ABSTRACT

Title of Dissertation:	DIVERSITY AND STRUCTURE OF *METROSIDEROS POLYMORPHA* CANOPY ARTHROPOD COMMUNITIES ACROSS SPACE AND TIME
	Elske Karolien Tielens, Doctor of Philosophy, 2019
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Global biodiversity is under pressure from climate change, habitat fragmentation and other anthropogenic change, and our ability to predict biodiversity responses to change requires a better understanding of the processes that drive diversity and structure local communities. However, quantifying these processes has proven to be challenging for multiple reasons; diversity is multidimensional, and both diversity and the processes that generate it vary across scale. In this dissertation, I examine temporal and spatial patterns in community structure to test hypotheses about the drivers of local diversity and composition in communities of varying age, focusing on arthropod communities associated with the native tree *Metrosideros polymorpha* on the Hawaiian Islands. Analysis of Hemiptera (true bug) communities reveals a temporal pattern in community structure, where young substrate communities were variable in species composition and beta dispersion decreased with substrate age, indicating convergence. However, substrate age did not correlate with community dissimilarity in a directional way. Similarly, geographic distance did not correlate with compositional dissimilarity, suggesting a lack of dispersal limitation. I confirmed this result by examining connections between arthropod communities in a historically fragmented ‘kīpuka’ landscape, using species-area relationships and graph theory analyses. Finally, if canopy arthropods are dispersive and differences in species composition across sites are not driven by substrate age, local habitat characteristics may influence species composition. I determined the role of local beta diversity and identified habitat characteristics regarding forest structure and host leaf traits that are strong drivers of beta diversity and species composition. Then, to further explore local habitat drivers I examined forests with high intraspecific variation in co-occurring *Metrosideros*. In this hybrid zone, insect life history traits shape species’ response to intraspecific variation in host plant characteristics, highlighting the importance of including dimensions of biodiversity beyond taxonomic diversity. Together, these results demonstrate the importance of local habitat conditions for canopy arthropods, suggest that canopy arthropod communities are highly connected and that substrate age plays a limited role in determining local arthropod communities. Such insights into biodiversity and plant-insect interactions across temporal and spatial scale are integral to understanding and conserving our natural world.

DIVERSITY AND STRUCTURE OF *METROSIDEROS POLYMORPHA* CANOPY ARTHROPOD COMMUNITIES ACROSS SPACE AND TIME

by

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Preface

This dissertation contains an introduction (Chapter I), three research chapters (Chapters II-IV), and a conclusion (Chapter V). Chapter III was previously published in the open access journal Ecosphere. For this manuscript, my contribution included conceptual development of the chapter, data analysis, writing and manuscript preparation. I thank my co-authors for their contributions to setting up the study, data collection, data extraction and editing. Chapter III is reprinted here in full under Creative Commons Attribution License (CC-BY). Assistance in funding, editing and data collection for all other chapters is stated in the acknowledgements. Appendices to all chapters are provided at the end of the dissertation as well as a single bibliography for literature cited throughout.

Dedication

For ʻōhiʻa lehua; the strong, resourceful and beautiful tree that forms the foundation of so much Hawaiian life

“One describes a tale best by telling the tale. You see? The way one describes a story, to oneself or to the world, is by telling the story. It is a balancing act and it is a dream. The more accurate the map, the more it resembles the territory. The most accurate map possible would be the territory, and thus would be perfectly accurate and perfectly useless.

The tale is the map that is the territory.
You must remember this.”

- Neil Gaiman 2001

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I would not have learned as much as I have without the input from the Evolab at UC Berkeley. Rosemary Gillespie and George Roderick have been generous with their time, thoughts and resources to help me sharpen my ideas around evolution on the Hawaiian Islands, and I am grateful to all the graduate and undergraduate Evolab members that helped with data collection and fieldwork.

The Gruner lab has been a wonderful place to spend these past years, and I am grateful for the university community. Kristen made this dissertation possible with her skills in insect identification, with her many stories that kept me sane in lonely times, and her willingness to even share a 10 m^2 living space with me. I want to thank Alex Forde for his snark and his critical scientific insight (in that order), Mayda for her thorough edits, Gussie for her unfailing faith in my work, and Cora for all things, from boxing to brainstorming. Nicola contributed a touch of Europe and great biking commutes. Alex Novarro blazed the trail for me and is still in all things my example.

I am deeply grateful for the love and support of my friends and family, in the United States and at home. I will not mention everyone here, but you all brighten my life. I am not sure I would have finished this process if it weren't for the faith community I found at St Stephen and the Incarnation in Washington D.C. Lastly, I am grateful to Casey for being my partner in adventures big and small.

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Chapter 1 : Introduction

Conceptual background

At the core of ecology is the concept of biological diversity, and the observations that in a given area some species are common and many species are rare, species differ in their distributions, and species differ in their interactions with one another as well as their environment (Hutchinson 1959). Biodiversity plays a role in ecosystem functioning such as maintaining biomass, stabilizing species networks, and protecting biodiversity has become an important conservation goal. Whereas categorizing and understanding the wealth and richness of biological life forms is a core component of ecology, we have not gotten very far in determining general 'laws'. Hutchinson's seminal question remains as relevant as ever; 'Why are there so many kinds of animals'; or in other words, what determines the diversity and composition of local communities (Hutchinson 1959).

Understanding the processes that generate diversity and developing a predictive framework remains challenging for many reasons. First, biodiversity is multidimensional, encompassing the number of species that occur in an area, the evenness of an assemblage, the species abundance distribution as well as genetic, functional and phylogenetic measures of diversity. Furthermore, ecological processes operate on various spatial and temporal scales, which interact to determine local diversity (Ricklefs 1987, McGill 2010). Thus, to understand where diversity comes from, it is important to incorporate various aspects of diversity, and how these vary across space and time.

In the first section of this introductory chapter, I will explain the importance of scale dependence in ecology, and discuss ecological and evolutionary drivers of biodiversity, as well as the importance of dispersal in bridging these scales. Then, I will discuss approaches that I use to characterize and analyze community structure across temporal and spatial scales. Lastly, I will detail my study system; the Hawaiian Islands, and outline the various chapters in this dissertation.

Biodiversity across spatial scales

Biodiversity is inherently scale dependent, and the importance of various processes in driving biodiversity varies across spatial scales (McGill 2010, Wiens 1989). Local richness increases with area, whereas the magnitude of beta diversity depends on the types of communities being compared. Effects of biodiversity drivers such as climate, habitat, dispersal and species interactions also depend on scale. For example, species interactions predominantly affect local diversity at the scale species interact with one another, but have also been show to influence biodiversity at regional scales (Gotelli et al. 2010). At larger scales productivity increases diversity, while this effect was much weaker at smaller spatial scales (Chase & Leibold 2002). The inverse is true of invasive species, which have been found to strongly influence diversity at small scales, with much weaker effects at large scales (Powell 2013).

This scale dependence of biodiversity makes comparing across space or time difficult. A recent meta-analysis showed that the majority of studies of biodiversity drivers that included multiple scales showed changes across scales in the magnitude of effects, and in 11-33% of studies the sign of the relationship even reversed (Chase et al 2018). Another issue complicating comparison is that the choice of sampling scale and biodiversity measure affects findings. Species richness increases nonlinearly with sampling effort and spatial scale, simply based on sampling likelihood. Understanding the shape of this nonlinear relationship, and how it varies across cases and studies, is key to reliable comparisons of diversity across studies.

Understanding the processes driving diversity and how they scale is not just a theoretical exercise. Differences in measurement of diversity and the importance of its drivers affects policy and public perception of current biodiversity declines. At global scales, habitat loss, land use change and other anthropogenic effects have increased extinction rates. However, most studies of biodiversity at local scales do not show a similar pattern of decline (Vellend et al. 2013, 2017). Recent publications have argued that this mismatch is due to a decrease in beta diversity (Dornelas et al. 2014). Locally, richness decreases through the loss of rare species, while richness increases through gain of invasive species. Moreover, biotic homogenization where communities regionally share more and more the same species results in decreased global diversity while local diversity is maintained (Dornelas et al. 2014). An alternative explanation is that the way we measure diversity does not accurately represent communities (McGill et al. 2015, Larsen et al. 2018), and that the bias of scientific studies to focus on ‘natural’ or ‘pristine’ areas results in an underestimation of biodiversity loss, neglecting urbanized or agricultural areas where biodiversity changes are greatest (Larsen et al. 2018). This discussion is ongoing, and will benefit from a better understanding of both scale dependence in biodiversity research, as well as processes driving diversity at various scales.

Biodiversity drivers

At broad spatial scales, species are gained through colonization from outside the region, species formation from within, and they are lost by (local) extinction. Locally, within a single habitat and community, the traditional view is that dispersal from a regional pool is followed by a series of consecutive abiotic and biotic filters, limiting which species can successfully colonize and persist in a community.

The regional species pool is determined by historic and current evolutionary, ecological and climatic conditions (Ricklefs 1987, 2007, Carroll et al. 2007). Geographic or ecological isolation can add to the species pool through speciation, such as in anole lizards in Caribbean islands (Losos et al. 1996). Speciation rates vary across regions, and several hypotheses exist to explain differences in speciation rates, including area (Rosenzweig 1995), age (Cadena et al 2005), climate (Rohde 1992, Wiens and Graham 2005) local richness (Emerson and Kolm 2005, 2007, but see Pereira et al. 2007, Gruner et al. 2008) and species interactions (Mcpeek 1996). Together speciation, colonization and extinction produce the local species pool.

Locally, species from the species pool may persist in a community dependent on their abiotic tolerances and species interactions. These interactions with the environment and co-occurring species are mediated by species traits.

These contemporary, local ecological processes are influenced by evolution. First, both positive (facilitation) and negative (competition, parasitism) species interactions are influenced by evolutionary history and phylogenetic relatedness

(Valiente-Banuet and Verdú 2008, Beltrán et al. 2012). Secondly, evolutionary history shapes species traits (Swenson and Enquist 2007, Bonte et al. 2010). Species shape their morphology, physiology, and phenology in response to their biotic and abiotic environment, and past adaptive traits are passed on to future generations. For example, competition can lead to character displacement, such as in Galapagos Islands finches, and tightly linked species interactions can lead to evolution of defense compounds against herbivory in plants (Nyman et al 2012).

In summary, ecological processes take place across a variety of scales, and are difficult to disentangle with evolutionary processes. As a result, understanding the processes that give rise to local biodiversity and community structure requires a multiscale approach that incorporates ecological and evolutionary perspectives. In the following section, I will discuss the role of dispersal in connecting communities at various scales and maintaining diversity. before detailing how this dissertation will go about addressing these questions.

Dispersal

The theory of island biogeography, one of the most influential ideas in modern ecology (MacArthur and Wilson 1967, Hubbell 2001, Haila 2002, Warren et al. 2014, Patiño et al. 2017), posits that island diversity can be described through processes of immigration and extinction (MacArthur and Wilson 1967). After initial colonization periods islands exist in dynamic equilibrium where the identity of species occupying an island community may change, but the number of species is balanced between immigration and extinction. This number of species is determined by island area and proximity to source populations (i.e. mainland), whereas species identity is dynamic because of the assumption of species equivalency. This theory has led to advances in community ecology (Hubbell 2001, Volkov et al. 2003), island biology (Warren et al. 2014, Patiño et al. 2017), landscape ecology (Cook et al. 2002, Haila 2002, Kupfer et al. 2006), conservation (Gilbert et al. 1998) and many other subfields of ecology, and has brought the role of dispersal and stochastic processes in ecological systems to the forefront.

Local communities are not closed systems, but are linked across space through dispersal. Organisms external to the local community can influence internal dynamics. For example, habitat heterogeneity and movement between patches allows for coexistence (Huffaker 1958), while mass effects can maintain populations in areas that they may not be the best adapted for or most competitive (Leibold et al. 2004). Dispersal also allows populations to select for optimal habitat (Cottenie et al. 2003, Shurin et al. 2004), thus enabling community composition to track environmental changes (Cottenie 2005). Lastly, dispersal influences evolutionary processes; lack of dispersal reduces gene flow, providing reproductive barriers and leading to speciation. When multiple communities are connected to each other by dispersal, spatial dynamics influence local processes.

Spatial dynamics in metacommunities can take various forms, depending on the nature of the patches and the importance of environmental conditions and competition for the communities in question. Spatial dynamics can be neutral, where colonization of a patch is dependent purely on colonization order, and demographic rates are assumed to be similar across species. Within a species-sorting perspective, environmental conditions are assumed to be heterogeneous, and with sufficient dispersal species sort into the communities to which they are best adapted (Cottenie et al. 2003). In contrast, a mass effects model of metacommunities assumes a sizeable role of dispersal, with source-sink dynamics between local patches (Pulliam 1988). Here, local populations are supplemented by immigration, allowing these to persist in a community. In all these frameworks, the rate of dispersal plays an important role (Winegardner et al. 2012). At low dispersal rates, the greatest effect of communities being connected will be colonization events, and those species first to arrive will establish and shape the assembly history of a community (MacArthur and Wilson 1967). In contrast, at high dispersal rates species should be able to perfectly track the optimal environmental and competitive conditions, functionally acting as a single large community. Most systems exist in an intermediate state between those extremes, where connectivity between communities and species' dispersal ability influence final community structure.

Approaches in this dissertation

Examining patterns in species diversity and the role of evolutionary history, geography, dispersal, biotic and abiotic interactions in shaping communities requires use of a system that explicitly integrates across spatial and temporal scales. Furthermore, our understanding of biological communities is enhanced by incorporating several attributes of biodiversity in; including species richness, abundance, dominance and rareness as well as functional composition. Several characteristics of my research have facilitated this: making use of a model system archipelago, using a space-for-time chronosequence and incorporating trait-based approaches.

Archipelagoes as model systems

To study processes that structure communities across spatial and temporal scales, it is helpful to have a model system where some variables can be held constant, while the variables of interest vary or can be manipulated (Vitousek 2002). Islands are great model systems, in particular for studying the integration of ecology and evolution. Islands provide small areas to study as a complete unit, that are geographically distinct and as a result generally have clear boundaries to species distributions. Islands that arose *de novo,* such as oceanic islands, provide substrate for colonization from a clean slate, where often the age of substrate and of lineages can be inferred, and *in situ* speciation can be identified (Gillespie & Baldwin 2010). Archipelagoes provide various instances to examine processes of diversification, immigration and extinction, with replicates of varying size and distances to other communities Fukami 2007, Rosindell & Philmore 2011, Losos & Schluter 2000. Lastly, the often depauperate fauna on oceanic islands makes it easier to examine entire communities.

The limitations of chronosequences

The volcanic nature of oceanic archipelagoes results in a system where different islands, volcanoes and substrates vary in their geological age. As a result, these systems lend themselves well for use as a space-for-time chronosequence; a system in which different areas that vary in age are used as sequential stages in development. This approach is built on the assumption that there is a fixed temporal path of development and that current sites at younger stages of development follow a temporal pattern that resembles the prior development of older sites. A space for time chronosequence takes a series of sites that vary in time since a specific event, often a disturbance, and treats these spatial sites as different stages along a shared history. The assumption is that each site has traced the same history, and infers a time sequence of development from the collection of sites.

The Hawaiian chronosequence has been a model system for evolution, biogeography, ecosystem ecology, as well as to understand forest vegetation and productivity (Kitayama and Mueller-Dombois 1995, Herbert et al. 1999), invasive species (Gruner 2005, Nogueira-Filho et al. 2009, Funk and Throop 2010) and trophic interactions (Gruner 2004, Wilson and Holway 2010, Meyer and Yeung 2011). Many of these studies have made use of Hawaiʻi's varied and well documented geological history as a space-for-time chronosequence (Crews et al. 1995, Vitousek 1995, Hedin 2003, Gruner 2007, Wardle et al. 2009).

While space for time chronosequences are powerful tools for studying processes that take place over time scales that are too long to examine directly (Pickett 1989), it is key to evaluate the assumptions of similar development, and of constant conditions throughout the time period of interest. Many classic succession studies making use of chronosequences have been invalidated (Chazden 2007, Roozen & Westhoff 1985), and the assumptions underlying this approach should be carefully examined (Johnson and Miyanishi 2008, Walker et al. 2010). The 'Long Substrate Age Gradient' (LSAG) used for studying temporal questions on Hawaiʻi (Vitousek 1995, Reed et al. 2011) encompasses sites in similar contemporary environmental conditions across substrate ages. However, there is some indication that historic conditions have fluctuated, particularly over the long time scales of development of the current high islands.

Glacial cycles have produced large variation in climate, and there is evidence for 0-6° C cooling as well as much drier conditions during the previous glacial period (Hotchkiss & Juvik, Porter 1979). Subsidence of the islands after formation means that historic sites that are currently at similar elevations across substrate ages, existed for a period of time at higher elevations. Similarly, subsidence also affects precipitation levels. Rainfall on the Hawaiian Islands is concentrated on the windward side and predominantly occurs from sea level to the trade wind inversion layer at approximately 2200 m, where warm air prevents clouds from rising any further. The relative regions of the island where this inversion layer occurs will change as subsidence lowers the island substrate, and this results in fluctuations in the distribution of rainfall (Gavenda 1992, Hotchkiss et al. 2000). As a result of this climatic variation the distribution of tropical forest has also varied (Selling 1948), as evidenced by the pollen record (Hotchkiss and Juvik 1999), and different trajectories of soil development, as well as higher rates of leaching in historic development than on current young substrate sites (Hotchkiss 1998).

While these are important considerations to keep in mind, extensive comparative studies across different types of substrates (a‘a lava, pahoehoe lava, ash), elevations, and climate as well as within site replication can provide an understanding of ways that chronosequence assumptions are not met (Walker et al. 2010). Comparisons are further facilitated by dominance of a single tree species across the chronosequence. Lastly, though this system may not be precise enough for some age-specific processes, but may still be relevant for studying ecological patterns that are less dependent on the precise age of the site. For studies interested in comparing dynamics across one of several *possible* developmental pathways, this chronosequence provides valuable information on what temporal dynamics on older substrates *can* look like.

Trait-based approaches

Inferring ecological processes from observed patterns in nature is challenging, and it is particularly difficult to produce general predictions (Keddy 1992, Ricklefs 2008). If the adaptations of organisms reflect ecological relationships with the environment and between organisms (Ricklefs and Travis 1980), such traits can provide information on processes. Trait-based approaches can be more generalizable than taxonomic studies because they allow for comparison across systems with different species (McGill et al. 2006). Morphological, physiological and phenological traits form the link between species abundance and ecological or evolutionary processes (Schluter 2000; Ackerly 2009; Ellers *et al.* 2012). Traits result from current and past selection pressures as well as past evolutionary trajectory, diversification and interactions (Chapin III *et al.* 1993; Ackerly 2004; Emerson & Gillespie 2008). Species traits can provide a link between organism and environment and affect the outcome of niche based processes (Chapin III *et al.* 1993; Lavorel & Garnier 2002; Thompson & Townsend 2006). Similarly traits such as seed or fruit size and dispersal mode in plants or wing morphology and life history traits in animals impact dispersal limitation (Augspurger & Franson 1987; Forsythe 1987; Zera & Denno 1997; Horn *et al.* 2001). Patterns in species traits can provide a mechanistic understanding of processes driving community assembly across scales (McGill *et al.* 2006; Kraft *et al.* 2007; Messier *et al.* 2010; Adler *et al.* 2013).

Community ecology has a long history of utilizing traits, particularly in birds

(Ricklefs and Travis 1980), bats (Findley 1973, Fenton 2008) and plants (Raunkiær 1934, Diaz et al. 1998). Early approaches focused on relating qualitative life history traits to species interactions or environmental gradients (Statzner et al. 2001). More recently quantitative frameworks for trait-based approaches have provided a predictive basis to community ecology as well as stronger theoretical linkages between community and ecosystem ecology (Lavorel and Garnier 2002, Petchey and Gaston 2006, Messier et al. 2010, Violle et al. 2012, Adler et al. 2013). Insights from this framework include community assembly processes and niche space in tropical forests (Kraft et al. 2011, Swenson and Weiser 2014, Swenson et al. 2016, Schliep et al. 2018), consistent patterns in leaf morphological and physiological traits across environmental gradients (Wright et al. 2004, Cavender-Bares et al. 2004), and the importance of intraspecific trait variation in traits (Jung et al. 2010, Violle et al. 2012, Siefert et al. 2015, Umaña et al. 2015). Evolutionary history and niche conservatism has been included in our understanding of community assembly processes by incorporating phylogenetic ecology in the analysis of trait distributions (Webb et al. 2002, Cavender-Bares et al. 2009). However, despite an explosion of research and significant progress in modeling and testing community structure (Kraft et al. 2011, Swenson 2014, Umaña et al. 2015), modern trait based approaches have been largely restricted to plant communities.

In part this might be because the field of plant ecology has been able to identify a clear relationship between trait and function. Standardized approaches (Cornelissen et al. 2003, Swenson and Enquist 2007), well documented trait databases (Kleyer et al. 2008, Kattge et al. 2011), make approaches more easily reproducible across systems. Further, the conceptual framework of plant ecology- focusing predominantly on competition, facilitation and abiotic limits- lends itself well to trait based approaches, avoiding vast differences in life history and processes such as predation and parasitism.

However, in the last 5 years significant advances have been made in applying trait based approaches to insect communities. Development of trait databases (Homburg et al. 2013a, Gossner et al. 2015), early efforts at standardized approaches (Moretti et al. 2016), and attempts to fit this work in a more rigorous theoretical frameworks (Fountain-Jones et al. 2015, Brousseau et al. 2018) are promising developments. In particular, links have been developed between insect traits and habitat use (Tack et al. 2010, Arnan et al. 2011, Barton et al. 2011, Pakeman and Stockan 2014), patchiness (Barton et al. 2013, Pakeman and Stockan 2013), land use change (Sackett et al. 2011, Bartomeus et al. 2018), across spatial scales (Brooks et al. 2012, Homburg et al. 2013b) and in response to vegetation structure (Gibb and Parr 2013, Janssen et al. 2017). While promising, trait-based approaches in arthropod systems are still in their infancy and further testing is needed to confirm their utility (McGill 2015).

Study system

Islands have provided scientists with inspiration and insight into ecological processes throughout history. As a model system, islands are tractable and generally contain a broad range of habitats in a small area, with well-defined boundaries. The Hawaiian archipelago is highly isolated, located more than 3800 km from the nearest landmass. The islands originated as volcanoes above a hotspot in the Pacific tectonic plate and plate movements resulted in a chain of volcanic islands, atolls and submerged seamounts (Clague and Dalrymple 1987, Carson and Clague 1995). Starting from the hotspot under the southeastern part of Hawai‘i, each island is progressively older in northwest direction. The Hawaiian archipelago spans an expanse of substrate ages ranging from historic (<50 years) to more than four million years (Kaua‘i), as based on potassium-argon dating (Clague and Dalrymple 1987). Young substrate on the islands exist in a state of dynamic flux, with contemporary volcanic activity generating new substrate, fragmenting forests, and providing opportunities for establishment or recolonization. As islands age, they slowly erode and subside, reducing island area and topographic complexity (Vitousek 2004, Whittaker et al. 2008).

Hawai‘i community development & succession

After new substrate arises, plants colonize young volcanic flows and produce biogeochemical changes in substrate and soil (Vitousek 2004). On young flows, there is little soil and nitrogen is limiting (Vitousek 1999). Productivity rates, decomposition, and soil nutrients increase over time, peaking at sites of intermediate age (20,000- 1.4 million years; Vitousek and Farrington 1997, Chadwick et al. 1999). After this stage, productivity is limited by phosphorus, which becomes increasing depleted and is only added to the system through aerial deposition (Crews et al. 1995, Austin and Vitousek 1998, Chadwick et al. 1999). Mesic and wet forests on Hawai‘i are dominated across elevation and substrate by the native tree *Metrosideros polymorpha* (Myrtaceae, Gaudich), which in many places makes up 80% of the basal area in the forest (Mueller-Dombois 1987, Crews et al. 1995). High phenotypic variability in physiology and morphology enables *M. polymorpha* to thrive in various environmental conditions (Cordell et al. 1998, James et al. 2004, Vitousek 2004, Morrison and Stacy 2014). Productivity and plant richness increases across succession and the forest structure develops with an understory (Mueller-Dombois 1987, Drake and Mueller-Dombois 1993, Vitousek et al. 1993). Mature forest is multilevel, dominated by *Metrosideros polymorpha* with a subcanopy of among others *Cibotium glaucum* (Cibotiaceae, Sm.), *Cheirodendron trigynum* (Araliaceae, Gaudich), *Ilex anomala* (Aquifoliaceae, Hook & Arn.) and *Myrsine spp* (Primulaceae, Hillebr.). *M. polymorpha* tree stature and diameter increase across substrate age, until approximately 10.000 years substrate age (Mueller-Dombois 1987, Kitayama and Mueller-Dombois 1995, Vitousek 2004).

Many large lineages on Hawaiʻi are monophyletic (Baldwin and Sanderson 1998, Price and Clague 2002, Baldwin and Wagner 2010), indicating that they arose from a single colonization, and it is likely that their establishment prevented other species establishment through competition and niche pre-emption (MacArthur and Wilson 1967, Silvertown 2004). Many species originally colonized the oldest island, Kauaʻi, and from there colonized the island chain following formation of new islands. This pattern of successive colonization, from old age to younger islands, is termed the ‘progression rule’ (Funk and Wagner 1995), and holds for many Hawaiian taxa, although more complex patterns within that progression are also common (Roderick and Gillespie 1998).

Metrosideros polymorpha, commonly known as ōhiʻa, likely arrived on the Hawaiian Islands 2.4-3.9 million years ago (Percy et al. 2008). The *Metrosideros* genus (Myrtaceae) is diverse and common in New Zealand, which is also where the oldest known fossils of *Metrosideros* have been found (Pole 1993). Phylogenetics indicate that this species likely dispersed to the Hawaiian islands from New Zealand to French Polynesia, with the Marquesas as a likely nearest stepping stone to colonization of Hawaiʻi (Wright et al. 2001, Percy et al. 2008). The monophyly of *Metrosideros* lineages within Hawaiʻi suggests single island colonization and then progressive dispersal and radiation within the island chain (Percy et al. 2008), in a pattern aligning with the progression rule (Funk and Wagner 1995).

Arthropod colonization of Hawaiʻi

Arthropods make up a major part of terrestrial food webs and productivity within the Hawaiian archipelago (Howarth 1990). The insect fauna is constrained by the isolation and age of the Hawaiian islands, resulting in restricted immigration. For most taxa, initial colonization likely occurred through aerial plankton (Harrell and Holzapfel 1966, Holzapfel and Harrell 1968, Peck 1994), and as a result smaller and vagile species are predominately represented among the native Hawaiian insects, while larger species are often missing (Howarth 1990). Those that established successfully often diversified to make use of the full diversity of habitats available. Adaptive shifts and new selection pressure have resulted in rapid morphological change for many groups, and high rates of diversification and speciation (Roderick and Gillespie 1998, Gillespie 2004a, Vandergast et al. 2004). While some groups are missing from Hawaiian native fauna (most notable the social insects, Blattodea and

Ephemeroptera), others have evolved in large adaptive radiations (Drosophila, Hyposmocoma, Proterhinus, Tetragnatha) (Ziegler 2002). This high degree of endemism (99% of native arthropods are said to be endemic; Elredge & Miller 1995, in Hormiga 2003) as well the prevalence of arthropods and their importance for nutrient cycling on island systems such as Hawaiʻi (Howarth 1985, Wilson 1987, from Howarth 1990) means that this is an important group to study.

For the current Hawaiian fauna, biogeographic patterns suggest that most taxa recently colonized the current high islands from other archipelagoes or mainland, rather than historic dispersal from older, now predominantly submerged, islands (Price and Clague 2002). Extant endemic Hawaiian taxa generally arrived by colonizing Kauaʻi, spreading and diversifying from there, although not all taxa: see Givnish (2009), Rubinoff & Schmitz (2010). The specific speciation patterns after establishment differ between Hawaiian arthropod taxa. Some taxa are only represented by a single endemic species across the archipelago, for example the Miridae *Hyalopeplus pellucides* (Hemiptera), the Odonata *Anax strenuous* (Aeshnidae) and the Lepidoptera *Vanessa tameamea* (Nymphalidae). Other lineages colonize Kauaʻi and radiate within the islands from there, with varying frequency of intra and interisland diversification (Roderick and Gillespie 1998). *Orsonwelles*, a genus of Linyphiidae spiders, is highly diverse with more than 13 species and present throughout the Hawaiian islands, and each species is a single island endemic (Hormiga et al. 2003). In contrast, the ‘spiny leg’ clade within the spider genus *Tetragnatha*, consists of 16 species, and has experienced extensive sympatric as well as allopatric speciation (Gillespie 2004a). Some ecomorphs in this clade fulfill the same ecological function across islands and appear to have dispersed between islands, while other ecomorphs speciate in situ from an original ‘spiny leg’ colonizer into one of the ‘open’ ecomorph or niche spaces on the island (Gillespie 2004a).

Evolution of Hawaiian Hemiptera

The evolutionary history of phytophagous insects is particularly interesting because they are highly dependent on their hosts, especially if they are specialists, offering opportunities for adaptive radiation. Species diversification can occur through host switching, for example in *Orthotylus* and *Sarona*, two highly host specific genera of Miridae that have expanded their host range beyond their host of origin to utilize novel or endemic plant species (Polhemus 2011). Speciation patterns in the planthopper genus *Nesosydne* (Hemiptera: Delphacidae) parallel speciation in their hosts in the silversword alliance (Roderick 1997). Hawaiian *Nesosydne* have high diversity; there are approximately 80 species of Nesosydne on Hawai‘i, feeding on 28 plant families (Zimmerman 1948). Fifteen of the Hawaiian *Nesosydne* species feed only on plants in the silversword alliance (Zimmerman 1948, Swezey 1954). These species are highly host-specific, but phylogenetics suggest does not currently provide evidence of reciprocal adaptation (Roderick 1997). Similarly, host availability likely influenced diversification in the highly diverse genus *Nesophrosyne* (Hemiptera: Cicadellidae; approximately 200 species; Bennett and O’Grady 2012). This taxon likely arose from a single colonization event, is almost exclusively single host-specific, and most species occur as single island or volcano endemics (Bennett and O’Grady 2012). Many of these species have likely made repeated independent shifts to the same hosts after allopatric speciation. Shifts between hosts are more likely when host taxa are in close geographic proximity. For example, *Nesophrosyne* on Kauaʻi demonstrate frequent host plant switching among different co-occurring Urticaceae genera (Percy et al. 2004, Bennett and O'Grady 2013). Lastly, some lineages remain on a single host plant, and instead allopatric speciation might take place within a single host plant on different volcanoes or geological formations. The genus *Pariaconus* is an example of this, where diversification has occurred without switching from the *Metrosideros* host of origin, but speciation occurred allopatrically across different substrates and volcanoes (Percy 2017).

In contrast, lineages may have limited diversification because ecological opportunity is limited (Bennett and O'Grady 2013). There is some evidence that diversification and distribution of Hemiptera on Hawaiʻi is restricted by insect-insect interactions. For example, the ecologically similar Cicadellidae *Nesophrosyne* and Delphacidae *Nesosydne* do not overlap in host use of Asteraceae or Lobeliads (Bennett and O'Grady 2013). It is possible that one lineage is pre-emptively excluded by early arrival of another, ecologically similar taxon. Similarly, the dominant tree *Metrosideros polymorpha* is not a host to either *Nesosydne* or *Nesophrosyne* hoppers, in spite of the fact that both groups have highly diverse host plants across the herbivore radiation on Hawaiʻi (Bennett and O'Grady 2013)

Overall, the evolutionary and biogeographical history of Hawaiian arthropods suggests that many extant lineages are of recent origin, following variation of the progression rule pattern in colonizing the island chain (Funk and Wagner 1995, Price and Clague 2002). Host switching has likely led to large adaptive radiations, and it appears that open niches on younger islands are more often filled by local adaptation of already present, related species, than by dispersal of specialized taxa from other islands. This diversification is stimulated by vicariance on the dynamic volcanic landscape (Vandergast et al. 2004, Roesch Goodman et al. 2012), inter-specific interactions with other species (Bennett and O'Grady 2013) and possibly host plant morphology (Percy 2017). Unfortunately, while for some lineages the evolutionary history has been well established, most taxa have many species awaiting description and lack information on their life history and phylogenetics, hampering ecological research on Hawaiian arthropods as well.

Outline of this dissertation

The majority of eukaryote biodiversity on Earth is composed of insect species, and yet theories describing the structure and development of biological communities have largely focused on plants or other primary producers. In contrast, while insect ecology is a productive subfield that has provided wide insight into various ecological topics, including plant defenses (Stamp 2003), trophic interactions (Novotny 2009, Harvey et al. 2011), island biogeography (Simberloff et al. 1970, Simberloff 1976), and metapopulation dynamics (Moilanen and Hanski 1998, Tscharntke et al. 2002); many other traditional community ecology questions (Sutherland et al. 2013) are often neglected. Examples of such questions are the relative roles of deterministic and stochastic processes, scale dependency of processes, successional patterns, and functional traits (Kitching 2013).

Focusing on plant-insect interactions on a single dominant host plant, *Metrosideros polymorpha*, this dissertation provides insight on local, forest and landscape scale drivers of community structure. The phenotypic diversity of *Metrosideros polymorpha* and its ability to flourish in a wide range of habitats drove me to explore how geological age, succession and other temporal factors affect insect communities through their highly variable host. Secondly, to understand community structure in the broad diversity of habitats co-occurring in a small spatial extent on Hawaiʻi, it is key to understand how communities are connected across space, and what the role is of dispersal limitation. Together, these questions highlight interactions processes affecting community assembly over time and space.

In Chapter 2, I investigate beta diversity across a space-for-time chronosequence. Specifically, I explore temporal patterns in community attributes, and examine hypotheses regarding the role of substrate age, habitat factors and geographic distance in driving of species dissimilarity.

In Chapter 3, I explore the effects of dispersal limitation and landscape connectivity on diversity. I examine species area relationships in a patchy landscape to understand whether the theory of island biogeography accurately predicts local patch diversity, and what deviations from that pattern can teach us. Next, to quantify connections between patches at the scale of entire communities, I use a graph theory approach and examine connectivity at varying threshold ‘dispersal’ distances.

Finally, in Chapter 4, I take a closer look at plant-insect interactions and examine communities associated with a wide range of plant phenotypes. I look at insect life history traits and correlate these directly with host plant characteristics, providing generalization across communities and insight into why environmental responses differ across species.

In Chapter 5, I bring together insights across these different studies, providing further context on abundance, taxonomic and functional diversity of Hawaiian canopy arthropods, and I discuss some of the outstanding questions that, although not answered in this dissertation, provide further opportunities to deepen our understanding of community ecology of Hawaiian canopy arthropods.

Chapter 2 : Local habitat, not dispersal limitation or geological substrate age, drives insect β-diversity

Abstract

Differentiation in species composition across communities, or beta diversity, can provide key insights into the processes that generate and maintain biodiversity. The contribution of different processes is predicted to shift across space and time. Although community ecologists have long studied development of plant communities over time, our understanding of temporal changes in diversity and composition at higher trophic levels is underdeveloped. To address this gap, I use an island space-for-time chronosequence to understand how canopy arthropod communities structure changes with increasing geological substrate age. In particular, I explore whether insect communities assemble and change in a predictable temporal sequence by examining community convergence, nestedness and turnover, as well as variation in species composition. I test whether communities of similar ages are similar in species composition, suggesting an important role of time or substrate age in community assembly. I also explore alternative hypotheses; that dispersal is limiting, such that communities in close proximity are more similar, and whether species composition is better predicted by forest structure or local leaf traits. I examine these hypotheses in an herbivorous insect community associated with the dominant host tree *Metrosideros polymorpha* on Hawaiʻi. This unique system, with a single dominant host across the chronosequence, allows me to examine consumer communities across broad spatial and temporal scale, encompassing multiple oceanic islands and forty to four million years in substrate age. I sampled *M. polymorpha* canopies and collected Hemiptera across twelve sites on Big Island, and one site each on Maui, Moloka‘i and Kaua‘i. I found that the strongest predictors of community structure were forest complexity and local leaf traits, supporting the hypothesis that local species are sorting across habitats. In contrast, I found no support for the hypothesis that communities close in age had similar species composition. Furthermore, site level beta diversity was highest in dynamic, early succession communities, and decreased linearly across the chronosequence. Together, these results suggest that canopy Hemiptera are not dispersal limited, and are primarily structured by habitat conditions. Surprisingly, similarity in site age did not correlate with community similarity. It is possible that the species pool for *M. polymorpha* herbivores is not geographically restricted within the islands, perhaps due to the general dispersiveness of the species involved, as well as the ubiquity of *M. polymorpha* habitat across the Hawaiian archipelago. These results provide insight in the structure of plant-associated insect communities across successional time, in particular emphasizing the importance of local habitat characteristics providing resources and structure.

Keywords: *beta diversity, Hawai‘i, community structure, forest structural complexity, LiDAR, spatial scale, succession, Hemiptera*

<u>Introduction</u>

Differences in species composition, i.e. beta diversity, can provide key insights into the processes that generate and maintain biodiversity (Condit et al. 2002, Kraft et al. 2008, Tuomisto 2010, Chase et al. 2011). Patterns of species turnover vary across geographic distance and environmental gradients (Harrison et al. 1992, Maaß et al. 2015, Zellweger et al. 2017). Along environmental gradients, variation in the survival and persistence of organisms produces directional turnover in species composition (Cottenie 2005, Anderson et al 2011, Tuomisto 2003). Likewise, dispersal limitation affects colonization and establishment, and is expected to generate patterns in community similarity across distance, where closer sites are more similar in species composition (Chave & Leigh, 2002; Condit et al, 2002). The relative importance of these processes of dispersal limitation and environmental filtering (Keddy 1992) vary across latitude (Kraft et al. 2011, Myers et al. 2013), spatial scales (Chase et al. 2018), and time (Stegen and Swenson 2009, Swenson et al. 2012).

