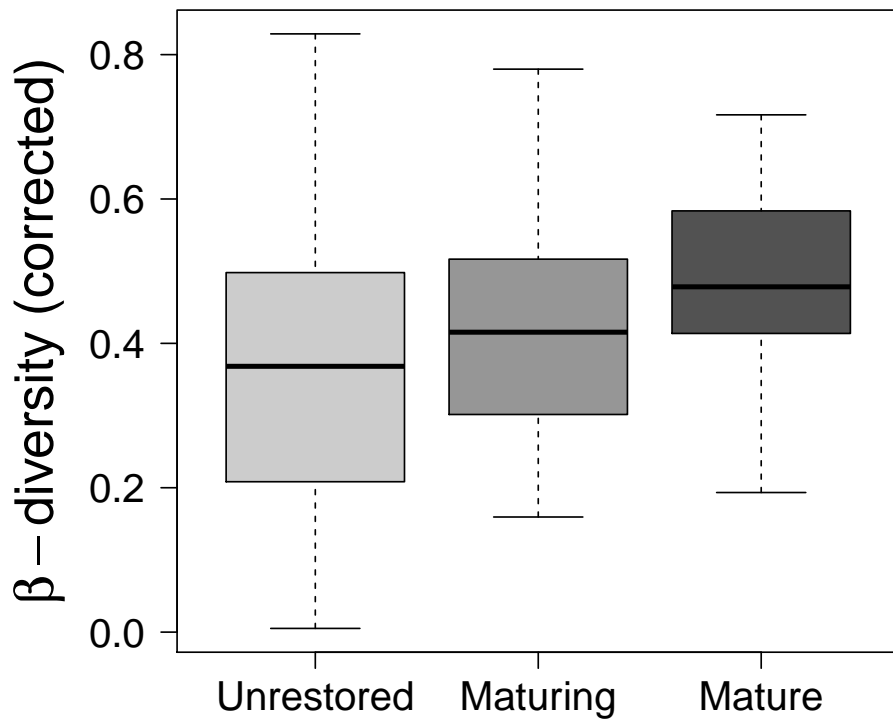


Fig. 2.7: The β -diversity (corrected using random communities that have the same number of individual as observed communities) at unrestored controls, maturing hedgerows and mature hedgerows. Corrected β -diversity is significantly higher in mature hedgerows than in unrestored controls (estimate \pm standard error, 0.130 ± 0.044 , p -value= 0.005). Boxplots represent medians (black horizontal line) first and third quartiles (box perimeter) and extremes (whiskers).

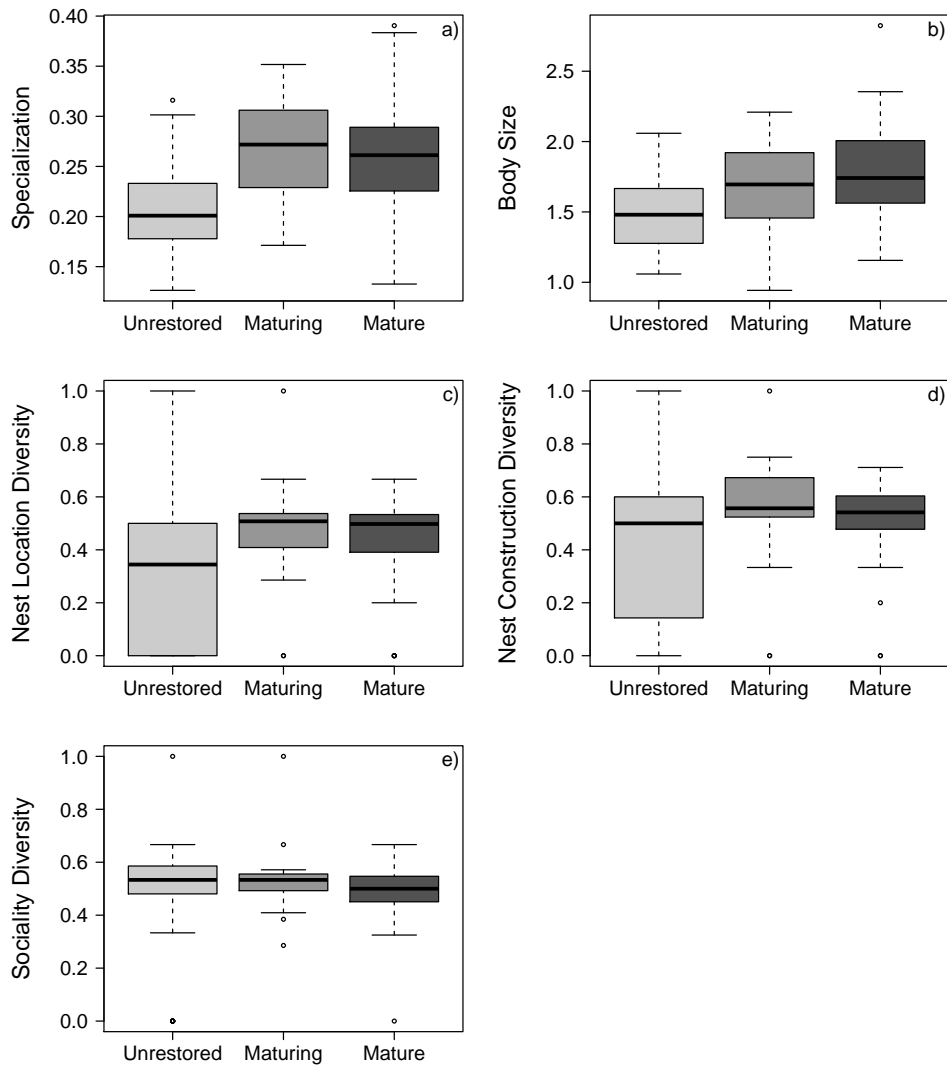


Fig. 2.8: The mean trait value (a-b) and trait diversity (c-e) of pollinator communities at different site types. Mature and maturing hedgerows supported significantly higher trait values and diversity for all of the trait groups investigated expect sociality diversity.

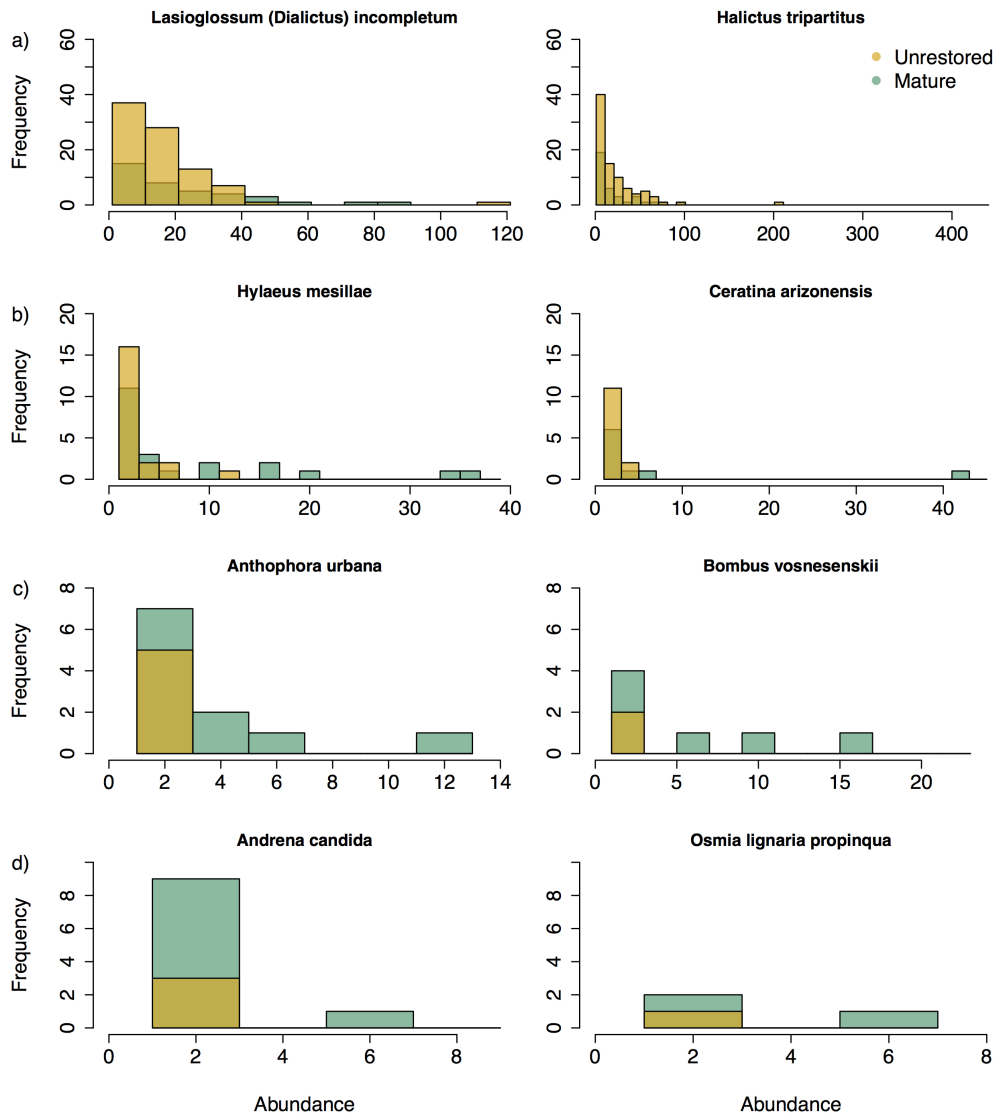


Fig. 2.9: The frequency of observing specific abundances at a site across years of a sample of species found in both hedgerows and controls. The top panel, (a), are the two most abundant species (total abundance > 100 individuals), panel (b) are relatively common species (abundance between 20 – 50 individuals), panel (c) are relatively infrequent (abundance between 10 – 20 individuals), and panel (d) are very infrequent (< 10 individuals).

Chapter 3

Coevolution leaves a weak signal on ecological networks

3.1 Transition

To fully understand the mechanisms maintaining communities we must combine our understanding of the ecological processes enabling their persistence with the evolutionary processes that assembled those communities. Coevolution is a key process producing and maintaining complex networks of interacting species. To inform restoration we must understand whether communities re-assembled through restoration are predicted to exhibit the same dynamics as tightly coevolved communities.

3.2 Abstract

One of the major challenges in evolutionary ecology is to understand how coevolution shapes species interaction networks. Important topological properties of networks, such as nestedness and modularity, are thought to be affected by coevolution. However, there has been no test whether coevolution does, in fact, lead to predictable network structure. Here we investigate the structure of simulated bipartite networks generated under different modes of coevolution. We ask whether evolutionary processes influence network structure and, furthermore, whether any emergent trends are influenced by the strength or “intimacy” of the species interactions. We find that coevolution leaves a weak and variable signal on network topology, which was not strongly affected by the intimacy of interactions. Our findings indicate that network metrics, on their own, should not be used to make inferences about processes underlying the evolutionary history of communities. Instead, a more holistic approach that combines network approaches with traditional phylogenetic and biogeographic reconstructions is needed.

3.3 Introduction

Dynamics of ecological communities are fundamentally shaped by their networks of interacting species (Thompson, 2005). The study of these networks, which involves the classification of interspecific relationships and the strength of their reliance upon one another, have important implications for ecology and conservation — informing, for example, the ability of communities to maintain ecosystem function in the face of disturbance. Specifically, interaction patterns, are thought to affect the resilience of a network to disturbances such as fluctuating species abundances, the introduction of new species, or the extinction of existing species.

Ecological networks exhibit two main topologies — modularity and nestedness. Modular community interactions are more insular, occurring within separate groups or “modules” more often than between modules. Conversely, nested networks are like pyramid of interactions, where there are some species that interact with many species, other species that interact with a subset of those species, and so on. Different types of ecological networks, ranging from mutualistic to antagonistic, exhibit nested (e.g., plants and pollinators, Bascombe *et al.*, 2006, 2003; hosts and parasites, Vázquez *et al.*, 2005) or modular (e.g., plants and pollinators, Olesen *et al.*, 2007; hosts and parasites, Krasnov *et al.*, 2012; plants and seed dispersers, Donatti *et al.*, 2011) interaction patterns. Both nested and modular communities may also exhibit phylogenetically structured interactions, where closely related species

have more similar interaction patterns than distantly related species (Rezende *et al.*, 2007; Donatti *et al.*, 2011). A strong phylogenetic signal indicates that network patterns are constrained by past evolutionary history (e.g., by trait conservatism).

Coevolutionary dynamics likely play a critical role in determining how communities are structured, because coevolution shapes and maintains the traits involved in species interactions. Modules can be created through coevolution by a combination of phylogenetic history (Lewinsohn *et al.*, 2006) and/or trait convergence of phylogenetically unrelated species (Danieli-Silva *et al.*, 2012; Donatti *et al.*, 2011). Coevolution can alternatively lead to nestedness if phenotypes constrain interactions (i.e., some links are “forbidden”, Jordano *et al.*, 2003; Santamaría & Rodríguez-Gironés, 2007). Coevolution can also affect the degree of dependence between interacting groups, or the “intimacy” of species associations, which can also affect network structure indirectly (Fontaine *et al.*, 2011; Guimarães *et al.*, 2007; Ollerton, 2006). The combined effects selection that leads to the avoidance of sharing interaction partners (so called, partner overlap) and biological limits that influence how many partners a species can have (interaction niche breath) are expected to lead to more intimate interactions. For example, antagonistic coevolution favors parasites that are able to overcome host defenses, which can subsequently lead to parasites visiting only a few mutually exclusive host species (e.g., overcoming one host’s defenses might come at the expense of the ability to overcome other host’s defenses, Nuismer & Thompson, 2006; Fontaine *et al.*, 2011). In contrast, more generalized interactions with considerable partner overlap may evolve if selection favors phenotypes that are compatible with traits common to many species in the community, as might be the case for free-living mutualists (Thompson, 2005; Guimarães *et al.*, 2011; Fontaine *et al.*, 2011). Actual networks exhibit levels of interaction intimacy that lie along a continuous spectrum, with varying degrees of interaction niche breath and partner overlap (Fontaine *et al.*, 2011).

A variety of processes other than coevolution are thought to affect species interaction patterns as well, including ecological dynamics (Thébaud & Fontaine, 2010; Bastolla *et al.*, 2009; Krause *et al.*, 2003), spatio-temporal species distributions (Pillai *et al.*, 2011; Vázquez *et al.*, 2009; Pimm *et al.*, 1991; Encinas-Viso *et al.*, 2012), stochastic processes (Canard *et al.*, 2012; Johnson *et al.*, 2013; Krishna *et al.*, 2008), sampling artifacts (Vázquez *et al.*, 2009), or combinations thereof (Suweis *et al.*, 2013; Vázquez *et al.*, 2009). Understanding which ecological, evolutionary, and stochastic processes have consistent effects on interaction patterns (i.e., the degree to which communities are nested or modular) is critical for elucidating the mechanisms that structure communities, as an interaction’s structure affects its stability. Compared to randomly assembled communities, nested communities may be more resilient to species extinction and fluctuations in abundance (Memmott *et al.*, 2004; Burgos *et al.*, 2007; Thébaud & Fontaine, 2010; Fortuna & Bascompte, 2006; Valdovinos *et al.*, 2013a, but see Allesina & Tang, 2012; James *et al.*, 2012). Modular interaction patterns are also thought to be more stable than random interactions (May, 1972; Krause *et al.*, 2003) because fluctuations in species abundance are largely contained within modules and are less likely to spread throughout an entire community (Krause *et al.*, 2003, but see Pimm & Lawton, 1980; Thébaud & Fontaine, 2010). Additionally, theoretical work suggests that when interactions are phylogenetically structured, species extinction may trigger extinction cascades of related species and a more pronounced loss of taxonomic diversity (Rezende *et al.*, 2007).

Recently, several authors have used theoretical models to explore the effect of evolution on networks (Guimarães *et al.*, 2011; Nuismer *et al.*, 2013; Loeuille, 2010). However, there have been no explicit tests of how different evolutionary assembly mechanisms may lead to predictably different network topologies. Here, we develop and analyze a model of coevolution and community assembly to test whether coevolution leads to predictable network structures. We also examine whether interaction intimacy, measured as the degree of interaction niche breath and partner sharing between species, accentuates the signal of these different assembly mechanisms on the structure of networks.

3.4 Material and methods

COMMUNITY GENERATION APPROACH

We simulate coevolution and community assembly of two interacting clades of species under four different modes of coevolution, each of which corresponds to a limiting case of the possible coevolutionary mechanisms. We then build interaction networks, using trait values to determine which pairs of species can interact. Finally, we calculate network metrics. All simulations were conducted in R version 3.2 (R Core Team, 2015).

We do not explicitly make a distinction between predatory, mutualistic, parasitic, or commensal interactions. These scenarios differ in how species interactions affect fitness. Because species’ fitnesses are not a component of our data simulation process, our conclusions should apply to networks containing interactions of all

types. To facilitate biological intuition, however, we will develop our methods using language most appropriate for mutualistic interactions.

Phylogeny and trait generation

We begin by generating phylogenetic trees for a fixed number of resource-providing species (e.g., plants) and resource-seeking species (e.g., pollinators). We do this using a birth-death process (Stadler, 2012) which approximates diversification of clades by assuming homogeneous rates of speciation (birth, λ) and extinction (death, μ) across taxa and time (Stadler, 2012). The shape of phylogenetic trees has the potential to affect the structure of networks (Chamberlain *et al.*, 2014), so we generated birth-death trees for a range of extinction and speciation rates (Fig. 3.1). Specifically we simulated trees with primarily deep or primarily shallow divergences (Fig. 3.1).

We next simulated trait evolution along these trees under a Brownian motion process (Paradis, 2012) except in one scenario (described below) where we also used an Ornstein-Uhlenbeck process (Gillespie, 1996; Nuismer & Harmon, 2015). Because trait variance and tree age are linearly related under a Brownian motion model, we altered the variance of the Brownian motion process while holding the tree age constant. The four scenarios under which we simulated trait evolution we as follows:

1. **Coevolution and cospeciation** (Fig. 3.2a): High levels of interaction specificity lead to tight coevolution and cospeciation and, consequently, evolution of congruent phylogenies (Fahrenholz, 1913). The plausibility of this scenario has been extensively criticized for its lack of realism (e.g., Klassen, 1992). Recently even obligate mutualisms have been shown to deviate from predictions of this model (e.g., figs and fig wasps, Machado *et al.*, 2005; Cruaud *et al.*, 2011; oil producing orchids and Euglossine bees, Ramírez *et al.*, 2011, yucca plants and yucca moths, Althoff *et al.*, 2012). Different groups of parasites, including macro-parasites (internal and external) and their vertebrate hosts also do not exhibit a strong signal of cospeciation (for a review see Hoberg & Brooks, 2008). However, this scenario provides a useful benchmark, because communities assembled under this strict scenario represent an extreme outcome of coevolution. We simulate this mode of coevolution by generating communities where the tree topology and trait values of interacting taxa are identical (Fig. 3.2a).
2. **Coevolution without cospeciation** (Fig. 3.2b): Trait complementarity is the result of natural selection honing the traits involved in interactions across many lineages (e.g., corolla tubes of plants and the length of pollinators' proboscises). Interacting communities are composed of phylogenetically related and unrelated species that have converged on similar traits (Donatti *et al.*, 2011; Olesen *et al.*, 2007; Danieli-Silva *et al.*, 2012; Krasnov *et al.*, 2012, 2014). This pattern of trait convergence is often observed in interacting species, such as patterns of fruit design in unrelated plant species (Jordano, 1995), oil production in orchids (Ramírez *et al.*, 2011), and ecto-parasites of mammals (Krasnov *et al.*, 2012). To investigate this scenario, we generate communities where the speciation of the mutualistic partners occurs independently and thus phylogenetic topologies differ between the two groups, but trait distributions of interacting species are probabilistically matched (Fig. 3.2b). To link the trait distributions, the traits of one interacting group are first simulated under Brownian motion evolution. The traits of this group are then used as lineage-specific optima in an Ornstein-Uhlenbeck process to generate the traits in the other interacting group. To approximate reciprocal selection, we then use the traits of the second group as optima in another Ornstein-Uhlenbeck process to re-generate traits for the first group.
3. **Cospeciation without coevolution** (Fig. 3.2c): Concurrent allopatric speciation of lineages across a shared biogeographic and climatic landscape leads to congruence between phylogenies of interacting species, without reciprocal selection on species' traits (Althoff *et al.*, 2012; Smith *et al.*, 2008). For example, the phylogenetic congruence between yuccas and yucca moths is likely due to shared biogeographic history rather than coevolutionary selection (Althoff *et al.*, 2012). When species co-occur geographically, it is likely that they evolve or coevolve. However, we present an extreme case where no coevolution takes place to explore the effect of cospeciation alone. To model this, we generate communities where interacting taxa share the same tree topology, but the traits of the partners evolve independently via Brownian motion along each tree (Fig. 3.2c).
4. **No coevolution, no cospeciation** (Fig. 3.2d): Speciation and trait evolution proceed independently of one another. Such independent evolution could occur if environmental or developmental constraints on the traits involved in interactions (e.g., the body size of pollinators and the flower size of plants) enable interactions

to occur without coevolution taking place. To construct communities under this scenario, we generate trees and traits of interacting taxa independently (Fig. 3.2d).