The question of what makes communities more or less similar to one another over time has not been fully resolved. Theory predicts that over time and community development the importance of different assembly processes for determining community structure will shift (Connell and Slatyer 1977, Webb et al. 2002). Therefore, different assembly processes are expected to dominate in communities differing in successional stage. Dispersal will be particularly important for communities in early stages of succession, and dispersal capacity determines which species reaches a given area. Establishment after dispersal is likely dependent on abiotic factors; research in post-disturbance successional systems show that in early stages of recovery environmental conditions are limiting (Dinnage 2009, Helmus et al. 2010). Research on plant communities indicates that during early successional stages communities primarily consist of short lived pioneer species and turnover is expected to be high between successional stages (Clements 1916, Chapin et al. 1994). In contrast, for communities in later successional stages, dispersal limitation and abiotic filtering are expected to be less important than in prior succession, while processes such as niche partitioning assume greater importance (Purschke et al. 2013).

These insights on temporal patterns in beta diversity primarily result from descriptions of plant sequences across succession and other work in plant communities, and temporal patterns in beta diversity in higher trophic levels are poorly studied (Novotný and Weiblen 2005). Successional changes in soil, nutrient availability, species composition and plant composition likely affect herbivore communities, but it is unclear whether these factors drive predictable shifts in consumer community composition.

Temporal patterns in local insect diversity vary across taxa and the resources on which the taxon specializes (Grove 2002, Heyborne et al. 2003, Inoue 2003). Similar to results from plants, many studies have found general increases in insect alpha diversity with time since disturbance or colonization (Siemann et al. 1999, Inoue 2003, Jeffries et al. 2006, Howard et al. 2018). Similarly, alpha diversity of arthropods on oceanic islands generally increases with island age (Borges and Brown 1999, Gruner 2007). Research on beta diversity of insects over time is more limited. There is some support for successional patterns in the plant community driving insect beta diversity (Siemann et al. 1999), and for dispersal limitation in late successional communities (Gobbi et al. 2010).

Variation in beta diversity across time may be driven by a number of different causes. Herbivore diversity may be influenced by assembly time via direct effects, for example because of species interactions or changes in the insect species pool. Indirect effects over time include successional vegetation changes in plant community composition, habitat structural complexity, and plant quality and defenses. Insect herbivore diversity and composition is frequently correlated with plant diversity in successional series (Southwood et al. 1979, Steffan-Dewenter and Tscharntke 1997), and is the largest driver of herbivore beta diversity in some systems (Siemann et al. 1999, Lewinsohn and Roslin 2008). Secondly, habitat structure develops with succession, and insect diversity is generally higher in more complex, heterogeneous environments (Lawton 1983, Lassau et al. 2005, Simonson et al. 2014, Stein et al. 2014). Alternatively, resource quality and plant defenses also change across successional time. Early successional species frequently grow more quickly and are generally poorly defended (Reader & Southwood 1981), with lower C:N ratios (Tilman 1990). Theory predicts lower growth rates for late successional plants, as well as higher C:N ratios, and lower palatability relative to early colonizers (Reader & Southwood 1981; Tilman 1990, Walker and del Moral 2003). This variation in resource quality and palatability influence both diversity and composition of herbivore communities. Lastly, variation in insect species composition across forests on different aged substrate may be independent of vegetation and succession, and driven instead by dispersal limitation based on proximity between sites.

This study aims to understand the processes that structure insect herbivore communities across temporal scales. I examine the herbivorous Hemiptera community associated with a single host plant species (*Metrosideros polymorpha*) across a 4 million year old space-for-time chronosequence in the Hawaiian archipelago. This model system provides an opportunity to study beta diversity in insect communities across succession *an sich*, independent of turnover in vegetation.

To understand beta diversity across this chronosequence, I address the following questions (i) What are the contributions of variation in species composition at different spatial scales to overall beta diversity? In other words, is beta diversity greatest at the scale of neighboring trees, between different forests or between different volcanoes?; (ii) How does community structure change across time? In particular, I address whether communities become more similar, less similar, or show no trend through time. I also examine whether evenness increases, decreases or shows no trend. And lastly, I ask (iii) What is the importance of geological substrate age, habitat structure, tree traits and dispersal limitation in explaining patterns in species composition? To address the latter question, I examine whether species turnover is predictable across the chronosequence such that communities that are similar in age are also similar in species composition. I examine whether variation in species composition is correlated with local habitat, in the form of forest structure and host leaf traits. Then, I evaluate the importance of dispersal limitation, and whether communities in close proximity are more similar.

Methods

Study site

The Hawaiian Island chain is the result of volcanic activity in the Pacific Ocean (Juvik and Juvik 1998). The chain is age progressive, with currently active volcanoes in the southeast, and the oldest islands to the northwest, which are estimated to be more than four million years old (Clague and Dalrymple 1987, Carson and Clague 1995, Neall and Trewick 2008). The volcanic activity that produced the Hawaiian Islands resulted in substrates of successive age both within and across islands (Clague and Dalrymple 1987). Successional changes occur across this age gradient, and plant colonization of young volcanic flows produces biogeochemical changes in substrate and soil (Vitousek 2004). Productivity and decomposition rates, as well as soil and foliar nutrients peak at sites of intermediate age (20,000- 1.4 million years); on younger substrates nitrogen is limiting, while on older sites phosphorus is increasingly depleted and only added to the system through aerial deposition (Crews et al. 1995, Austin and Vitousek 1998, Chadwick et al. 1999, Vitousek 2004).

Vegetation in wet and mesic zones are dominated by an endemic tree, *Metrosideros polymorpha* Gaudich. (Myrtaceae). *Metrosideros polymorpha* is one of the first plants to colonize new lava flows, and remains dominant across substrate ages (Stemmermann 1983, Dawson and Stemmermann 1999). This tree is phenotypically variable and thrives across elevations from sea level to 2500 m (Vitousek et al. 1992), and across rainfall from 400-10.000 mm (Stemmermann and Ihsle 1993, Cordell et al. 1998). The broad ecological distribution of *M. polymorpha* is enabled by high morphological and physiological variation (Cordell et al. 1998, Cornwell et al. 2007). This morphological variation includes differences in specific leaf area, foliar nutrients, leaf water content, and degree of leaf pubescence.

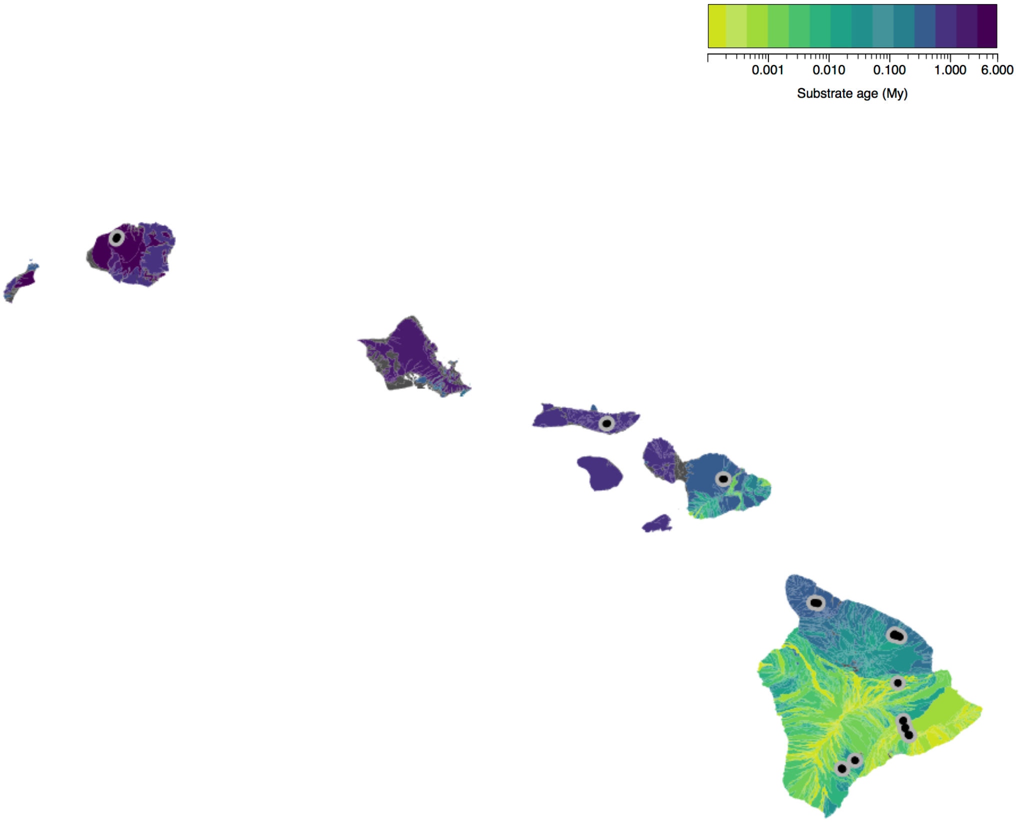

Figure 2.1: Map of sampling sites on Hawai'i, Maui, Moloka'i and Kaua'i. Dots represent sites where sampling occurred, colors indicate substrate age (log scale, in million years).

I made use of the progression of geological substrate ages on the Hawaiian Islands as a space for time chronosequence and sampled four islands ranging in age from new substrates (< 50 years old on Kilauea) to Kauaʻi (approximately four million years old). Ecosystem state variables were held as constant as possible to focus on turnover as a result of temporal community development. Sites were selected in mesic forest at similar precipitation (2500-4600 mm/year), elevation (950-1200 m), and dominant vegetation (i.e. predominantly native species with *M. polymorpha* canopy. See Appendix Table S1 and Table S2 for site details). Site selection resulted in 12 sites on Hawaiʻi Island and one each on Maui, Molokaʻi and Kauaʻi (Figure 2.1). Each site consisted of 6 plots of 15 m radius centered around a focal *M. polymorpha* tree, and plots were located at least 80 m from one another. Plots within the site were selected through a randomized procedure using LiDAR (Light Detection And Ranging) remote sensing data to locate trees with large canopies.

Sampling

Arthropods were collected from the outer canopy of the focal *M. polymorpha* tree at the center of each plot. Each tree on Hawaiʻi Island was sampled in 2014 and 2015; trees on Maui, Molokaʻi and Kauaʻi were sampled in 2015 only. Canopies were accessed using single rope technique (Perry 1978). Nylon ripstop fabric bags of one meter diameter and two meter deep were attached to a large hoop with a handle to access branches in the outer canopy. Samples were collected by quickly bagging multiple branches from various areas of the outer canopy, and using a pole pruner to clip and remove branches (Gruner et al. 2005). Bags were closed and stored in a cool place until transport to the lab. Samples were collected under predominately dry weather conditions.

Foliage samples were transported to the lab and arthropod specimens were extracted within 48 hours of collection. Specimens were extracted by gently shaking branches on an enclosed white surface and aspirating individuals that emerged. Foliage samples were carefully searched, but herbivores feeding completely enclosed within leaves or buds (galls for example) were not manually extracted. Specimens were kept in 95% ethanol until identification. Specimens were identified to (morpho)species in the lab.

Habitat variables

To quantify *Metrosideros polymorpha* leaf characteristics, 20 leaves were selected from the foliage collected during each sampling event. The leaves were undamaged and representative of the sample in size, color and trichome presence. Leaves were selected from the penultimate leaves to ensure fully developed young leaves. I measured fresh weight to the nearest 0.01 g and leaf area to the nearest mm, then dried leaves at 60°C for 96 hours and reweighed them for dry weight. I calculated specific leaf area as the ratio of leaf area to dry mass to quantify leaf 'toughness', a biomechanical property. Specific leaf area is closely correlated with metrics such as work to punch and work to shear (Edwards et al. 2000, Díaz et al. 2001, Wright and Westoby 2002). Mean SLA per tree was calculated by averaging SLA from approximately 20 leaves from each sample. For leaf nutrient analysis, I pooled ten leaves per sample, ground them to fine powder using a Retsch MM 400 Oscillating Mixer Mill and kept them at 60°C until analysis. An Exeter Analytical

CE- 440 CHN Elemental Analyzer was used for foliar carbon and nitrogen analysis at the Parker lab at the Smithsonian Environmental Research Center in Edgewater, MD (USA). Leaf phosphorus percentage by mass was determined by placing a known mass (~2 mg) of dried, ground leaf material in a muffle furnace at 550°C for two hours (Miller 1998), followed by colorimetric analysis using the ammonium molybdate method (Clesceri et al. 1998).

In June 2017, the Carnegie Airborne Observatory CAO3 system was flown to collect LiDAR (Light Detection and Ranging) data on all Hawaiʻi Island sites (Asner et al. 2012). This system was flown at 2000 meter above ground level, with a pulse repetition frequency set to 200 Mhz and scan frequency of 31 Hz. Up to four discrete pulses per return were recorded. The system operates at 1024 nm wavelength with a laser beam divergence of 0.5 MRad and a 34 degree field of view (FOV). Previous analysis with this system has estimated errors of 16 cm horizontal and 7 cm vertical RMSE. Using the point cloud data resulting from this campaign, I generated a canopy height model and normalized the height of each point with respect to the ground surface by making and combining the digital surface model and digital terrain model. I computed descriptive statistics within each pixel using the grid_metrics() function in the package 'lidR' (Roussel and Auty 2018), including mean, median, maximum, standard deviation, skew and kurtosis of tree height.

Analyses

All data analysis and statistics were conducted in R (R Core Team 2017). I calculated alpha diversity using the estimated Shannon index in the 'iNEXT' package (Hsieh et al. 2016), which was then converted to its number equivalent (H for $q = 1$;

Jost 2006, Chao et al. 2014). I tested for differences in alpha diversity between sites and differences across years in sampling effort and arthropod abundance using generalized linear models. I examined alpha diversity for trends across the chronosequence using linear mixed effect models in the package ‘lme4’, including site as a random effect and an offset for sampling effort (Bates et al. 2015).

For this study, I was interested in a number of aspects of beta diversity, including both variation and turnover components of beta diversity (Anderson et al. 2011). I studied variation in species composition across a hierarchical series of spatial scales (i.e. variation between trees, sites, volcanoes, islands); variation in species composition within sites across geological substrate age; directional turnover across an explicit gradient of substrate age, distance, and successional dissimilarity in habitat and leaf traits; and lastly variation in species composition as a function of age, location, habitat and leaf traits (independent of any explicit gradient).

(i) What are the contributions of variation in species composition at different spatial scales to overall beta diversity?

To examine diversity across hierarchical scales, I used multiplicative partitioning with the function multipart() in the package ‘vegan’ (Oksanen et al. 2018). Multiplicative partitioning results in alpha and beta components of biodiversity that are independent of one another (Baselga 2010a, Jost et al. 2010), a key requirement in this system where species richness differs strongly across the sites. This beta diversity measure gives the effective number of distinct communities at scale n within the next hierarchical scale $n+1$, culminating in the regional data set (Baselga 2010a). In this study, partitioning provides a beta diversity value quantifying variation within a site, variation within a volcano, and variation within an island. I compared these observed diversity values to expected values based on 1000 randomizations. For this, individuals were randomly assigned to samples at each level, while maintaining original sample sizes and species abundances. These random assemblages were then partitioned to calculate null expectations for beta diversity across scales, and compared to observed values. Beta diversity was calculated relative to the local gamma value (i.e. relative to one level higher than the beta scale in question), with weighting proportionate to sample abundances. Beta diversity is intrinsically scale dependent, and as a result sensitive to the selection of which scales to include. I analyzed beta diversity separately within Hawaiʻi Island, where replication is greatest, as well as across all sampled islands to incorporate inter-island turnover in the analysis. Beta diversity partitioning gave similar results in the analysis of Hawaiʻi Island and the analysis across all four islands, confirming that artefacts of the sampling design and differences in replication across islands were not driving results. Then, to examine the role of rare or endemic species, I also partitioned beta diversity into species turnover and nestedness components, In this analysis, species turnover incorporates species that are unique to a sampling unit, while the nestedness component quantifies how much of the community is a subset of other, more species rich communities. This analysis used presence absence data and Sørensen dissimilarity in the package ‘betapart’ (Baselga 2010b).

(ii) How does community structure change across time?

To characterize changes in community structure across time, I described species richness, abundance, evenness, and convergence in the community. Convergence or divergence in community composition was analyzed through beta dispersion, or within site turnover in species composition, across the chronosequence. If the amount of variation in species composition at the local (ie within site) scale varies across the chronosequence, that would suggest that different processes determine community composition across time. The function betadisper() in 'vegan' examines this by analyzing the multivariate homogeneity of variance (Anderson et al. 2006, Oksanen et al. 2018). I first standardized for abundance using Hellinger standardization, and chose to calculate the distance matrix with the Horn-Morisita index. This index handles multisite abundance data, gives importance to rare species, and is not sensitive to differences in alpha diversity. I calculated this distance to centroid using data sampled in 2014 and 2015. Number of samples differed across sites (6-13 samples), but analysis of the 2014 data, which was more evenly sampled (11 sites with 6 samples, one with 5), gave qualitatively similar results.

(iii) What is the importance of geological substrate age, habitat structure, tree traits and dispersal limitation in explaining patterns in species composition?

I analyzed variation in species composition by comparing the pairwise dissimilarity between Hemiptera communities with dissimilarity in age, spatial distance and habitat through LiDAR and *Metrosideros polymorpha* leaf traits. These analyses were conducted only on samples from Hawai'i Island, because forest structure and leaf trait data was lacking for the other islands. Hemiptera community dissimilarity was based on Hellinger transformed data and using Bray Curtis dissimilarity (Oksanen et al. 2018). I quantified spatial distance between plots using the function 'Imap' to generate a matrix of distances between points (Wallace 2012).

Dissimilarity in forest structure was calculated based on mean vegetation height, standard deviation in vegetation height, kurtosis and skew. Dissimilarity in leaf traits was calculated based on foliar nitrogen, phosphorus, specific leaf area, water content, and leaf morphotype. These dissimilarities were compared to dissimilarity in Hemiptera community composition using mantel tests. I then further explored these predictors using redundancy analysis, with functions dbRDA(), and varpart() in vegan. To use the geographic distance matrix in constrained ordination, distance data needs to be converted to independent, orthogonal spatial variables. To do so, I calculated a principal components of neighborhood matrix to transform the spatial distances into rectangular data, using the function pcnm() in 'vegan' (Oksanen et al. 2018).

Results

The samples consisted of 7754 insects across 15 families in the order Hemiptera, which were identified to 64 (morpho)species. Mean plot abundance was 49.18 individuals in 2014 and 42.66 in 2015. Mean sampling effort was 518.35 g of *M. polymorpha* foliage in 2014 and 498.50 g in 2015. Sampling effort did not differ between years (LM, $F_{2,168}$=0.522, P=0.471). Insect abundance did not differ between years when including an offset for sampling effort (LM, $F_{2,168}$=1.7688, P=0.1854). Mean richness per tree sampled also did not differ between 2014 and 2015 (2014: 5.81, 2015: 6.59, $F_{2,168}$=1.08, P=0.3).

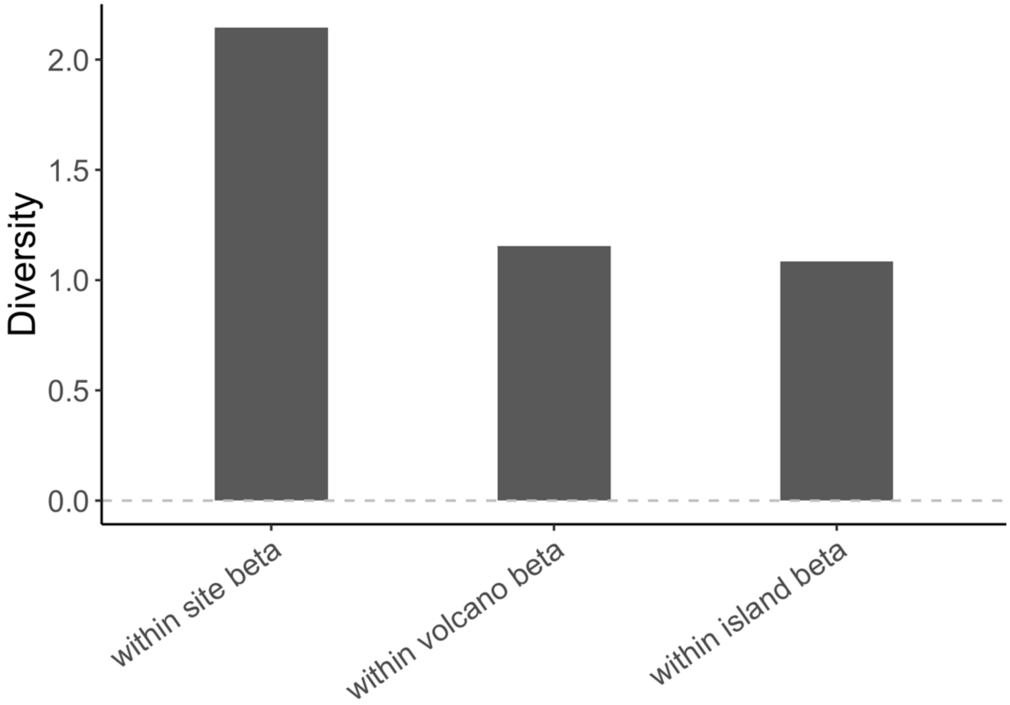

Figure 2.2: Multiplicative diversity partitioning across Hawai'i, Maui, Moloka'i and Kaua'i, showing beta diversity at different spatial scales. Beta diversity values are relative to gamma (ie global=T).

Table 2.1: Nestedness and turnover components of beta diversity.

	Turnover component	Nestedness component	Total Sørensen
All sites	0.969	0.0134	0.983
Within Hawai'i	0.967	0.0141	0.981
Within outer islands	0.726	0.124	0.850

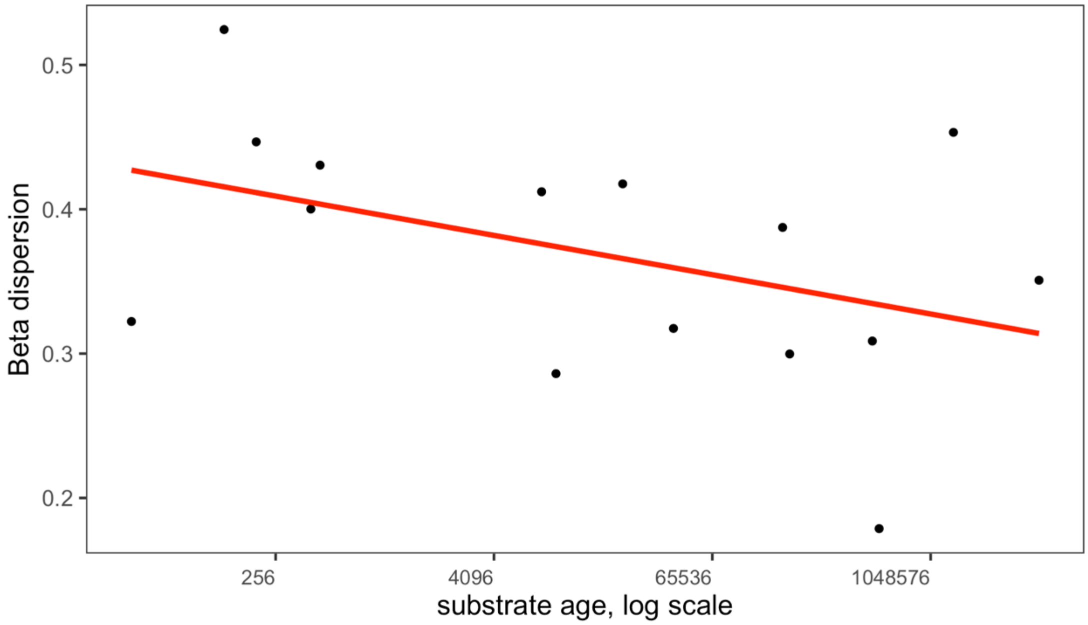

Figure 2.3: Rate of species turnover across the chronosequence. Each point represents the within site beta dispersion as a function of substrate age (years on log scale). P = *0.0346*

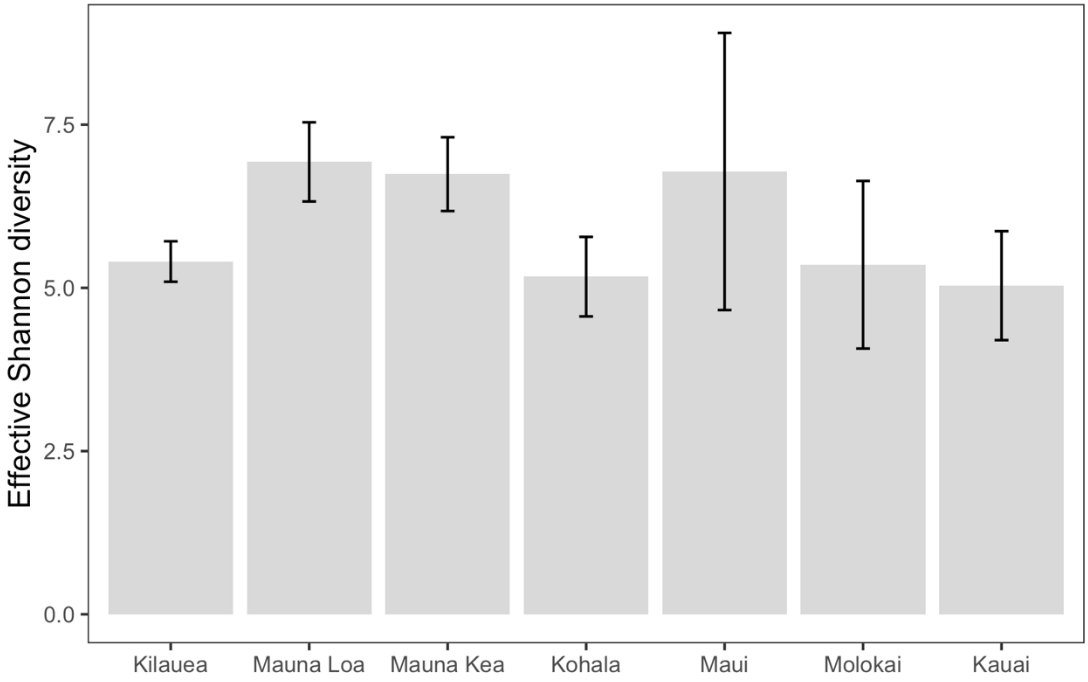

Figure 2.4: Mean effective Shannon diversity per sample across the chronosequence from youngest (Kilauea) to oldest (Kaua'i) volcano.

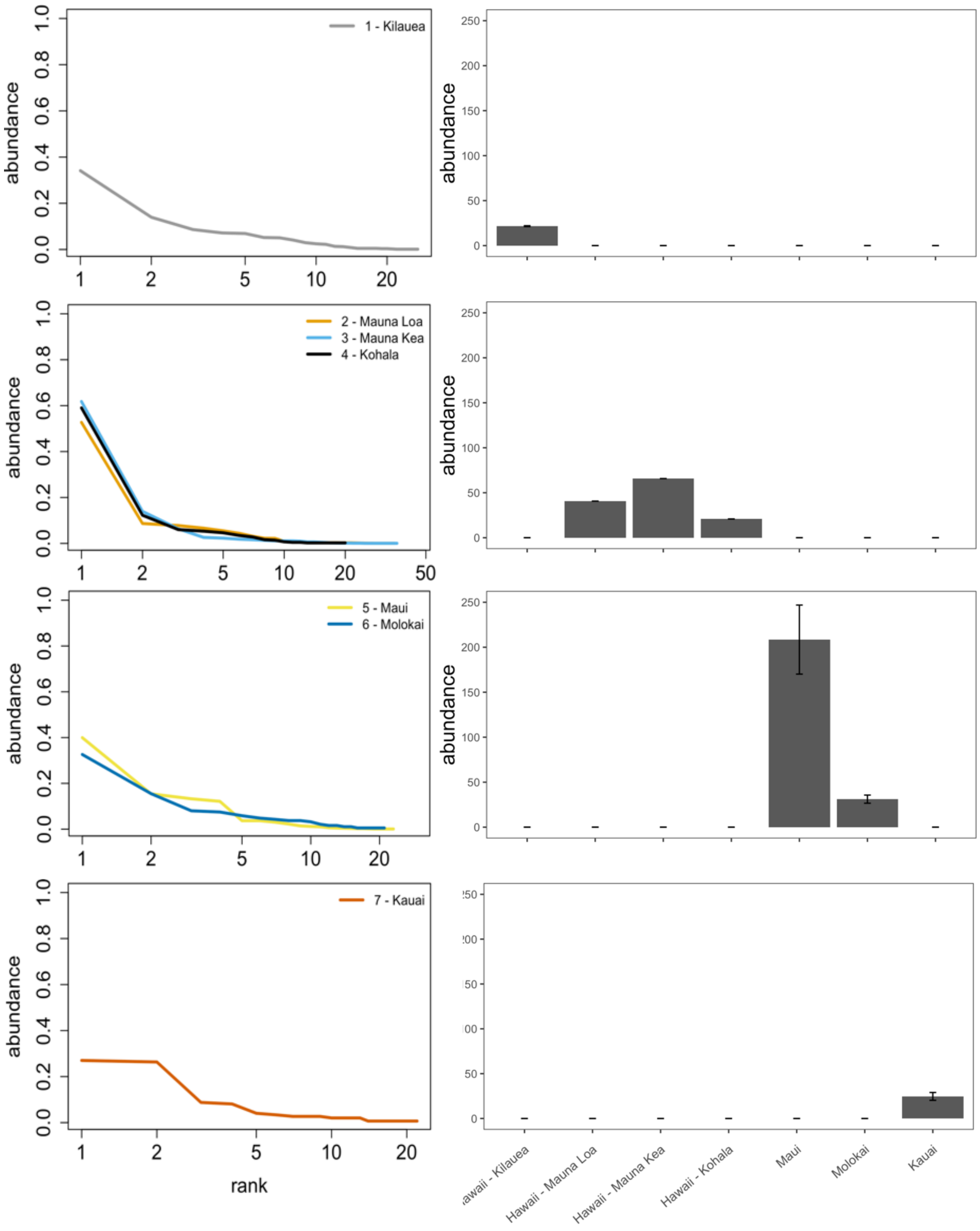

Figure 2.5: Rank abundance curve (left column)and mean sample abundance (right column) per volcano across the chronosequence. Panels are grouped to ease comparison, showing similar aged volcanoes with similar patterns in the same panel, and groups are ordered chronologically from top (youngest) to bottom (oldest).

Species richness and effective Simpson diversity differed among sites (GLMM including year as random effect and an offset for sampling effort; Richness $F_{15,154}$=1. 960 *P=0.02174*; effective Shannon $F_{15,154}$=1.173 *P*=0.2983; effective Simpson $F_{15,154}$=1.8287 *P= 0.03521*), but richness, Shannon and Simpson diversity did not change directionally across the chronosequence (GLMM including site and year as random effect and an offset for sampling effort; species richness $F_{15,154}$=0.1646 *P*=0.6854; effective Shannon F=0.1772 *P*=0.6743; effective Simpson $F_{15,154}$=0.205 *P*=0.6513; Figure 2.4).

(ii) At what spatial scale does turnover occur?

Absolute beta diversity decreased with spatial scale, with highest beta diversity among trees within a site (Figure 2.2). Observed beta diversity was greater than the null expectation at the among trees, among sites, and among volcanoes scale (*P*=0.0001 for all levels).

(ii) How does community structure change temporally?

Hemiptera species composition differed significantly across substrate age (PERMANOVA: *P*=0.001). The mean distance from individual tree assemblages to the site centroid decreased across the chronosequence, indicating decreasing species turnover with geological age (Betadisper: Figure 2.3, *P*=0.002).

Community structure varied across volcanoes (Figure 2.5, Figure S 3, Figure S 4). The oldest (Kaua‘i) and youngest (Kilauea) sites had shallow rank abundance curves, while the rank abundance curve for all intermediate age volcanoes were steeper (Figure 2.5, Figure S 3). The intermediate age volcanoes on Hawai‘i Island

(Mauna Kea at 7-165 ky and Kohala at 175-450 ky) had the steepest rank abundance curves (Figure 2.5, Figure S 3). Hemiptera abundance per tree differed across volcanoes (*P*=0.008), and was highest on Mauna Kea and Maui (Figure 2.5, Figure S 4).

The turnover component of beta diversity on the Hawaiian Islands was greater than the nestedness component (Table 2.1), indicating that variation among communities was primarily due to species replacement rather than differences in species number. Next, I examined how the nestedness and turnover components of beta diversity differed between sites on Hawaiʻi and on the older islands. Sites within Hawaiʻi exist in close proximity to other sites and differ in age by only a couple orders of magnitude, while Maui, Molokaʻi, Kauaʻi are more separated spatially and have much longer evolutionary histories. If these differences had led to different drivers of community assembly between Hawaiʻi and the older islands, this would result in differences in patterns of species turnover and nestedness. If these temporal and spatial differences result in different community assembly drivers, the species turnover component of beta diversity is expected to be greater on the older islands than on Hawaiʻi Island. I compared nestedness and turnover components within Hawaiʻi Island, within the older islands and within the entire chronosequence (Table 2.1). When comparing across the entire chronosequence and when comparing across Hawaiʻi Island only, beta diversity primarily consisted of species turnover. However, across Maui, Molokaʻi and Kauaʻi the turnover component was lower than across Hawaiʻi, as well as the chronosequence in its entirety.

(iii) What is the importance of habitat, geological age and dispersal limitation in explaining patterns in species composition within Hawai‘i Island?

Pairwise distance among sites on Hawai‘i Island was correlated with Hemiptera community dissimilarity, indicating that samples in closer geographic proximity were more similar (Mantel statistic r: 0.1213, $P = 0.001$, Figure 2.6a). This correlation was consistent but not very strong. Sites of similar geological substrate age were not more similar in their species composition, as pairwise dissimilarity in substrate age did not correlate with dissimilarity in community composition (Mantel statistic r=-0.0377, P=0.766, Figure 2.6b). Dissimilarity in species composition did correlate with dissimilarity in habitat structure, indicating that structurally similar sites had more similar communities (Mantel statistic r=0.2225, P=0.001, Figure 2.6c). Lastly, dissimilarity in leaf traits also correlated with dissimilarity in community composition (Figure 2.6d; Mantel statistic r=0.1542, P=0.001).

I used ordination to examine the importance of different predictors in driving Hemiptera community structure. I partitioned the variation in community composition into components for substrate age, spatial, leaf traits and forest structure (LiDAR), using redundancy analysis. Leaf traits and forest structure were the largest components (Figure 2.7; leaf traits: 0.16 overall and 0.07 after accounting for other predictors, forest structure 0.19 overall and 0.12 after accounting for all other predictors). Distance based redundancy analysis indicated that the constrained components explained 44% of variation, predominantly along the first two axes ($F_{11,59}$=3.4561, P=0.001).