Linkage rules and interaction intimacy

Several ecological “linkage rules” have been suggested for determining how a species’ trait values mediate its interactions (Santamaría & Rodríguez-Gironés, 2007). Here, we assume that interactions are dependent on the complementarity between the trait values of the resource producing species and the reward seeking species (matching traits, Santamaría & Rodríguez-Gironés, 2007; Nuismer *et al.*, 2013; Stang *et al.*, 2007, Fig. 3.2) and, further, that the range of acceptable trait values in a partner is proportional to the magnitude of a species’ evolved trait values (Williams & Martinez, 2000a; Pires *et al.*, 2011; Santamaría & Rodríguez-Gironés, 2007). Our formulation of matching traits is similar to the niche model (Williams & Martinez, 2000a) or to the “single trait complementary model” (Santamaría & Rodríguez-Gironés, 2007), both of which have been shown to generate empirically feasible bipartite networks (Santamaría & Rodríguez-Gironés, 2007; Pires *et al.*, 2011). Depending on the variance in trait values and the structure of the phylogenetic tree, the distribution of traits was normal to right-skewed, which also matches the empirical literature (Stang *et al.*, 2009, 2006). Our formulation of trait ranges also reflects the observation that species with larger traits (e.g., proboscises length) are able to interact more widely (e.g., access to a greater variety of nectar depths, Stang *et al.*, 2009).

The degree of interaction intimacy in a community is determined by the amount of partner overlap in the community and the interaction niche breadth of the constituent species. We varied both components of interaction intimacy by changing the specificity of the interactions which we did by changing the maximum acceptable difference in trait values that would still enable two potential partners to interact (Fig. 3.3). Specifically, we varied the range of acceptable trait values in a partner from $\pm 10\%$ of a focal individual’s trait value (narrow trait range) to $\pm 100\%$ (wide trait range). For example, if the trait value of a species is 2, with a narrow trait range, the species would interact with partners whose trait values fell within the range $2 \pm 2 * 0.1$. With a wide trait range, however, acceptable partner trait values would lie in the interval $2 \pm 2 * 1$. Trait ranges above 100% or below 10% yielded interaction matrices where nearly all or nearly none of the species interacted and, thus, they were not considered.

We also generated weighted networks, in which partners interact in proportion to the amount of overlap in their trait ranges, and unweighted networks, in which species interact equally frequently with all others whose trait ranges overlap. In the weighted case, a species with a trait range of 2 ± 2 would interact twice as much with a species with a trait range of 3 ± 3 (an overlap of 4) than a species with a trait range of 1 ± 1 (an overlap of 2).

We calculated niche breadth as $S = \bar{d}$ where \bar{d} denotes the mean proportion of potential interaction partners a species interacts with, from the total possible (i.e., the mean species degree). We calculated partner overlap as $P = \bar{s}_{ij}$ where \bar{s}_{ij} denotes the mean trophic similarity of pairs of species belonging to the same interaction group (Gower, 1971; Oksanen *et al.*, 2013a).

Because we assume that interactions require complementarity of traits between partner species (Stang *et al.*, 2007; Santamaría & Rodríguez-Gironés, 2007; Nuismer *et al.*, 2013), traits of interacting lineages are positively correlated in each of the coevolutionary scenarios. For hosts and parasites, this positive correlation might correspond to a match between traits that govern susceptibility in hosts and mode of attack in parasites. Traits such as the depth of nectar tube in a flower and the length of a pollinator’s tongue would also be expected to positively correlate when interactions are mutualistic.

When simulating phylogenies, we began with a 1:1 ratio of resource-providing species to resource-seeking species. We did this in order to facilitate comparisons between scenarios where there is necessarily a one-to-one congruence (e.g., the coevolution and cospeciation scenario) with those where there is not. However, species that evolve to possess trait values that prohibit them from interacting with any members of the community were not included in the network. Thus the communities vary in the number of species in each group of interacting species. We would expect this feedback between species’ traits community composition when species with ill-suited trait values are unable to persist in that community.

CHARACTERIZING NETWORK TOPOLOGIES

For each of the resulting interaction networks, we calculated topological descriptors, focusing in particular on nestedness and modularity. We use NODF (weighted or unweighted) to evaluate network nestedness (Almeida-Neto *et al.*, 2008). NODF evaluates whether species with fewer partners interact with subsets of partners with which more connected species interact (Almeida-Neto *et al.*, 2008). Many methods exist for partitioning networks into sub-communities for modularity computation, and all have potential pitfalls (Fortunato, 2010). We, therefore, considered three community partitioning methods: 1) a dynamic algorithm via a random walk (Pons & Latapy,

2005; Csardi & Nepusz, 2006), 2) a greedy modularity optimization (Clauset *et al.*, 2004; Csardi & Nepusz, 2006), and 3) a hierarchical clustering algorithm (Newman & Girvan, 2004; Csardi & Nepusz, 2006).

We calculated standardized z-scores so that network metrics could be compared between communities. The z-scores were calculated by generating an ensemble of 99 randomly assembled communities, subtracting the mean of the statistic calculated across these communities from the observed value, and then dividing by the standard deviation. To assemble random communities, we reshuffled the interactions between species but fixed the total number of interactions and species, and, in quantitative networks, the distribution of the interaction frequencies (Galeano *et al.*, 2009). Simulating > 99 for all analyses presented here was too computationally intensive. However, we verified that conclusions did not differ qualitatively for a subset of scenarios when using 999 vs. 99 null communities.

We estimated the strength of the phylogenetic interaction signal as the correlation between the evolutionary time separating species and the dissimilarity of their interaction partners. The evolutionary distance between two species is proportional to their phylogenetic distance – the sum of the branch lengths connecting those species (Paradis *et al.*, 2004). We measured the dissimilarity of interaction partners by calculating the relative overlap of interaction partners between pairs of species (Oksanen *et al.*, 2013a). We then calculated phylogenetic interaction signal as the correlation between the phylogenetic distance matrix and the interaction dissimilarity matrix using a Mantel test (Rezende *et al.*, 2007). A high correlation indicates that species with older divergence times are less likely to share interaction partners.

To calculate the effect of coevolution, we selected random pairs of communities that shared the same cospeciation history but had evolved traits under different coevolutionary conditions (one community had coevolved whereas the other had not). We then calculated the difference between metric scores between those paired communities. The mean and standard deviation of these differences across replicate pairs of communities was used as an estimate of the effect of coevolution.

3.5 Results

We found that the coevolutionary history of a community can have consistent and detectable effects on the structure of interactions (Fig. 3.4, Tables 3.2 – 3.4). Specifically, when interaction probabilities were not weighted by the degree of overlap between partner traits, communities that coevolved and cospeciated were more modular and anti-nested (Fig. 3.4a,c). This is likely because cospeciating clades form interacting modules (for example, see Fig. 3.2a). The metric used for calculating modularity (edge-betweenness, greedy optimization, and random walk) did not qualitatively affect the relative differences between coevolutionary scenarios (Fig. 3.7).

In addition, communities that cospeciated had the highest phylogenetic interaction signal (Fig. 3.4e-f, Table 3.4). That a strong phylogenetic interaction signal characterizes cospeciating communities is likely a consequence of the fact that shared tree topologies between interaction groups constrain trait evolution such that closely related species will have similar traits and thus share interaction partners, with or without coevolution.

The effect of coevolution did not depend strongly on phylogenetic tree structure or the variance in evolved trait values, (Tables 3.1). Because these community characteristics did not have distinct effects on the differences between coevolutionary communities, we restrict our focus to community with shallow divergences between species within interaction groups and a low variance in evolved trait values (see Fig. 3.1 for parameter details in all figures).

There was also no detectable effect of coevolution on network structure in communities with the same cospeciation history. In both communities that cospeciated and those that did not, the mean effect size of coevolution (calculated as the difference in network metrics between communities with and without coevolution) was smaller than the standard deviation of the difference (Tables 3.1). Thus the effect of coevolution was never significantly different from zero. In addition, at any level of interaction niche breadth or partner overlap, the effect of coevolution was highly variable and not significantly different from zero (Figs. 3.5 – 3.6).

3.6 Discussion

We found that coevolution leaves a weak signal on network topology in four coevolutionary community assembly scenarios. These scenarios represent extreme possibilities, ranging from coevolution and cospeciation to completely independent evolution and speciation. Real-world communities likely fall somewhere between these extremes and are, thus, likely to exhibit intermediate patterns to those reported here. Because the topological differences reported here are small, detecting signals of coevolution will likely be difficult. Thus, caution should be

taken when using only the most common network topology descriptors (nestedness, modularity, and phylogenetic interaction signal) to make inferences about the processes that underlie the evolutionary history of a community.

Because communities with coevolved species were not consistently more nested or modular than communities that did not coevolve, we would be reluctant to make predictions about resilience of coevolved communities expected based on interaction structure (Memmott *et al.*, 2004; Burgos *et al.*, 2007; Fortuna & Bascompte, 2006). However, cospeciation left a relatively strong phylogenetic interaction signal. Because closely related species share interaction partners, this may make communities that cospeciate more vulnerable to coextinction cascades (Rezende *et al.*, 2007).

By assembling evolutionary communities both with and without coevolution in the same framework, our approach differs from those that consider coevolutionary dynamics in isolation (e.g., Nuismer *et al.*, 2013; Loeuille, 2010; Guimarães *et al.*, 2011). Here, coevolutionary feedbacks between phylogenies, traits, and interactions were modeled implicitly, so that the same framework can be used for communities that did and did not coevolve. However, our coevolutionary communities exhibit similar structural properties to communities generated by explicit coevolutionary models of bipartite networks (Nuismer *et al.*, 2013). We found that trait matching based species interactions led to anti-nested networks (Fig. 3.4) — this result is consistent with other studies (Nuismer *et al.*, 2013).

Our finding that different coevolutionary processes do not lead to drastically different interaction patterns in networks sheds light on why other studies have found it difficult to distinguish mechanisms (e.g., Althoff *et al.*, 2012; Machado *et al.*, 2005; Cruaud *et al.*, 2011; Ramírez *et al.*, 2011). Until recently, coevolution and cospeciation were thought to play a critical role in structuring many one-to-one symbiotic relationships, such as those between figs and fig wasps or yucca and yucca moths. Evidence was largely based on the congruence between traits of interacting species and their phylogenies. Recent work using more synthetic approaches and diverse data sources, however, has shown that these apparent patterns were largely due cospeciation of interacting lineages due to a shared biogeographic history, and not coevolution (Althoff *et al.*, 2012) and/or incomplete sampling (Machado *et al.*, 2005; Cruaud *et al.*, 2011).

Because so many mechanisms give rise to the same interaction patterns, additional tests have to be devised and undertaken to assess the contribution of different assembly mechanisms. Specially, determining whether assembly processes structure interactions will require a synthetic approach — combining network approaches with more traditional phylogenetic, trait and biogeographic reconstructions (e.g., Ramírez *et al.*, 2011).

Tree divergences	Variance in evolved trait values		Interaction weights		Coevolution		Modularity		Nestedness		Phylo int Signal	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Shallow	Low		Unweighted		With cospeciation		-0.47	6.286	-3.618	5.603	0.012	0.294
Shallow	Low		Unweighted		Without cospeciation		2.144	5.759	1.471	6.436	0.02	0.121
Shallow	Low		Weighted		With cospeciation		1.431	3.765	-3.568	5.121	0.005	0.302
Shallow	Low		Weighted		Without cospeciation		0.676	4.232	1.995	5.687	0.019	0.119
Shallow	High		Unweighted		With cospeciation		-0.454	6.383	-3.592	5.614	0.01	0.294
Shallow	High		Unweighted		Without cospeciation		2.142	5.69	1.499	6.672	0.021	0.124
Shallow	High		Weighted		With cospeciation		1.423	3.833	-3.572	5.115	0.001	0.302
Shallow	High		Weighted		Without cospeciation		0.691	4.334	2.065	5.892	0.018	0.123
Deep	Low		Unweighted		With cospeciation		-0.576	6.464	-3.403	5.595	0.015	0.291
Deep	Low		Unweighted		Without cospeciation		-0.22	5.499	0.348	6.419	0.006	0.137
Deep	Low		Weighted		With cospeciation		1.444	3.853	-3.457	5.062	0.005	0.294
Deep	Low		Weighted		Without cospeciation		-0.342	3.982	0.419	6.071	0.004	0.132
Deep	High		Unweighted		With cospeciation		-0.521	6.334	-3.413	5.649	0.016	0.29
Deep	High		Unweighted		Without cospeciation		3.599	5.324	-3.986	6.301	-0.003	0.169
Deep	High		Weighted		With cospeciation		1.418	3.728	-3.447	5.141	0.006	0.295
Deep	High		Weighted		Without cospeciation		3.923	5.007	-3.153	6.751	-0.009	0.169

Table 3.1: The mean and standard deviation of the difference in modularity (z -scores), nestedness (z -scores), and phylogenetic interaction signal between coevolved and non-coevolved communities, controlling for whether the interaction groups cospeciated (see Fig. 3.1 for details on the parameters governing tree divergence and the variance in evolved trait values). The effect of coevolution with cospeciation is calculated as the difference between communities that coevolved and cospeciated and those that only cospeciated. Similarly, the effect of coevolution without cospeciation is calculated as the difference between coevolved communities that did not cospeciate and those with interaction partners that did not coevolve or cospeciate. SD represents the standard deviation. The mean differences are always less than the standard deviation.

Tree divergences	Trait evolution variance	vari-	Coevolutionary community	Interaction weights	Mean	Standard deviation
Shallow	Low		No coevolution, no cospeciation	Unweighted	5.313	3.342
Shallow	Low		Coevolution, no cospeciation	Unweighted	6.05	3.163
Shallow	Low		No coevolution, cospeciation	Unweighted	6.053	3.169
Shallow	Low		Coevolution, cospeciation	Unweighted	7.54	2.311
Deep	Low		No coevolution, no cospeciation	Unweighted	6.327	2.926
Deep	Low		Coevolution, no cospeciation	Unweighted	6.015	3.167
Deep	Low		No coevolution, cospeciation	Unweighted	6.04	3.223
Deep	Low		Coevolution, cospeciation	Unweighted	7.489	2.34
Deep	High		No coevolution, no cospeciation	Unweighted	1.866	4.271
Deep	High		Coevolution, no cospeciation	Unweighted	6.112	3.142
Deep	High		No coevolution, cospeciation	Unweighted	6.129	3.123
Deep	High		Coevolution, cospeciation	Unweighted	7.56	2.288
Shallow	High		No coevolution, no cospeciation	Unweighted	5.27	3.354
Shallow	High		Coevolution, no cospeciation	Unweighted	6.002	3.188
Shallow	High		No coevolution, cospeciation	Unweighted	6.055	3.204
Shallow	High		Coevolution, cospeciation	Unweighted	7.496	2.343
Shallow	Low		No coevolution, no cospeciation	Weighted	0.932	4.239
Shallow	Low		Coevolution, no cospeciation	Weighted	3.101	3.927
Shallow	Low		No coevolution, cospeciation	Weighted	3.116	3.917
Shallow	Low		Coevolution, cospeciation	Weighted	2.709	4.985
Deep	Low		No coevolution, no cospeciation	Weighted	3.306	3.851
Deep	Low		Coevolution, no cospeciation	Weighted	3.153	3.887
Deep	Low		No coevolution, cospeciation	Weighted	3.276	3.883
Deep	Low		Coevolution, cospeciation	Weighted	2.696	5.051
Deep	High		No coevolution, no cospeciation	Weighted	-0.525	3.697
Deep	High		Coevolution, no cospeciation	Weighted	3.145	3.851
Deep	High		No coevolution, cospeciation	Weighted	3.183	3.849
Deep	High		Coevolution, cospeciation	Weighted	2.772	4.929
Shallow	High		No coevolution, no cospeciation	Weighted	0.807	4.246
Shallow	High		Coevolution, no cospeciation	Weighted	2.992	3.908
Shallow	High		No coevolution, cospeciation	Weighted	3.083	3.887
Shallow	High		Coevolution, cospeciation	Weighted	2.655	5.015

Table 3.2: The mean and standard deviation of the relative modularity (z-scores) of different coevolutionary communities (see Table 1 for parameter details).

Tree divergences	Trait evolution variance	vari-	Coevolutionary community	Interaction weights	Mean	Standard deviation
Shallow	Low		No coevolution, no cospeciation	Unweighted	-4.499	3.798
Shallow	Low		Coevolution, no cospeciation	Unweighted	-2.701	5.251
Shallow	Low		No coevolution, cospeciation	Unweighted	-2.738	5.218
Shallow	Low		Coevolution, cospeciation	Unweighted	-6.274	2.671
Deep	Low		No coevolution, no cospeciation	Unweighted	-3.165	4.877
Deep	Low		Coevolution, no cospeciation	Unweighted	-2.699	5.254
Deep	Low		No coevolution, cospeciation	Unweighted	-2.823	5.169
Deep	Low		Coevolution, cospeciation	Unweighted	-6.257	2.68
Deep	High		No coevolution, no cospeciation	Unweighted	0.84	6.298
Deep	High		Coevolution, no cospeciation	Unweighted	-2.66	5.275
Deep	High		No coevolution, cospeciation	Unweighted	-2.795	5.191
Deep	High		Coevolution, cospeciation	Unweighted	-6.242	2.694
Shallow	High		No coevolution, no cospeciation	Unweighted	-4.706	3.739
Shallow	High		Coevolution, no cospeciation	Unweighted	-2.699	5.257
Shallow	High		No coevolution, cospeciation	Unweighted	-2.722	5.278
Shallow	High		Coevolution, cospeciation	Unweighted	-6.255	2.695
Shallow	Low		No coevolution, no cospeciation	Weighted	-1.964	5.106
Shallow	Low		Coevolution, no cospeciation	Weighted	-0.712	5.688
Shallow	Low		No coevolution, cospeciation	Weighted	-0.76	5.674
Shallow	Low		Coevolution, cospeciation	Weighted	-4.371	3.759
Deep	Low		No coevolution, no cospeciation	Weighted	-1.14	5.42
Deep	Low		Coevolution, no cospeciation	Weighted	-0.717	5.703
Deep	Low		No coevolution, cospeciation	Weighted	-0.873	5.6
Deep	Low		Coevolution, cospeciation	Weighted	-4.288	3.778
Deep	High		No coevolution, no cospeciation	Weighted	3.725	6.258
Deep	High		Coevolution, no cospeciation	Weighted	-0.715	5.704
Deep	High		No coevolution, cospeciation	Weighted	-0.885	5.603
Deep	High		Coevolution, cospeciation	Weighted	-4.348	3.753
Shallow	High		No coevolution, no cospeciation	Weighted	-2.16	5.061
Shallow	High		Coevolution, no cospeciation	Weighted	-0.713	5.679
Shallow	High		No coevolution, cospeciation	Weighted	-0.82	5.675
Shallow	High		Coevolution, cospeciation	Weighted	-4.374	3.765

Table 3.3: The mean and standard deviation of the relative nestedness (z-scores) of different coevolutionary communities (see Table 1) for parameter details).

Tree divergences	Trait evolution variance	vari-	Coevolutionary community	Interaction weights	Mean	Standard deviation
Shallow	Low		No coevolution, no cospeciation	Unweighted	0.004	0.075
Shallow	Low		Coevolution, no cospeciation	Unweighted	0.025	0.096
Shallow	Low		No coevolution, cospeciation	Unweighted	0.211	0.22
Shallow	Low		Coevolution, cospeciation	Unweighted	0.215	0.213
Deep	Low		No coevolution, no cospeciation	Unweighted	0.022	0.089
Deep	Low		Coevolution, no cospeciation	Unweighted	0.024	0.097
Deep	Low		No coevolution, cospeciation	Unweighted	0.205	0.214
Deep	Low		Coevolution, cospeciation	Unweighted	0.21	0.214
Deep	High		No coevolution, no cospeciation	Unweighted	0.038	0.142
Deep	High		Coevolution, no cospeciation	Unweighted	0.026	0.101
Deep	High		No coevolution, cospeciation	Unweighted	0.202	0.212
Deep	High		Coevolution, cospeciation	Unweighted	0.21	0.21
Shallow	High		No coevolution, no cospeciation	Unweighted	0.005	0.076
Shallow	High		Coevolution, no cospeciation	Unweighted	0.024	0.097
Shallow	High		No coevolution, cospeciation	Unweighted	0.213	0.217
Shallow	High		Coevolution, cospeciation	Unweighted	0.216	0.215
Shallow	Low		No coevolution, no cospeciation	Weighted	0.004	0.072
Shallow	Low		Coevolution, no cospeciation	Weighted	0.027	0.101
Shallow	Low		No coevolution, cospeciation	Weighted	0.21	0.219
Shallow	Low		Coevolution, cospeciation	Weighted	0.223	0.211
Deep	Low		No coevolution, no cospeciation	Weighted	0.023	0.092
Deep	Low		Coevolution, no cospeciation	Weighted	0.026	0.101
Deep	Low		No coevolution, cospeciation	Weighted	0.205	0.213
Deep	Low		Coevolution, cospeciation	Weighted	0.219	0.213
Deep	High		No coevolution, no cospeciation	Weighted	0.034	0.142
Deep	High		Coevolution, no cospeciation	Weighted	0.028	0.103
Deep	High		No coevolution, cospeciation	Weighted	0.201	0.214
Deep	High		Coevolution, cospeciation	Weighted	0.219	0.21
Shallow	High		No coevolution, no cospeciation	Weighted	0.005	0.071
Shallow	High		Coevolution, no cospeciation	Weighted	0.026	0.102
Shallow	High		No coevolution, cospeciation	Weighted	0.211	0.217
Shallow	High		Coevolution, cospeciation	Weighted	0.223	0.213

Table 3.4: The mean and standard deviation of the phylogenetic interaction signal of different coevolutionary communities (see Table 1 for parameter details).