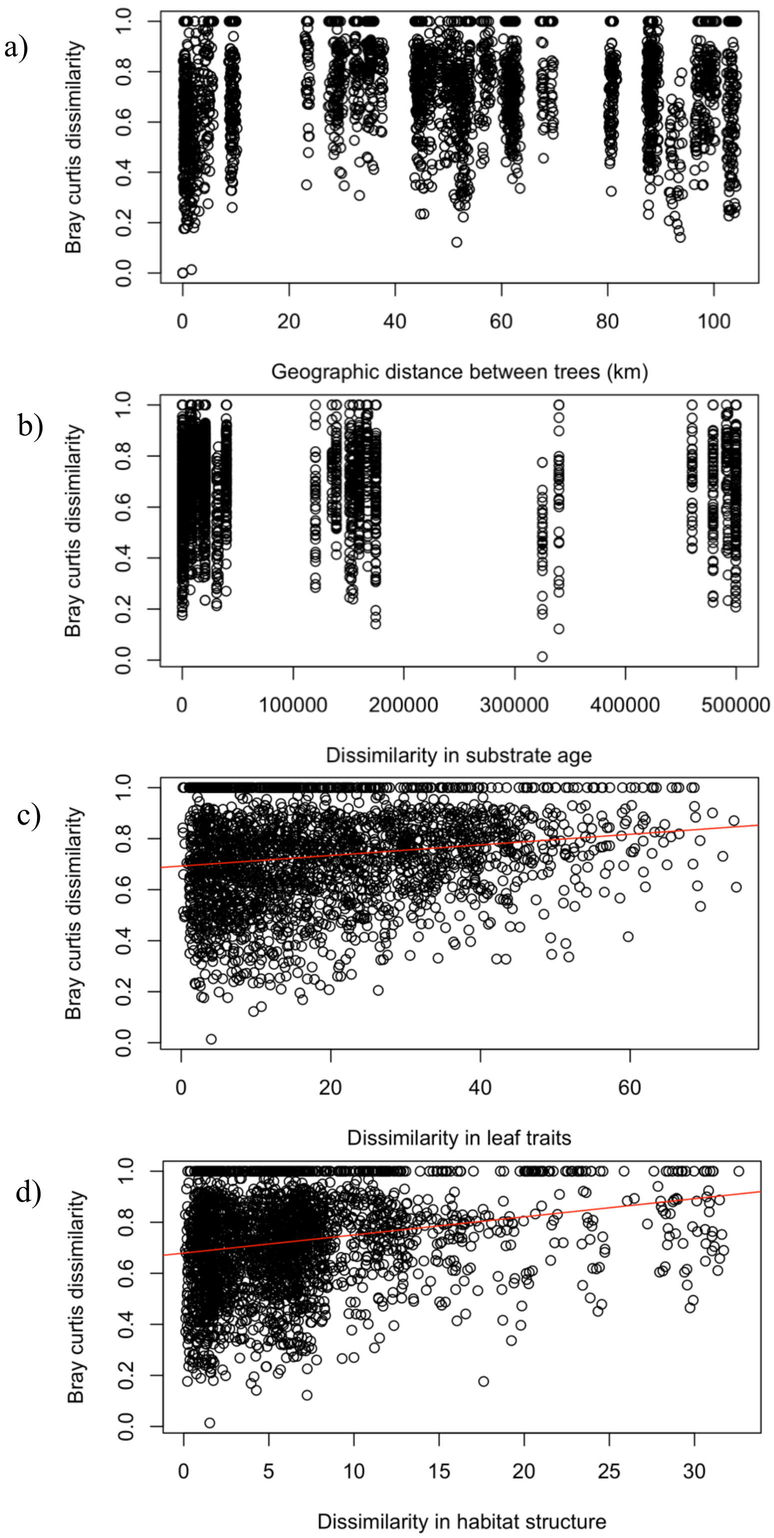

Figure 2.6: Pairwise dissimilarity in community composition as a function of (a) pairwise geographic distance (mantel statistic r=*0.1114,* P=*0.001), (b) pairwise dissimilarity in substrate age (mantel* r= *-0.0377,* P=*0.782), (c) pairwise dissimilarity in leaf traits (leaf nitrogen, phosphorus, water content, SLA and morphotype; mantel* r=*0. 1662,* P=*0.001), and pairwise dissimilarity in forest structure (mean tree height, standard deviation, kurtosis and skew; mantel statistic* r=*0. 2225,* P=*0.001).*

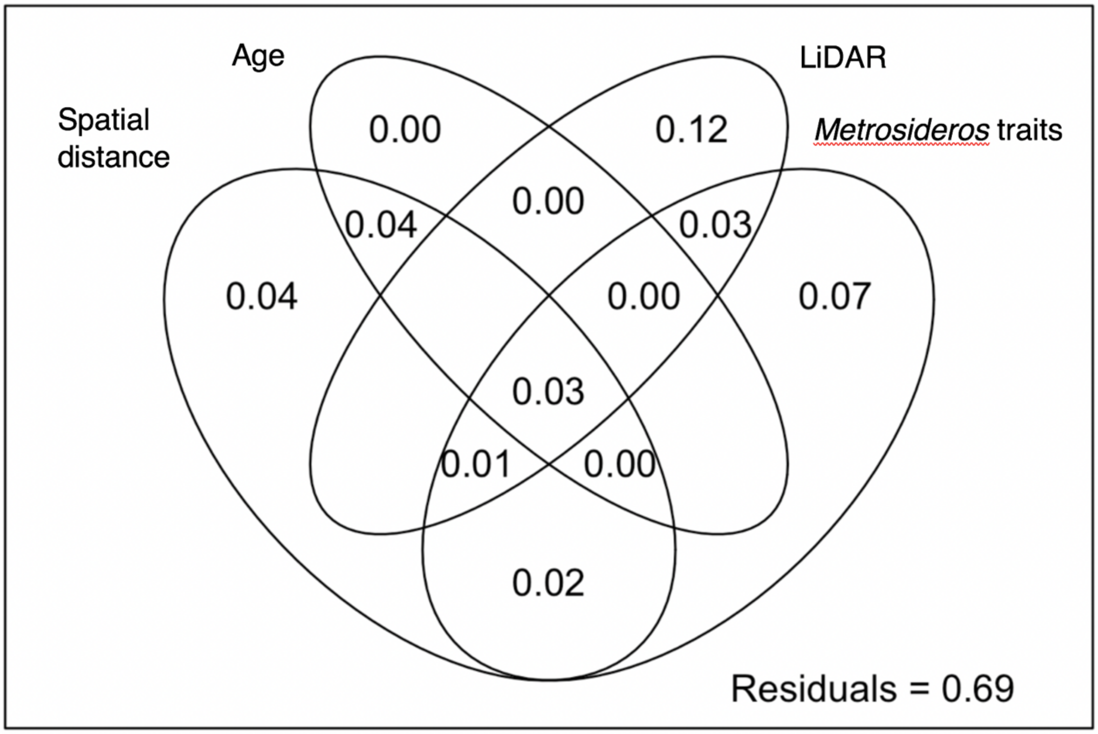

Figure 2.7: Variance partitioning of site level predictors, from left to right: geographic distance based on PCNM axes 1 and 2; substrate age; LiDAR (mean, standard deviation, kurtosis and skew of tree height), and leaf traits (nitrogen, phosphorus, water, specific leaf area and morphotype). dbRDA indicates 44% of variation is explained, F *= 3.456,* P *= 0.001.*

Lastly, I used PERMANOVA to analyze variance in species composition. Variation in community composition was significantly explained by substrate age, latitude, longitude, mean tree height, kurtosis of tree height, skew of tree height, leaf nitrogen and specific leaf area (full model with all predictors: $R^2 = 0.431$).

Discussion

Patterns in community composition of Hemiptera associated with *Metrosideros polymorpha* canopies varied across successional stage and space. Beta diversity was greatest at the within site scale, indicating that variation between trees is more important than larger scale differences. These results were supported by analysis of species dissimilarity matrices, where insect communities were more similar in community composition to communities in similar habitats, rather than their closest neighbors or communities on similar substrate ages. However, a spatial pattern in community structure was present, resulting from the interaction between assembly on dynamic young flows, site productivity, insect abundance, evenness and the size of the regional species pool. Analyzing insect communities on a single host plant along a chronosequence, and combining this with detailed information on forest structure and host traits identified temporal patterns in the complex community structure of canopy arthropods on Hawaiian *Metrosideros polymorpha*.

Hypotheses for drivers of community structure

This study examined the hypotheses that environmental conditions, successional stage and dispersal limitation are important determinants of community composition.

My results provided strong support for the hypothesis that habitat drives community structure in *Metrosideros polymorpha* canopy Hemiptera, both in host traits for nutrition and palatability of leaves as well as in physical habitat structure. Diversity of Hawaiian canopy arthropods had previously been shown to increase with foliar nutrients and productivity (Gruner et al. 2005), although habitat structure data used in Gruner 2007 lacked the resolution to provide conclusive answers regarding forest structure (Gruner 2007). Habitat structure is positively correlated with arthropod diversity in many systems (Lawton 1983, Tamme et al. 2010, Stein et al. 2014), with unique communities at different forest stages as a result from specialization of insect species on vegetation types or structure specific to a successional stage (Inoue 2003, Jeffries et al. 2006), such as saproxylic beetles on large trees in late succession (Grove 2002). Changes in forest complexity result in variation in canopy layers (Basset et al. 2003), unique niches and greater habitat availability (MacArthur 1958, Stein et al. 2014, Müller et al. 2018), and as such can drive species composition and diversity of arthropods.

Furthermore, there was only a weak signature of dispersal limitation on beta diversity patterns. Dispersal distances are largely unknown for Hawaiian arthropod taxa, but lack of dispersal limitation is in line with previous work on *Metrosideros* canopy arthropods (see Chapter III). However, the role of dispersal limitation is supported by studies of population genetic structure in various Hawaiian arthropod lineages. For example, genetic structure in spider communities in contiguous forest suggests limited gene flow at small spatial scales (Vandergast et al. 2004). Limited gene flow, and consequently dispersal, among volcanos is also indicated by several examples of single volcano endemics of *Metrosideros polymorpha* specialists (for example the psyllid *Pariaconus wyvernus*; Percy 2017). For some Hawaiian taxa dispersal limitation does play a greater role; for example flightlessness has evolved in Hawaiian taxa such as lacewings (Tauber et al. 2007) and cave moths (Medeiros et al. 2009). Lastly, work on delphacid plant hoppers has found incipient speciation on adjacent lava flows in spite of common hosts, suggesting that dispersal limitation rather than host differences is driving local speciation (Roesch Goodman et al. 2012). These various examples suggest that the importance of dispersal limitation varies greatly across taxa.

Finally, although many studies on arthropod lineages emphasize single island endemics and diversification between islands (Polhemus 1997, Hormiga et al. 2003, Gillespie 2004b), these results surprisingly did not indicate an important role for island identity or substrate age in determining variation in Hemiptera community composition. However, when evaluating the Hawaiian islands as a chronosequence there was a temporal pattern in Hemiptera communities (discussed below), suggesting that communities converge and with time become more similar in composition at the local scale.

Temporal patterns across volcanos

To further understand temporal patterns in community structure I examined mean species richness, abundance and evenness for each volcano, and found a general developmental sequence across the chronosequence (Figure 2.5). Progressing from young to older substrates on Hawaiʻi Island, evenness decreased, and communities were more dominated by a subset of Hemiptera species, that perhaps were better adapted or specialized. Communities on the young and dynamic landscape of Kilauea, the youngest volcano, had high evenness and beta dispersion, likely due to high rates of immigration and an unstable community, or lack of an established community. This pattern may result from a high abundance of recruitment opportunities on young substrate (i.e. available ecological space Horn and MacArthur 1972, Gillespie 2002, Ricklefs and Bermingham 2007), or mass effects, where migration of individuals from source environments enhances diversity within sink environments by reducing local extinction (Pulliam 1988, Leibold 2004).

Sites at intermediate age and high productivity (Chadwick et al. 1999), Hemiptera abundance was also high, and communities were characterized by a subset of dominant species in high abundances. Number of individuals is one component contributing to species richness (Chase et al. 2018), and elevated abundances likely drive the high species richness on productive, intermediate age sites. Then, on progressively older substrates, as phosphorus availability limits productivity on the oldest sites on Hawaiʻi Island (Vitousek and Farrington 1997, Hedin 2003), Hemiptera abundances decreased and communities were made up of a number of common species. This pattern of reduced abundance and richness continued on volcanoes on older islands.

Older islands have both had more time for diversification to take place (Funk and Wagner 1995, Cowie and Holland 2008), and are physically separated from other sampled sites by 50-500 km of ocean. In general, rates of arthropod single island endemics are higher on Maui, Molokaʻi and Kauaʻi (Gruner 2007). Diversity was particularly high on Maui, where Hemiptera abundances were tenfold higher than abundances on other sites. On the oldest islands, Moloka‘i and Kaua‘i, number of individuals was lower than on Maui, resulting in a more even community.

Overall, I find that shifts in abundance and evenness were an important component of species turnover between different volcanoes on Hawai‘i Island. The driver of beta diversity among volcanoes on the older islands was less clear. Nestedness was greater within the older islands than in Hawai‘i Island, indicating that turnover into assemblages with different or unique species is less important on the older islands, and that communities have a stronger component where lower richness assemblages are subsets of higher richness samples. This suggests that while single island endemics are more common on older islands than on Hawai‘i Island, they are a small portion of the community and contribute relatively little to overall Hemiptera community structure.

Evolutionary studies of diversity on Hawai‘i and other oceanic archipelagos show that geological age or evolutionary time influences community composition through speciation (Borges and Brown 1999, Price 2004, Ricklefs and Bermingham 2007, Cowie and Holland 2008, Bennett and O’Grady 2012). However, my results on Hemiptera diversity do not show a strong signal of substrate age. This surprising result may be due to a number of reasons; for example, in situ speciation in phytophagous insects frequently takes place through host switching (Bennett and O’Grady 2012, Hardy and Otto 2014, though see Roesch Goodman et al. 2012). Therefore, the structure of Hemiptera communities interacting locally on a single host may not be strongly affected by evolutionary time. Also, frequent volcanic activity and isolation of populations on young flows may result in high speciation rates on younger substrates, producing a different temporal signature than hypothesized (Roderick et al. 2012, Roesch Goodman et al. 2012). Lastly, it is possible that my sampling was insufficient to capture rare or endemic species, biasing the results at older sites. While species accumulation curves were generally saturated or close to saturated (Figure S 1), the asymptote was not reached for some sites on the older end of the chronosequence and in particular for the Maui, Molokaʻi and Kauaʻi sites. However, the general patterns across geologic age are likely accurate; further sampling and increasing the number of singletons in the data for the oldest sites would support my conclusions of low abundances and increased evenness in later stages of the chronosequence.

Ecological succession

Studies on ecological succession in plant communities have also found that early successional stages are characterized by shifts in abundance and evenness (Norden et al. 2012). Herbivore communities on woody species in a succession of abandoned gardens were found to be dominated in later stages of succession by a few highly abundant species (Basset et al. 2001). I found similar patterns of high abundances at high productivity sites, but in the Hawaiʻi system these are found at mid-, rather than late-succession sites, due to the greater length of the chronosequence (millions of years versus hundreds in conventional succession studies). With longer time and stronger dispersal limitation between islands, later successional sites support many endemic species, increasing evenness and overall richness. Siemann et al (1999) also found increasing evenness as succession continues, which they suggested to be due to increases in plant defense; this study was unable to examine this hypothesis due to a lack of leaf chemistry data.

Early successional communities are generally characterized by a subset of species with traits that allow them to thrive under disturbed conditions. This has not been well documented for insect communities, but plant succession find that early succession species generally have high dispersal and growth rates, trading off in late succession with traits associated with survival under lower resource conditions or high competition (Tilman 1988, Rees et al. 2001). This question has received some attention in the context of competition- colonization tradeoffs, as well as work on invasive species. Insect traits associated with early succession or colonization ability include dispersal ability, host breadth, and growth rate or life history traits to do with rapid reproduction (Novotný and Weiblen 2005, Mondor et al. 2007). Good colonizers are thought to be polyphagous species, because in an environment with patchy resource availability the abundance of suitable host plants is likely to be greater for polyphagous than for highly specialized insects (Lawton and Strong 1981, Siemann et al. 1999, but see Basset et al. 2001). Similarly, body size is related to dispersal ability and metabolic efficiency, and may decrease across succession (Steffan-Dewenter and Tscharntke 1997, Siemann et al. 1999, Mondor et al. 2007). However, I did not find a strong pattern in body size (Supplemental Figure S 2). Lastly, there is one example of trait research on Hawai‘i insects relating to colonization and establishment. Aphids are thought to have been successful in colonizing Hawai‘i in part because of their ability to reproduce asexually at a rapid pace (Mondor et al. 2007). Similarly, on early successional sites these traits of asexual reproduction, high fecundity and short generation times are also likely to be beneficial. Overall, understanding shifts in insect traits across succession will require further taxonomic work as well as a focus on natural history of Hawaiian arthropods, much of which has not been documented.

Understanding beta diversity patterns is complicated by the fact that beta diversity is inherently scale dependent. Definitions or concepts of beta diversity depend on the communities being compared (Anderson et al. 2011). Similarly, differences between systems in the severity of environmental gradient, in the scale considered or in host diversity have limited our ability to generalize regarding beta diversity drivers. This chapter addresses a gap in our understanding of insect beta diversity by controlling for the effects of vegetation change across space and time. Beta diversity of tropical herbivores has generally been examined in relation to latitude (Novotny et al. 2007), altitude (Hulcr et al. 2008) or across broad scales with differences in host plant abundance (Weiblen et al. 2006, Forister et al. 2014), and most studies have found high beta diversity. It is difficult to interpret these results more broadly, because the observed beta diversity is dependent on the degree of dissimilarity among the various sites. Similarly, when succession results in increases in plant richness, insect richness tracks these changes in the plant community (Lewinsohn et al. 2005), providing information on how insects respond to changes in host plant richness and abundance rather than temporal patterns per se. This chapter uses a system dominated by a single host plant, thereby focusing on turnover associated with space and substrate age, within a single habitat and community type.

Such comparisons of herbivore assemblages present on a single host across ecological conditions are rare.

Summary

Understanding the main drivers of diversity across time and space is an ongoing question in community ecology. For Hawaiian canopy Hemiptera, I examined community progression from young, dynamic communities dominated by high dispersal and mass effects to more productive sites with higher dominance and abundance. Then, at the oldest end of the chronosequence, communities were more even, the species pool was likely greater, although in general communities did not differ greatly in their species composition from those on younger substrate. Across this progression, habitat changes in leaf traits and forest structure correlated with dissimilarity in species composition, mediating the interaction between changes in substrate and the Hemiptera community. These results de-emphasize the importance of speciation for community structure of canopy Hemiptera, likely due to a lack of dispersal limitation, and suggest that common species shared across the chronosequence sketch the broad outlines of community structure while shifts in abundance and evenness, as a result of productivity and variation in the species pool, color in the details.

Chapter 3 : Multiscale analysis of canopy arthropod diversity in a volcanically fragmented landscape

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Abstract

Habitat fragmentation resulting in habitat loss and increased isolation is a dominant driver of global species declines. Habitat isolation and connectivity vary across scales, and understanding how connectivity affects biodiversity can be challenging because the relevant scale depends on the taxa involved. A multiscale analysis can provide insight in biodiversity patterns across spatial scale when information on dispersal ability is not available, in particular for community-level studies focusing on multiple taxa. In this study, we examine the relationship between arthropod diversity, patch area, and connectivity using a multiscale approach. We make use of a natural experiment on Hawaiʻi Island, where historic volcanic activity has transformed contiguous native forests to lava matrix and discrete forest patches. This landscape of patches has persisted for 150 years, and we selected 10,000 ha consisting of 863 patches to analyze landscape connectivity using a graph theory approach. We collected arthropod samples from *Metrosideros polymorpha* tree canopies in 34 forest patches during multiple years. We analyzed the relationship of arthropod diversity with area, as well as with connectivity across increasing scales, or dispersal threshold distances. In contrast to well-established ecological theory as well as prior work on birds and fungi in this system, we did not find support for a canonical species–area relationship. Next, we calculated connectivity across spatial scales and found lower Shannon diversity with higher connectivity at small scales, but no effect at increased dispersal threshold distances. We examined the landscape structure and found all habitat patches connected into three subnetworks at a 350 m threshold distance. All patches were connected at 700 m threshold distance, indicating structural dispersal limitation only at small scales. Our findings suggest that canopy arthropods are not dispersal limited at scales shown to impact both soil fungi and birds in this system. Instead, Hawaiian canopy arthropods may perceive the landscape as a connected area where discrete forest patches and the early-successional matrix contribute resources that vary spatially with regard to habitat quality. We argue for the utility of multiscale approaches, and the importance of examining maintenance of biodiversity in fragmented landscapes that persist for hundreds of years.

Keywords: *biodiversity; canopy arthropods; connectivity; fragmented landscapes; graph theory; Hawai‘i;* Metrosideros polymorpha*; patch isolation; spatial scale; species area relationship*

Introduction

Change in land use is a leading driver of declining biodiversity worldwide, and most species now occur in fragmented landscapes of degraded habitat (Pereira et al.

2010, Haddad et al. 2015). Fragmented landscapes are widespread, for example 70% of all forests globally are within one km of a forest edge, and nearly 20% are within 100 m of an edge (Haddad et al. 2015). Habitat fragmentation generally occurs in conjunction with habitat loss, and it has been difficult to quantify the contribution of loss of area relative to changes in spatial configuration of patches, patch shape and isolation. Reductions in area result in a decline in biodiversity, for example because smaller patches have fewer resources, smaller populations, lower genetic diversity and likely attract fewer new colonizing species (Simberloff and Wilson 1969, Simberloff 1976, Gibb and Hochuli 2002, Steffan-Dewenter et al. 2002). While negative effects of habitat loss on biodiversity are widely supported (Curtis 1956, Preston 1962, Watling and Donnelly 2006, Didham et al. 2012), the effects of fragmentation independent of area are less clear (Tscharntke et al. 2002, Haddad et al. 2017b, 2017a). Habitat fragmentation was long considered unimportant in comparison to the effects of loss of area (Fahrig 2003), but recent reviews on this subject have reopened this question and led to vigorous debate (Fahrig 2017, Fletcher et al. 2018, Fahrig et al. 2019). Researchers disagree on appropriate definitions, whether studies should take place at landscape or patch scale, and how fragmentation should be quantified, and consensus has not yet emerged (Tscharntke et al. 2002, Fahrig 2003, 2017, Haddad et al. 2017b, 2017a, Fletcher et al. 2018, Fahrig et al. 2019).

Habitat fragmentation can affect diversity by reducing landscape connectivity, or the degree to which the landscape facilitates or impedes movement among resource patches (Taylor et al. 1993). A decrease in landscape connectivity can reduce movement between patches (Collinge 2000), increasing extinction rates (Rybicki and Hanski 2013), reducing recolonization rates (Simberloff and Wilson 1969, Berggren et al. 2001), and decreasing species persistence (Ferraz et al. 2003, Orrock and Watling 2010). However, the prevalence and magnitude of these effects depends on the spatial scale in question as well as species' characteristics (Tischendorf and Fahrig 2000).

Alongside the landscape's physical attributes, including structural connectivity, functional connectivity of the landscape depends on the behavioral response of organisms to the landscape structure. Discrete habitat patches may still be connected for species that disperse over the intervening distances, whereas species that operate on smaller scales and disperse below inter-patch distances will be isolated on individual patches. Thus, life history and behavioral characteristics, such as species movement ability, foraging patterns, and seed dispersal syndromes influence the spatial scale at which a species interacts with the landscape (Henle et al. 2004, Umetsu et al. 2008, Jones et al. 2015). Despite its importance, dispersal ability is often an unknown parameter that is difficult to measure directly for many species. In such cases, community patterns can be examined by analyzing connectivity as a function of increasing spatial scale.

Graph theory approaches are well suited to such multi-scale analyses because they allow integrated interpretation of patch-level, class- and landscape-level connectivity across an array of potential dispersal distances (Keitt et al. 1997, Tischendorf and Fahrig 2000, Calabrese and Fagan 2004). While recent debate on the effects of fragmentation on biodiversity focuses strongly on the relative value of patch versus landscape scale studies (Fahrig 2017, Fletcher et al. 2018, Fahrig et al. 2019), multiscale graph theory allows for specifically incorporating the contribution of spatial scale in comparing connectivity between habitat fragments. Graph theory approaches connectivity by creating a spatially explicit depiction of the landscape (the graph) with individual patches existing as nodes and edges among them representing possible movement (Keitt et al. 1997). Metrics are calculated that summarize spatial relationships among nodes and allows overall landscape connectivity and the contribution of particular nodes to be quantified. Graph theory metrics can incorporate proximity, number and size of neighbors, and their centrality to the bigger network across a defined set of threshold distances. These variables can provide information on the role of connectivity in maintaining biodiversity, given the differences in scale across which organisms may operate.

Here, we present a multiscale graph analysis of habitat connectivity and biodiversity, combining landscape scale remote sensing data with local sampling of arthropod communities. We utilize a patchy landscape of mature forest and primary successional volcanic substrate on Hawai‘i island, where historic volcanic activity and two resulting lava flows in 1852 and 1881 have created a model fragmentation system of natural replicate forest patches, called kīpuka, that vary widely in size, shape and isolation. The acute effects of this historic disturbance event have long since stabilized, and we can examine the role of area and connectivity among kīpuka independent of the habitat loss process. In particular, using a historically fragmented system allows us to avoid erroneous conclusions due to delayed effects of fragmentation on biodiversity over time and extinction debt (Tilman et al. 1994, Ewers and Didham 2006, Fletcher et al. 2018). The relatively homogeneous matrix surrounding kīpuka eliminates the need to incorporate the well-known effects of differential landscape resistance (Ricketts 2001, Kennedy et al. 2010) into our analyses. Prior work in the kīpuka landscape has demonstrated a canonical log-log species area relationship for forest birds (Flaspohler et al. 2010), as well as correlations between kīpuka area, connectivity, and soil fungal diversity and composition (Vannette et al. 2016). However, we examine the effects of connectivity and area on canopy arthropods because these have very different life histories from the previously discussed taxa, including variation in dispersal ability, such as winged and unwinged species. We examine the role of area as well as connectivity between kīpuka in this model fragmentation study system to address the following questions with regards to canopy arthropods: (1) Does arthropod species richness increase with habitat kīpuka area? (2) How do the importance of connectivity and kīpuka area as predictors of arthropod diversity vary across spatial scale? (3) How does connectivity among discrete forest patches vary across spatial scale?

Methods

Study site

The study landscape was located on the northeast flank of Mauna Loa in the Upper Waiakea Forest Reserve on Hawaiʻi Island (19°38–410 N, 155°20–230 W). Two historic lava flows (c. 1852 and 1881) converted relatively continuous native wet forest dominated by *Metrosideros polymorpha* Gaudich. (Myrtaceae) into a series of remnant patches (Fig. 1; Wolfe and Morris 1996). The forest remnants left intact (termed kīpuka) are separated by a matrix consisting of ‘a’ā and pāhoehoe basalt substrates (Harris et al. 2017). The matrix, in early primary succession, differs strongly from the 3000-to5000-yr-old kipuka forest with respect to microclimate and soil and vegetation composition (Carson and Clague 1995, Vandergast and Gillespie 2004) and is relatively consistent across the landscape. Matrix vegetation is predominately <2 m in height and characterized by shrubs such as *Vaccinium reticulatum* Sm. (Ericaceae), *Leptecophylla tameiameiae* Cham. & Schltdl. (Ericaceae), and scattered small-statured *M. polymorpha* trees. The native kīpuka forest is dominated in the overstory by *M. polymorpha* with a subcanopy of, among others, *Cibotium glaucum* Sm. (Cibotiaceae) and *Cheirodendron trigynum* Gaudich. (Araliaceae; Gruner 2004, Flaspohler et al. 2010).

We chose a 10,000-ha landscape for our analyses and used kīpuka boundaries determined by Vaughn et al. (2014). We selected focal kīpuka across the landscape to span the variation in size (0.1–10.2 ha) and relative isolation (Figure 3.1). We chose focal *M. polymorpha* trees that represented the modal size and forest canopy tree architecture. Within each kīpuka, we chose the representative canopy tree nearest the GPS point of the kīpuka centroid. For all kīpuka larger than 0.2 ha (n = 24), we selected a second tree by following a random compass bearing to within 10 m of the kīpuka edge and choosing the closest representative canopy tree. For each focal tree, we recorded tree height to the nearest meter using a clinometer and tape measure.

Arthropod sampling details

We sampled arthropods from the canopies of focal *Metrosideros polymorpha* trees within the kīpuka. In 2009, we sampled from interior (n = 32) and edge (n = 24) trees in 32 kīpuka. In 2010, we selected a subset of the previously sampled kīpuka, ensuring subset spanned both the range of kīpuka area and the full spatial extent of the study region. The 2010 kīpuka were sampled from both interior (n = 16) and edge (n = 10) trees. There was no difference in mean area between kīpuka that were included vs. excluded in 2010 ($\text{mean}_{\text{overall}} = 1.88$, $\text{mean}_{\text{included}} = 2.23$, $\text{mean}_{\text{excluded}} = 1.19$, $t = 1.143$, $P > 0.1$).

Arthropods were collected by branch clipping and bagging samples from focal trees from July to August each year, following the methods in Gruner (2004). We took composite samples consisting of 4–6 upper-canopy terminal branches, containing ~0.25 m3 of foliage, for each focal tree. We sampled branches with a custom pole-pruner and net to catch clipped branches. When necessary, we accessed the canopy using the single- rope climbing technique (Perry 1978). All branch clips were collected directly into doubled 13- gallon, white polyethylene trash bags, which were sealed and stored in a shaded location to prevent arthropod escape and limit mortality before transport to the USDA Forest Service's Institute of Pacific Island Forestry in Hilo, HI, for processing on the same day of collection.

Arthropods were extracted from each sample by shaking portions of foliage over a table lined with a white sheet and collecting dislodged arthropods in vials filled with 70% ethanol. We repeated this process until all foliage and the collection bag were thoroughly searched. To quantify sampling intensity across samples, we recorded the total dry mass of separated leaves and stems after drying to constant mass at 70°C. Arthropods were sorted, counted, and identified to taxonomic species or morphospecies. A full list of collected arthropods can be found in Appendix S2. We

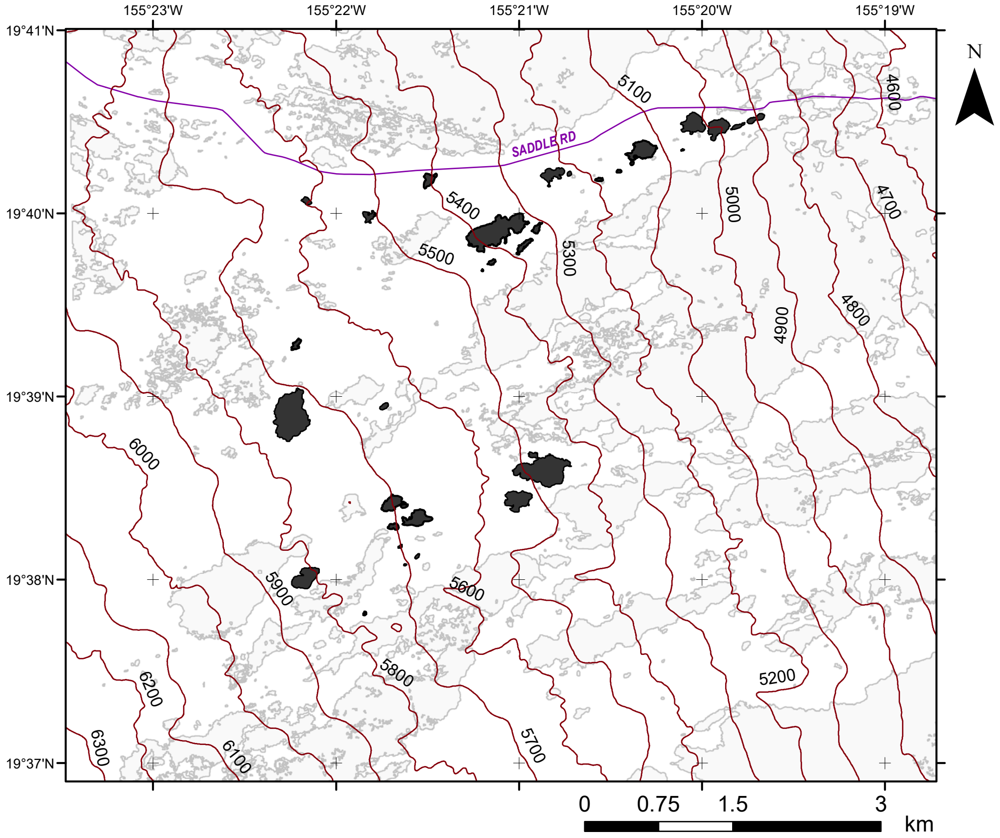

Figure 3.1: Topographic map of the kīpuka landscape with forest fragments in gray, matrix in white, and forest fragments where arthropods were sampled in black. Elevation bands are included and labeled in feet. Map boundaries based on LiDAR remote sensing methods (Vaughn et al. 2014).

measured specimen body length with an ocular micrometer to the nearest millimeter size class. We then estimated biomass using taxon-specific regression equations developed from species in this study system (Gruner 2003).

Diversity and species-area relationship

We examined the relationship of diversity to kīpuka area for the 34 sampled kīpuka. We assessed arthropod diversity using three measures of Hill or effective species numbers (Hill 1973, Jost 2006): estimated asymptotic species richness using the nonparametric function ChaoRichness(), estimated asymptotic Shannon index using function ChaoShannon(), and estimated asymptotic Simpson index using function ChaoSimpson() (Chao et al. 2014), in the package iNEXT in R (Hsieh et al. 2016). These measures estimate the species richness curve asymptote as a measure of richness to compare across incompletely sampled assemblages (Chao et al. 2014). Species rarefaction curves were assessed before proceeding with extrapolated diversity values (Appendix S 3: Figure S3.1). We converted these diversity metrics to effective species numbers (Hill numbers for $q = 0$, $q = 1$and $q = 2$).We assessed Pielou’s evenness by dividing raw Shannon diversity by species number, using package vegan in R (Oksanen et al. 2018). We also estimated species density as the species count per unit plant mass, defined as load (Root 1973). We tested the hypothesis that area was correlated with various diversity indices and species density using linear mixed models with a fixed effect for kīpuka identity and an offset for foliage mass, and using log likelihood ratio tests, using package lmer. We compared species composition between edge and center trees using a PERMANOVA in the package vegan in R.

Graph theory

We used ArcGIS 10.1 to project the GIS layer of the 10,000-ha kīpuka landscape into PCS Universal Transverse Mercator Zone 5 to calculate patch area and select all kīpuka larger than 0.01 ha containing mature native forest as nodes (ESRI 2012). Pairwise distances among nodes were calculated from spherical weighted centroids using the Conefor Inputs extension for ArcGIS (Saura and Torné 2009). We calculated graph theoretic metrics (described below and in Table 3.1) at threshold distances at 50-m increments from 50 to 5500 m to provide a comprehensive description of the landscape and of each node. Nodes were considered connected by edges when they were within a chosen threshold distance. These edges signify ecological flux or potential dispersal of organisms between patches (Urban and Keitt 2001), and we considered all habitat patches within a subnetwork of nodes connected by edges (together known as a component) available to organisms capable of dispersing that distance. We specifically looked for threshold distances at which the metric changed dramatically, indicating the landscape was rapidly shifting from unconnected to connected coincident with varying dispersal capacity. All landscape-level metrics were quantified across the range of threshold distances mentioned above using the command line version of Conefor Sensinode V.2.6 (Saura and Torné 2009).We used custom Perl scripts to generate the commands for each Conefor run and custom R scripts to process the resulting data files.

First, we quantified the number of subnetworks in the landscape (number of components, NC) and connections among nodes (number of links, NL). To provide comprehensive connectivity measures, we used habitat availability (reachability) metrics based on the integral index of connectivity (IIC; Pascual-Hortal and Saura 2006, Saura and Rubio 2010). Integral index of connectivity describes landscape connectivity by weighing patch area and number of links between all pairs of patches in a landscape for a given dispersal distance (Pascual-Hortal and Saura 2006, Neel et al. 2014). It increases monotonically with area and proximity across the entire fragmentation gradient and thus is easy to interpret. Because it is a binary metric (the landscape is either connected or not connected at a given distance), it emphasizes threshold distances at which network connectivity changes dramatically (Pascual-Hortal and Saura 2006, Saura and Rubio 2010, Neel et al. 2014). We chose IIC because metrics that include area within a threshold distance are more accurate at estimating movement (Moilanen and Nieminen 2002, Bender et al. 2003) and immigration (Bender et al. 2003) of animals between patches than purely distance-based metrics such as nearest-neighbor distances. We used EC(IIC), a formulation of IIC that gives the area of one continuous patch that would yield the same value of IIC as the observed, fragmented IIC (Pascual-Hortal and Saura 2006).

To examine individual node importance for overall landscape connectivity, we calculated the percentage change in the value of NC, NL, and IIC before and after removal of each node (denoted as dNC, dNL, and dIIC). The larger the percentage change from the full network when a node is removed, the greater the contribution of that node to overall network connectivity. Integral index of connectivity is of particular interest because it also takes into account the existence of alternative paths when evaluating the effect of patch removal. Further, IIC can be partitioned into three independent portions: IICintra, representing the contribution of habitat within a patch;

IICflux, the portion of connectivity for pairs of patches where the focal patch is a potential source or destination; and IICconnector, quantifying the degree to which a patch connects other patches, or functions as stepping-stone in the landscape (Bodin and Saura 2010, Saura and Rubio 2010, Neel et al. 2014). IICconnector is based on the area of the patches being connected and number of links needed to connect them but is independent of focal patch area. This metric is sensitive to landscape configuration and the location of the patch in the larger landscape. Because these dIIC metrics are additive, the sum of values across all patches gives insight into the sensitivity to losses of patches and thus quantifies how robust or fragile the network is in terms of different aspects of connectivity. The three dIIC metrics provide a comprehensive and non-redundant view of the changes in different aspects of patch contributions to connectivity patches as measured by the consequence of their loss.

Relating arthropod communities to graph networks

To examine the relationship between our predictors and arthropod diversity, abundance, and species density, we modeled diversity measures using mixed-effect models and a model-averaging approach. We used generalized linear mixed models with Shannon diversity, abundance and species density as response variables and connectivity and area as fixed effects, kīpuka identifier as random effect, and log foliage mass as offset for sampling effort. We included the following predictors: kīpuka area, sampled tree height, change in number of components (dNC), change in the flux portion of integral index of connectivity (dIICflux), and change in the connector portion of integral index of connectivity (dIICconnector). We included tree height to explore the possibility that hyperlocalized area— approximated by focal tree

Table 3.1: Connectivity metrics used to analyze the kīpuka landscape as a whole and connectivity values for individual patches.