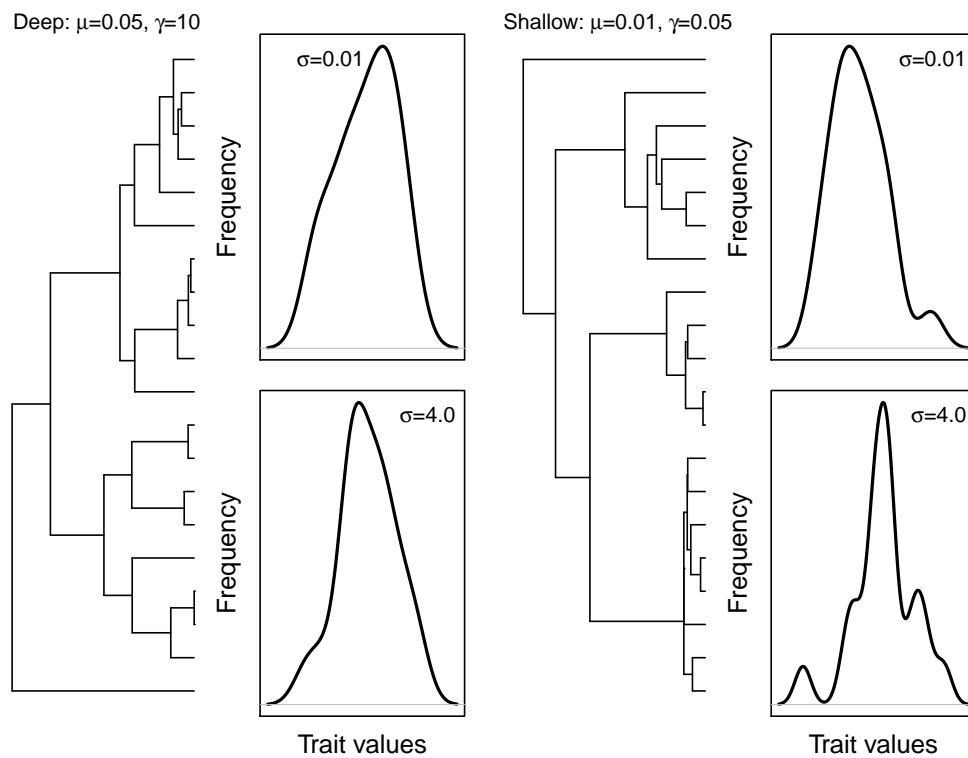


Fig. 3.1: Dependence of tree shape on speciation (μ) and extinction rates (λ). The low values of μ and λ generated trees with shallow divergences, and the high values generated deep divergences. The panels show the distribution of trait values generated by the different combinations of phylogenetic tree structure and Brownian motion variance.

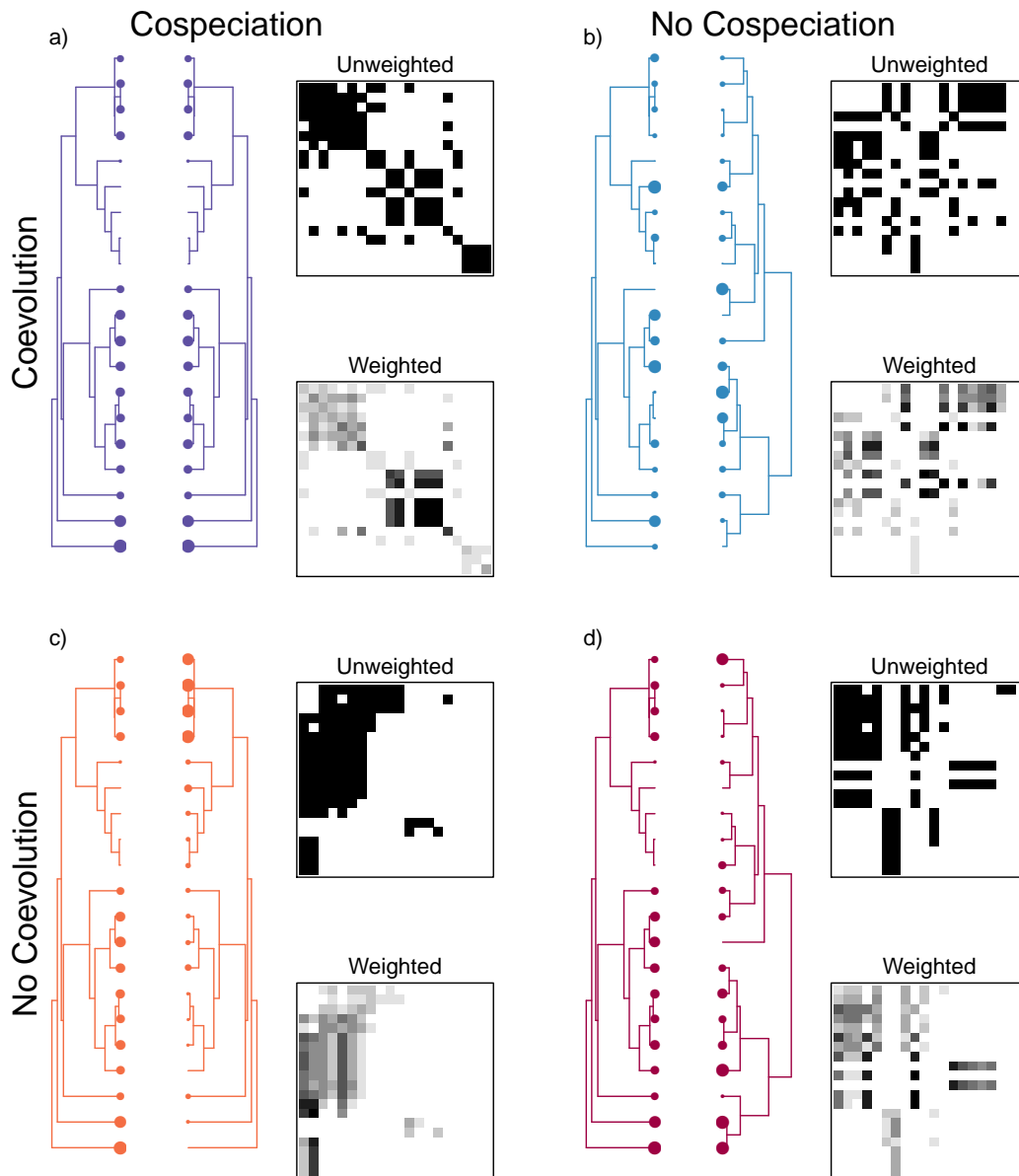


Fig. 3.2: Coevolutionary and non-coevolutionary phylogeny-trait combinations and linkage rules. Trait values are represented by circle size on the phylogenetic tree branch tips. The matrix of interactions (for example, plants and pollinators where pollinators are the columns and plant are the rows) is depicted with interaction frequency of interaction represented by colored squares. Unweighted interactions result in only 0s (white) or 1s (black).

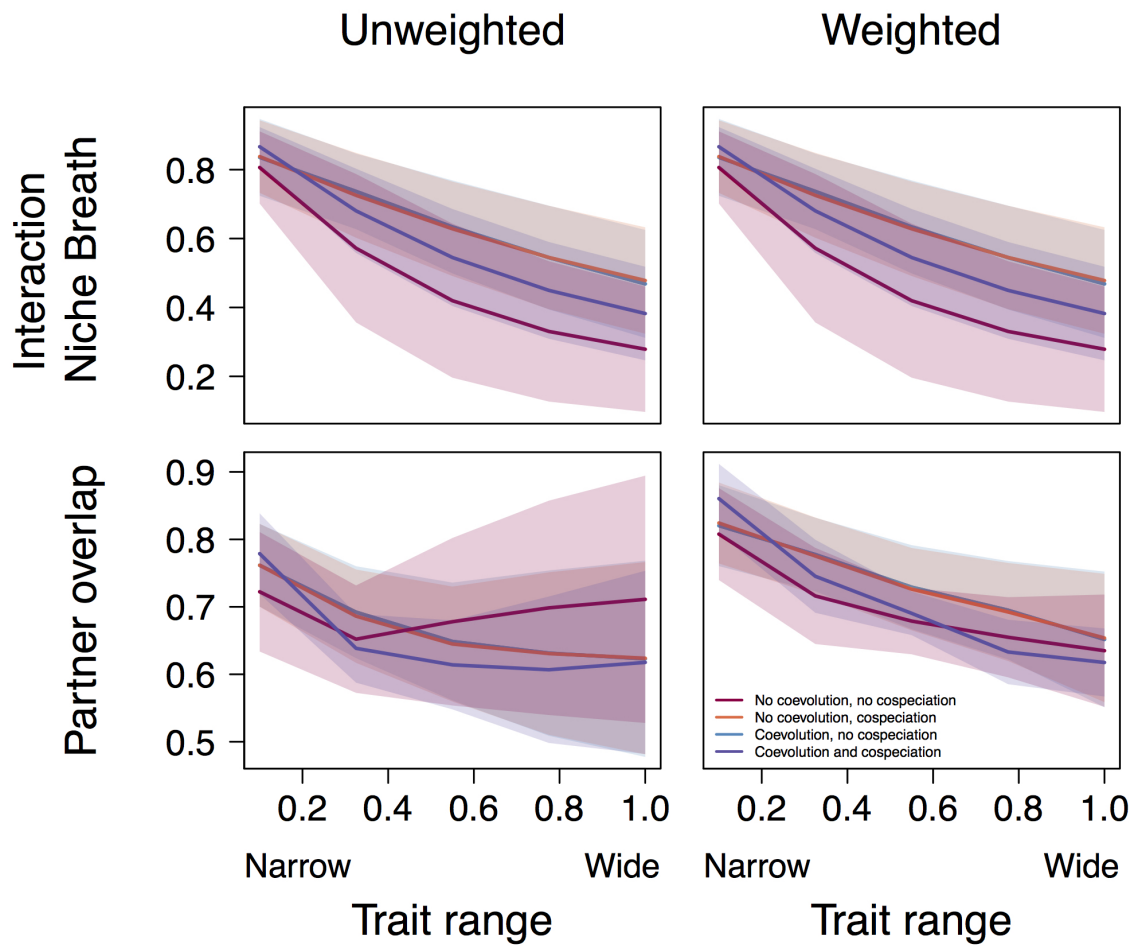


Fig. 3.3: The interaction niche breadth and partner overlap of communities as the range of trait values a species can interact with is varied from wide to narrow.