Type	Metric	Abbrev.	Definition	Literature
Landscape	Number of edges	NL	Total number of edges (i.e. connections between patches) in the landscape.	
	Number of components	NC	Total number of components (i.e. subnetworks) in the landscape.	
	Integral index of connectivity	IIC	The possibility of dispersal between different pairs of patches, as a function of patch area and overall landscape size. Quantifies the possibility that two points in the landscape are connected- either because they are in the same patch or in different patches that are connected. Dispersal is binary; ie patches are either connected or not. The numerator of the equation calculating IIC measures habitat amount and possibility of connection, without taking into account overall landscape area.	(Pascual-Hortal and Saura 2006)
	Equivalent connected area of integral index of connectivity	EC(IIC)	The area of a single patch of habitat that would yield the same IIC value as is seen in the observed landscape.	(Pascual-Hortal and Saura 2006)
	Change in integral index of connectivity	dIIC	The sum of IIC across all patches when one patch is removed. Quantifies how much connectivity is prone to decrease if changes in the landscape occur.	(Pascual-Hortal and Saura 2006)
Node	Change in number of edges	dNL	Change in number of edges in the landscape when patch k is removed.	
	Change in Number of components	dNC	Change in number of components in the landscape when patch k is removed.	
	Change in Integral index of connectivity	dIIC	Change in integral index of connectivity, i.e. change in overall habitat reachability in the landscape when patch k is removed.	(Pascual-Hortal and Saura 2006)
	Intra portion of change in integral index of connectivity	dIICintra	Contribution of habitat area within a patch to the change in integral index of connectivity when patch k is removed.	(Bodin and Saura 2010, Saura and Rubio 2010)
	Connector portion of change in integral index of connectivity	dIICconnector	Contribution of the degree to which a patch connects other patches to the change in integral index of connectivity. Calculated based on the area of patches connected and the	(Bodin and Saura 2010, Saura and Rubio 2010)

		number of links needed to connect them.	
Flux portion of change in integral index of connectivity	dIICflux	Flux contribution to the change in integral index of connectivity. Calculates the connectivity for pairs of patches where the focal patch is either a source or destination.	(Bodin and Saura 2010, Saura and Rubio 2010)

maximum height—is a more relevant measure of habitat size. Tree height has previously been shown to be linearly related to canopy volume in kīpuka (Flaspohler et al. 2010). Correlation coefficients for connectivity metrics included in the model analysis were ≤ 0.3. We used the same predictors for mixed models explaining species density but excluded the offset.

All explanatory variables were centered and standardized to z values before use in models. We used the function dredge in the R package MuMIn to come to the best model (Bartoń 2018), and for global models without a model of clear best fit (ΔAICc > 4), we used model averaging. We calculated variable estimates, confidence intervals (CIs), and relative importance for the averaged model using the package lmer (Appendix S1; Bates et al. 2015). Coefficient of determination was based on corrected R^2 using the function r.squaredGLMM in package lmerTest.

Results

Arthropod community description

We sampled 21,365 individuals for this analysis, across four different classes (Arachnida, Insecta, Diplopoda, and Malacostraca), 15 orders, and 106 species and morphospecies. Species richness in samples ranged from 11 to 33 species, with median richness of 22 species. Overall mean species richness was slightly higher in samples collected in 2010 than in 2009 (< 1 standard deviation), but per kīpuka richness was similar. Pielou's evenness across samples was high with a mean of 0.84 for samples taken in 2009 and 0.87 for samples from 2010. Kīpuka edge and interior trees did not differ with respect to arthropod community composition (PERMANOVA pseudo-F = 0.9727, $P > 0.05$).

Species-area relationship

Kīpuka Shannon diversity did not correlate with kīpuka habitat area (Hill q = 1; likelihood ratio: $\chi^2 = 1.8919$, estimate = 0.2246, 2.5% CI = 0.09745, 97.5% CI = 0.2661, $P > 0.01$; Figure 3.2). Other diversity measures showed similar patterns (effective species richness and Simpson diversity; Appendix S 3: Table S 3.1). In contrast to Shannon diversity, species density did slightly increase with kīpuka area (likelihood ratio: $\chi^2 = 6.7003$, estimate = 0.1573, 2.5% CI 0.04394, 97.5% 0.2661, $P < 0.05$; Appendix S 3: Figure S 3.2).

Arthropod richness, abundance and biomass across spatial scales

Significant predictors of arthropod diversity and abundance varied across spatial scales (Figure 3.3, Tables 3.2, 3.3). Although connectivity in the land- scape increased with dispersal threshold until 750 m, the subset of kīpuka where we sampled arthropods were connected in a single component at 350 m. As a result, connectivity metrics for sampled kīpuka did not vary above 350 m threshold distance and are not included here.

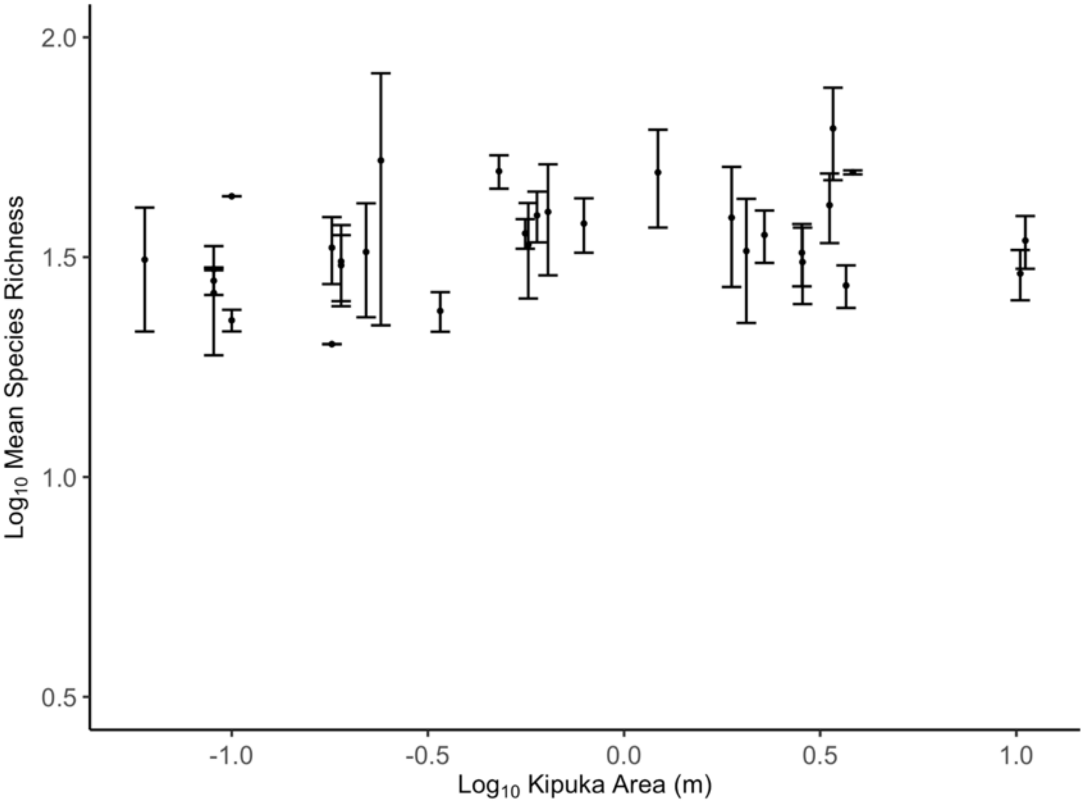

Figure 3.2: Log$_{10}$ mean species richness as a function of log$_{10}$ kīpuka area (m). Mean kīpuka species richness is based on center and edge trees sampled in 2009 and 2010. Error bars indicate standard error of the mean.

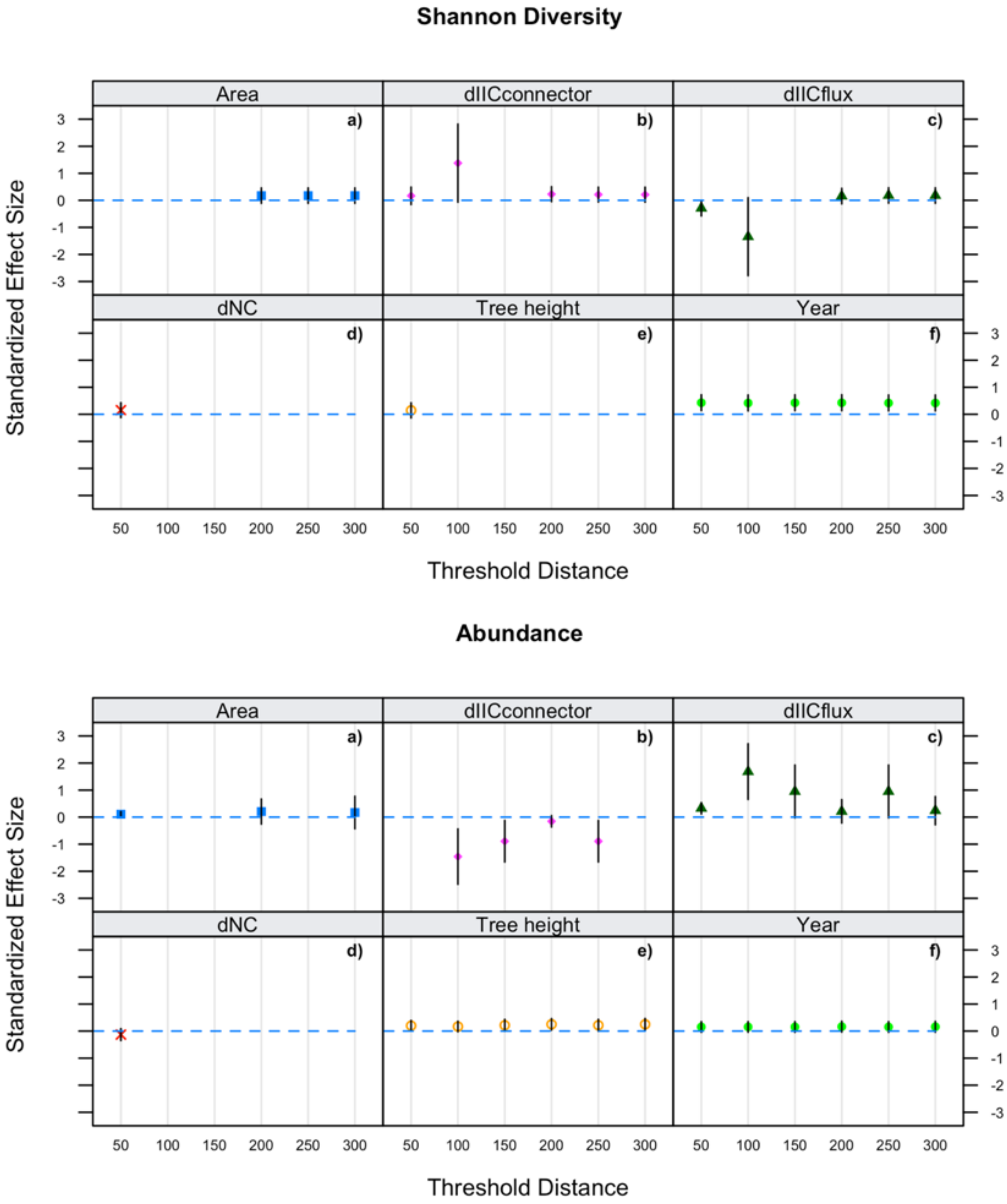

Figure 3.3: Effect sizes for the relationship between connectivity and effective Shannon diversity (top) and abundance (bottom) across threshold distances. Effect sizes are standardized to z values (mean and variance) of data. Panels show (a) area, (b) connector portion of integral index of connectivity after patch removal, (c) flux portion of integral index of connectivity after patch removal, (d) change in number of components, (e) tree height, and (f) year.

Table 3.2: Model coefficients of response variables included in averaged model explaining effective estimated Shannon diversity (Hill 1).

Shannon Diversity

Distance	Year	Area	Tree height	dIICconnector	dIICflux	dNC
50	0.4289 ± 0.1471 **	-	0.1463 ± 0.1416	0.1681 ± 0.1620	-0.2886 ± 0.1445 *	0.1550 ± 0.1388
100	0.4190 ± 0.1484 **	-	-	1.376 ± 0.7250	-1.343 ± 0.7239	-
150	0.4267 ± 0.1477 **	-	-	-	-	-
200	0.4279 ± 0.1490 **	0.1745 ± 0.1438	-	0.2289 ± 0.1391	0.1570 ± 0.1452	-
250	0.4191 ± 0.1482 **	0.1745 ± 0.1438	-	0.2138 ± 0.1380	0.1802 ± 0.1440	-
300	0.4190 ± 0.1482 **	0.1745 ± 0.1438	-	0.2115 ± 0.1441	0.1774 ± 0.1441	-

Notes: Values represent averaged standardized model estimates and standard errors (unitless). We used linear mixed effect models, averaging all models for which $\Delta AICc < 4$. Variables not included in best models are indicated by -. Estimates, standard errors, confidence intervals and importance of the variable in the averaged model can be found in Appendix. * $P < 0.05$, ** $P < 0.01$

Table 3.3: Model coefficients of response variables included in averaged model for abundance.

Arthropod Abundance

Distance	Year	Area	Tree height	dIICconnector	dIICflux	dNC
50	0.1543 ± 0.09861	0.1082 ± 0.0476*	0.1999 ± 0.0975 *	-	0.3287 ± 0.1044 **	-
100	0.1554 ± 0.09914	-	0.1699 ± 0.0985	-1.458 ± 0.5144 **	1.685 ± 0.5175 **	-
150	0.1544± 0.09959	-	0.2160 ± 0.1117	-0.8906 ± 0.3854*	0.9502 ± 0.4646	-
200	0.1652 ± 0.1015	0.2072 ± 0.2329	0.2520 ± 0.1076 *	-0.1517 ± 0.1064	0.2157 ± 0.2169	-
250	0.1544 ± 0.09959	-	0.2160 ± 0.1117	-0.8906 ± 0.3854*	0.9502 ± 0.4946	-
300	0.1611 ± 0.1016	0.1723 ± 0.3026	0.2513 ± 0.1088 *	-	0.2417 ± 0.2621	-

Notes: Values represent averaged standardized model estimates and standard errors (unitless). We used linear mixed effect models, averaging all models for which $\Delta AICc < 4$. Variables not included in best models are indicated by -. Estimates, standard errors, confidence intervals and importance of the variable in the averaged model can be found in the Appendix. * $P < 0.05$, ** $P < 0.01$

With increasing dispersal threshold, the importance of connectivity as explanatory variable for Shannon diversity decreased (Figure 3.3, Table 3.2). While dIICflux was negatively correlated with Shannon diversity at 50 m dispersal thresholds, above 50 m this relationship no longer occurred (Fig. 3.3). Partitioning dIIC into intra, connector, and flux portions indicated that this relationship primarily results from changes in dIICflux, which quantifies the role of a patch as source or destination and weighs patch area as well as the number of edges between them (Table 1, Figure 3.3). Besides dIICflux, the averaged model explaining Shannon index at 50 m included sampling year as significant predictor (year, 0.4289 ± 0.1471, $P < 0.05$; dIICflux 0.2886 ± 0.1445, $P < 0.05$; Table 3.2). Above 50 m threshold distance, only sampling year was a significant predictor (at 100 m, year 0.4190 ± 0.1484, $P < 0.01$; at 150 m, year 0.4267 ± 0.1477, $P < 0.01$; at 200 m, year 0.4279 ± 0.1490, $P < 0.01$; at 250 m, year 0.4279 ± 0.1490, $P < 0.01$; at 250 m, year 0.4191 ± 0.1482, $P < 0.01$; at 300 m, year 0.4190 ± 0.1482, $P < 0.01$; Figure 3.3, Table 3.2).

Landscape graph description

The landscape consisted of 863 kīpuka in 10,000 ha. The kīpuka size distribution ranged from 0.01 to 1011 ha, and median kīpuka size was 0.07 ha. The distribution of pairwise distances between kīpuka was relatively uniform as a result of the high patch number in the land- scape. Interpatch distances range from 9.90 to 12172 m with a median of 4982 m.

At 350 m dispersal threshold, the landscape consisted of three components (i.e., three subnetworks with all nodes connected to at least one other node; Figure 3.4).

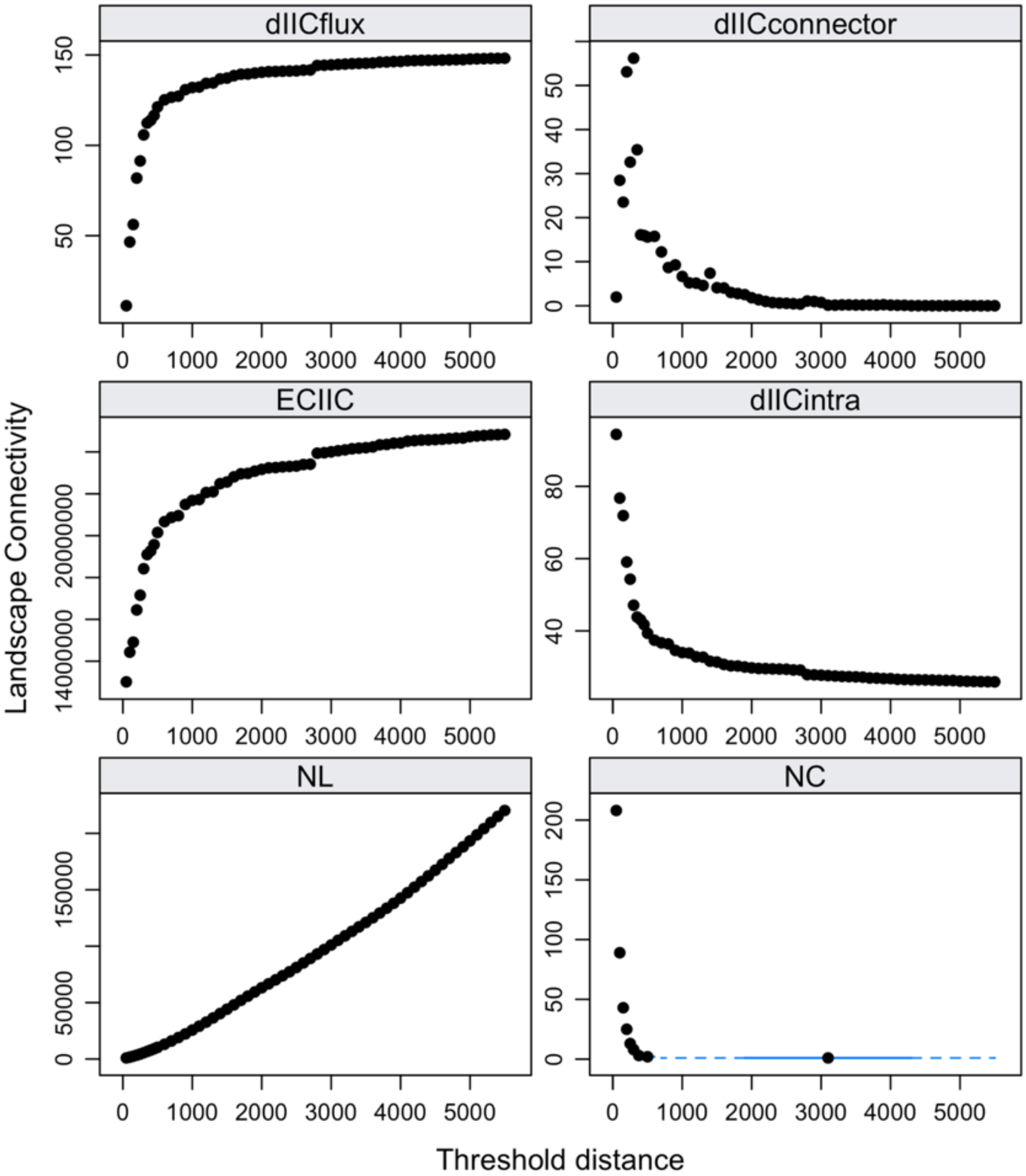

Figure 3.4: Landscape connectivity as a function of dispersal threshold. Panels show (a) change in flux portion of the integral index of connectivity, (b) change in connector portion of the integral index of connectivity, (c) change in equivalent area of the integral index of connectivity, or the amount of connected habitat necessary to provide the same amount of connectivity as a given IIC, (d) change in intra portion of the integral index of connectivity, (e) change in number of links in the landscape, and (f) change in number of components in the landscape.

At dispersal threshold distances ≥ 350 m dispersal distance, the graph was highly interconnected with many redundant paths connecting nodes, suggesting decreasing importance of any single node for overall connectivity. At a threshold of 700 m, the landscape was connected in a single component. Number of links among kīpuka increased linearly with threshold distance (Figure 3.4). EC(IIC), which represents the size of a single contiguous patch that would have a given IIC value, increased with threshold distance, indicating increasing habitat availability (Figure 3.4). When the landscape was completely disconnected, EC(IIC) was 1301.19 ha, increasing to 2086.96 ha at the lowest threshold at which all patches were uni- ted in one component (700 m). Maximum EC(IIC) was found at 5500 m when all kīpuka were directly connected to one another. With increasing threshold distance, dispersal limitation was reduced, resulting in a decrease in dIICintra while an increasing proportion of connectivity was contributed by movement among kīpuka: dIICflux. dIICconnector peaked when distance was below 350 m, and then decreased as the number of redundant pathways among kīpuka increased, and consequently, the importance of individual kīpuka as stepping-stones decreased (Figure 3.4).

Discussion

Although the species–area relationship is often regarded as a general law in ecology (McGuinness 1984, Rosenzweig 1995, Drakare et al. 2006) and has been supported for other taxa in the kīpuka landscape (Vandergast and Gillespie 2004, Vandergast et al. 2004, Flaspohler et al. 2010, Mueller 2015, Vannette et al. 2016), we did not find a correlation between canopy arthropod richness and kīpuka area. Furthermore, patch connectivity did not correlate strongly with observed diversity.

Lastly, we found that small expansions in dispersal threshold rapidly increase landscape connectivity. Together, these results suggest that the kipuka landscape is both structurally and functionally connected for canopy arthropods. This landscape-level diversity pattern results from three interacting variables: the nature of the matrix, Hawaiian canopy arthropod dispersal ability, and structural connectivity in the kīpuka landscape.

One explanation for the lack of species–area relationship is that the matrix may not serve as a barrier to dispersal. The kīpuka and the matrix differ both in structure and in microhabitat (Vandergast and Gillespie 2004, Flaspohler et al. 2010), but small-statured *M. polymorpha* (shrubs < 3 m) occur across the matrix. Functional connectivity is higher in landscapes where vegetation structure or microclimate is similar for the matrix and the habitat (Ricketts 2001, Prevedello and Vieira 2010, Eycott et al. 2012, Öckinger et al. 2012). Second, matrix landscapes often act as sinks or even sources of organisms (Haynes et al. 2007, Schmidt et al. 2008, Umetsu et al. 2008). *M. polymorpha* trees occurring in the matrix supported higher abundances of arthropods than trees in the kīpuka, but with strong differences in community composition (unpublished data). We conclude that canopy arthropods do differentiate between the two habitats, but we hypothesize that contrary to other kīpuka-dwelling taxa and our assumptions (Flaspohler et al. 2010, Mueller 2015, Vannette et al. 2016, Knowlton et al. 2017), canopy arthropods do not experience the matrix as strongly hostile. Although we cannot determine conclusively without measuring dispersal, our results suggest that the matrix is permeable and there is a high degree of movement across the landscape.

Dispersal ability and life history characteristics determine how organisms perceive and interact with landscape patchiness and may explain differences in species–area relationship between our work and many other studies in fragmented landscapes (Rosenzweig 1995, Holt et al. 1999, Cagnolo et al. 2009, Phillips et al. 2017), including other taxa in the same kīpuka system. For example, species richness increases with area for root fungi associated with *M. polymorpha* (Vannette et al. 2016), for Drosophila flies (Mueller 2015), and for birds, particularly non-native species (Flaspohler et al. 2010). Additionally, gene flow is limited between understory Tetragnatha spider populations in the kīpuka (Vandergast and Gillespie 2004, Vandergast et al. 2004). Also, fungal communities (Vannette et al. 2016) and understory spiders (Vandergast and Gillespie 2004, Vandergast et al. 2004) in more connected patches are more similar to one another in species composition, indicating possible dispersal limitation. However, these taxa may have very different habitat use from canopy arthropods. Fungi may be dispersal-limited, particularly those with specialist resource or habitat requirements (Norros et al. 2012, Nielsen et al. 2016), and while Drosophila are active flyers, they do not make use of *M. polymorpha* (Mueller 2015) and may perceive the matrix to be more impermeable. Bird species, on the other hand, are highly dispersive (Knowlton et al. 2017) and select kīpuka for foraging, and will be sensitive to differences in conditions between kīpuka and the matrix. Our study combines a highly patchy landscape with taxa that are likely moderate dispersers, for which the matrix may be more permeable due to the ability of canopy arthropods associated with *M. polymorpha* to make short- term use of the matrix. For canopy arthropods, we found no evidence for variation in the species–area relationship across dispersal strategies or body size (Appendix S1: Table S2). This contrasts with expectations based on theory (Holt et al. 1999, Tscharntke and Brandl 2004, Jones et al. 2015, van Noordwijk et al. 2015) as well as prior findings in kīpuka fungal communities (Vannette et al. 2016). It is possible that canopy arthropods are sufficiently dispersive due to their relatively small size. For many Hawaiian canopy arthropods, wind is hypothesized to be the main mode of dispersal (Howarth 1987, 1990), and as a result, body size and dispersal ability do not affect their mobility between kīpuka.

The large number of patches and short distances among kīpuka result in a landscape that is structurally connected at small spatial scales. Connectivity among the kīpuka increases rapidly with threshold distance, as the number of components in the landscape decreases. The slope of the equivalent connected area of the integral index of connectivity is steep at low dispersal thresholds. At threshold distances larger than 350 m, the sampled kīpuka are all connected in a single network component. At this threshold distance, the network has many redundant connections, so individual kīpuka contribute little to overall landscape connectivity. Partitioning the integral index of connectivity supported this, where the dIIC portion quantifying the importance of nodes as stepping-stones connecting other nodes, dIICconnector, peaked at 350 m before rapidly declining, while connectivity provided by area within a node, dIICintra, decreased consistently with increasing dispersal threshold. Canopy arthropod diversity and abundance only correlates with connectivity for threshold distances ≤100 m. We conclude that the kīpuka landscape is functionally well connected for canopy arthropods, as dispersal in similar taxa commonly exceeds those distances (Hanski 1994, Denno et al. 1996, Eber 2004).

For canopy arthropods, the kīpuka landscape may be best understood as a heterogeneous landscape of varying resource quality, rather than a series of disconnected fragments. Variation in arthropod diversity across kipuka can be driven by differences in arthropod abundances as a result of resource availability or quality. Specifically, canopy arthropod communities are directly (for primary consumers) or indirectly (for higher trophic levels) dependent on tree or canopy size. Tree height roughly corresponds to canopy volume (Flaspohler et al. 2010) and is also positively correlated with foliar nitrogen content (D. Gruner, unpublished data). Fertilization of *M. polymorpha* trees in the matrix increases foliar biomass relative growth rate and arthropod density (Gruner 2004). Although tree height does not directly correlate with species richness, tree height may affect diversity by increasing arthro- pod abundance. By necessity, kīpuka with higher abundance of individuals have a higher likelihood of containing more species (Gotelli and Colwell 2001, Chase et al. 2018). If kīpuka size correlates with an increase in resource availability or quality, we would expect a higher species richness purely on the basis of number of individuals. Kīpuka species density significantly increases with tree height across all spatial scales, further supporting that variation in resource availability or quality drives differences in arthropod abundance and consequently species richness. These results highlight that diversity patterns can be strongly affected by numbers of individuals (Gotelli and Colwell 2001).

Arthropod diversity at small scales was negatively correlated with kīpuka connectivity. Although we did not examine the cause for this negative relationship, metacommunity theory predicts a unimodal relationship between dispersal frequency and diversity (Mouquet and Loreau 2003, Leibold et al. 2004). When patches are isolated, increasing connectivity will promote local coexistence and allow for rescue effects, resulting in higher alpha diversity, as well as variation across patches in species composition and increased beta diversity. However, at higher dispersal levels or in well-connected landscapes, dispersal can increase metacommunity homogenization, reduce coexistence, and decrease local diversity. Furthermore, beta diversity would also decrease as a result of increased homogenization. Experimental work on zooplankton has found that dispersal can enhance or reduce species coexistence in metacommunities (Forbes and Chase 2002, Cottenie et al. 2003). Similarly, work on pitcher plants has shown a negative relation- ship between dispersal and local diversity in pitcher plant inquilines (Kneitel and Chase 2004). In line with the literature, we found small-scale variation in the effect size between diversity and connectivity measures, and low arthropod alpha diversity in highly connected kīpuka.

Our study exemplifies how the landscape structure, through patch configuration and nature of the matrix, interacts with focal organism characteristics to produce patterns in biodiversity. We do not find support for a species–area relationship in canopy arthropods, suggesting that *Metrosideros polymorpha* canopy arthropods are not dispersal-limited, in contrast to other taxa in this kīpuka landscape. Movement between kīpuka patches is likely not restricted enough to structure the makeup of these communities of organisms that disperse readily, can make use of sporadic low-quality resources in the matrix, and can use small kīpuka as stepping-stones. As such, our findings highlight the importance of considering the landscape perception of focal organisms. We suggest that providing connectivity through high numbers of smaller, proximate patches can be a promising management strategy to conserve biodiversity in patchy landscapes, but that within systems with a broad range of taxa, the ecological outcome may vary depending on scale of the organism. Our results show that the relationship between connectivity and diversity varies across relatively small spatial scales, and emphasize the utility of multiscale landscape analyses when dispersal information is unavailable or difficult to acquire. By shedding light on how habitat availability and connectivity vary across scales, multiscale approaches help us better understand the varied empirical results when studying biodiversity in patchy landscapes.

Chapter 4 : Intraspecific variation in host plant traits determines taxonomic and functional composition of the local insect herbivore community

Abstract

Intraspecific variation in host plant phenotype has a strong effect on the structure of the associated consumer community. Distinct herbivore assemblages between host plants within the same population are often researched in relation to host genotypic variation, but species interactions are mediated through their phenotypic traits, However, a mechanistic understanding of the host characteristics that drive herbivore community response is lacking. I address this by modeling the relationship between host and insect traits using a multilevel model in a GLM framework.

I compare herbivore assemblages from the canopy of the phenotypically variable tree *Metrosideros polymorpha* in four forests on southeastern Hawaiʻi Island. Two varieties of *M. polymorpha* co-occur on young flows in this area, and regular hybridization results in a zone where different varieties and their hybrids occur alongside each other with large variation in morphological traits. I identify host and insect traits that underlie patterns of herbivore species abundance, and quantify the strength of host-insect trait interactions.

This work examines plant-insect interactions at a community scale, across a broad diversity of 36 herbivore species in three orders, comprising four feeding guilds. Results show that distinct herbivore communities are supported on co-occurring trees that vary in phenotype. Plant traits, including leaf water content, specific leaf area, trichome presence, leaf nitrogen and leaf phosphorus content, explain 46% of variation in insect communities, and glabrous, pubescent and hybrid morphotypes have distinct insect communities in two of the four forests examined. I detect insect traits that are correlated with host plant traits, in particular body size, feeding guild and nymphal life history, and find that model predictions are improved by including the interaction between insect traits and host traits.

This study demonstrates that insect herbivore phenotypic traits that mediate community response to morphologically variable hosts can isolate relevant host plant traits and test hypotheses about their importance across herbivore communities. Further, my results suggest that intraspecific variation in hosts due to environmental heterogeneity and gene flow can scale up to affect herbivore community structure and diversity.

Key words: *plant-insect interactions, biodiversity, Hemiptera, herbivory, functional traits, intraspecific variation, fourth corner, Hawaiian Islands*

Introduction

Community ecology has traditionally focused on differences between species, but in recent years there has been a growing awareness of the importance of intraspecific variation to a wide range of ecological processes, including population demography (Umaña et al. 2015), productivity (Cook-Patton et al 2011, Reiss and Drinkwater 2017), and multitrophic interactions (Bolnick et al. 2011). For plant-herbivore interactions, intraspecific variation within a host species provides variation in accessibility and quality of resources for insect herbivores, and can result in neighboring plants with widely diverging consumer communities (Agrawal 2005, Johnson and Agrawal 2005, Crutsinger et al. 2006, Johnson et al. 2006). Most studies examining intraspecific variation in host plants, however, focus on plant genotype and fail to quantify host plant phenotype (Hughes et al. 2008, Barbour et al. 2015). While host plant genotype can affect richness (Bangert et al. 2005, Hughes et al. 2008, Johnson 2008), abundance (Johnson and Agrawal 2005, Johnson 2008), behavior (Zerebecki et al. 2017) and structure (Johnson and Agrawal 2005) of consumer communities, host plants and herbivores affect one another through interaction of their phenotypes. Quantifying the host phenotype can provide information on what plant traits the herbivore community is responding to (Hersch-Green et al. 2011).

Host phenotype affects herbivore populations and communities through resource quality, leaf chemistry and structural defenses, habitat architectural diversity and variation in niche diversity (Martinsen and Whitham 1994, Stamp 2003, Reusch et al. 2005, Wimp et al. 2005, Johnson et al. 2006). Host phenotypes are shaped by genotype and environment, and the drivers underlying a specific set of traits are not always well understood. Plant allocation is limited by resource availability and many theories exist regarding plant allocation to defense (e.g. optimal defense theory; Feeny 1976), but plant traits can be adaptive for many purposes and are likely the result of a much more complex set of selection pressures. Research in recent years does not find support for either tradeoffs between traits or highly correlated 'defense syndromes' (Moles et al 2013). Instead, a variety of selection pressures operate.

Producing and maintaining defense traits against insect herbivory brings costs with it, but frequently primarily or in addition serve other functions. For example, leaf trichomes reflect light, which reduces light stress and photoinhibition in high UV environments (Jordan et al. 2005, Liakopoulos et al. 2006), trichomes increase water use efficiency by reducing boundary layer stomatal conductance (Amada et al. 2017), and maintain leaf temperature (Ehleringer and Mooney 1978, Pérez-Estrada et al. 2000). Other host plant traits with strong effects on herbivores include leaf nutrient quality, water content, and presence of spines or latex (Agrawal and Fishbein 2006, Hanley et al. 2007). Various selection pressures have shaped the current plant phenotype, resulting in the current interactions between the plant and the biotic and abiotic environment.

Herbivore response to plant phenotypic traits varies across insect species; for example, high trichome density on *Oenothera* (Onagraceae) increases aphid abundance (Johnson 2008), while density of chewing herbivores is negatively correlated with trichome presence on *Asclepius* (Apocynaceae) (Agrawal 2005). This can be related to differences in insect feeding strategy; while chewers often consume whole leaves and are exposed to toxins across the leaf material, sap-sucking insects can circumvent defense traits such as latex by selectively piercing tissue (Schoonhoven et al. 2005). Insect morphology can also play a role, for example in soapberry bugs where proboscis (mouthpart) length is adapted to their native host plant (Carroll and Boyd 1992). These examples suggest that both host plant traits as well as insect traits are important in the plant-herbivore interaction, and that insect responses can be categorized into 'suites' (Maddox and Boot 1990).

Environmental filtering is considered an important process structuring communities, where environmental conditions shape the distribution of species across habitats. Species traits can provide information on both *how* species differ in their response to environmental variables, as well as *why* (Legendre et al. 1997, Dray and Legendre 2008). In recent years, many different ways have been developed to use multilevel model-based approaches for this so-called "fourth corner" problem (i.e. Jamil et al. 2013, Brown et al. 2014, Dray et al. 2014, Warton et al. 2015), with ongoing debate on the merits and limitations of different types of model approaches (Peres-Neto et al. 2017, ter Braak et al. 2017, Löbel et al. 2018, Miller et al. 2018). Multilevel models allow analyses of community response to the environment (or host plant traits) by accounting for all species abundances, rather than examining species one at a time (Dray et al. 2014). As such, this approach can identify traits or variation in the host plant phenotype that are important drivers of species abundance, and quantify the strength of the interaction between host plant phenotype and herbivore community traits (Jamil et al. 2013, Renner and Warton 2013, Brown et al. 2014, Dray et al. 2014).

In this study, I examine herbivore communities across host plant phenotype, and quantify to what degree this relationship is mediated by their respective traits. I make use of a model system on Hawai‘i Island where the dominant endemic tree in mesic forests, *Metrosideros polymorpha* Gaud., exists across broad ecological breadth and displays a high degree of polymorphism. This provides an opportune system to examine host plant polymorphism and its relationship to herbivore communities. This work examines the effects of host phenotypic traits on phytophagous insect abundance and diversity (i); identifies *M. polymorpha* characteristics that are associated with arthropod community composition (ii); and explores the relationship between insect traits and host characteristics. I hypothesized that different *Metrosideros polymorpha* phenotypes are correlated to insect traits, and that increases in resource accessibility and quality would induce a shift in insect community composition from internal to external feeding and from sap sucking to leaf chewing species. To test my hypothesis, I used data collected across four hybrid zones on Hawaiʻi Island, where *M. polymorpha* trees of varying phenotype occur in sympatry. First, I compared insect communities across hosts with different levels of leaf trichomes. I examined host plant phenotype to identify plant traits that drive insect herbivore community composition. Lastly, I used a trait-modeling approach to quantify correlations between insect traits and host traits.

Methods

Study site

Mesic forests on Hawaiʻi are dominated by the native tree *Metrosideros polymorpha* Gaudich. (Myrtaceae). This phenotypically variable tree occurs across succession on all Hawaiian high islands (Stemmermann 1983, Dawson and Stemmermann 1999), from sea level to high-elevation tree line (Vitousek et al. 1992) and across rainfall gradients from 400-10.000 mm (Stemmermann and Ihsle 1993, Cordell et al. 1998). The range of environmental conditions under which *Metrosideros polymorpha* can grow is likely related to the broad morphological and physiological variation displayed in this species. Eight varieties are recognized, two of which dominate on mid-elevational young substrate on Hawaiʻi Island (Stacy et al. 2017). At low to middle elevations, newly created volcanic substrate is colonized by the early-successional variety *incana.* Over the course of succession and soil development, the late successional variety *glaberrima* becomes established, existing as a monodominant stand after 1400-3000 years (Drake and Mueller-Dombois 1993). This landscape of lava flows is dynamic and different substrate ages occur close together. Viable and fertile hybrids are frequently produced in areas where the ranges of these *Metrosideros polymorpha* varieties overlap and incipient radiation is likely (Stacy et al. 2014, 2017). The *glaberrima*, *incana* and hybrid varieties are ecologically and morphologically differentiated; var. *glaberrima* has a glabrous morphotype with large thin leaves and lacks trichomes; var. *incana* has a pubescent morphotype with small thick leaves and high trichome density; and hybrids between the two possess thick leaves and intermediate trichome density (Stacy et al. 2017). The phenotypic characters that distinguish these varieties have a genetic basis (Cordell et al. 1998), and these characters have been used to identify the varieties in the field and for previous studies (Gruner et al. 2005). There are some variable patterns in phenotypic variation across substrates, elevation, light availability and nutrient availability (Cordell et al. 1998, Morrison and Stacy 2014). I selected four focal sites on the west and southwest side of Hawaiʻi Island where multiple varieties and phenotypes co-occur (Figure 4.1) and hybrids occur (Stacy et al. 2017); in Hawaiʻi Volcanoes National Park (2 sites; Ola’a and Escape Road), in Kaʻū Kaiholena Forest Reserve (1 site) and Kau Alili Springs Forest Reserve (1 site).

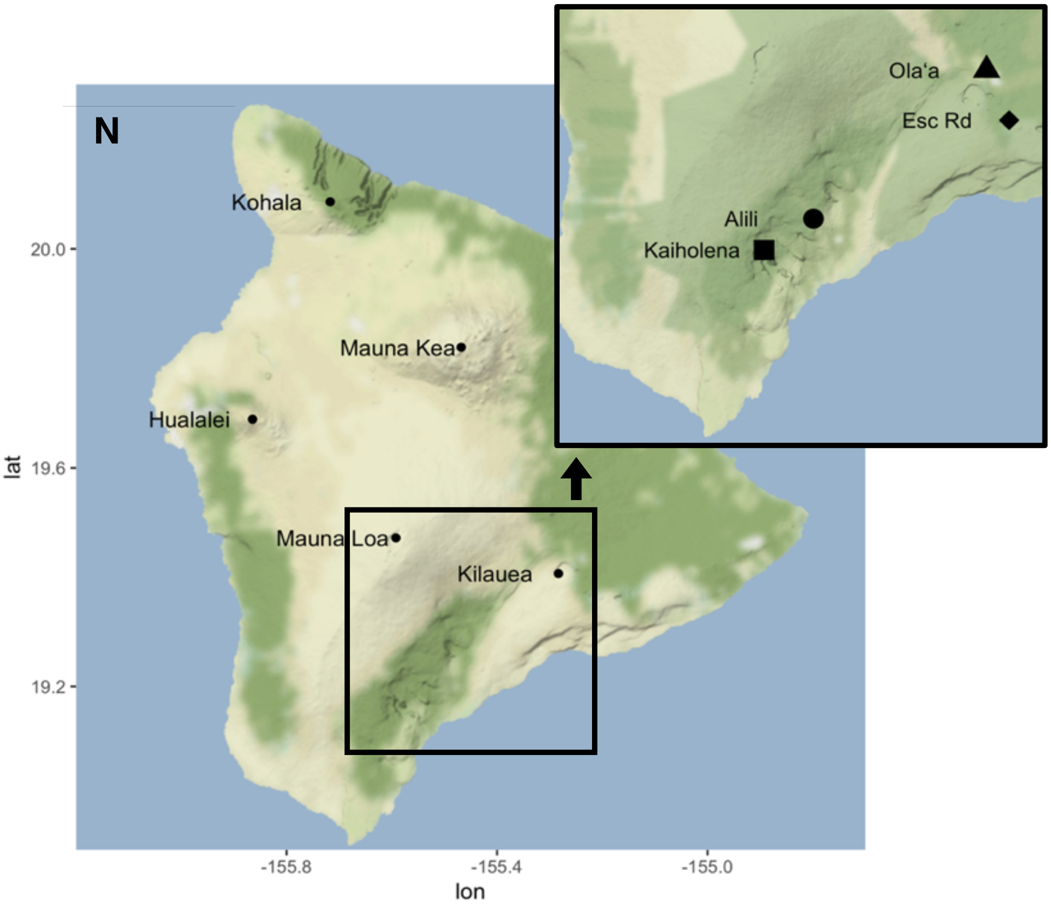

Figure 4.1: Location of sampling sites on Hawai'i Island. From north to south, 'Ola'a (triangle), Escape Road (diamond), Alili Springs (circle) and Kaiholena (square).

Sites were selected to have similar forest composition (wet forest dominated by *Metrosideros polymorpha*), elevation (1000-1200 m), and precipitation (2500-3100 mm per year). Sites differed in substrate type, substrate age (from 200-21000 years), and consequentially forest successional stage (see Table S 13 for site details). Each site consisted of 6 plots of 15m in radius, each with a focal *M. polymorpha* tree, and plots were located at least 80 m from one another.

Specimen collection

Arthropods were collected from the outer canopy of the focal *M. polymorpha* tree at the center of each plot. Each tree was sampled in 2014 and 2015. Canopies were accessed using single rope technique (Perry 1978). Nylon ripstop fabric bags of 1m diameter and 2m deep were attached to a large hoop with a handle to access branches in the outer canopy. Samples were collected by quickly bagging multiple branches in the canopy and from multiple areas of the outer canopy, and using a pole pruner to clip and remove branches (Gruner et al. 2005). Bags were tied shut and stored in a cool place until being transported to the lab. Samples were only collected when weather conditions were predominantly dry.

Samples were transported to the lab and specimens were extracted on the same day as collection. Specimens were extracted by gently shaking branches on an enclosed white surface and aspirating individuals that emerged. Foliage samples were carefully searched, but herbivores feeding completely enclosed within leaves or buds were not manually extracted (galls for example). Specimens were kept in 95% ethanol until identification. Specimens were identified in the lab; Hemiptera specimens were identified to (morpho)species, while Lepidoptera and Coleoptera were identified to family or morphotype. *Hyposmocoma* (Cosmopterigidae) were assigned a morphospecies based on the size and material of their case. Foliage collected with each sample was later dried and massed to account for sampling effort.

Trait database (host plant and insect)

In 2014, I collected foliage along with the arthropod samples and quantified several leaf traits (Table S 14). I selected twenty leaves from the foliage collected during each sampling event. These leaves were undamaged and representative of the sample in size, color and trichome presence. Leaves were selected from the penultimate leaves to ensure fully developed young leaves. I measured fresh weight to the nearest 0.01 g and leaf area to the nearest mm, then dried leaves at 60°C for 96 hours and reweighed them for dry weight. I calculated specific leaf area as the ratio of leaf area to dry mass to quantify leaf 'toughness', a biomechanical property. Specific leaf area is closely correlated with metrics such as work to punch and work to shear (Edwards et al. 2000, Díaz et al. 2001, Wright and Westoby 2002). Mean SLA per tree was calculated by averaging SLA from approximately 20 leaves from each sample. For leaf nutrient analysis, I pooled ten leaves per sample, ground them to fine powder using a Retsch MM 400 Oscillating Mixer Mill and kept them at 60°C until analysis. An Exeter Analytical CE- 440 CHN Elemental Analyzer was used for foliar carbon and nitrogen analysis at the Parker lab at the Smithsonian Environmental Research Center in Edgewater, MD (USA). Leaf phosphorus percentage by mass was determined by placing a known mass (~2 mg) of dried, ground leaf material in a muffle furnace at 550°C for two hours (Miller 1998), followed by colorimetric analysis using the ammonium molybdate method (Clesceri et al. 1998). Some leaf traits were correlated (Table 4.2).

A list of species present was compiled and insect traits were added based upon direct measurement (body size) or the literature (Table S 15). Where possible, data at the species level was used, however for poorly described species I based trait information on the nearest taxonomic level for which information was available, no coarser than at the family level. I measured body size to a resolution of 0.1 mm and then calculated mean body size for a species across all samples.

Statistical Analysis

Sampling effort

While data on Hemiptera communities were collected during 2014 and 2015, data from both years was used only to analyze overall abundance and diversity, as well as for within site comparisons. Further analyses were then completed with data from 2014 only, the year for which I also had leaf trait data. I included adult and juvenile Hemiptera but only juvenile Lepidoptera and Coleoptera since adults within this order do not typically feed on *Metrosideros polymorpha*. Predaceous Hemiptera (e.g., Nabidae), Lepidoptera (e.g., Geometridae: *Eupithecia*), and Coleoptera (e.g., Coccinellidae) were also excluded. I assessed insect abundance and diversity using three orders of Hill or effective species numbers (Hill 1973, Jost 2006); estimated asymptotic species richness ($q = 0$), effective estimated Shannon ($q = 1$) and Simpson ($q = 2$) diversity with the package ‘iNext’ (Hsieh et al. 2016) in R software (R Core Team 2017).

Table 4.1: Traits for the herbivore community and Metrosideros polymorpha

Traits		**Trait levels**
Herbivore community	Diet breadth	generalist (n=15)
Species-level variation		specialist (n=21)
	Feeding guild	sap feeder (n=25)
		leaf chewer (n=9)
		seed feeder (n=1)
		flower / bud feeder (n=1)
	Location juvenile	free living (n=26)
		gall (n=4)
		litter (n=4)
		shelter (n=1)
	Body size	in mm, range = 1.0-10.5
Metrosideros polymorpha	Leaf trichomes	glabrous (G) (n=10)
Individual based variation		pubescent (P) (n=8)
		hybrid (H) (n=6)
	Specific leaf area	in cm^2/g, range = 31.4-91.5
	Foliar nitrogen	mean = 1.175%; range = 0.61-1.91 %
	Foliar phosphorus	mean = 0.0676%; range = 0.03-0.16 %
	Leaf water content	in grams, range = 0.08-0.5 g

Table 4.2: Correlation coefficients between foliar leaf traits.

	Foliar nitrogen	Foliar phosphorus	Specific leaf area
Foliar nitrogen content	-	-	-
Foliar phosphorus content	0.8052	-	-
Specific leaf area	0.8377	0.8316	-
Water content	0.1344	0.2912	0.1770

(i) *How do plant phenotypic traits affect phytophagous insect abundance and diversity?*

To identify differences in insect diversity and abundance across sites, I used generalized linear mixed effect models with site as random effect and an offset with the log of dry foliage mass to quantify sampling effort, using package 'lme4' in R (Bates et al. 2015). I scaled and centered continuous predictor variables to z-scores with mean zero and unit variance.

(ii) What host plant traits are associated with arthropod community composition?

To identify differences in insect herbivore communities across host traits, I used generalized linear mixed effect models with site as random effect, z-scores for continuous predictors and an offset of foliage mass. To examine whether there were differences between species in their response to host plant characteristics, I used generalized linear mixed effect models with species-specific random slopes and intercepts (GLMM). In contrast to the previous section (i), here insect abundance is used as a response variable for each species individually, as opposed to using total abundance. I used a negative binomial distribution with site as random effect and an offset for sampling effort. I tested a Poisson distribution as well as a zero inflated negative binomial, but rejected these due to a poor fit. I ran diagnostics on all models and confirmed the absence of overdispersion, zero inflation and temporal and spatial autocorrelation using Kolmogorov-Smirnov test and simulated data (package 'DHARMa', as well as ratio between Pearson χ^2 and degrees of freedom). I tested the models with and without species-specific slopes and intercept using likelihood-ratio testing and did backward model selection using ΔAICc to evaluate plant predictors as fixed effects. I used a cutoff of ΔAICc = 3 per degree of freedom, and used a bobyqa optimizer to speed up processing and increase model convergence (Bobyqa is the default in lmer() but not in glmer(); Bates et al. 2015), although some models still did not converge. I visualized differences between sites in species composition using non-parametric multi-dimensional scaling (NMDS, Bray-Curtis dissimilarity), and analyzed differences in multivariate group mean across sites using the function adonis() in the package 'vegan' in R (Bray-Curtis dissimilarity, assessing marginal terms) (Oksanen et al. 2018). I reported partial R^2, pseudo-F values and P-values based on permutations.

I visualized differences in abundance between specific herbivore species in response to host plant traits by plotting linear relationships between z-scores for continuous host plant traits and the ten most abundant herbivore species.

(iii) Does the relationship between insect traits and host characteristics further explain community composition?

While ordination of species dissimilarity matrices is helpful to visualize multivariate data, converting data to dissimilarity matrices reduces power to detect patterns, in particular for relationships with low variance. I circumvented this problem by using a generalized linear mixed model approach, allowing us to use raw count data. To analyze the effects and interaction between host plant characteristics and insect species traits, I applied a trait-modeling approach as proposed by Brown et al. (2014), generating generalized linear models with a term for the environment by trait interaction. Using the function traitglm() in the package 'mvabund' in R, I fit a generalized linear model for all species and all sites simultaneously, as a function of

M. polymorpha host plant characteristics measured for each tree, insect traits at the species level, and the insect trait by host characteristic interaction (Wang et al. 2017). I used a negative binomial family and least absolute shrinkage penalty (LASSO) to do model selection and evaluate model predictors, and used the method manyglm() for resampling-based testing of the host plant characteristics by insect traits interaction term (Wang et al. 2017). LASSO is a method of penalized likelihood that works to shrink terms that do not explain variation to zero, improving the predictive performance (Hastie et al. 2009). To deal with the assumption in generalized linear models of independence of samples, I used anova.traitglm() which resamples sites but maintains all species from a site together, as such making the assumption that abundances are independent across sites, though not across species (Warton et al. 2015, Löbel et al. 2018). I examined residuals of the traitglm model to confirm homogeneity of variance of both models, used to test analysis of deviance and variable selection using LASSO (Figure S 13), as well as testing different family distributions before selecting a negative binomial distribution.

Results

Sampling effort

I took canopy arthropod samples from 24 trees in 2014 and 2015, collecting 49 samples and a total of 2698 individuals across 42 taxa or morphospecies. The collected insect herbivores were predominantly Hemiptera (97.68%), with small proportions of Lepidoptera (14 species, 1.78% of individuals) and Coleoptera (2 species, 0.54% of individuals). The most abundant species were Hemiptera:

Greenidea psidii (Aphididae), *Opuna sp*. (Miridae), and *Oceanides vulcan* (Lygaeidae). Average richness was 11.56 per tree sample in 2014 and 9.35 in 2015.

Sampling effort was similar across sites (mean dry mass of sampled foliage = 605 g SD 204 g, $F_{2,21} = 1.22$, $P = 0.315$) and across years ($F_{1,43}$=1.481, $P = 0.230$). Sampling effort was not correlated with leaf trichome morphotype ($F_{2,22} = 1.22$, $P = 0.352$), specific leaf area ($F_{1,22} = 2.293$, $P = 0.144$), mean water content ($F_{1,22}$ =2.97, $P = 0.099$) or percentage phosphorus ($F_{1,22} = 2.85$, $P = 0.105$), but was correlated positively with foliar nitrogen content ($F_{1,21} = 13$, $P = 0.0015$, Figure S 8.

Leaves from trees in populations differed significantly in foliar nitrogen content, phosphorus content, trichome presence and specific leaf area across sites (Supplemental Figure S 8, Figure S 9, Figure S 10, Figure S 11). Water content did not differ between sites (n=24; only measurements in 2014 for leaf traits; Table S 14).

(i) *How do plant phenotypic traits affect phytophagous insect abundance and diversity?*

Insect species richness was marginally greater on trees without trichomes than on other tree morphs ($q = 0$; GLMM: $n = 49$, $\chi^2= 5.8086$, ΔAICc likelihood-ratio test = 1.81, $P = 0.0548$, with trichome presence as fixed effects, site as random effect and an offset for sampling effort; Figure 4.2). Species richness was not correlated with foliar nitrogen content, mean specific leaf area or leaf water content (Hill $q = 0$; GLMM: n = 24 for 2014 and 2015 data, site as random effect and an offset for sampling effort;

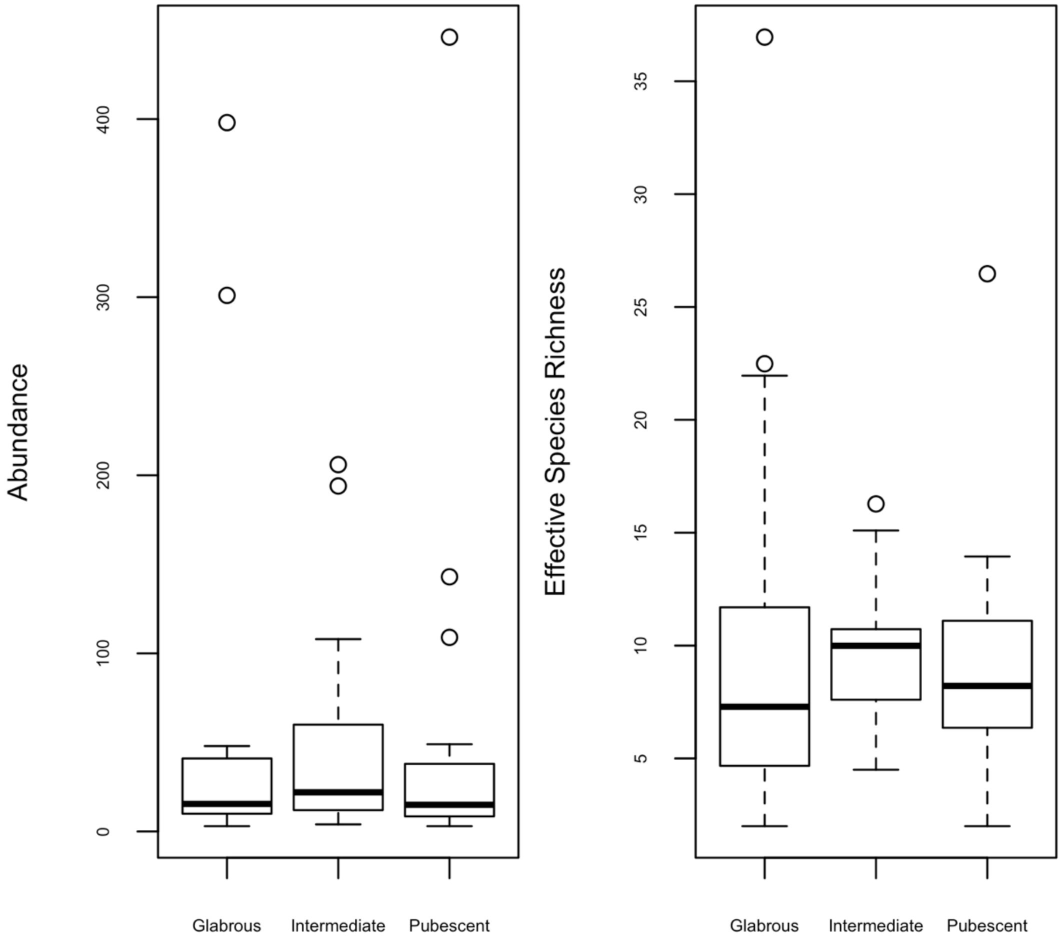

Figure 4.2: Herbivore abundance (left) and effective herbivore species richness (ChaoRichness(); right) as a function of trichome presence, for Hawai'i hybrid zone sites across 2014 and 2015.

nitrogen $\chi^2 = 0.3581$, ΔAICc to null model = -1.64, $P = 0.5496$; SLA $\chi^2 = 1.6535$, ΔAICc to null model = - 0.35, $P = 0.1985$; leaf water content $\chi^2 = 0.0015$, ΔAICc to null model = -2, $P = 0.9694$). Species richness increased with leaf phosphorus content ($\chi^2 = 5.6152$, ΔAICc to null model = 3.61, $P = 0.01781$). Host plant leaf traits did not affect Shannon ($q = 1$) or Simpson index ($q = 2$) (GLMM with site as random effect, $n = 24$, sample years 2014 and 2015). Insect abundance was not influenced by host leaf traits (GLMM with site as random effect and an offset for sampling effort; Figure 4.2).

(ii) What host plant traits are associated with arthropod community composition?

Herbivore community composition varied with host traits. To analyze multivariate response across the community, I used generalized mixed effect models with species specific intercepts, where the abundance of each species is the response variable. The multivariate response to host phenotypic traits differed from the response of total insect abundance. When analyzing across species, foliar nitrogen, phosphorus, mean water content, and trichome presence affected insect species abundances across all sites, and in particular species abundances across trees varied with foliar nitrogen content (GLMM with species specific intercept, site as random effect and an offset; likelihood-ratio test, $\chi^2 = 61.431$, ΔAICc = 47.5, $P < 0.0001$; foliar nitrogen $F_{1,42} = 2.185$, $P = 0.0254$; trichome presence $F_{2,42} = 21.847$, $P < 0.0005$, Figure 4.4; water content $F_{1,42} = 8.633$, $P = 0.0017$; foliar phosphorus $F_{1,42} = 6.899$, $P = 0.0136$). Responses to *Metrosideros polymorpha* host characteristics varied across insect species, and model fit improved when taking this into account; generalized linear mixed effect models with species specific slopes and intercepts performed better than models without species specific slope and intercept (ΔAICc = 1480, χ^2 =463.94, $P < 0.0001$) or with only species specific intercept (ΔAICc = 13.2, χ^2 = 17.148, $P < 0.00019$). Almost half of the variation in species composition across sampled trees can be explained by leaf traits (PERMANOVA cumulative $R^2 = 0.4635$, trichome presence: $R^2 = 0.16495$, $P = 0.003$; foliar nitrogen $R^2 = 0.07547$, $P = 0.023$; leaf water content: $R^2 = 0.06736$, $P = 0.034$; specific leaf area $R^2 = 0.04552$, P = 0.188; foliar phosphorus $R^2 = 0.0750$, $P = 0.024$). Another 14% of variation is explained by predictors associated with site that were not included in the traits I measured ($R^2 = 0.60187$ for leaf traits and site).

Within sites, with limited inference due to small sample size, results vary. For Kaiholena, herbivore communities differ between trees with high pubescence and without pubescence (PERMANOVA, samples from 2014 and 2015, $n = 18$, $F_{2,16}$ = 2.5311, $R^2 = 0.2403$, $P < 0.005$). Herbivore communities in ‘Ola‘a also differ between trees with no and with intermediate levels of pubescence (PERMANOVA, n =12, $F_{1,12} = 2.5677$, $R^2 = 0.204$, $P = 0.046$). Communities do not differ significantly with tree trichome presence on other sites (Escape Road Old $F_{1,12} = 1.367$, Alili $F_{1,12}$ = 1.471). I did not analyze effects of other leaf traits on species composition within sites because I lacked 2015 leaf trait measurements beyond pubescence.

Common families such as Aphididae, Miridae, Delphacidae, Triozidae and Lygaeidae differed in their response to leaf trichomes (

Figure 4.4). Most insect species increased in abundance with specific leaf area (Figure 4.6a), though *Oliarus* sp. and *Orthotylus metrosideri* decreased with increasing SLA.

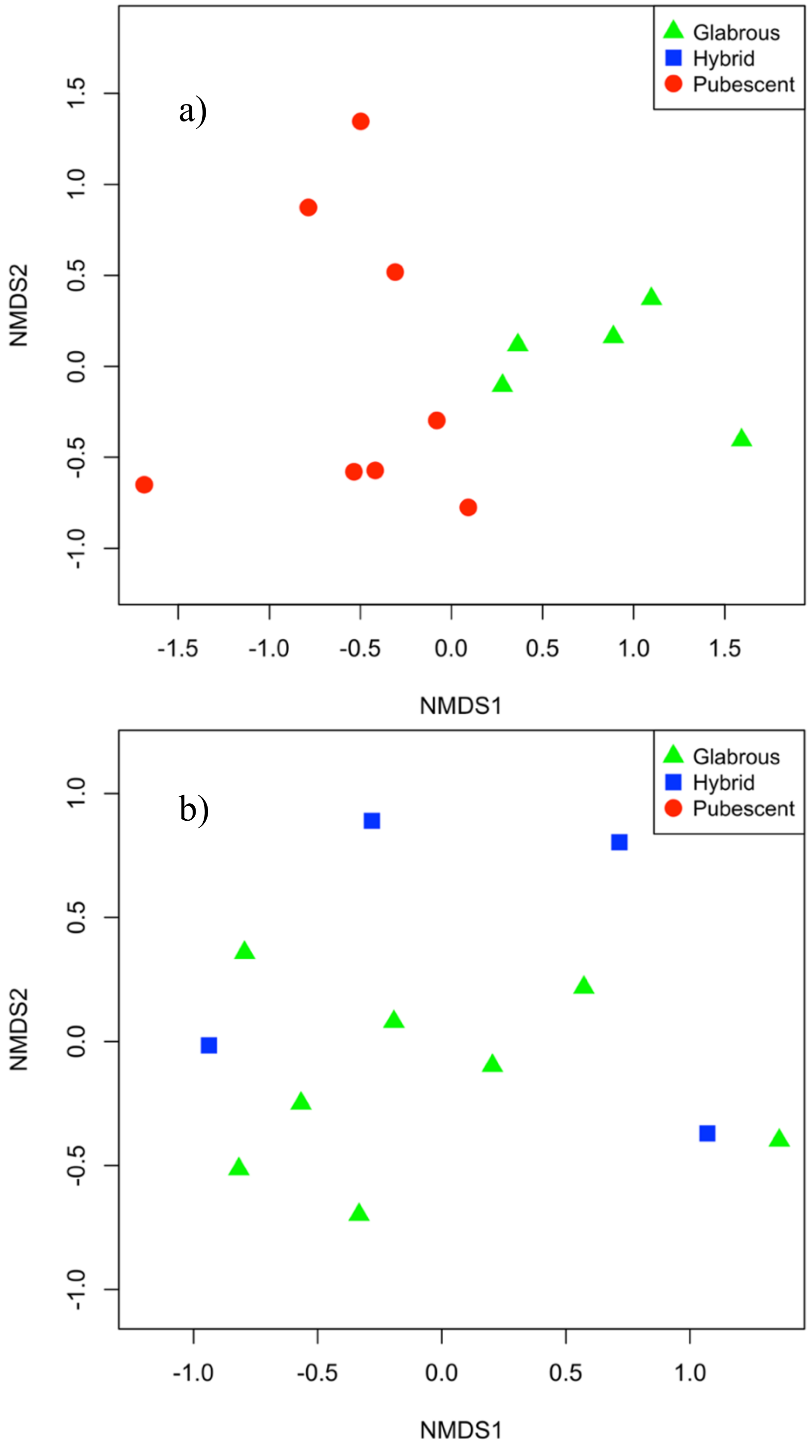

Figure 4.3: NMDS of herbivore species composition for each leaf trichome category in sites a) Kaiholena and b) ʻOlaʻa. Red circles are pubescent trees, green squares are glabrous and blue triangles are intermediate.

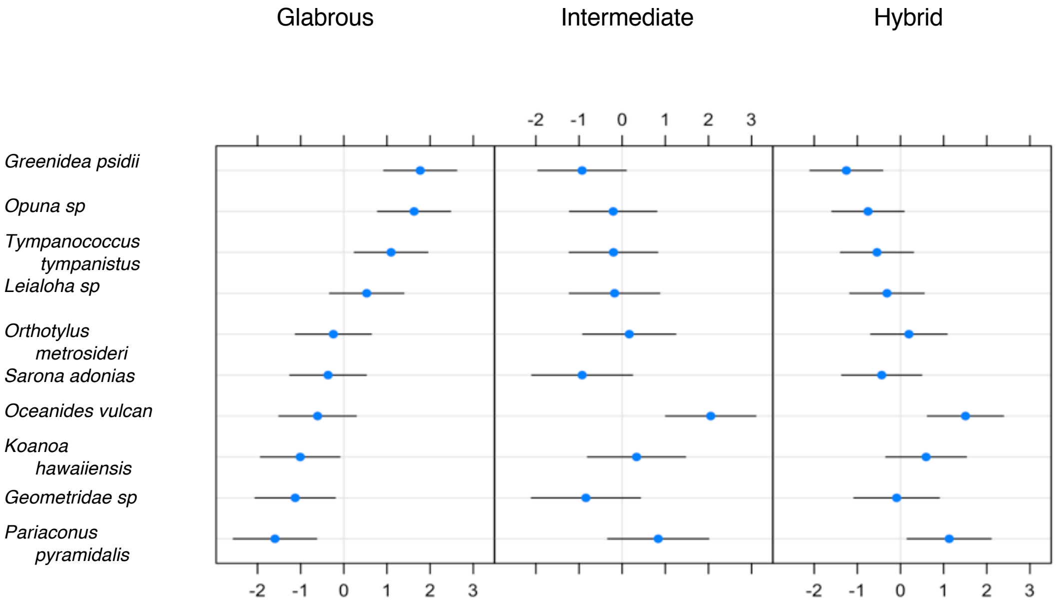

Figure 4.4: Model output for generalized linear mixed effect models with species-specific slope and intercept. Dots show conditional mean and conditional standard deviation for the most abundant insect species in relation to plant trichomes, with glabrous morphotype as intercept.

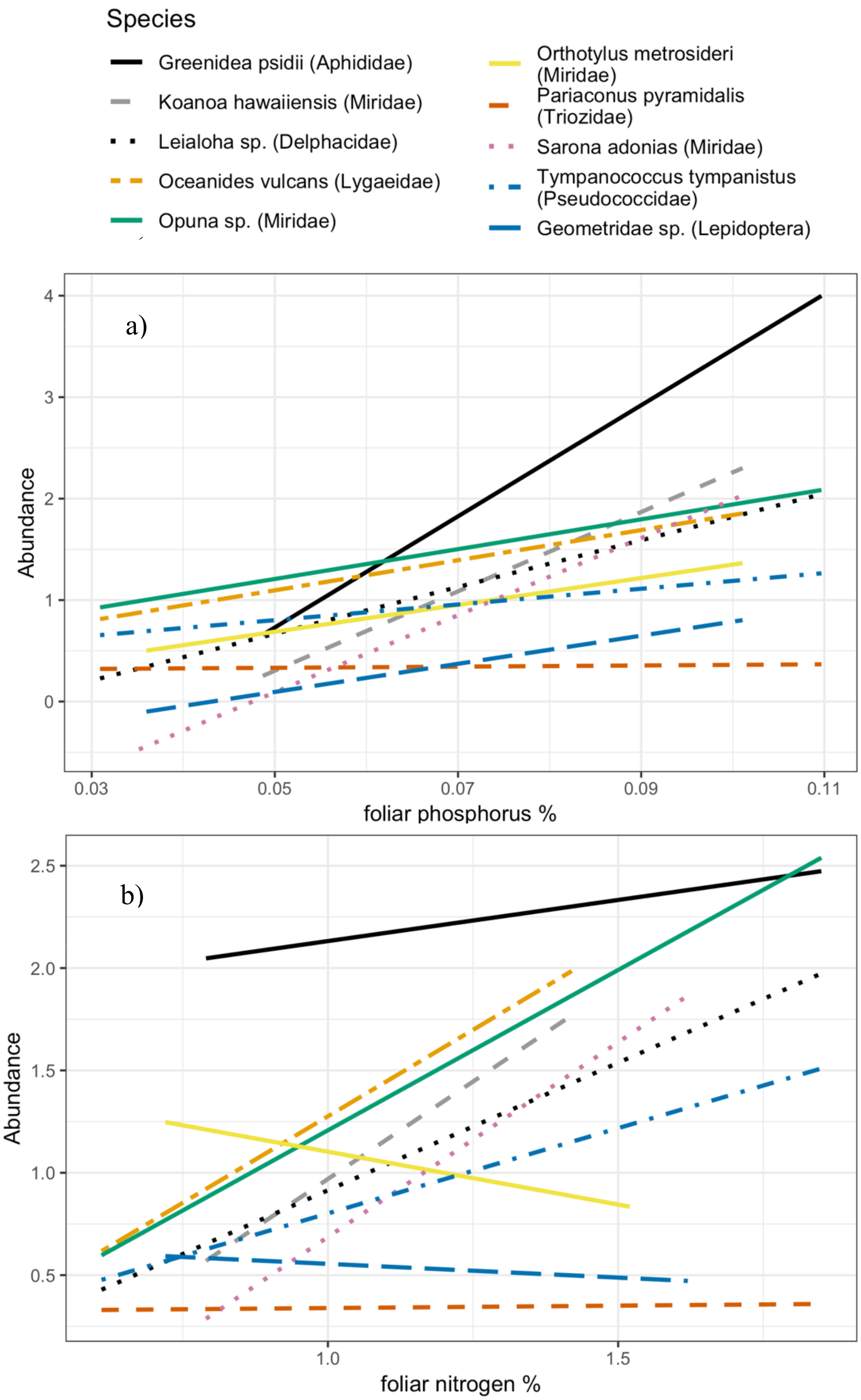

Figure 4.5: Abundance of the ten most abundant species as a function of standardized foliar phosphorus (a) and nitrogen (b).

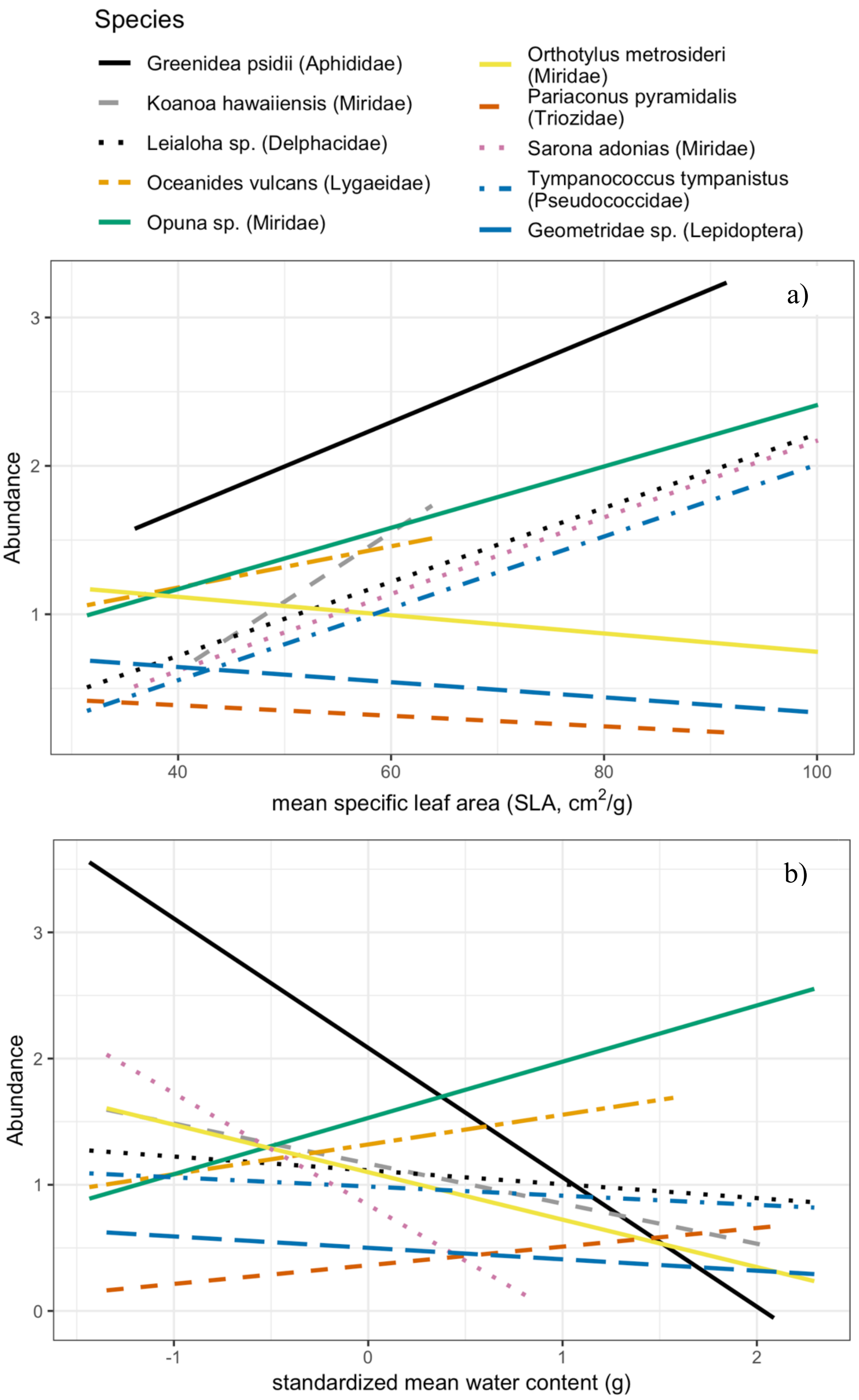

Figure 4.6: Abundance of the ten most abundant species as a function of mean specific leaf area (a) and mean water content (b).