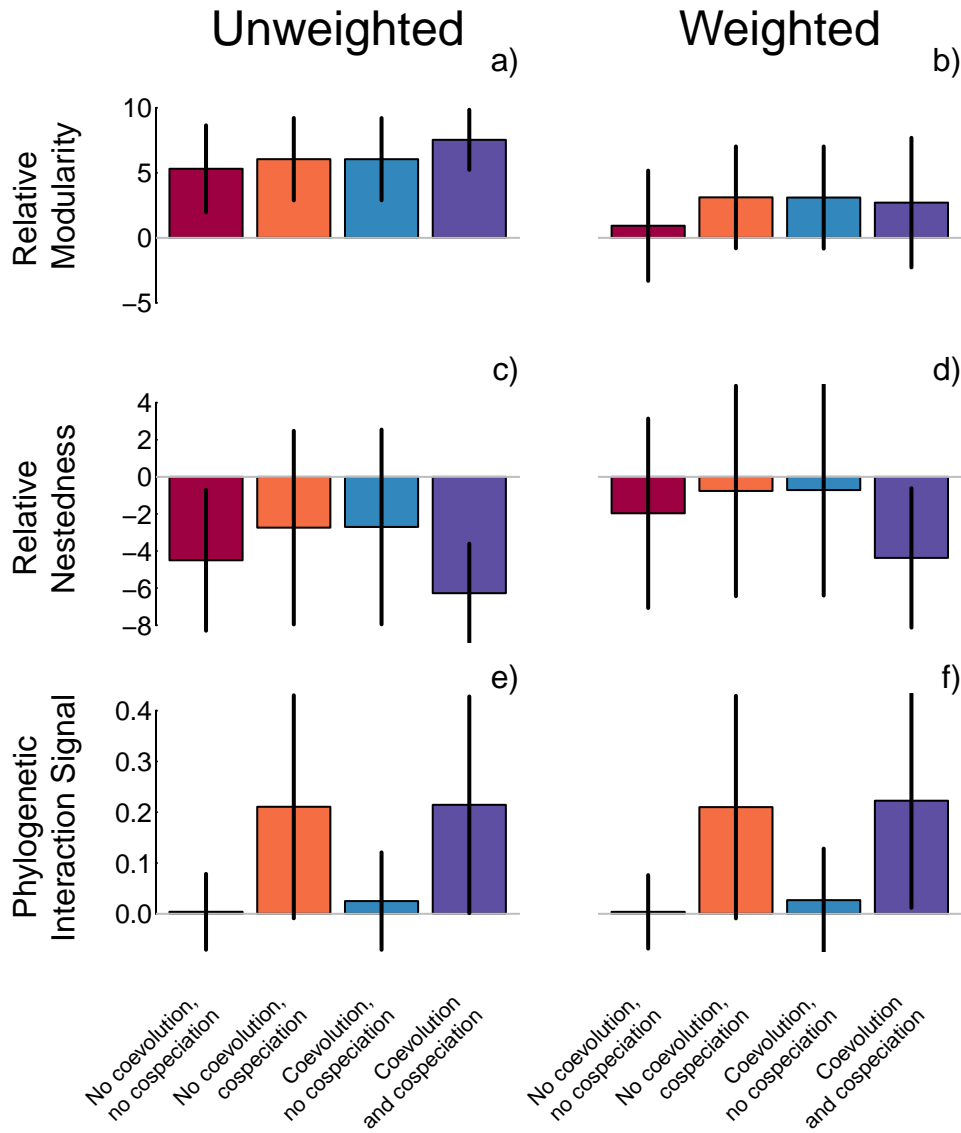


Fig. 3.4: Mean relative modularity, nestedness, and phylogenetic interaction signal of 10,000 simulated communities. Communities comprised 30 species in each interaction group. Colors correspond to different coevolutionary scenarios. In left panels, all species interactions were equally frequent, whereas in right panels the interaction probability depended on the degree of trait overlap between potentially interacting pairs of species. Relative nestedness and modularity are corrected for the null expectation, given the number of interactions and species in the interaction network (z -scores, top two panels). Scores greater than ~ 2 or less than ~ -2 are significantly more or less structured than randomly assembled communities. Vertical bars denote the 95% confidence intervals. Modularity was calculated using a hierarchical clustering algorithm.

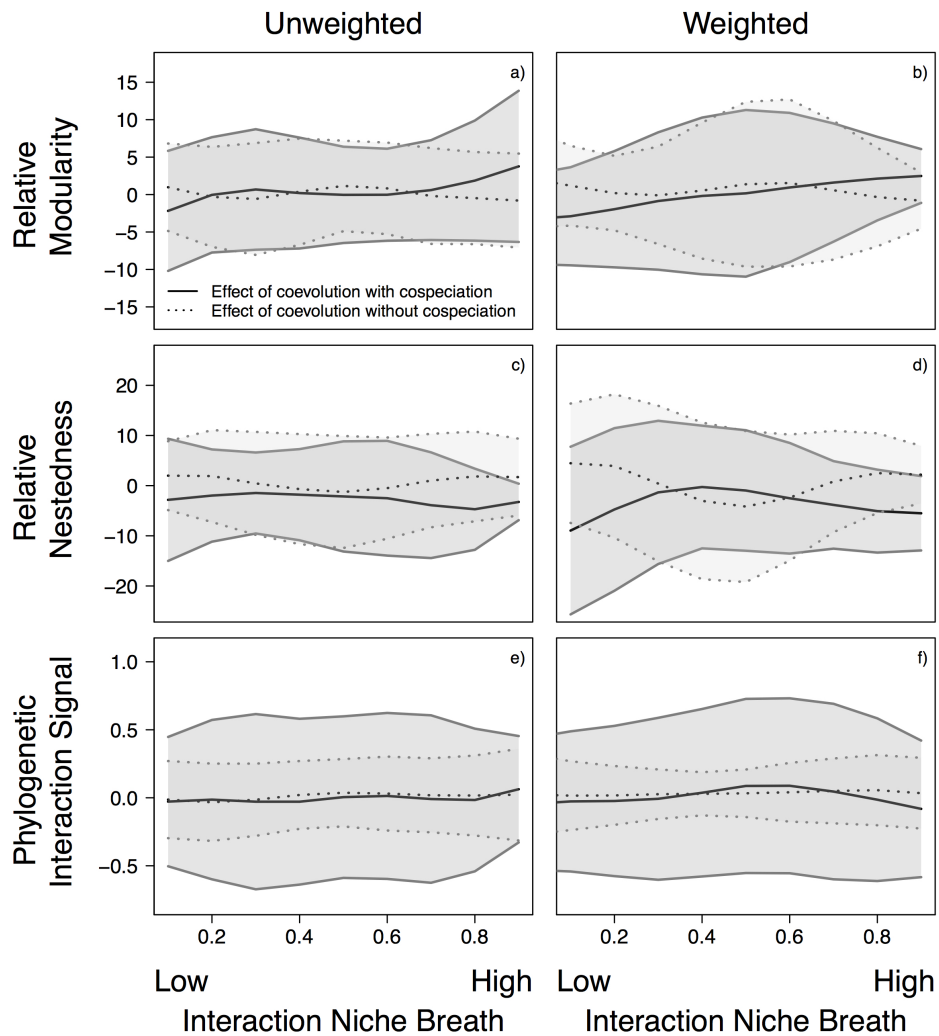


Fig. 3.5: The effect of coevolution on the relative modularity, nestedness, and phylogenetic interaction signal across a range of levels of mean interaction niche breath. Interaction niche breath is measured the mean proportion of potential interaction partners a species interacts with out of the total possible. The solid curves represent smoothed mean differences between randomly selected pairs of communities and the filled area corresponds to 95% confidence intervals. Note that we do not directly vary interaction niche breath, but instead do so indirectly by varying the size of the range of trait values that a species will accept in a partner (see Fig. S2 for further interpretation of these values).

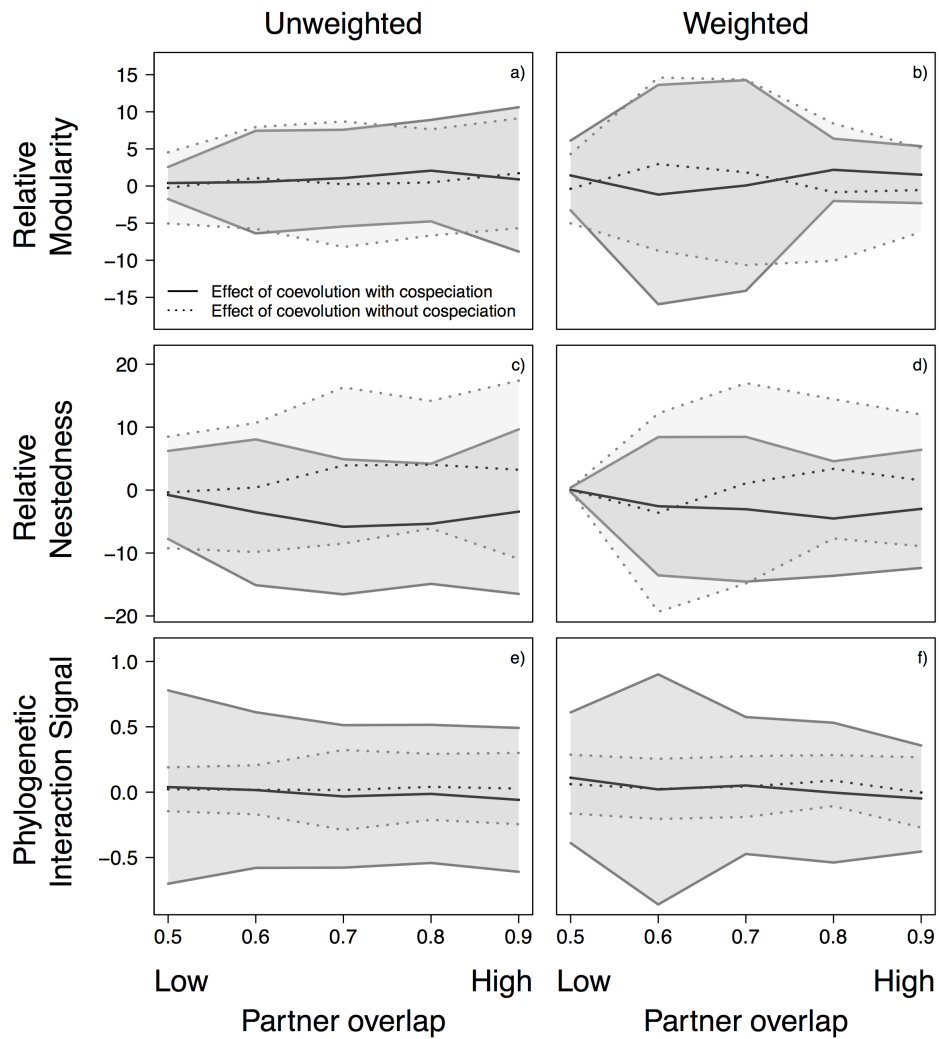


Fig. 3.6: The effect of coevolution on the relative modularity, nestedness, and phylogenetic interaction signal for simulated communities across a range of partner overlap values. Partner overlap is measured the mean tropic similarity of pairs of species belonging to the same interaction group. Curves were calculated as described in the caption to Fig. 3.5. The solid curves represent smoothed means and the filled area corresponds to 95% confidence intervals.

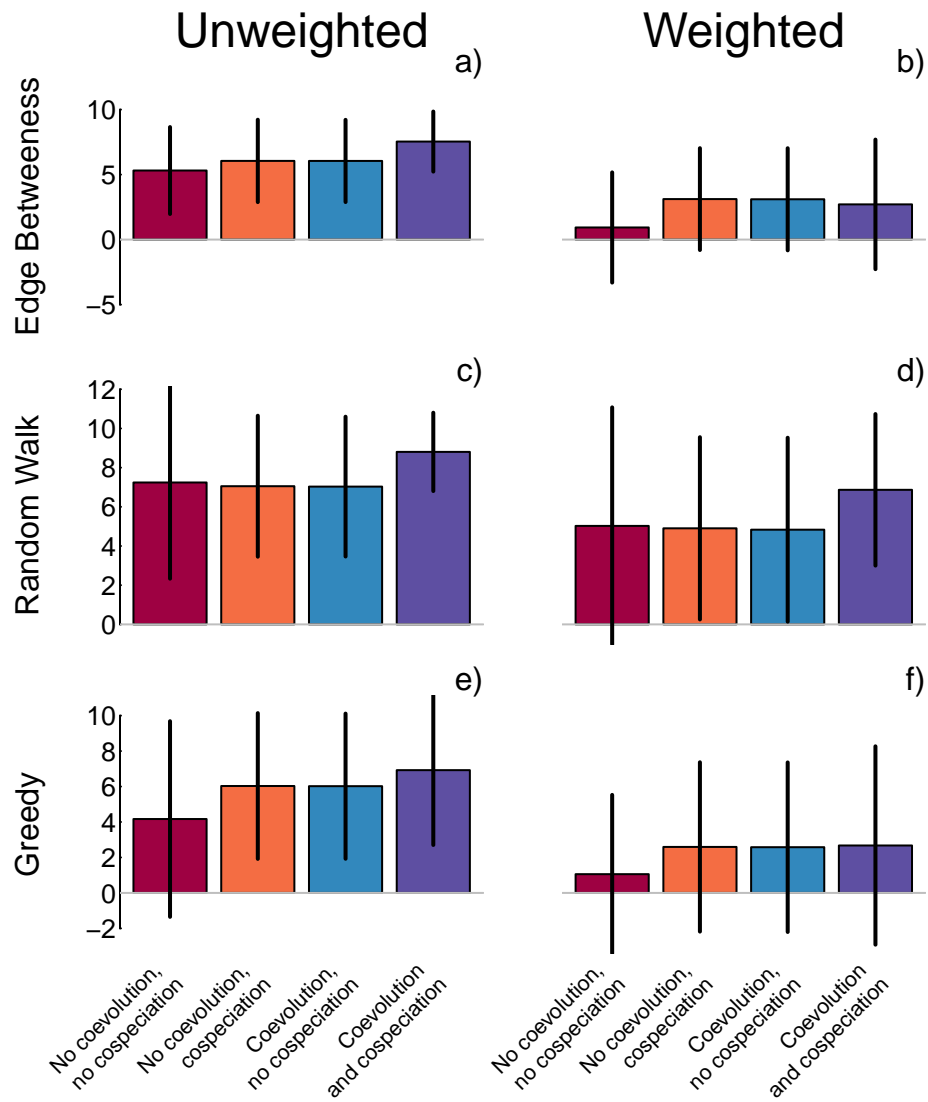


Fig. 3.7: The modularity of different coevolution communities calculated with different community partitioning methods. Communities evolved with a low trait evolution variance and shallow divergences between species of the same interaction group is represented as an example.

Chapter 4

Conclusion

Throughout my thesis, I found that species interactions have a profound influence on the ecological dynamics of communities (e.g., Thompson, 2005). In both Yosemite and the Central Valley, the diversity of plants and pollinators was correlated, and the geographic distribution of pollinators tracked their floral hosts. I am now seeking to move past these correlative relationships to uncover the mechanisms underlying the assembly of different interaction patterns. Ecological networks have emerged as a powerful method to understand the dynamics of the myriad species and their interactions that comprise complex ecosystems. In particular, modeling communities as networks enables us to develop our understanding of how the species-level interactions led to emergent patterns of interaction. The structure of interactions is in turn related to the community resilience to disturbance, and the ability of the system to avoid collapse (e.g., Montoya *et al.*, 2006). To predict the response to communities to global change, it is thus important to elucidate the mechanisms that underlie the patterns of interactions observed in communities.

NETWORK ASSEMBLY

To explore the mechanisms that influence network topology, I am examining how foraging decisions of species change as a community assembles, and the subsequent impacts on network topology. Specifically, I modified an adaptive foraging network model (Valdovinos *et al.*, 2013b, 2010) to allow for the colonization and extinction of species to reflect the community assembly conditions on the hedgerows in the Central Valley. The empirical data supports the prediction of the optimum foraging model that more generalized species begin to niche partition and limit their diet breadth as the community develops (Ponisio and Valdovinos, *in prep*). This shift in species foraging causes the network topology to become more specialized and less nested. By examining how patterns of interactions change as the community develops, we can make predictions about how resilience of these communities evolves through time to better set targets for restoration.

Next I hope to isolate whether specific mechanisms of assembly give rise to different patterns on interaction, building on my work in Chapter 3. Models incorporating both ecological and evolutionary dynamics, so-called large community evolution models, reproduce the observed structure of networks (e.g., Allhoff *et al.*, 2015; Guimarães *et al.*, 2011; Loeuille, 2010; Brännström *et al.*, 2011). Much simpler models, however, that incorporate only ecological dynamics (population dynamics, Thébault & Fontaine, 2010; Bastolla *et al.*, 2009; Krause *et al.*, 2003; spatio-temporal species distributions, Pillai *et al.*, 2011; Pimm *et al.*, 1991; Encinas-Viso *et al.*, 2012; stochastic processes Canard *et al.*, 2012; Jonhson *et al.*, 2013; Krishna *et al.*, 2008) or even just simple interaction rules (e.g. static community models, Williams & Martinez, 2000b; Cattin *et al.*, 2004) also generate networks with properties comparable to those found in empirical communities.

To develop the framework that would be necessary to disentangle different assembly mechanisms, I lead an interdisciplinary workshop in collaboration with the Berkeley institute for Data Science on network approaches to community assembly. I brought together theoreticians (e.g., Neo Martinez and Robert Holt) and empiricists (e.g., Rosemary Gillespie) to discuss approaches to develop new theory and analyze data describing networks of ecological interactions to propel a new synthesis of our understanding of ecological and evolutionary assembly of communities. Our discussion provided the basis for an Ideas and Perspectives article for *Ecology Letters*, currently in preparation. We suggest that to elucidate the mechanisms shaping interaction patterns, we must examine the process of network assembly through time both through modeling and empirical work, and how community characteristics affect that process.

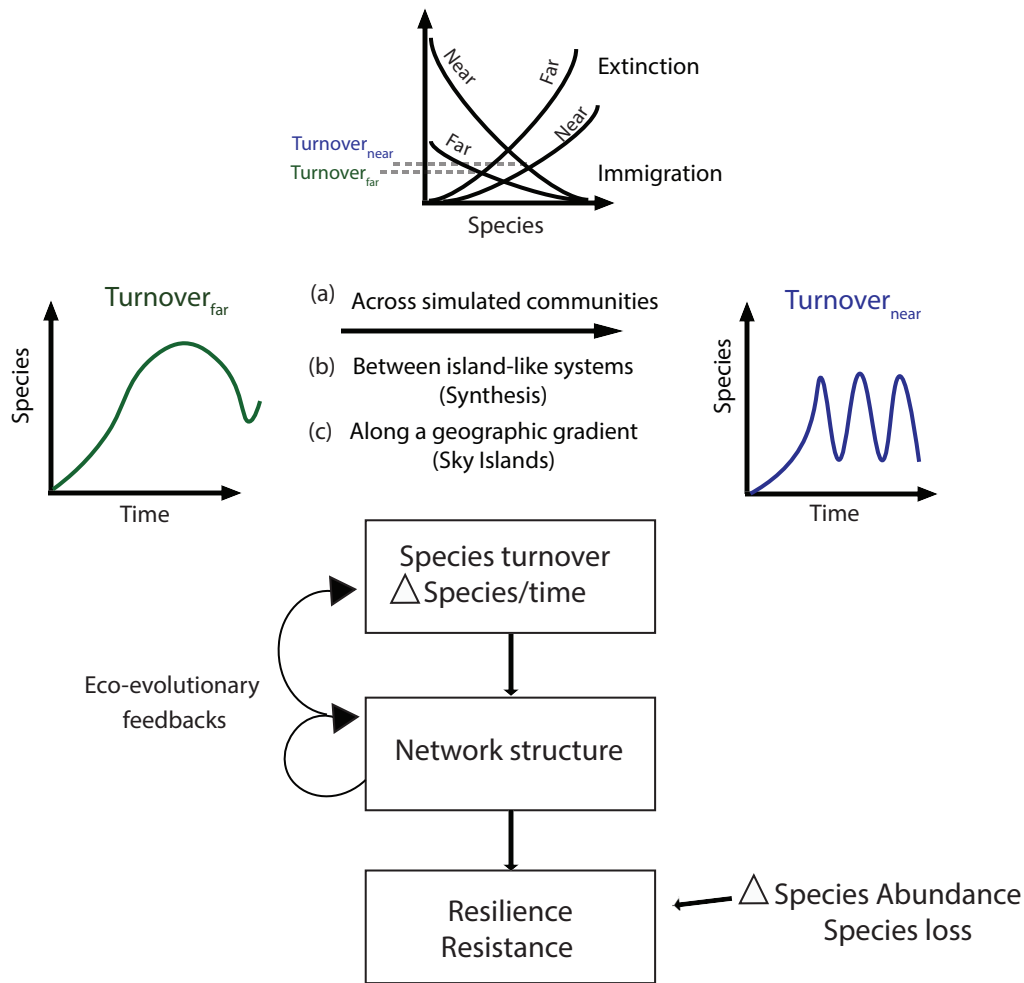


Fig. 4.1: A conceptual outline of future research.