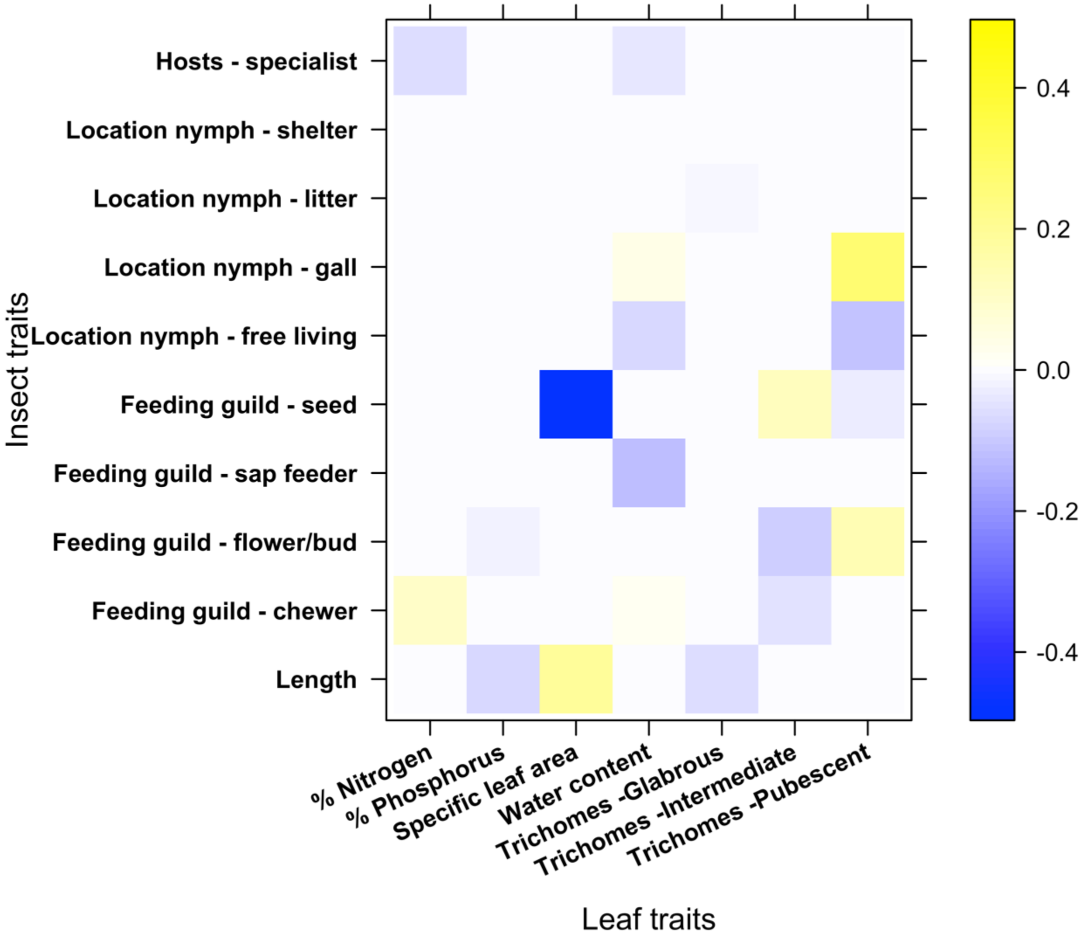

Figure 4.7: Interactions coefficients from model output of traitGLM fourth corner model with LASSO testing.

Further, *Greenidea psidii* and *Oliarus sp*. responded the strongest to variation in specific leaf area. Insect responses to water content varied strongly, with some taxa increasing and others decreasing in abundance in response to increases in mean water content (Figure 4.6b), including some Miridae taxa (*S. adonias, O. metrosideri, K. hawaiienses*), as well as *Greenidea psidii*, and *Pariaconus pyramidalis. Oceanides vulcans* and *Opuna sp.* increased in abundance on sites with higher leaf water content. Most insect species responded positively to foliar nitrogen, although a species of Cixiidae, Miridae and of Triozidae decreased with increasing foliar nitrogen content (Figure 4.5b). Similarly, most insect taxa responded positively to increased foliar phosphorus content, with only *Pariaconus pyramidalis* and *Oliarus sp*. decreasing in abundance on trees with higher foliar phosphorus content (Figure 4.5a).

(iii) Does the relationship between insect traits and host characteristics further explain community composition?

The host plant-insect trait interaction explains significantly more variation in insect abundance across trees than taxonomic data only (TraitGLM, *n* =24, *P* = 0.003). Herbivores responded differently to host traits depending on their feeding guild. Sap feeder abundance was negatively associated with leaf water content (LASSO, *r* = -0.1222, Figure 4.7), while abundance of leaf chewers was positively correlated with foliar nitrogen (*r* = 0. 09882) and water content (*r* = 0.02416), and negatively correlated with leaves with intermediate trichome presence (*r* = -0.04922**).** Seed eater abundance was negatively correlated with specific leaf area (*r* = 0.4968), and was associated with intermediate and pubescent leaves (*r* = 0.1206, r = -0.03414). Flower feeder abundances were also associated with intermediate and pubescent leaves (*r* = -

0.09350, *r* = 0.1362), as well as foliar phosphorus content (*r* = -0.01997). For nymph location, free living nymphs were negatively correlated with water content (*r* = -0.06898, Figure 4.7), and pubescent leaves (*r* = -0.1057). Insects forming galls were associated with pubescent leaves (*r* = 0.2675) and leaf water content (*r* = 0.04214). Shelter building species were lightly correlated with foliar nitrogen (*r* = 0.003734). Insects with juveniles developing in leaf litter were associated with glabrous leaves (*r* = -0.006217). Degree of specialization was lightly negatively associated with foliar nitrogen (*r* = -0.06079) and water content (*r* = -0.04206). Lastly, body size was positively correlated with specific leaf area (*r* = 0.1918), negatively with foliar phosphorus (*r* = -0.07427), and glabrous leaves (*r* = -0.06046; Figure 4.7). Other correlations between insect and host plant trait were present but were not retained in model selection using a LASSO penalty, which shrinks terms not explaining any variation in species response to zero.

Discussion

Intraspecific variation in the host plant *Metrosideros polymorpha* influences insect herbivore abundance, diversity and species composition. I found that phenotypic variation in hosts results in unique herbivore communities at a local scale, and that insect traits related to resource use and habitat are significant predictors of this relationship. Herbivore richness was greater on trees with high foliar nitrogen levels and lacking leaf pubescence, indicating a broader community persisted on accessible, nutritious hosts. My expectations were broadly supported, and host-insect trait correlations were particularly discernible for insect body size and feeding guild, and leaf water content and trichome presence in hosts. My results were consistent with environmental filtering at the local scale (Mittelbach and Schemske 2015), where species in a shared species pool sort locally to hosts with preferred phenotypes. Environmental filtering is particularly important given that prior research has shown little effect of top down control through predators or parasitoids on Hawaiian insect herbivore density and biomass (Gruner 2004).

Previous work in the Hawaiʻi *Metrosideros* system has described variation in phenotype across elevation (Vitousek et al. 1988), substrate age (Vitousek et al. 1988, Asner et al. 2005) and precipitation (Austin 2002, Cornwell et al. 2007). *Metrosideros polymorpha* varieties differ in their morphology, which common garden work indicates is predominantly genetically determined (Cordell et al. 1998, Stacy et al. 2016), while physiological plasticity allows varieties to exist alongside one another along a breadth of conditions. Physiological traits in *incana* are better suited for dry conditions (Hoof et al. 2008), while *glaberrima* is better suited to nutrient rich conditions. Similarly, var. *incana* has a whole host of traits better adapted to early successional conditions, including adaptations for dry conditions (Hoof et al. 2008), a strong response to light availability (Morrison and Stacy 2014), and little change in biomass or growth to nutrient addition. In contrast, the later successional variety *glaberrima* responds strongly to nutrient addition, with higher survivorship under low light conditions (Morrison and Stacy 2014). This tradeoff between rapid growth under high light and survivorship in shade is more commonly seen between species in a given environment rather than within a population, and is supported by research showing a negative correlation between trichome mass and lamina mass (leaf without trichomes) in co-occurring *Metrosideros polymorpha* (Tsujii et al. 2015). The distribution of *Metrosideros polymorpha* varieties across the landscape has been well documented, and is likely related to high environmental heterogeneity, gene flow and ecological tradeoffs. My results, and in particular the high amount of variation in community composition that was explained by plant traits, indicate that this heterogeneity in environment and distribution of *Metrosideros polymorpha* varieties scales up to the broader insect herbivore community. However, the consequences of this remarkable intraspecific variation in *Metrosideros polymorpha* for the consumer community have before now largely been neglected.

How do plant traits influence insects?

Nearly half (46%) of the variation in species composition across sites was explained by the specific plant traits examined. Host traits will affect insect abundance through different routes; by decreasing or increasing food quality, reducing palatability or by preventing access. Resource quality influenced *Metrosideros polymorpha* herbivore community composition, and response to foliar nitrogen and phosphorus content varied across species. Herbivore abundance followed expectations and was correlated with higher nitrogen availability (Mattson 1980, Bezemer and Jones 1998). Gruner et al also found that arthropod abundance on *M. polymorpha* increased with fertilization, however, the specific macronutrient responsible was not identified (Gruner et al. 2005). Specific leaf area (SLA) is related to leaf palatability, digestibility and herbivore preference (Grubb 1986, Iddles et al. 2003, Moles et al. 2013). I found increases in abundance with specific leaf area for dominant species, concurring with work in other field settings (Peeters et al. 2007).

Lastly, trichome presence was important in explaining variation in *Metrosideros polymorpha* herbivore communities. Trichomes generally limit access to leaf material, reduce herbivore growth rate and increase mortality (Levin 1973, Haddad and Hicks 2000), all of which may play a role in community composition across trichome presence in my study. I found higher abundance and higher diversity of herbivores on glabrous tree morphs than on intermediate or pubescent types. On Hawai‘i, trichomes are mainly hypothesized to be adaptive in extreme habitats, and pubescent morphs are mainly distributed on young, exposed flows that lack well developed soils and are likely water limited, as well as in montane regions with high solar irradiance (Joel et al. 1994, Tsujii et al. 2015). It is possible that the consequences of trichome presence on arthropod communities provides further advantages. Future work comparing intraspecific variation in host plants at local scales will provide further information on the effect of these host traits in sympatric phenotypes, however limited sample size prevented us from doing further within site comparisons in this study.

Variation in leaf traits across trees led to strong responses in a number of herbivore species. *Greenidea psidii* is a generalist invasive aphid (Messing et al. 2007), that is a successful invader in part because it frequently reproduces parthenogenically, allowing the aphid to rapidly increase in population size under favorable conditions (Mondor et al. 2007). This species responds strongly to nutrient availability; across samples and leaf traits, *Greenidea psidii* often had both the highest abundance and the steepest slope. Other generalist species, such as the Miridae *Opuna sp* and *Sarona adonias*, respond similarly though less strongly. In contrast, *Pariaconus pyramidalis* generally differed from the majority of other species in its response to leaf traits. The unique characters of its life history; ie a *Metrosideros polymorpha* specialist that induces gall production and provides an enclosed habitat for juveniles, may result in *Pariaconus* experiencing environmental pressures differently from other herbivore species. In contrast to most species, *Orthotylus metrosideri* responded negatively to leaf water content, specific leaf area and foliar nitrogen, and this specialist Miridae species may be best adapted to early successional low nutrient substrates and communities.

Trait-environment modeling

My results indicate that the interaction between plant and insect traits, rather than the effect of these predictors independently, best predicts herbivore community turnover. I found that specific herbivore traits related to feeding guild, nymph location and body size drive turnover in composition between host plants with distinct leaf trichome morphotypes. I expected feeding guild to be an important driver of species habitation, and this was confirmed by the trait modeling analysis showing correlations between herbivore feeding guild and plant traits such as foliar nutrients and trichome presence. Insect body size was negatively correlated with percentage phosphorus and with trichome presence, such that plants with high nutrient content that lack trichomes were associated with smaller insect body size. High trichome density plants generally have insect herbivores with larger body size (Schoonhoven et al. 2005, Stam et al. 2014), likely because trichomes impede the ability of smaller insects to navigate the leaf surface. Unexpectedly, although I did not have specific predictions for insect response to leaf water content, this predictor was retained as correlation with various insect traits even after shrinkage using LASSO. While some results, such as the importance of feeding guild, were expected and well established, these surprising results in my study indicate that considering host traits together with insect traits can provide valuable insights for understanding ecological responses to environmental variation.

While trait based approaches are common tools to understand patterns in species composition across environmental gradients (McGill 2005), there are various statistical approaches to incorporate traits. Multilevel modeling of the trait environment relationship is preferable to alternatives such as community weighted means (CWM) because multilevel model approaches (ie Pollock et al 2012, Jamil et al 2013, Brown et al 2014) explicitly account for nonindependence among species in their abundances (Miller et al. 2018). Furthermore, because these models are based on a GLM framework, they allow for flexibility in the types of data they can handle, as well as model selection and prediction (ter Braak et al. 2017). By being able to predict occurrence of species in unstudied locations or future settings, this approach combines the strength of multivariate methods with species distribution modeling (Brown et al. 2014). On Hawai‘i in particular, *M. polymorpha* leaf traits such as trichome presence or foliar nutrients vary predictably with elevation, precipitation and substrate age. Given the strong relationship between leaf traits and herbivore traits, it is possible to predict species composition based on *M. polymorpha* traits. Because of the strength of using a trait based approach, it may also be possible to predict community composition in regions where the herbivore species pool differs, such as some of the older Hawaiian islands. While I examine trait-environment relationships at a local scale, this approach has successfully been applied at broader scales as well. Pollock, Morris & Vesk (Pollock et al. 2012) showed that this type of model can explain species variation in environmental response in Eucalypt communities at a broad scale, while Auffret et al use a fourth corner model to predict long term patterns in community turnover as a function of biogeography and plant traits (Auffret et al. 2017).

Do dominant species drive the results?

While my analysis was conducted on 36 herbivore morphospecies, the majority of those are low in abundance across each site. In particular, two species of Miridae, a psyllid, a family of Lepidoptera larvae and an invasive aphid were highly abundant and had a disproportionate contribution to the outcome. As a result, it is possible that my trait analysis does not reflect the community response as much as it reflects the response of a subset of dominant species that drive the observed patterns. However, when conducting the analysis using presence/absence instead of abundance data, I find qualitatively similar results. In fact, I find the same associations with stronger interaction coefficients when excluding abundance from the analysis, indicating that my results are if anything, conservative, and that any bias due to highly abundant species would strengthen support for the patterns found.

Chemical defenses

Theory predicts that herbivore diet breadth is connected to host chemical defenses, where specialist species may be adapted to a host plant's leaf chemistry, and will be less impacted than generalists. In this study, I did not measure secondary metabolites in *M. polymorpha*. No comprehensive work has been done on chemical defense in *M. polymorpha*, although in general native Hawaiian plants have lower tannin and phenolic content than invasive species (Funk and Throop 2010, Peñuelas et al. 2010). As such the role of chemical defenses in mediating plant-herbivore interactions on *M. polymorpha* is unknown, but given the prevalence of structural defenses in low-resource conditions (Agrawal and Fishbein 2006), and on Hawaiʻi in general (Funk and Throop 2010), I expect chemical defenses to be of lesser importance relative to structural defenses such as trichome presence or leaf toughness. In particular, in areas where resources are low or herbivore pressure is limited, structural defenses that perform multiple functions can be cost effective (Funk and Throop 2010). However, I did not find a relationship between insect specialization and the structural *M. polymorpha* traits that I examined, and it is possible that patterns in abundance of generalist and specialist species would become apparent when incorporating chemical defenses.

Early stages evolution

The role of genetic and plastic mechanisms in maintaining the high degree of polymorphism in *Metrosideros polymorpha* has been well examined (Cordell et al. 1998, Morrison and Stacy 2014). Gross leaf morphology is predominantly genetically determined in *M. polymorpha* (Stacy et al. 2016), and it is likely that variation in genotype is driving the intraspecific variation in host leaf morphology that I observed, thus indirectly structuring herbivore communities. Intraspecific variation in leaf traits plays an important role in the ecological breadth of conditions where *M. polymorpha* occurs, but these traits also affect herbivore density and filtering herbivore community composition, possibly resulting in further fitness advantages to the host.

In parallel to this, differential sorting across phenotypically different hosts within a population can translate into genetic structure in herbivore populations and may eventually lead to diversification. The herbivore traits related to feeding guild, body size and protection for juveniles that are correlated with turnover in insect communities between morphologically different hosts could over time generate larger-scale patterns in distributions. If over longer time periods herbivores become exclusive consumers of a certain *M. polymorpha* phenotype, or if other ecological barriers arise, differentiation may take place between herbivore populations across *M. polymorpha* phenotypes. Percy and others have hypothesized that this may be a mechanism for diversification in *Pariaconus* psyllids (Percy 2017). Percy suggests that diversification among *Pariaconus* on different *M. polymorpha* leaf trichome morphotypes may be the result of variation in oviposition site selection, where ‘mistakes’ in site selection and the resulting physiological sinks result in preference for particular *M. polymorpha* morphotypes (such as those observed in work by Gruner et al 2005 and Percy 2017) and eventual diversification. This could be a preliminary step in the process through which many endemic species on oceanic islands such as Hawai‘i have originated; through adaptive radiation and isolation after newly colonizing an area or new host plant. This process is particularly conceivable on the dynamic younger substrates of Kilauea and Mauna Loa such as those where this study was done. In this landscape, ongoing volcanic activity and changing habitat within small geographic areas produce a variable forest with many different selection pressures, resulting in high potential for local adaptation and intraspecific variation.

Summary

While the interaction between host phenotype and herbivore traits is frequently neglected (Barbour et al. 2015), in this study I demonstrate that explicitly examining this relationship can help identify relevant host plant traits and test hypotheses about their importance across herbivore communities. Further, I emphasize the importance of intraspecific, genetic and functional diversity when considering biodiversity conservation. Conservation of sources of intraspecific variation is of crucial importance for the maintenance of community interactions, and my study suggests that reductions in intraspecific variation within populations are likely to have immediate community level consequences.

Chapter 5 : Dimensions of *Metrosideros polymorpha* canopy arthropod diversity: In conclusion

Understanding the diversity of communities in their current form and predicting future community characteristics in response to global anthropogenic change requires knowledge of the processes that determine community structure. I use a model system of a phenotypically variable host occurring across substrates of varying age to examine arthropod communities and determine 1) the relative influences of substrate age and ecological sorting on assembly processes; 2) the importance of dispersal and connectivity between habitats for local diversity; and 3) the role of insect and host traits in shaping communities where variable phenotypes co- occur at local scales. This work contributes to our understanding of how communities are structured, and in particular how the dynamic effects of geology, evolution, forest succession and host and insect traits interact to produce local canopy arthropod communities.

Throughout this dissertation, I examine patterns in arthropod communities. Describing biological communities can be challenging, and ecologists have devised various ways to quantify community attributes and summarize their characteristics. A thorough understanding of a community requires analysis of multiple dimensions of diversity. I characterize Hawaiian canopy arthropod communities through their abundance of individuals, their taxonomic diversity and their functional diversity. Incorporating these three dimensions provides a broad perspective, and differences across dimensions provides information on the relative drivers of biodiversity. In this chapter, my objective is to synthesize across the previous chapters and current work in community ecology to discuss these three dimensions of biodiversity and their drivers in Hawaiian canopy arthropods.

Direct and indirect effects of substrate age

Community attributes of species composition, abundance of individuals, taxonomic and functional diversity are influenced by a range of variables. This dissertation demonstrates through various analyses that the direct effect of age on communities is limited. Geological substrate age does not correlate with patterns in species similarity or composition (Chapter II), and structural equation models show no direct effects of age on Hemiptera (Figure 5.1, Appendix S 5). Instead of age effects on community similarity, Hemiptera communities show a temporal pattern in community structure, with shifts in the proportion of dominant and of rare species as well as differences in abundance of individuals. These results suggest that the processes shaping arthropod communities vary across volcanoes.

Age effects on *Metrosideros polymorpha* traits

Metrosideros polymorpha leaf traits vary across substrate age. As volcanic rock is broken down across the chronosequence and organic material accumulates, soil nutrient availability and water holding capacity increases, with consequences for *Metrosideros polymorpha* leaf traits. Leaf traits explain a large amount of variation in Hemiptera community composition (Chapter II), and taking a closer look at a hybrid zone where various *Metrosideros polymorpha* morphotypes co-occur reveals a close relationship between specific host traits and Hemiptera life history traits (Chapter IV). Analyzing host leaf traits as well as several other predictors of Hemiptera abundance and diversity using a structural equation model demonstrates the importance of leaf traits (Figure 5.2, Appendix S 5), and suggests a correlation between volcano identity and leaf trait values (Appendix S 5).

Forest structure

Mesic forests across the chronosequence show high variation in forest structure (Appendix S 5). I quantified this forest structure using LiDAR data, to analyze the effects of structural characteristics on insect diversity, abundance and functional diversity. Forests more similar in physical structure had more similar Hemiptera communities (Chapter II). In particular, Hemiptera abundance and functional diversity were influenced by foliage density in the lower canopy (Structural equation model, Figure 5.1, Appendix S 5).

In spite of significant variation in forest structure across sites, the structural equation model did not support an effect of age on maximum tree height, tree height standard deviation, height entropy or understory foliage density (Figure 5.1). Substrate age likely interacts with many other variables to determine habitat structure, diffusing the direct relationship with age or succession.

Abundance

Hemiptera abundance showed a clear temporal pattern across the chronosequence. Abundance had a largely unimodal pattern on Hawaiʻi Island, with a peak at Laupāhoehoe (Chapter II, Figure 2.5). This site has highest productivity (Vitousek and Farrington 1997) due to the abundance of nitrogen through organic material while also not yet experiencing phosphorus depletion (Vitousek 1999). The mechanisms behind this temporal pattern- increasing and then decreasing insect abundance- are likely both increased plant biomass to support phytophagous insects (peak maximum tree height) and high leaf nutrient availability. Because number of individuals is a key component of species richness, statistically and functionally, this high abundance is translated to high local diversity as well. The structural equation model indicates that abundance is the strongest determinant of Shannon diversity, and that forest structure and most leaf traits do not directly determine Shannon diversity, but may do so through insect abundance (Figure 5.1, Figure 5.2).

Functional diversity

Community convergence

Communities converge across the chronosequence. I find that with increasing substrate age, assemblages become more similar within sites in their taxonomic composition, as evidenced by decreasing beta dispersion (Chapter II). Similarly, the species composition of a single assemblage also increases in functional similarity along the substrate age gradient (Figure 5.3), perhaps indicating that the community converges on an 'optimal' morphology and life history, or a more stable community. Together, these results suggest that as forests develop and become more structurally complex, the species composition changes directionally. However, this appears to be driven by habitat successional changes rather than by age; i.e. communities change in a predictable manner along a gradient of physical forest structure, whereas there is no correlation between similarity of species composition and age.

Environmental heterogeneity as diversity driver

Environmental heterogeneity supports higher diversity of organisms in many different habitats (MacArthur 1958, Lawton 1983, Tamme et al. 2010, Stein et al. 2014). Habitats with high structural heterogeneity are expected to result in high diversity because of increased niche space and coexistence. However, I find no relationship between taxonomic diversity and measures of forest structure (Figure 5.3). Unexpectedly, beta dispersion decreases with increasing structural complexity (in the form of tree height standard deviation, understory density, and height entropy, Figure 5.3, Appendix S 5). This counterintuitive result may be due to the narrow focus of my sampling, the difference between heterogeneity in physical structure and environmental heterogeneity, or may be related to changes in canopy arthropod communities. One hypothesis is that the increased niche space with higher structural complexity may be predominately found in the forest understory, thereby not enhancing canopy arthropod diversity and not detected in the sampling for this research. Alternatively, on dynamic young flows forest structural complexity is lower but leaf traits are also more heterogeneous. I find distinctly dissimilar communities on different morphotypes in the hybrid zone (Chapter IV). This high phenotypic diversity in *Metrosideros polymorpha* on the early side of the age gradient may drive a significant part of the high turnover in phytophagous communities between trees, and result in environmental heterogeneity other than forest structure. Lastly, forests with higher structural diversity likely have higher plant diversity. As such, these forests may support higher diversity of plants and arthropods, and may draw Hemiptera away from *Metrosideros polymorpha* by providing alternative habitat elsewhere for generalist species. Further analysis of existing data on plant diversity, structure and canopy volume can help differentiate these hypotheses.

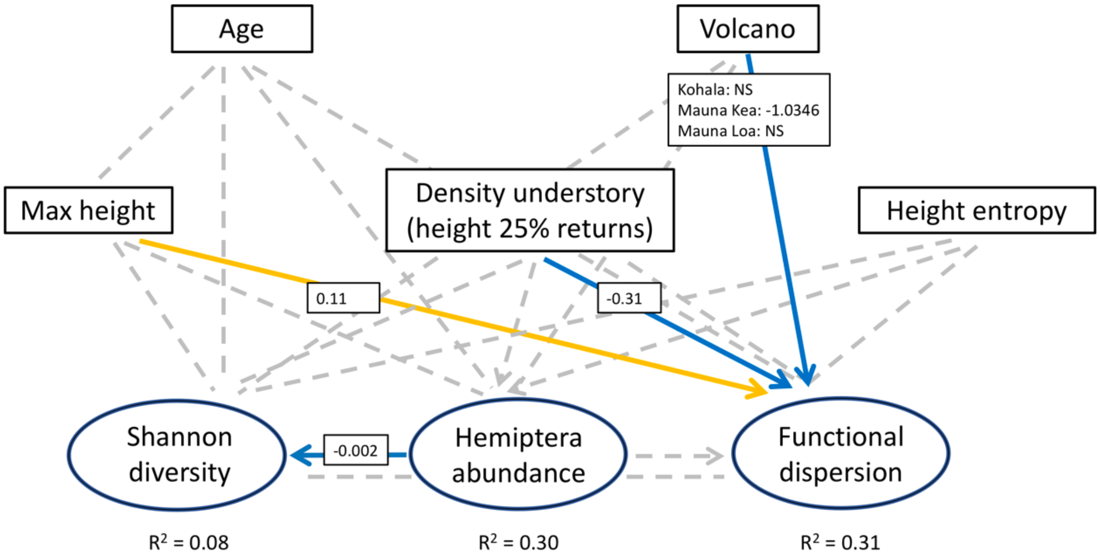

Figure 5.1: Structural equation model focusing on forest structure. Model includes multilevel predictors, community attributes and their relationships. Arrows for non-significant paths (P>0.05) are dashed. Significant positive relationships are indicated by yellow, and negative by blue arrows. Estimated coefficients are given in the associated boxes for significant paths, and R^2 values for component models are given below response variables.

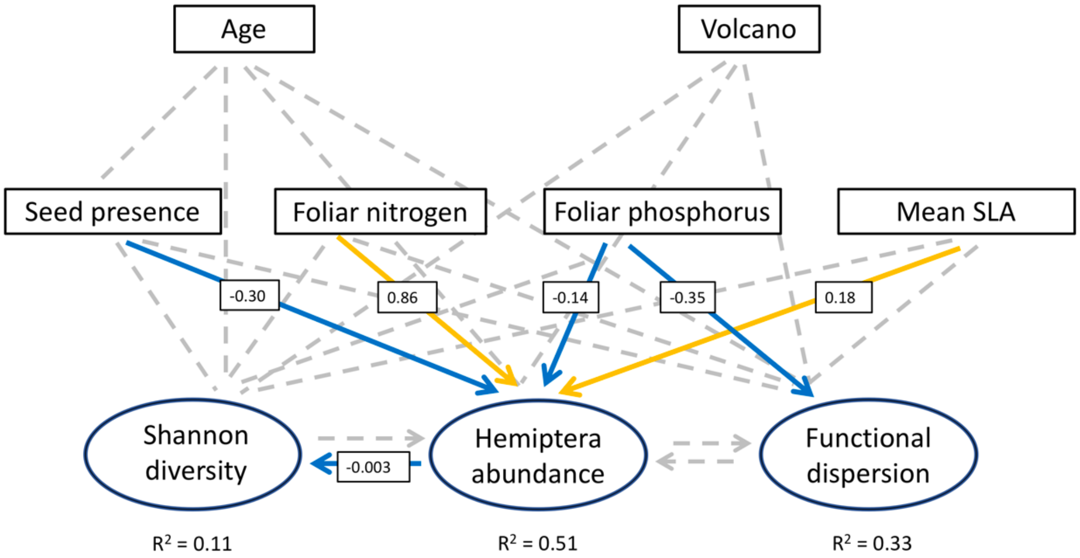

Figure 5.2: Structural equation model focusing on Metrosideros polymorpha leaf traits. Model includes multilevel predictors, community attributes and their relationships. Arrows for non-significant paths (P>0.05) are dashed. Significant positive relationships are indicated by yellow, and negative by blue arrows. Estimated coefficients are given in the associated boxes for significant paths, and R^2 values for component models are given below response variables.

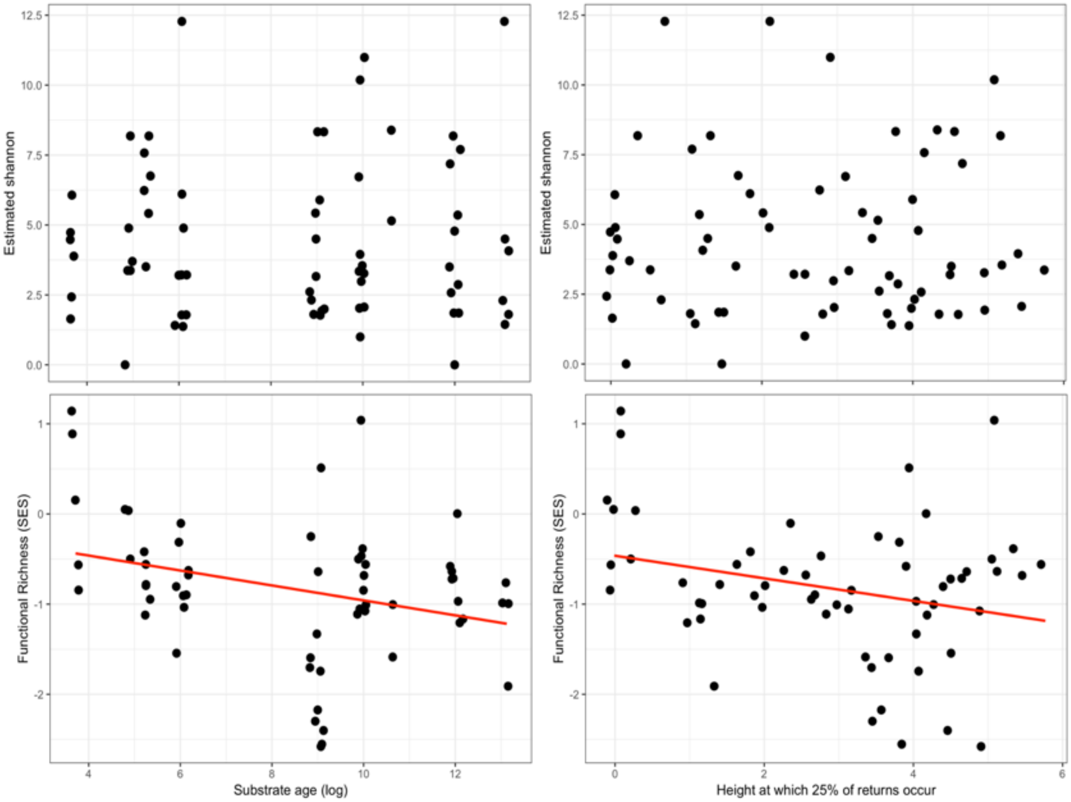

Figure 5.3: Taxonomic (top) and functional (bottom) Shannon diversity of Hemiptera as a function of substrate age (left) and forest structure (right). Hawai'i Island only, substrate age ranges from 41-500000 years.

Connecting communities

Dispersal

Connectivity appears to be high among *Metrosideros polymorpha* canopy arthropod communities (Chapter II, Chapter III). This is in contrast with other Hawaiian taxa, both in the kīpuka landscape and more broadly across Hawaiʻi. In the kīpuka, Drosophila, fungi and birds have strong species area relationships (Flaspohler et al. 2010, Mueller 2015, Vannette et al. 2016), while for spiders and fungi dissimilarity patterns and genetic structure suggest dispersal limitation (Vandergast and Gillespie 2004, Vandergast et al. 2004, Vannette et al. 2016). Besides these kīpuka examples, other Hawaiian plant and animal taxa also show signatures of dispersal limitation in their genetic structure (Roesch Goodman et al. 2012, Stacy et al. 2014, Percy 2017). Thus, the finding that *Metrosideros* canopy arthropods are not dispersal limited is rather unexpected.

While this difference is likely the result of differences in insect life history traits, information on Hawaiian arthropod dispersal ability is sparse, except for taxa that have lost the ability for flight (for example, brown lacewings in the genus *Micromus;* moths in the genus *Thyrocopa*; flightless cave moths in the genus *Schrankia*; Tauber et al. 2007, Medeiros et al. 2009, Medeiros and Gillespie 2011). In most studies of phytophagous insects however, insects are frequently assumed to be highly dispersive (Howarth 1990, Lewinsohn and Roslin 2008), and limited by the distribution of host plants rather than by geographic distance (Novotný and Weiblen 2005, Novotny et al. 2007, Whitfeld et al. 2012). Furthermore, ancestors of all arthropod taxa on Hawaiʻi arrived on the archipelago through dispersal, frequently as aerial plankton (Peck 1994), and so rare long-distance dispersal events have at least occurred in the past.

Deterministic versus stochastic processes

The importance of deterministic versus stochastic processes in driving community structure has been widely debated in the past decades (Hubbell 2001, Gravel et al. 2006, Adler et al. 2007, Swenson et al. 2012), although significantly less so among entomologists and insect ecologists (Kitching 2013). Because processes structuring diversity are scale dependent, the relative importance of deterministic versus stochastic processes may depend on the heterogeneity of the habitats compared (Chase and Myers 2011). In homogeneous habitats, stochastic models are more likely to describe patterns in community structure accurately (Gravel et al. 2006), while in heterogeneous habitats, the underlying environmental heterogeneity is likely to leave a deterministic signature on community composition. Surprisingly, although this study takes place in relatively homogenous habitat, consisting of a single host tree in wet forests across consistent elevation and precipitation, I find support for deterministic rather than stochastic processes. These results are consistent across both a long (Chapter II) and short (Chapter IV) temporal gradient. Although this study finds strong support for deterministic rather than stochastic processes, in general it is unlikely that only a single process would structure communities, and our theories of community structure should integrate both (Chase and Myers 2011). Ellwood et al argue that general models of these processes are only possible with detailed knowledge of the local environment and history of the community, as this allows selection of the appropriate resolution, both spatial and temporal, at which to test for such processes (Farnon Ellwood et al. 2009). While information is still lacking on the life history of Hawaiian arthropods associated with *Metrosideros polymorpha,* this dissertation is an important step in understanding fine scale environmental drivers and the role of deterministic and stochastic processes in arthropod assemblages.

Metacommunities

Dispersal is not limiting for *Metrosideros polymorpha* arthropod communities, suggesting that movement across the landscape is prevalent. Assemblages in close proximity to one another are dissimilar, particularly on dynamic, young substrate (Chapter II), suggesting that mass effects or source sink effects are important for community assembly (Leibold et al. 2004). The lack of a stable consistent community across trees within a site suggests that influx from outside populations may be prevalent. In contrast, on older substrates, Hemiptera communities converged, and this combined with the correlation between habitat and species dissimilarity suggests an important role for species sorting. Although I did not formally test metacommunity theory in this system (Leibold et al. 2004), the findings in this dissertation show the importance of understanding natural systems across scales and viewing communities within a connected network.

Species sorting

Although a species sorting paradigm aligns with patterns in Hemiptera community structure on older substrates, the mechanism behind this ‘sorting’ is unclear. Organisms may be preferentially selecting ideal habitats for oviposition sites, feeding, or predator and parasitoid avoidance, based on environmental stimuli (Singer 2004, Saint-Germain et al. 2009), insect perceptual ability (Singer 2004) and search costs (Stamps et al. 2005). Alternatively, habitat characteristics may shape arthropod mortality (Hawkins et al. 1997) or fecundity and survival of offspring (Rauscher 2004), resulting in the observed plant-insect associations. While I am unable to distinguish between these processes in this dissertation, further work on the mechanism behind patterns in insect habitat use will contribute to our understanding of insect community assembly.

Conclusion

Throughout this dissertation, I demonstrate that the effects of the species pool and substrate age are limited for canopy arthropod communities. Because of the high dispersal ability of canopy arthropods, the role of substrate age in determining community structure is relatively weak. Instead, effects of substrate age primarily trickle down to affect the phytophagous insect community through changes in host morphology and forest structure. By determining the relative importance of assembly processes across a space for time chronosequence (Chapter II), examining connectivity in a patchy landscape (Chapter III), the scales influencing community dissimilarity (Chapter II), (Chapter III), and testing effects of vegetation structure and host leaf traits on local habitat use and insect traits (Chapter II, IV), this study sheds light on the interactions between various community-structuring ecological processes in a dynamic landscape.

Outstanding questions

Having reached the end of the dissertation writing process, many questions still remain for me. I would like to better quantify movement between communities. Life history information for many canopy arthropod taxa is largely lacking, including dispersal distances. How does insect survival and fitness vary between different plant morphotypes. How actively can these Hemiptera select desirable host habitat? What do the higher trophic levels, in particular specialized Hemiptera parasitoids, look like? What will the colonization and establishment of the first communities on Lōʻihi look like, when this proto-volcano, the youngest member of the Hawaiian archipelago, breaks the ocean surface?

More urgently, over the course of my doctoral studies I have seen the Hawaiian forests become threatened by two fungal pathogens, *Ceratocystis lukuohia* and *Ceratocystis huliohia*, causing rapid and widespread population decline in *Metrosideros polymorpha* (Keith et al. 2015, Mortenson et al. 2016, Barnes et al. 2018). Many great scientists are currently working on how this disease (termed Rapid ʻŌhiʻa Death) spreads, how to stop it and how to preserve the genetic diversity of *Metrosideros polymorpha* as much as possible (Asner et al. 2018, Heller and Keith 2018, Roy et al. 2019). However, it is likely that mesic forests on Hawaiʻi have been irreversibly changed. This raises many more questions regarding the associated arthropod community. How does the reduction of this foundation species affect *Metrosideros polymorpha* associates, and in particular native species? This pathogen and the consequent mortality in *Metrosideros polymorpha* generate disturbance and habitat loss. This affects forest structure as well; reducing canopy density, creating light gaps and increasing standing wood and debris. Habitat loss, disturbance and changes in the forest structure will affect arthropod species differently, and to an unknown magnitude. Forests with declining populations of *Metrosideros polymorpha* are more prone to invasion by other tree species, with again broader community consequences. The long term consequences of Rapid ‘Ōhi‘a Death for Hawaiian mesic forests are dire, and difficult to predict. This dissertation provides valuable new information and a deeper understanding of the canopy arthropod community associated with this threatened foundational tree.