FUTURE WORK: THEORY

In my future work, I plan to undertake the theoretical work we identified in our workshop as lacking but critical for understanding network assembly. I am currently developing a template for studying community assembly based on network theory, the theory of island biogeography and coevolutionary theory.

I will build a large community evolution model to examine how community variables affect the structure of interactions. I will focus on two community characteristics — temporal turnover of species and community age (Figure 4.1a). The temporal turnover of species is ubiquitous across different types of interaction networks (pollination: Olesen *et al.*, 2011, 2008; Alarcón *et al.*, 2008; Petanidou *et al.*, 2008a; Fang & Huang, 2012; Burkle & Irwin, 2009; ant-plant: Díaz-Castelazo *et al.*, 2010; frugivore-plant: Carnicer *et al.*, 2009; host-parasite: Pilosof *et al.*, 2013; Saavedra *et al.*, 2015; predator-prey: (Owen-Smith & Mills, 2008). Temporal turnover is most fundamentally governed by the rates of immigration and extinction (Figure 4.2a, MacArthur & Wilson, 2015). Though large community evolution models have been employed to study community assembly (Allhoff *et al.*, 2015; Guimarães *et al.*, 2011; Loeuille, 2010; Brännström *et al.*, 2011), few have examined the effect of varying rates of immigration (Allhoff *et al.*, 2015). A more thorough exploration of the effects of species turnover on the trajectory of community assembly, and the species interactions that govern that trajectory has yet to be explored (Brännström *et al.*, 2012).

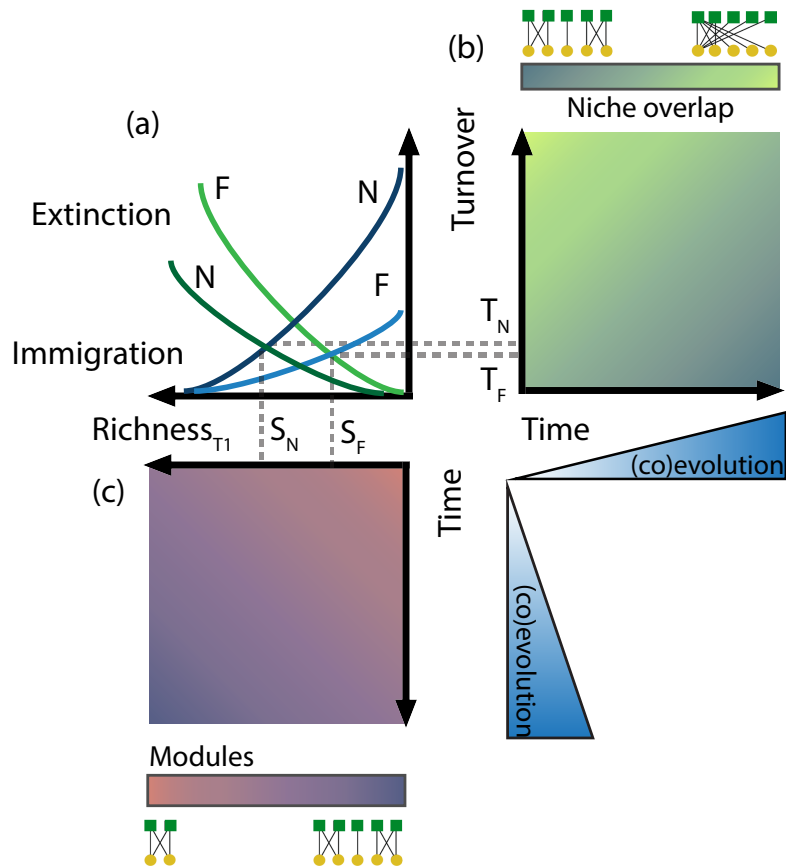


Fig. 4.2: Conceptual framework and hypothesis regarding how species turnover and evolution/coevolution influence the patterns of interactions in a community. (a) The rate of species turnover will depend on the rates of immigration and extinction into a community. The rate of extinction of species near source pools will be lower than those far from sources because of the rescue effect. Similarly, immigration rates will be lower for communities far from source pools. Here, the turnover of species in the community near the source pool (T_N) is higher than the more isolated community (T_F). Rates of immigration and extinction will also determine the species richness of a community at time T_1 (before speciation has had time to add new species). Here, the community far from the source pool (S_F) is lower than the near community (S_N). (b) Low rates of species turnover and many generations of evolution/coevolution will favor niche partitioning, whereas high turnover will favor niche overlap. (c) The richness of a community will limit number of compartments of interactions a community can support. With enough time for evolution/coevolution to occur, however, the community will itself before a source of new species as species diversify, allowing for greater modularity.

FUTURE WORK: SYNTHESIS

The proposed theoretical work will help lay the foundation for understanding the interaction patterns favored by assembly in real-world communities that vary in their rate of temporal species turnover. Based on island biogeography theory (MacArthur & Wilson, 2015), large islands far from sources (e.g., Hawaii) will have lower species temporal turnover than small islands near sources (e.g., habitat fragments). By using a synthesis approach to compare the assembly of true islands, natural island-like systems, and anthropogenically generated habitat islands, I will build on our understanding of how and why the interaction patterns vary between human modified and more natural landscapes. (Figure 4.1b).

I am working to compile and augment existing collections of plant-pollinator interaction networks from true islands such as the Channel Islands, natural island-like systems like montane meadows in the Sierra Nevada, and human generated islands like habitat fragments in agricultural matrices. I will test the predictions from my theoretical work on the effect of species temporal turnover on interaction patterns. I will also use the empirical data as starting points for my large community evolution model (Section 4.0.2), and examine the evolutionary trajectory of the communities through time. I can then explore how the stability and response to perturbations of the different island systems changes through time. An understanding of the differences in network structures between islands and islands-like systems will help elucidate any differences in resilience between these systems, as well as provide targets for restoration interventions.

FUTURE WORK: EMPIRICAL

Lastly, I also plan to test my theoretical predictions (Section 4.0.2) empirically by examining how similar types of ecological communities that vary along geographic gradient of species temporal turnover differ in their network structure (Figure 4.1c). The Madrean sky islands, an archipelago of mountains surrounded by “seas” of desert, provides an ideal system to explore these questions. The islands vary in their distance from the two source pools (the Rocky Mountains and the Sierra Madre) and thus likely their temporal species turnover (Figure 4.3). I plan to lead a highly interdisciplinary study, using genetic techniques to reconstruct patterns of species immigration across the sky islands, and examining how the structure of interaction networks changes along this spatial gradient. Though my original focus will be plant-pollinator communities, I also hope to examine other types of mutualistic systems (e.g., rhizome-legume) in collaboration with other researchers.

Similar to the island synthesis study, I will also use the empirical data from the different sky islands as starting points for my large community evolution model (Section 4.0.2), and examine the evolutionary trajectory and resilience of the communities through time. Island-systems are also both fundamental to theories of biogeography, and fascinating because of their endemic flora and fauna. At the same time, these systems are threatened by anthropogenic impacts such as climate and land-use change. My work presents a unique opportunity for elucidating the mechanisms sustaining the biodiversity of these systems and their ability to withstand disturbance to inform conservation efforts.

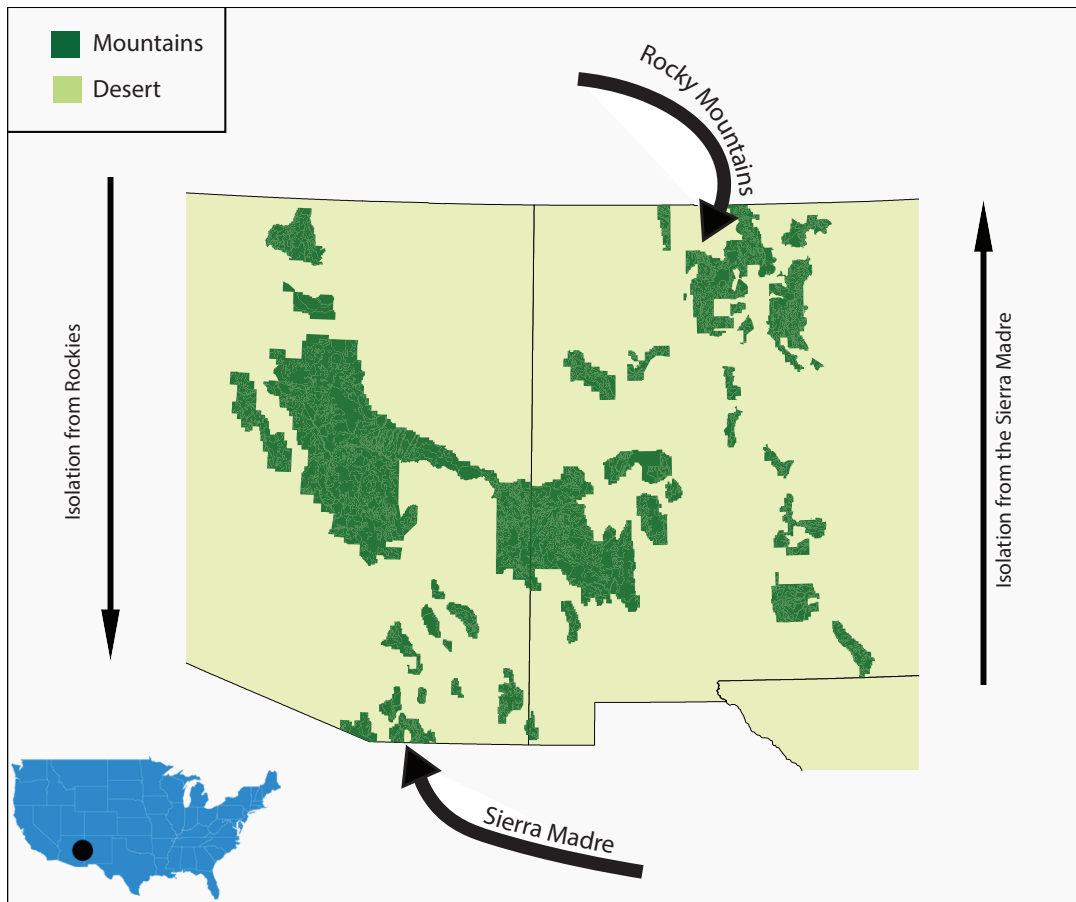


Fig. 4.3: The Madrean sky islands of the southwestern U.S. The mountain “islands” link the Rocky Mountains to the Sierra Madre.

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