Appendices

Appendix S 2: Chapter 2

Table S 1: Chronosequence site environmental information

Site	Volcano	Island	Age (years)	Elevation (m)	Rainfall (mm/year)	Sampling years
Escape Road 1973 flow	Kilauea	Hawai‘i	41	975	3750	2014, 2015
Tree planting road	Mauna Loa	Hawai‘i	133	1200	4600	2014, 2015
Escape road 200y	Kilauea	Hawai‘i	200	1005	2700	2014, 2015
Thurston	Kilauea	Hawai‘i	400	1186	2730	2014, 2015
Kaiholena 450y	Mauna Loa	Hawai‘i	450	1018	2900	2014, 2015
‘Ola‘a	Kilauea	Hawai‘i	7500	1176	3010	2014, 2015
Laupahoehoe LSAG	Mauna Kea	Hawai‘i	9000	1182	3250	2014, 2015
Kaiholena 21ky	Mauna Loa	Hawai‘i	21000	1000	2930	2014 only
Alili Spring	Mauna Loa	Hawai‘i	21000	948	2500	2014, 2015
Laupahoehoe Hippnet	Mauna Kea	Hawai‘i	40000	1171	3525	2014, 2015
Laupahoehoe 65-250 ky	Mauna Kea	Hawai‘i	165000	1058	4000	2014 only
Kohala 175 ky	Kohala	Hawai‘i	175000	1286	2920	2014, 2015
Kohala 450 ky	Kohala	Hawai‘i	450000	1307	3516	2014, 2015
Waikamoi	Haleakela	Maui	500000	1554	2810	2015 only
Kamakou	East Moloka‘i	Moloka‘i	1650000	1202	2890	2015 only
Kokee	Kaua‘i	Kaua‘i	4150000	1175	2602	2015 only

Table S 2: Chronosequence site vegetation information

Site	**Overstory**	**Understory**	**Cover**
Escape Road 1973 flow	*Metrosideros polymorpha*	matted ferns, native shrubs, bare lava flow	Open
Tree Planting Road	*Metrosideros polymorpha*	matted ferns, native shrubs, introduced grasses, bare lava flow	Open
Thurston	*Metrosideros polymorpha*, Native trees	native shrubs, native tree ferns, introduced sedges	Open
Escape Road 200y	*Metrosideros polymorpha*	matted ferns, native shrubs, introduced grasses	Open
Kaiholena 450y	*Metrosideros polymorpha*, Native trees	tree ferns, native shrubs	Dense
‘Ola‘a	*Metrosideros polymorpha*, Native trees	tree ferns, native shrubs	Medium
Laupahoehoe LSAG	*Metrosideros polymorpha*, *Acacia Koa,* native trees	tree ferns, native shrubs	Medium
Alili Spring	*Metrosideros polymorpha*, Native trees	tree ferns, native shrubs	Open
Kaiholena 21ky	*Metrosideros polymorpha*, Native trees	tree ferns, native shrubs	Dense
Laupahoehoe Hippnet	*Metrosideros polymorpha*, *Acacia Koa*, native trees	tree ferns, native shrubs, standing dead trees	Medium
Laupahoehoe 65-250 ky	*Metrosideros polymorpha*, *Acacia Koa*, native trees	tree ferns, native shrubs	Dense
Kohala 175 ky	*Metrosideros polymorpha*, Native trees	tree ferns, native shrubs	Medium
Kohala 450 ky	*Metrosideros polymorpha*, *Cheirodendron trugynum*, Native trees	native shrubs, *Sphagnum sp.*, tree ferns, matted ferns	Medium
Waikamoi	*Metrosideros polymorpha*, Native trees	native shrubs, standing dead trees, introduced grasses	Medium
Kamakou	*Metrosideros polymorpha*	native shrubs	Open
Kokee	*Metrosideros polymorpha*	native shrubs	Medium

Table S 3: Correlation coefficients for predictors used in variance partitioning

	Latitude	Longitude	Substrate age	Mean tree height	SD tree height	Skew tree height	Kurtosis tree height
Latitude	-	-	-	-	-	-	-
Longitude	-0.1829	-	-	-	-	-	-
Substrate age	0.6722	-0.5795	-	-	-	-	-
Mean tree height	0.1389	0.1274	-0.07909	-	-	-	-
SD tree height	0.3022	0.1342	-0.00323	0.9643	-	-	-
Skew tree height	-0.08219	0.2181	-0.1189	-0.7784	-0.7087	-	
Kurtosis tree height	-0.1862	0.2679	-0.1807	-0.5663	-0.5512	0.8625	-

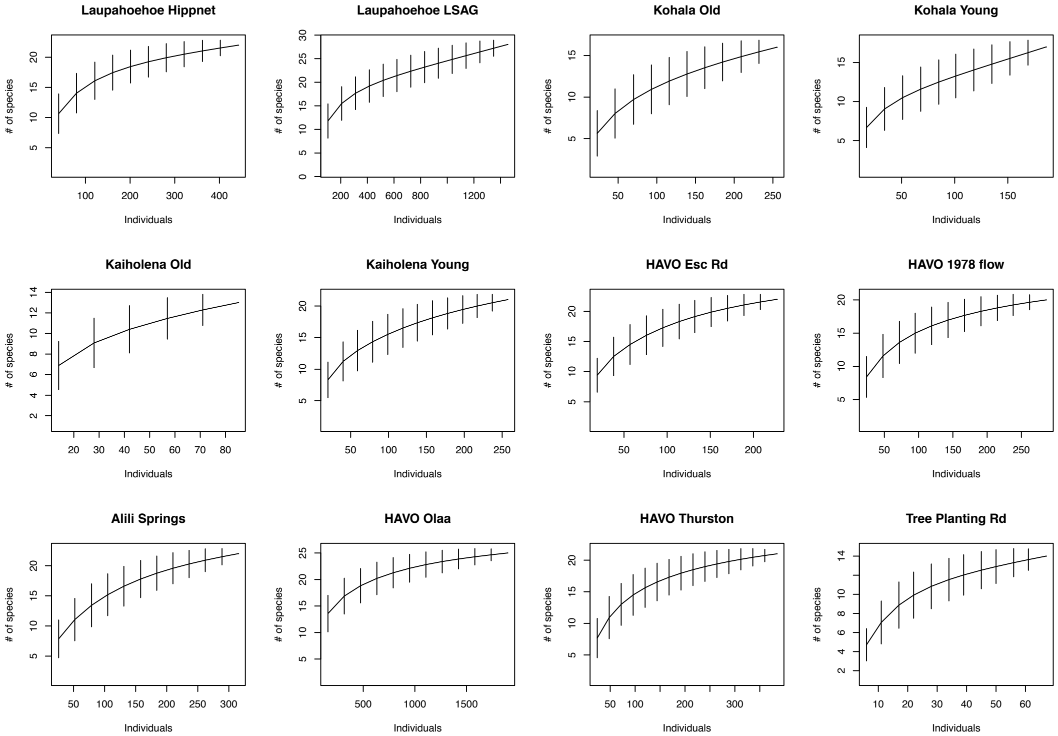

Figure S 1: Species accumulation curves for samples taken on Hawai'i Island.

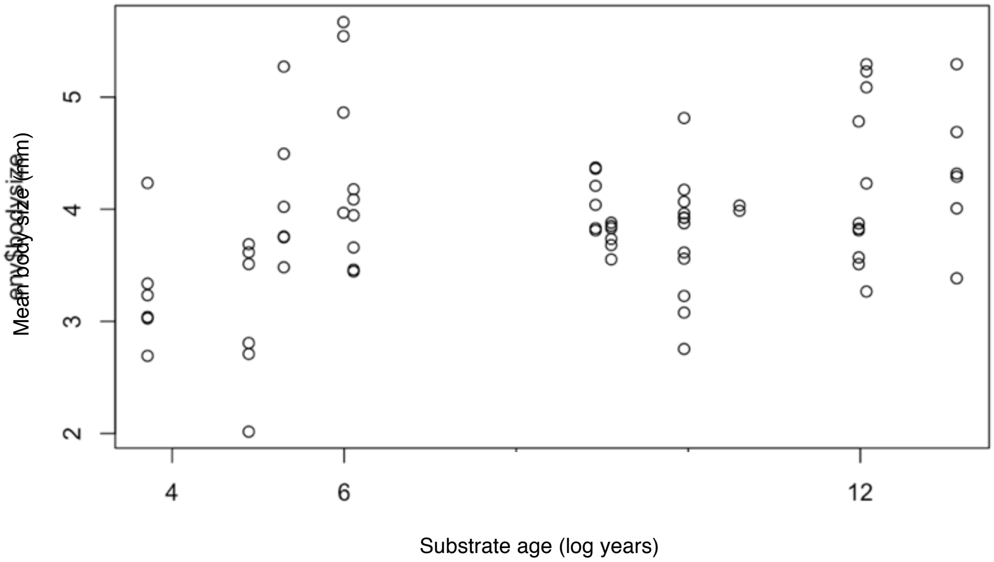

Figure S 2: Mean Hemiptera body size across the chronosequence.

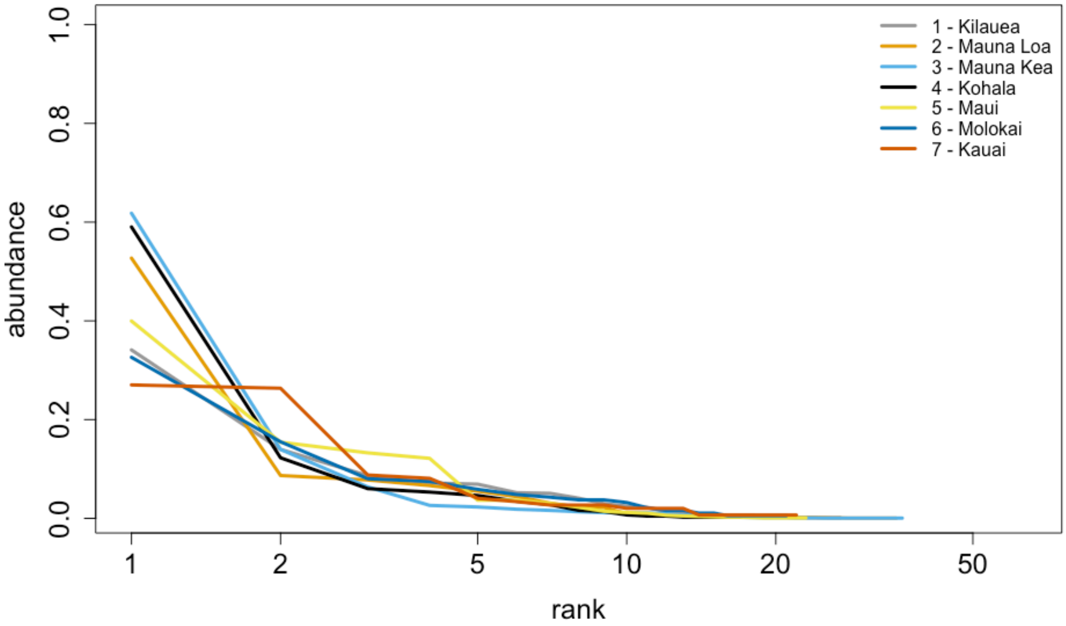

Figure S 3: Rank abundance curve per volcano across the chronosequence.

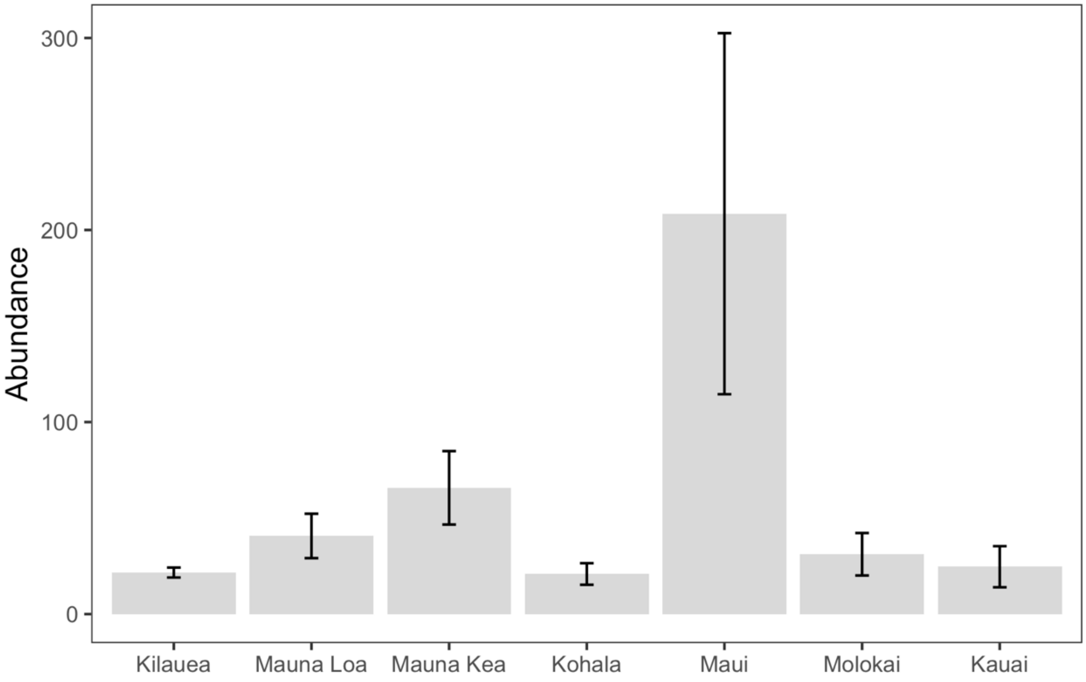

Figure S 4: Insect abundance per volcano across the chronosequence.

Appendix S 3: Chapter 3

Table S 4: Species codes, taxonomic information, and total abundance of all specimens in the kīpuka dataset collected in 2009 and 2010.

Species code	**Class**	**Order**	**Family**	**Genus**	**Species**	**Authority**	**Total abundance**
ACARI	Arachnida	Acari	Acari f.	Acari f.g.	spp.		562
arankapi	Arachnida	Araneae	Araneidae	*Araneus*	*kapiolaniae*	Simon, 1900	2
erigosp1	Arachnida	Araneae	Linyphiidae	*Erigone*	sp. 1		274
linyp001	Arachnida	Araneae	Linyphiidae	*Mermessus*	sp. 1		241
tenuisp1	Arachnida	Araneae	Linyphiidae	*Tenuiphantes*	sp. 1		114
cheimord	Arachnida	Araneae	Miturgidae	*Cheiracanthium*	*mordax*	L Koch, 1866	1
pagiatom	Arachnida	Araneae	Philodromidae	*Pagiopalus*	*atomarius*	Simon, 1900	116
paginigr	Arachnida	Araneae	Philodromidae	*Pagiopalus*	*nigriventris*	Simon, 1900	119
pediacul	Arachnida	Araneae	Philodromidae	*Pedinopistha*	*aculeata*	(Simon 1900)	10
havanava	Arachnida	Araneae	Salticidae	*Havaika*	*navata*	(Simon, 1900)	4
tetracut	Arachnida	Araneae	Tetragnathidae	*Tetragnatha*	*acuta*	Gillespie, 1992	55
tetrquas	Arachnida	Araneae	Tetragnathidae	*Tetragnatha*	*quasimodo*	Gillespie, 1992	207
tetrrest	Arachnida	Araneae	Tetragnathidae	*Tetragnatha*	*restricta*	Simon, 1900	1
ariawaik	Arachnida	Araneae	Theridiidae	*Ariamnes*	*waikula*	Gillespie & Rivera, 2007	1
crypripa	Arachnida	Araneae	Theridiidae	*Cryptachaea*	*riparia*	(Blackwall, 1834)	2
thermeli	Arachnida	Araneae	Theridiidae	*Theridion*	*melinum*	Simon, 1900	10
therprae	Arachnida	Araneae	Theridiidae	*Theridion*	*praetextum*	Simon, 1900	91
mecaangu	Arachnida	Araneae	Thomisidae	*Mecaphesa*	*anguliventris*	(Simon, 1900)	502

mecafacu	Arachnida	Araneae	Thomisidae	*Mecaphesa*	*facundus*	(Suman, 1970)	195
mecansp1	Arachnida	Araneae	Thomisidae	*Mecaphesa*	n sp. 1		16
nannosp1	Diplopoda	Spirostreptida	Cambalidae	*Nannolene*	sp. 1		3
xylet001	Insecta	Coleoptera	Anobiidae	*Xyletobius*	sp. 1		1
mecydeve	Insecta	Coleoptera	Carabidae	*Mecyclothorax*	*deverilli*	Liebherr, 2008	5
cis001	Insecta	Coleoptera	Ciidae	*Cis*	sp. 1		3
proso001	Insecta	Coleoptera	Nitidulidae	*Prosopeus*	sp. 1		1
stelgemi	Insecta	Coleoptera	Nitidulidae	*Stelidota*	*geminata*	(Say, 1825)	5
xylesaxe	Insecta	Coleoptera	Scolytidae	*Xyleborinus*	*saxeseni*	(Ratzeburg, 1837)	4
entomauk	Insecta	Collembola	Entomobryidae	*Entomobrya*	*mauka*	Christiansen & Bellinger, 1992	1
entomult	Insecta	Collembola	Entomobryidae	*Entomobrya*	*multifasciata*	(Tullberg, 1871)	253
entonyhu	Insecta	Collembola	Entomobryidae	*Entomobrya*	*nyhusae*	Christiansen & Bellinger, 1992	130
entosoci	Insecta	Collembola	Entomobryidae	*Entomobrya*	*socia*	Denis, 1929	1
collem004	Insecta	Collembola	Entomobryidae	Entomobryine g	sp. 4		2
salicele	Insecta	Collembola	Entomobryidae	*Salina*	*celebensis*	(Schaeffer, 1898)	3
tomomino	Insecta	Collembola	Entomobryidae	*Tomocerus*	*minor*	(Lubbock, 1862)	3
willkahl	Insecta	Collembola	Entomobryidae	*Willowsia*	*kahlertae*	Christiansen & Bellinger, 1992	303
crypther	Insecta	Collembola	Isotomidae	*Cryptopygus*	*thermophilus*	(Axelson, 1900)	3
isotsens	Insecta	Collembola	Isotomidae	*Isotoma*	*sensibilis*	Tullberg, 1876	3
chiro001	Insecta	Diptera	Chironomidae	*Orthocladius*	sp. 1		1
culequin	Insecta	Diptera	Culicidae	*Culex*	*quinquefasciatus*	Say, 1823	1
camps001	Insecta	Diptera	Dolichopodidae	*Campsicnemus*	sp. 1		2
scapt001	Insecta	Diptera	Drosophilidae	*Scaptomyza*	*?tumidula*		4

ctenhawa	Insecta	Diptera	Sciaridae	*Ctenosciara*	*hawaiiensis*	(Hardy, 1956)	1
hypemagn	Insecta	Diptera	Sciaridae	*Hyperlasion*	*magnisensoria*	(Hardy, 1965)	1
iolaperk	Insecta	Hemiptera	Cixiidae	*Iolania*	*perkinsi*	Kirkaldy, 1902	1
leiahawa	Insecta	Hemiptera	Delphacidae	*Leialoha*	*hawaiiensis*	Muir, 1916	13
leiaohia	Insecta	Hemiptera	Delphacidae	*Leialoha*	*ohiae*	(Kirkaldy, 1910)	346
siphacut	Insecta	Hemiptera	Flatidae	*Siphanta*	*acuta*	(Walker, 1851)	4
nysicoen	Insecta	Hemiptera	Lygaeidae	*Nysius*	*coenosulus*	Stal, 1859	1
oceapter	Insecta	Hemiptera	Lygaeidae	*Oceanides*	*pteridicola*	(White, 1881)	1
oceavulc	Insecta	Hemiptera	Lygaeidae	*Oceanides*	*vulcan*	(White, 1881)	949
hyalpell	Insecta	Hemiptera	Miridae	*Hyalopeplus*	*pellucida*	(Stal, 1859)	1
koanhawa	Insecta	Hemiptera	Miridae	*Koanoa*	*hawaiiensis*	Kirkaldy, 1902	13
miridjuv1	Insecta	Hemiptera	Miridae	Miridae g	juv sp. 1		285
opunshar	Insecta	Hemiptera	Miridae	*Opuna*	*sharpianus*	(Kirkaldy, 1902)	7
orthmetr	Insecta	Hemiptera	Miridae	*Orthotylus*	*metrosideri*	Polhemus, 2004	45
saroadon	Insecta	Hemiptera	Miridae	*Sarona*	*adonias*	Kirkaldy, 1902	50
nabiosci	Insecta	Hemiptera	Nabidae	*Nabis*	*oscillans*	Blackburn, 1888	111
tymptymp	Insecta	Hemiptera	Pseudococcidae	*Tympanococcus*	*tympanistus*	(Ferris, 1948)	77
parihawa	Insecta	Hemiptera	Triozidae	*Pariaconus*	*hawaiiensis*	(Crawford, 1918)	71
pariminu	Insecta	Hemiptera	Triozidae	*Pariaconus*	*minutus*	(Crawford, 1918)	14
paripele	Insecta	Hemiptera	Triozidae	*Pariaconus*	*pele*	Percy, 2017	11
pariprob	Insecta	Hemiptera	Triozidae	*Pariaconus*	*proboscideus*	Percy, 2017	14
paripyra	Insecta	Hemiptera	Triozidae	*Pariaconus*	*pyramidalis*	Percy, 2017	1
pariwyve	Insecta	Hemiptera	Triozidae	*Pariaconus*	*wyvernus*	Percy, 2017	2
siero001	Insecta	Hymenoptera	Bethylidae	*Sierola*	sp. 1		58

siero002	Insecta	Hymenoptera	Bethylidae	*Sierola*	sp. 2		20
braco001	Insecta	Hymenoptera	Braconidae	Braconidae g	sp. 1		1
dicoperk	Insecta	Hymenoptera	Dryinidae	*Dicondylus*	*perkinsi*	(Ashmead), 1901	5
encyr002	Insecta	Hymenoptera	Encyrtidae	Encyrtidae g.	sp. 2		11
encyr003	Insecta	Hymenoptera	Encyrtidae	Encyrtidae g.	sp. 3		37
encyr004	Insecta	Hymenoptera	Encyrtidae	Encyrtidae g.	sp. 4		2
plaghosp	Insecta	Hymenoptera	Encyrtidae	*Plagiomerus*	*hospes*	Timberlake, 1920	2
eudemeta	Insecta	Hymenoptera	Eulophidae	*Euderus*	*metallicus*	(Ashmead, 1901)	3
pauaswez	Insecta	Hymenoptera	Eulophidae	*Pauahiana*	*swezeyi*	Yoshimoto 1965	20
anopgrac	Insecta	Hymenoptera	Formicidae	*Anoplolepis*	*gracilipes*	(Smith, 1857)	1
formi001	Insecta	Hymenoptera	Formicidae	Formicidae g.	alate 1		1
wasmauro	Insecta	Hymenoptera	Formicidae	*Wasmannia*	*auropunctata*	(Roger, 1863)	1
sceli001	Insecta	Hymenoptera	Mymaridae	Mymaridae g.	sp. 2		1
polyn001	Insecta	Hymenoptera	Mymaridae	*Polynema*	sp. 1		16
baeus001	Insecta	Hymenoptera	Scelionidae	*Baeus*	sp. 1		22
telen001	Insecta	Hymenoptera	Scelionidae	*Telenomus*	sp. 1		138
signaspi	Insecta	Hymenoptera	Signiphoridae	*Signiphora*	*aspidioti*	Ashmead, 1900	1
leplarv2	Insecta	Lepidoptera	Carposinidae	*Carposina*	sp. 2		3
leplarv11	Insecta	Lepidoptera	Geometridae	*Eupethecia*	sp. 11		4
leplarv12	Insecta	Lepidoptera	Geometridae	*Scotorythra*	sp. 12		4
leplarv4	Insecta	Lepidoptera	Geometridae	*Scotorythra*	sp. 4		5
leplarv6	Insecta	Lepidoptera	Geometridae	*Scotorythra*	sp. 6		3
Lepidoptera	Insecta	Lepidoptera	Lepidoptera f.	Lepidoptera f.g.	spp.		51
leplarv3	Insecta	Lepidoptera	Oecophoridae	*Thyrocopa*	sp. 3		9

leplarv1	Insecta	Lepidoptera	Tortricidae	*Eccoptocera*	sp. 1		73
anomfulv	Insecta	Neuroptera	Chrysopidae	*Anomalochrysa*	*fulvescens rhododora*	Perkins, 1899	8
anomhepa	Insecta	Neuroptera	Chrysopidae	*Anomalochrysa*	*hepatica*	McLachlan, 1883	1
anoma001	Insecta	Neuroptera	Chrysopidae	*Anomalochrysa*	sp		28
hemer001	Insecta	Neuroptera	Hemerobiidae	*Hemerobius*	sp. 1		10
Orthoptera	Insecta	Orthoptera	Orthoptera f.	Orthoptera f.g.	spp.		1
ectocali	Insecta	Psocoptera	Ectopsocidae	*Ectopsocus*	*californicus*	(Banks, 1903)	1
ectomain	Insecta	Psocoptera	Ectopsocidae	*Ectopsocus*	*maindroni*	Badonnel, 1935	1
kilau001	Insecta	Psocoptera	Elipsocidae	*Kilauella*	sp. 1		359
kilau003	Insecta	Psocoptera	Elipsocidae	*Kilauella*	sp. 3		152
kilauspp	Insecta	Psocoptera	Elipsocidae	*Kilauella*	spp. juveniles		1213
propnsp1	Insecta	Psocoptera	Elipsocidae	*Propsocus*	n sp. 1		1
ptyclobo	Insecta	Psocoptera	Psocidae	*Ptycta*	*lobophora*	Thornton, 1984	13
ptycmacu	Insecta	Psocoptera	Psocidae	*Ptycta*	*maculifrons*	Thornton, 1984	2
ptyct002	Insecta	Psocoptera	Psocidae	*Ptycta*	sp. 2		9
Thysanoptera	Insecta	Thysanoptera	Thysanoptera f.	Thysanoptera f.g.	spp.		94
porcscab	Malacostraca	Isopoda	Porcellionidae	*Porcellio*	*scaber*	Latreille, 1804	36

Table S 5: Likelihood ratio tests and model output for the relationship between diversity (Hill number q=0, q=1, q=2) or species density with kīpuka area, using linear mixed effect models and kīpuka identity as random effect.

		Estimate	2.5% CI	97.5% CI	p value	Log ratio χ^2
Hill number	q = 0	0.0197	-0.9900	0.9837	0.9089	0.0131
	q = 1	0.2246	-0.09745	0.5466	0.169	1.8919
	q = 2	0.2683	-0.03679	0.5733	0.08392	2.9872
Species density		0.1573	0.04394	0. 2661	0.00964	6.67003

Table S 6: Model output of the species area relationship across various insect traits, using linear mixed effect models with kīpuka identity as random effect.

Category	Description	Levels	F statistic	*P* value
Dispersal ability	Wing presence	Absent / present	3.653	0.08494
Body size	Size class	Small(< 1.5 mm) / medium (1.5 mm < size < 4 mm) / large (> 4 mm)	2.082	0.1336

Table S 7: Correlation coefficients for predictors used in generalized linear mixed effect models.

	dNC	*dIICconnector*	*dIICintra*	*dIICflux*	Area	Tree height
dNC	-	-	-	-	-	-
dIICconnector	-0.2658	-	-	-	-	-
dIICintra	-0.0888	-0.0483	-	-	-	-
dIICflux	-0.4077	0.5398	-0.0695	-	-	-
Area	-0.2658	0.0142	0.9518	0.0821	-	-
Tree height	-0.0888	-0.0483	0.3056	0.3132	0.4882	-
Year	-0.0591	-0.0962	0.1450	0.0108	0.1380	-0.0054

Table S 8: Output for model averaging of linear mixed effect models for effective estimated Shannon index across dispersal thresholds from 50-300 m.[1]

Shannon index

50 m	Parameter	Estimate	Standard Error	Confidence Interval Lower	Confidence Interval Upper	Model Importance
	Year	0.4289 **	0.1471	0.1359	0.7220	0.93
	Area	-	-	-	-	-
	Tree height	0.1463	0.1416	-0.1360	0.4285	0.06
	dIICconnector	0.1681	0.1620	-0.1548	0.4910	0.07
	dIICflux	-0.2886 *	0.1445	-0.5763	-0.009517	0.43
	dNC	0.1545	0.1388	-0.1216	0.4316	0.08

---

[1] Significant predictors in the averaged model are indicated by * (p<0.05), ** (p<0.01), *** (p<0.001). Predictors not included in the averaged models are marked with -.

100 m	Parameter	Estimate	Standard Error	Confidence Interval Lower	Confidence Interval Upper	Model Importance
	Year	0.4190 **	0.1514	0.1192	0.7127	0.93
	Area	-	-	-	-	-
	Tree height	-	-	-	-	-
	dIICconnector	1.376	0.7249	-0.06895	2.821	0.24
	dIICflux	-1.343	0.7239	-2.786	0.1002	0.24
	dNC	-	-	-	-	-

150 m	Parameter	Estimate	Standard Error	Confidence Interval Lower	Confidence Interval Upper	Model Importance
	Year	0.4267 **	0.1477	0.1324	0.7211	0.87
	Area	-	-	-	-	-
	Tree height	-	-	-	-	-
	dIICconnector	-	-	-	-	-
	dIICflux	-	-	-	-	-
	dNC	-	-	-	-	-

200 m	Parameter	Estimate	Standard Error	Confidence Interval Lower	Confidence Interval Upper	Model Importance
	Year	0.4279 **	0.1490	0.1311	0.7247	0.92
	Area	0.1745	0.1438	-0.1120	0.4611	0.12
	Tree height	-	-	-	-	-
	dIICconnector	0.2289	0.1391	-0.04838	0.5062	0.21
	dIICflux	0.1569	0.1452	-0.1325	0.4464	0.1
	dNC	-	-	-	-	-

250 m	Parameter	Estimate	Standard Error	Confidence Interval Lower	Confidence Interval Upper	Model Importance
	Year	0.4191 **	0.1482	0.1239	0.7143	0.92
	Area	0.1745	0.1438	-0.1120	0.4611	0.12
	Tree height	-	-	-	-	-
	dIICconnector	0.2138	0.1380	-0.06122	0.4888	0.18
	dIICflux	0.1802	0.1440	-0.1067	0.4671	0.13
	dNC	-	-	-	-	-

300 m	Parameter	Estimate	Standard Error	Confidence Interval Lower	Confidence Interval Upper	Model Importance
	Year	0.4189 **	0.1482	0.1237	0.7142	0.92
	Area	0.1745	0.1438	-0.1120	0.4611	0.12
	Tree height	-	-	-	-	-
	dIICconnector	0.2114	0.1382	-0.06412	0.4870	0.17
	dIICflux	0.1774	0.1441	-0.1098	0.4647	0.12
	dNC	-	-	-	-	-

Table S 9: Model averaging output for linear mixed effect models for effective estimated Simpson index across dispersal thresholds from 50-300 m.[2]

Simpson index						
50 m	Parameter	Estimate	Standard Error	Confidence Interval Lower	Confidence Interval Upper	Model Importance
	Year	0.4462 **	0.1426	0.1620	0.7304	1
	Area	0.1055	0.06969	-0.03340	0.2444	0.09
	Tree height	-	-	-	-	-
	dIICconnector	-	-	-	-	-
	dIICflux	-0.2395	0.1347	-0.5041	0.02524	0.25
	dNC	0.1986	0.1383	-0.06983	0.4671	0.15
100 m	Parameter	Estimate	Standard Error	Confidence Interval Lower	Confidence Interval Upper	Model Importance
	Year	0.4300 **	0.1439	0.1433	0.7145	1
	Area	0.1467	0.0861	-0.02455	0.6289	0.22
	Tree height	-	-	-	-	-
	dIICconnector	1.413 *	0.7037	0.009717	2.815	0.33
	dIICflux	-1.457 *	0.7229	-2.897	-0.01670	0.33
	dNC	-	-	-	-	-
150 m	Parameter	Estimate	Standard Error	Confidence Interval Lower	Confidence Interval Upper	Model Importance
	Year	0.4415	0.1429	0.1568	0.7261	1
	Area	0.1055	0.06969	-0.03341	0.2444	0.15
	Tree height	-	-	-	-	-
	dIICconnector	-	-	-	-	-
	dIICflux	-	-	-	-	-
	dNC	-	-	-	-	-

---

[2] Significant predictors in the averaged model are indicated by * (p<0.05), ** (p<0.01), *** (p<0.001). Predictors not included in the averaged models are marked with -.

200 m	Parameter	Estimate	Standard Error	Confidence Interval Lower	Confidence Interval Upper	Model Importance
	Year	0.4429**	0.1438	0.1564	0.7294	1
	Area	0.3011	0.3166	-0.3277	0.9299	0.28
	Tree height	-	-	-	-	-
	dIICconnector	0.2330	0.1351	-0.03626	0.5023	0.25
	dIICflux	-0.04872	0.4368	-0.9141	0.8166	0.16
	dNC	-0.1038	0.1379	-0.3786	0.1710	0.06
250 m	Parameter	Estimate	Standard Error	Confidence Interval Lower	Confidence Interval Upper	Model Importance
	Year	0.4353**	0.1431	0.1502	0.7228	1
	Area	0.2754	0.3682	-0.4578	1.008	0.23
	Tree height	-	-	-	-	-
	dIICconnector	0.2203	0.1362	-0.05114	0.4917	0.18
	dIICflux	0.04701	0.4217	-0.7908	0.8848	0.21
	dNC	-	-	-	-	-
300 m	Parameter	Estimate	Standard Error	Confidence Interval Lower	Confidence Interval Upper	Model Importance
	Year	0.4349**	0.1431	0.1497	0.7200	1
	Area	0.3050	0.4033	-0.4976	1.108	0.24
	Tree height	-	-	-	-	-
	dIICconnector	0.2204	0.1364	-0.05146	0.4922	0.18
	dIICflux	0.05518	0.4654	-0.9186	0.9296	0.21
	dNC	-	-	-	-	-

Table S 10: Model averaging output for linear mixed effect models for effective species richness across dispersal thresholds from 50-300 m. [3]

Species Richness						
50 m	Parameter	Estimate	Standard Error	Confidence Interval Lower	Confidence Interval Upper	Model Importance
	Year	-	-	-	-	-
	Area	-	-	-	-	-
	Tree height	0.2850*	0.1206	-0.0015	0.5252	0.65
	dIICconnector	-	-	-	-	-
	dIICflux	-0.1048	0.1261	-0.3562	0.1465	0.07
	dNC	0.1166	0.1288	-0.1401	0.3733	0.08

---

[3] Significant predictors in the averaged model are indicated by * (p<0.05), ** (p<0.01), *** (p<0.001). Predictors not included in the averaged models are marked with -.

100 m	Parameter	Estimate	Standard Error	Confidence Interval Lower	Confidence Interval Upper	Model Importance
	Year	-	-	-	-	-
	Area	-	-	-	-	-
	Tree height	0.2751*	0.1169	0.04221	0.5081	0.59
	dIICconnector	-	-	-	-	-
	dIICflux	-	-	-	-	-
	dNC	-	-	-	-	-

150 m	Parameter	Estimate	Standard Error	Confidence Interval Lower	Confidence Interval Upper	Model Importance
	Year	-	-	-	-	-
	Area	-	-	-	-	-
	Tree height	0.2795*	0.1180	0.04446	0.5145	0.63
	dIICconnector	-	-	-	-	-
	dIICflux	-0.1227	0.1219	-0.3655	0.1202	0.09
	dNC	-	-	-	-	-

200 m	Parameter	Estimate	Standard Error	Confidence Interval Lower	Confidence Interval Upper	Model Importance
	Year	-	-	-	-	-
	Area	-0.1105	0.1370	-0.3836	0.1626	0.08
	Tree height	0.2871	0.1229	0.04237	0.3185	0.65
	dIICconnector	-	-	-	-	-
	dIICflux	-0.1062	0.1308	-0.3670	0.1546	0.07
	dNC	-	-	-	-	-

250 m	Parameter	Estimate	Standard Error	Confidence Interval Lower	Confidence Interval Upper	Model Importance
	Year	-	-	-	-	-
	Area	-0.1105	0.1370	-0.3836	0.1626	0.08
	Tree height	0.2827	0.1213	-0.0412	0.5242	0.62
	dIICconnector	-	-	-	-	-
	dIICflux	-	-	-	-	-
	dNC	-	-	-	-	-

300 m	Parameter	Estimate	Standard Error	Confidence Interval Lower	Confidence Interval Upper	Model Importance
	Year	-	-	-	-	-
	Area	-	-	-	-	-
	Tree height	0.2751*	0.1169	0.04222	0.0815	0.59
	dIICconnector	-	-	-	-	-
	dIICflux	-	-	-	-	-

	dNC	-	-	-	-	-

Table S 11: Model averaging output for linear mixed effect models for arthropod abundance across dispersal thresholds from 50-300 m. [4]

Abundance						
50 m	Parameter	Estimate	Standard Error	Confidence Interval Lower	Confidence Interval Upper	Model Importance
	Year	0.1543	0.09861	-0.04219	0.3509	0.1
	Area	0.1082*	0.04762	0.01333	0.2032	0.18
	Tree height	0.2000 *	0.09749	0.005657	0.3942	0.23
	dIICconnector	-	-	-	-	-
	dIICflux	0.3287 **	0.1044	0.1208	0.5365	1
	dNC	-0.1281	0.1103	-0.3479	0.09162	-
100 m	Parameter	Estimate	Standard Error	Confidence Interval Lower	Confidence Interval Upper	Model Importance
	Year	0.1554	0.09914	-0.04219	0.3531	0.16
	Area	-	-	-	-	-
	Tree height	0.1699	0.0985	-0.02643	0.3663	0.21
	dIICconnector	-1.4581 **	0.5144	-2.482	-0.4337	1
	dIICflux	1.685 **	0.5175	0.6542	2.715	1
	dNC	-	-	-	-	-
150 m	Parameter	Estimate	Standard Error	Confidence Interval Lower	Confidence Interval Upper	Model Importance
	Year	0.1544	0.0996	-0.04411	0.3530	0.11
	Area	-	-	-	-	-
	Tree height	0.2160	0.1117	-0.005939	0.4380	0.31
	dIICconnector	-0.8906*	0.3854	-1.658	-0.1231	0.71
	dIICflux	0.9502	0.4946	-0.02694	1.927	0.89
	dNC	-	-	-	-	-
200 m	Parameter	Estimate	Standard Error	Confidence Interval Lower	Confidence Interval Upper	Model Importance
	Year	0.1652	0.1015	-0.0370	0.3674	0.11
	Area	0.2072	0.2329	-0.2564	0.6709	0.22

---

[4] Significant predictors in the averaged model are indicated by * (p<0.05), ** (p<0.01), *** (p<0.001). Predictors not included in the averaged models are marked with -.

	Tree height	0.2520*	0.1076	0.03785	0.4660	0.44
	dIICconnector	-0.1517	0.1064	-0.3638	0.06032	0.12
	dIICflux	0.2157	0.2169	-0.2161	0.6475	0.27
	dNC	-	-	-	-	-
250 m	Parameter	Estimate	Standard Error	Confidence Interval Lower	Confidence Interval Upper	Model Importance
	Year	0.1544	0.09959	-0.04411	0.3523	0.11
	Area	-	-	-	-	-
	Tree height	0.2160	0.1117	-0.005939	0.4380	0.31
	dIICconnector	-0.8906*	0.3854	-1.658	-0.1231	0.71
	dIICflux	0.9502	0.4946	-0.0269	1.927	0.89
	dNC	-	-	-	-	-
300 m	Parameter	Estimate	Standard Error	Confidence Interval Lower	Confidence Interval Upper	Model Importance
	Year	0.1611	0.1016	-0.04144	0.3636	0.15
	Area	0.1723	0.3026	-0.4297	0.7742	0.25
	Tree height	0.2513 *	0.1088	0.03470	0.4678	0.42
	dIICconnector	-	-	-	-	-
	dIICflux	0.2417	0.2621	-0.2805	0.7639	0.31
	dNC	-	-	-	-	-

Table S 12: Model averaging output for linear mixed effect models for arthropod species density across dispersal thresholds from 50-300 m. [5]

Species Density						
50 m	Parameter	Estimate	Standard Error	Confidence Interval Lower	Confidence Interval Upper	Model Importance
	Year	0.4368 ***	0.1057	0.2263	0.6473	1
	Area	0.1394 *	0.06419	0.01145	0.2673	0.16
	Tree height	0.2675 *	0.1113	0.04580	0.4892	0.51
	dIICconnector	-	-	-	-	-
	dIICflux	-0.1295	0.1262	-0.3811	0.1220	0.07
	dNC	-	-	-	-	-

---

[5] Significant predictors in the averaged model are indicated by * ($p<0.05$), ** ($p<0.01$), *** ($p<0.001$). Predictors not included in the averaged models are marked with -.

100 m	Parameter	Estimate	Standard Error	Confidence Interval Lower	Confidence Interval Upper	Model Importance
	Year	0.6160 ***	0.1504	0.3163	0.9157	1
	Area	0.1659	0.08863	-0.0107	0.3426	0.10
	Tree height	0.3010	0.1616	-0.0210	0.6230	0.31
	dIICconnector	0.8647	0.9139	-0.9446	2.674	0.31
	dIICflux	-0.7630	1.015	-2.771	1.245	0.25
	dNC	-0.2146	0.1769	-0.5672	0.1379	0.08

150 m	Parameter	Estimate	Standard Error	Confidence Interval Lower	Confidence Interval Upper	Model Importance
	Year	0.6190 ***	0.1504	0.3192	0.9187	1
	Area	0.1660	0.0886	-0.0107	0.3426	0.12
	Tree height	0.2776	0.1564	-0.03408	0.5892	0.25
	dIICconnector	0.2720	0.3939	-0.5127	1.056	0.21
	dIICflux	0.06260	0.4815	-0.8948	1.020	0.15
	dNC	-0.1518	0.1810	-0.5125	0.2090	0.07

200 m	Parameter	Estimate	Standard Error	Confidence Interval Lower	Confidence Interval Upper	Model Importance
	Year	0.6116 ***	0.1504	0.	0.	1
	Area	0.2913	0.3880	-0.	1.	0.35
	Tree height	0.2484	0.1684	0.	0.	0.26
	dIICconnector	-	-	-	-	-
	dIICflux	0.2460	0.4034	-0.	1.	0.34
	dNC	-	-	-	-	-

250 m	Parameter	Estimate	Standard Error	Confidence Interval Lower	Confidence Interval Upper	Model Importance
	Year	0.6109 ***	0.1503	0.3114	0.9103	1
	Area	0.04961	0.6085	-1.158	1.257	0.35
	Tree height	0.2412	0.1719	-0.1011	0.5836	0.25
	dIICconnector	0.03869	0.2020	-0.3631	0.4405	0.07
	dIICflux	0.4350	0.4941	-0.5487	1.4188	0.44
	dNC	-	-	-	-	-

300 m	Parameter	Estimate	Standard Error	Confidence Interval Lower	Confidence Interval Upper	Model Importance
	Year	0.6106 ***	0.1503	0.3111	0.9100	1
	Area	-0.0267	0.6428	-1.249	1.303	0.36
	Tree height	0.2402	0.1721	-0.1025	0.5829	0.25
	dIICconnector	0.03111	0.2052	-0.3769	0.4392	0.07
	dIICflux	0.4510	0.5258	-0.5956	1.4976	0.44
	dNC	-	-	-	-	-

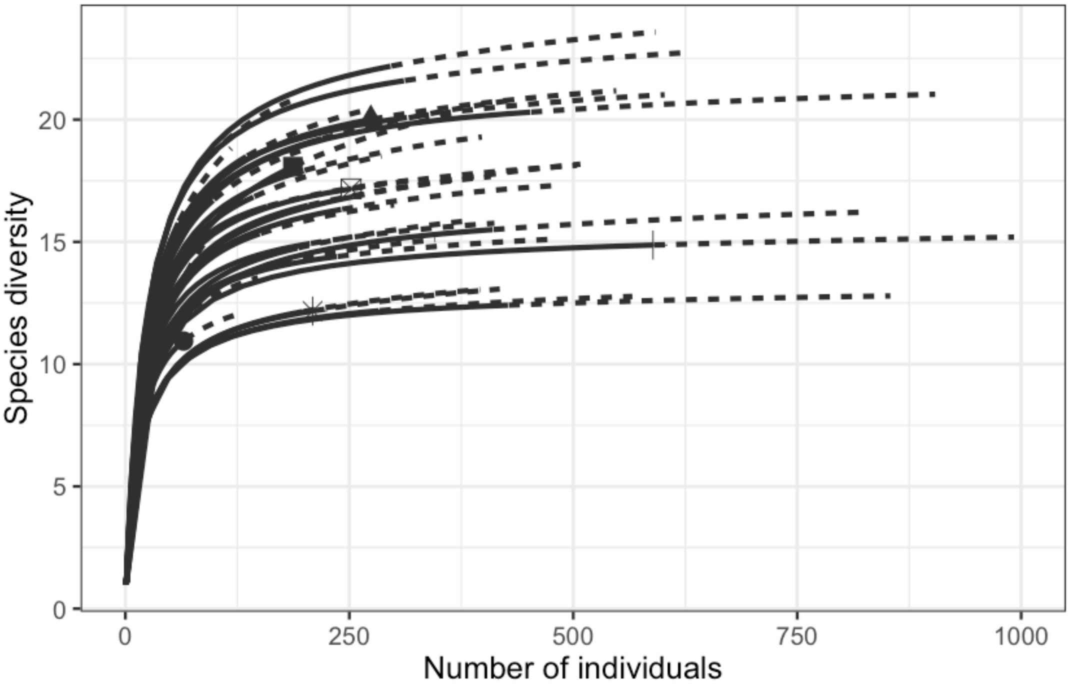

Figure S 5: Species extrapolation curve for arthropod sampling for species richness. Each line represents a single tree sample. The solid lines are interpolated, the dashed lines are extrapolated richness.

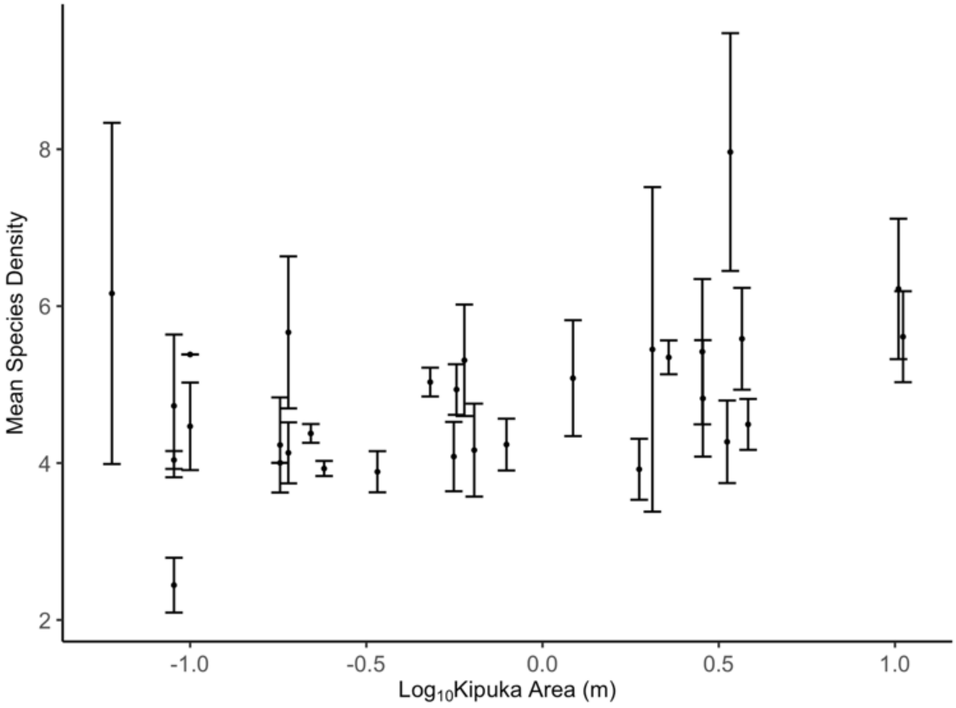

Figure S 6: Mean species density as a function of log$_{10}$ kīpuka area (m). Mean kīpuka species density is based on center and edge trees sampled in 2009 and 2010. Error bars indicate standard error of the mean.

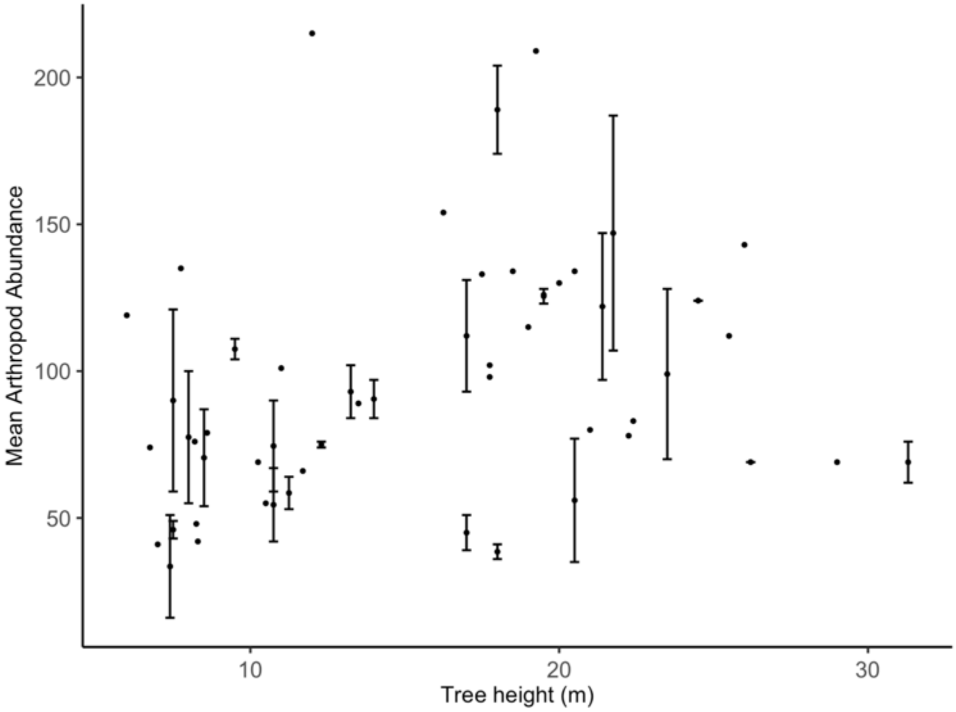

Figure S 7: Mean arthropod abundance per tree (across 2009 and 2010) as a function of sampling tree height (m). Error bars indicate standard error of the mean, points without error bars were only sampled a single time.

Appendix S 4:

Table S 13: Site information.

site	Elevation (m)	Rainfall (mm)	Substrate age (years)	Volcano
HAVO Escape Road	1006	2700	200	Kilauea
HAVO ‘Ola’a	1174	3000	7500	Kilauea
Kau Alili	948 m	2500	450	Mauna Loa
Kau Kaiholena	1018	2900	21000	Mauna Loa

Table S 14: Metrosideros polymorpha *mean trait value per site.*

site	n trees G	n trees H	n trees P	Specific leaf area	water content	foliar nitrogen	foliar phosphorus
HAVO Escape Road	0	2	4	43.2646	0.245208	0.848333	0.0539964
HAVO ‘Ola’a	4	2	0	53.6232	0.217028	1.171667	0.0787297
Kau Alili	3	3	0	80.1229	0.264236	1.56	0.0893019
Kau Kaiholena	2	0	4	41.8357	0.280167	1.048333	0.0545438

Sites at Hawai‘i Volcanoes National Park (HAVO) and Kau Forest Reserve. Morphotype codes are as following: G- glabrous tree, H- hybrid or intermediate trichome presence and P- pubescent tree.

Table S 15: Insect taxonomic and trait information

Species code	Order	Family	Genus	Species	Length	Feeding guild	Location of nymph	Generalist/ specialist
CIC_SP	Hemiptera	Cicadellidae	Sp	Sp	3	sap feeder	NA	NA
COL_BLA	Hemiptera	Pentatomidae	Coleotichus	Blackburniae	3.667	sap feeder	free living	specialist
DAR_HEA	Lepidoptera	Sp	Sp	Dark head	3.25	chewer	free living	generalist
FLA_CUR	Lepidoptera	Sp	Sp	Flat curve	9.333	chewer	free living	generalist
GEO_SP	Lepidoptera	Geometridae	Sp	SP	9.946	chewer	free living	specialist
GRE_PSI	Hemiptera	Aphididae	Greenidea	Psidii	1.495	sap feeder	free living	generalist
HYA_PEL	Hemiptera	Miridae	Hyalopeplus	Pelucidus	3.073	flower / bud	free living	generalist
HYP_SPO	Lepidoptera	Cosmopterigidae	Hyposmocoma	Spotty	6.1	chewer	shelter	specialist
IOL_PER	Hemiptera	Cixiidae	Iolania	Perkinsi	4.133	sap feeder	litter	generalist
KOA_HAW	Hemiptera	Miridae	Koanoa	Hawaiiensis	2.636	sap feeder	free living	generalist
LEI_HAW	Hemiptera	Delphacidae	Leialoha	Hawaiiensis	3.222	sap feeder	free living	specialist
LEI_OHI	Hemiptera	Delphacidae	Leialoha	Ohiae	3.6	sap feeder	free living	specialist
LEI_SP	Hemiptera	Delphacidae	Leialoha	Sp	3	sap feeder	free living	specialist
LEP_SP	Lepidoptera	Sp	Sp	Sp	6.354	chewer	free living	generalist
LIG_SP	Coleoptera	Sp	Sp	Light morph	3.75	chewer	free living	generalist
MIR_SP	Hemiptera	Miridae	Sp	Sp	3.667	sap feeder	NA	NA
MOR_SP	Lepidoptera	Sp	Sp		4.75	chewer	free living	generalist
NES_GIF	Hemiptera	Cicadellidae	Nesophrosyne	Giffardi	4.667	sap feeder	free living	NA
NES_INS	Hemiptera	Cicadellidae	Nesophrosyne	Insularis	5	sap feeder	free living	NA
OCE_VUL	Hemiptera	Lygaeidae	Oceanidae	Vulcan	4.396	seed feeder	free living	specialist
OLI_FIL	Hemiptera	Cixiidae	Oliarus	Filicola/ Koanoa	5	sap feeder	litter	specialist
OLI_INA	Hemiptera	Cixiidae	Oliarus	Inaequalis	5.667	sap feeder	litter	generalist

OLI_SP	Hemiptera	Cixiidae	Oliarus	Sp	5	sap feeder	litter	generalist
OPU_SHA	Hemiptera	Miridae	Opuna	Sharpianus	2.421	sap feeder	free living	generalist
OPU_SP	Hemiptera	Miridae	Opuna	Sp	2.421	sap feeder	free living	generalist
ORT_MET	Hemiptera	Miridae	Orthotylus	Metrosiderii	2.741	sap feeder	free living	specialist
PAR_HAW	Hemiptera	Triozidae	Pariaconus	Hawaiiensis	3.027	sap feeder	stem/bud galler	specialist
PAR_MIN	Hemiptera	Triozidae	Pariaconus	Minutus	1.545	sap feeder	leaf gall	specialist
PAR_NIG	Hemiptera	Triozidae	Pariaconus	Nigrilineatus	1.5	sap feeder	free living	specialist
PAR_PEL	Hemiptera	Triozidae	Pariaconus	Pele	2.397	sap feeder	leaf gall	specialist
PAR_PYR	Hemiptera	Triozidae	Pariaconus	Pyramidalis	2.367	sap feeder	leaf gall	specialist
PAR_SP	Hemiptera	Triozidae	Pariaconus	SP	2	sap feeder	free living	specialist
SAR_ADO	Hemiptera	Miridae	Sarona	Adonias	3.903	sap feeder	free living	specialist
SIP_ACU	Hemiptera	Flatidae	Siphanta	Acuta	6.27	sap feeder	free living	generalist
SPO_HEA	Lepidoptera	Sp	SP	Spotty head	10.5	chewer	free living	generalist
TIN_SP	Lepidoptera	Sp	SP	Tiny morph	4.167	chewer	free living	generalist
TYM_TYM	Hemiptera	Pseudococcidae	Tympanococcus	Tympanistus	2.207	sap feeder	free living	specialist

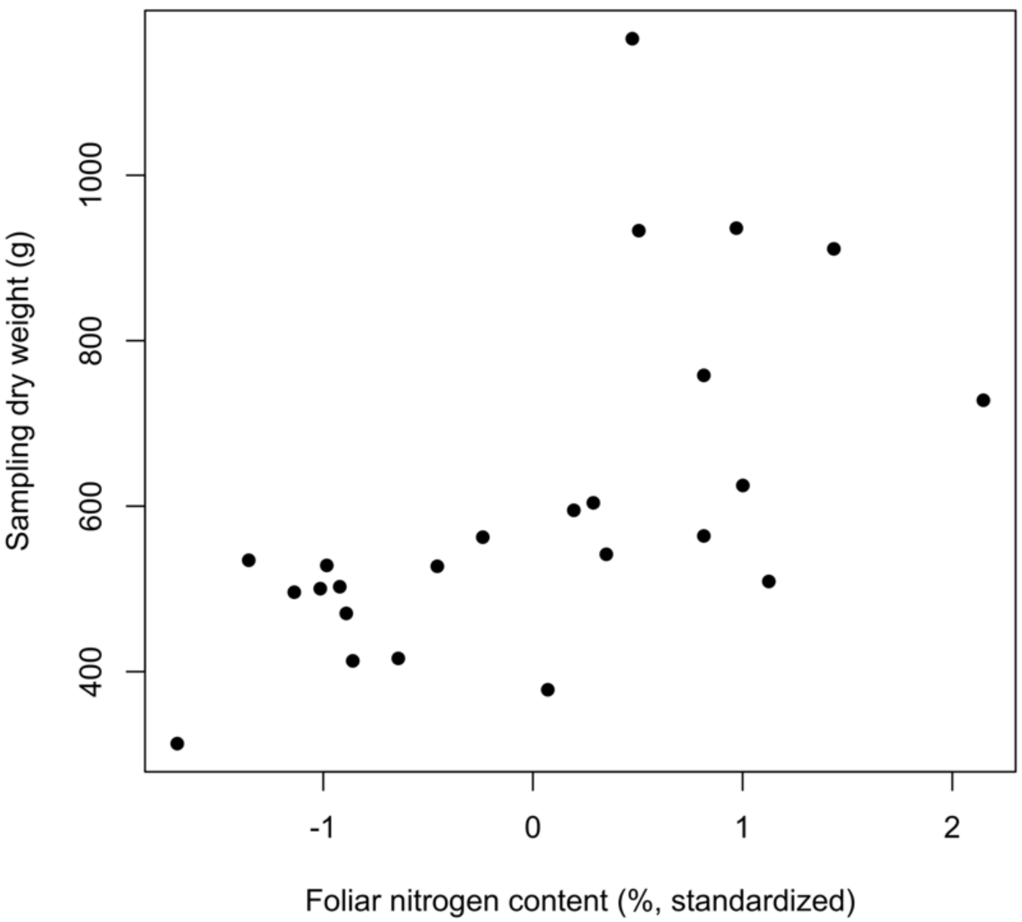

Figure S 8: Dry weight as a function of nitrogen

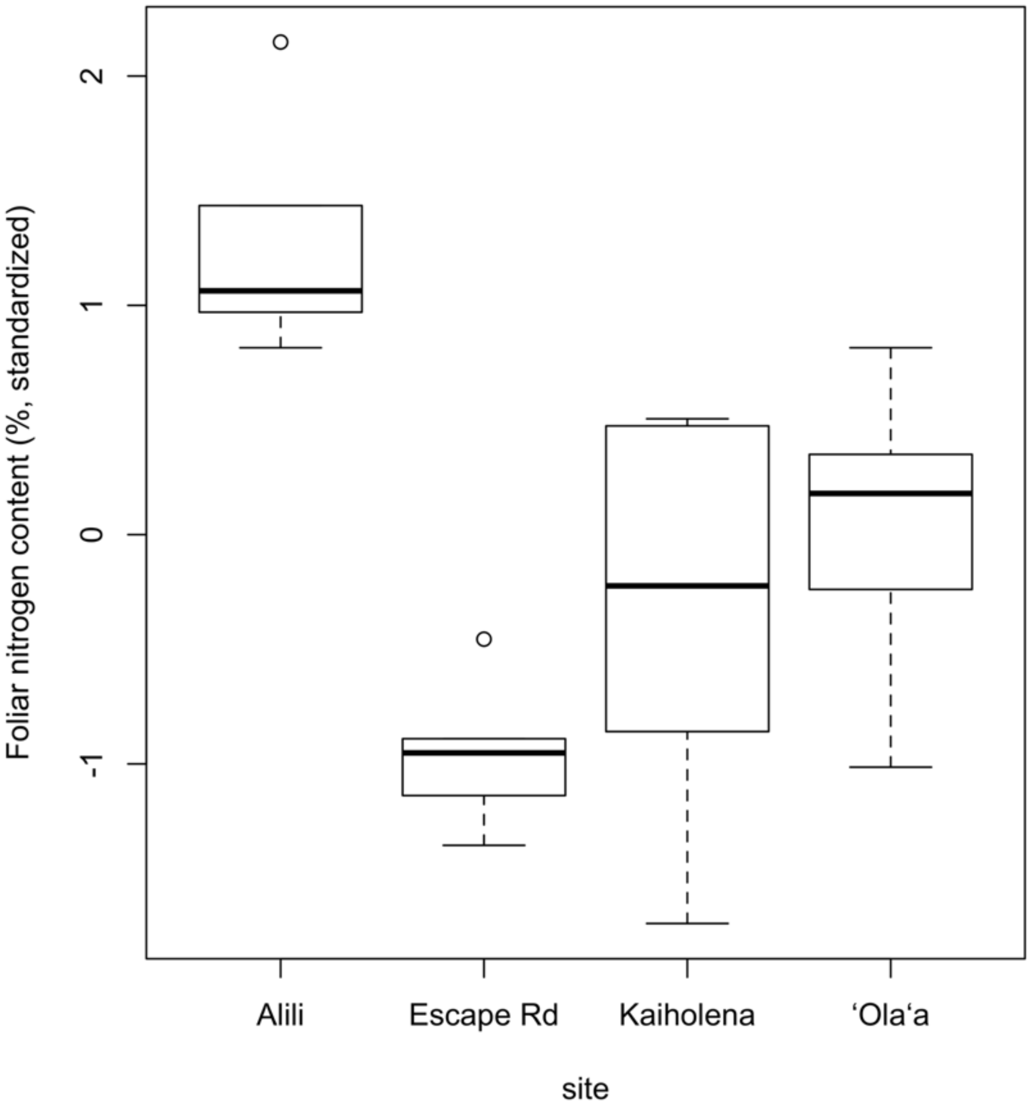

Figure S 9: Nitrogen percentage across sites

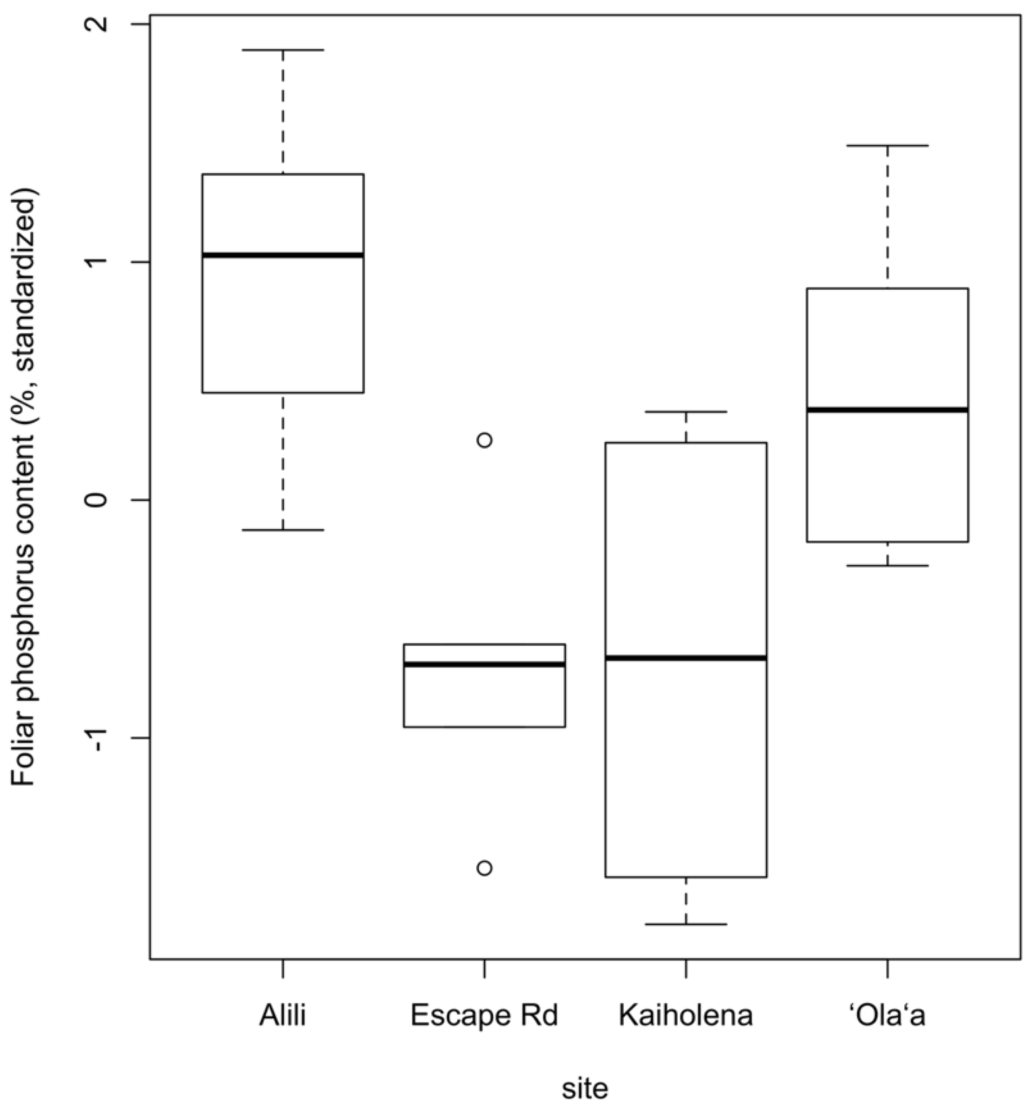

Figure S 10: Foliar phosphorus content across sites

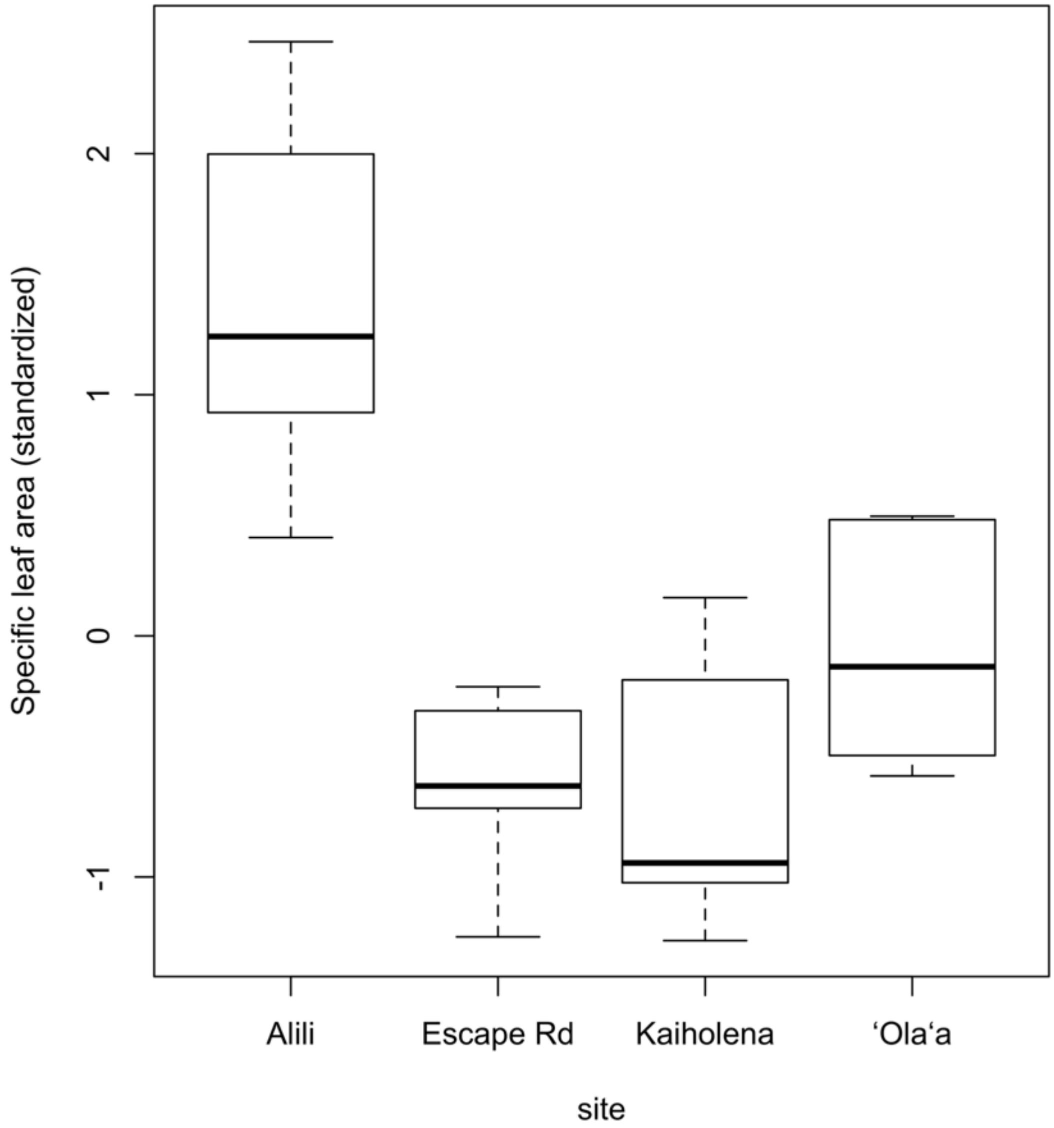

Figure S 11: Mean specific leaf area per site

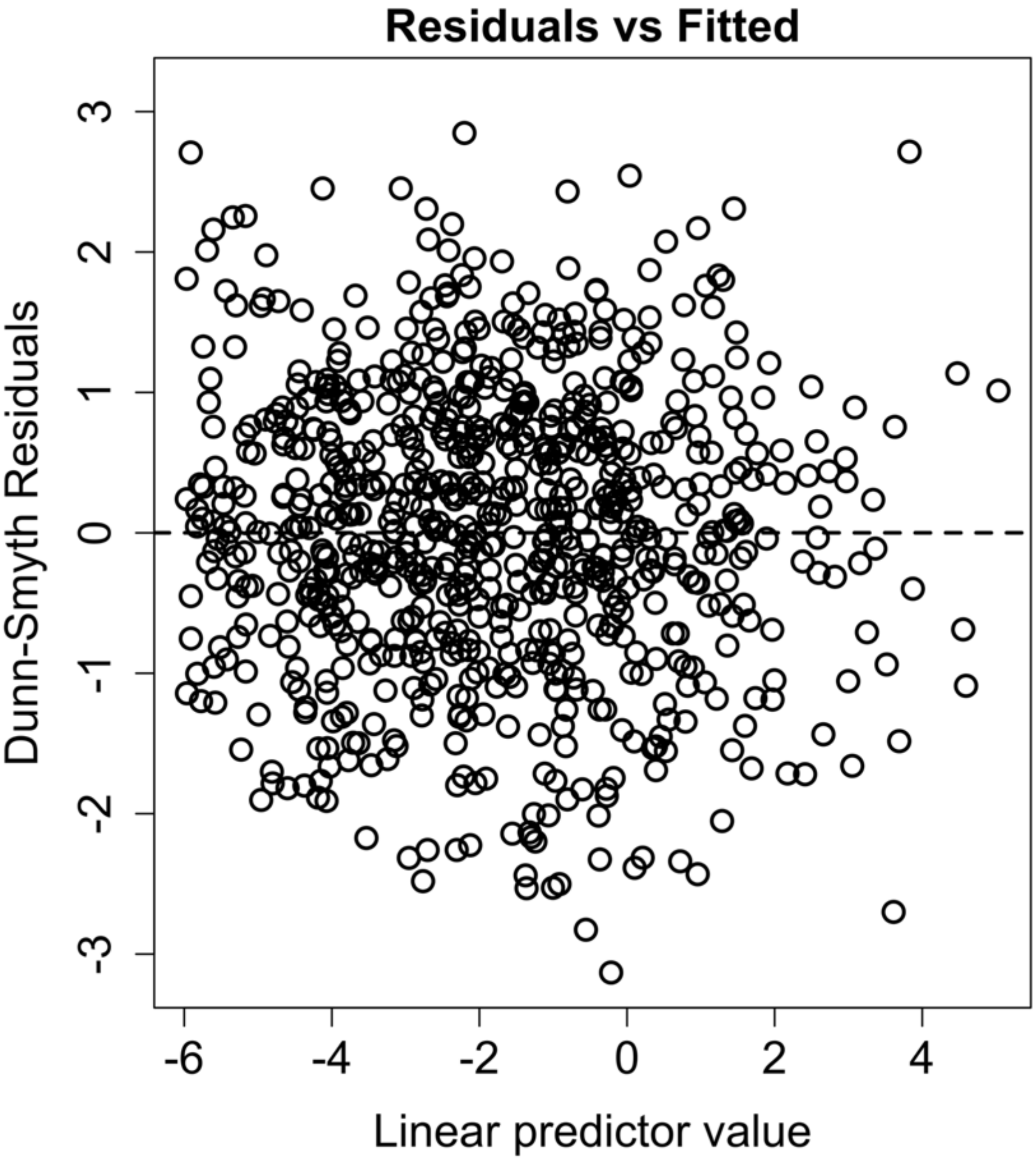

Figure S 12: Residuals from the traitGLM model using method='manyglm', to allow for analysis of deviance and calculating significance using PIT-trap resampling.

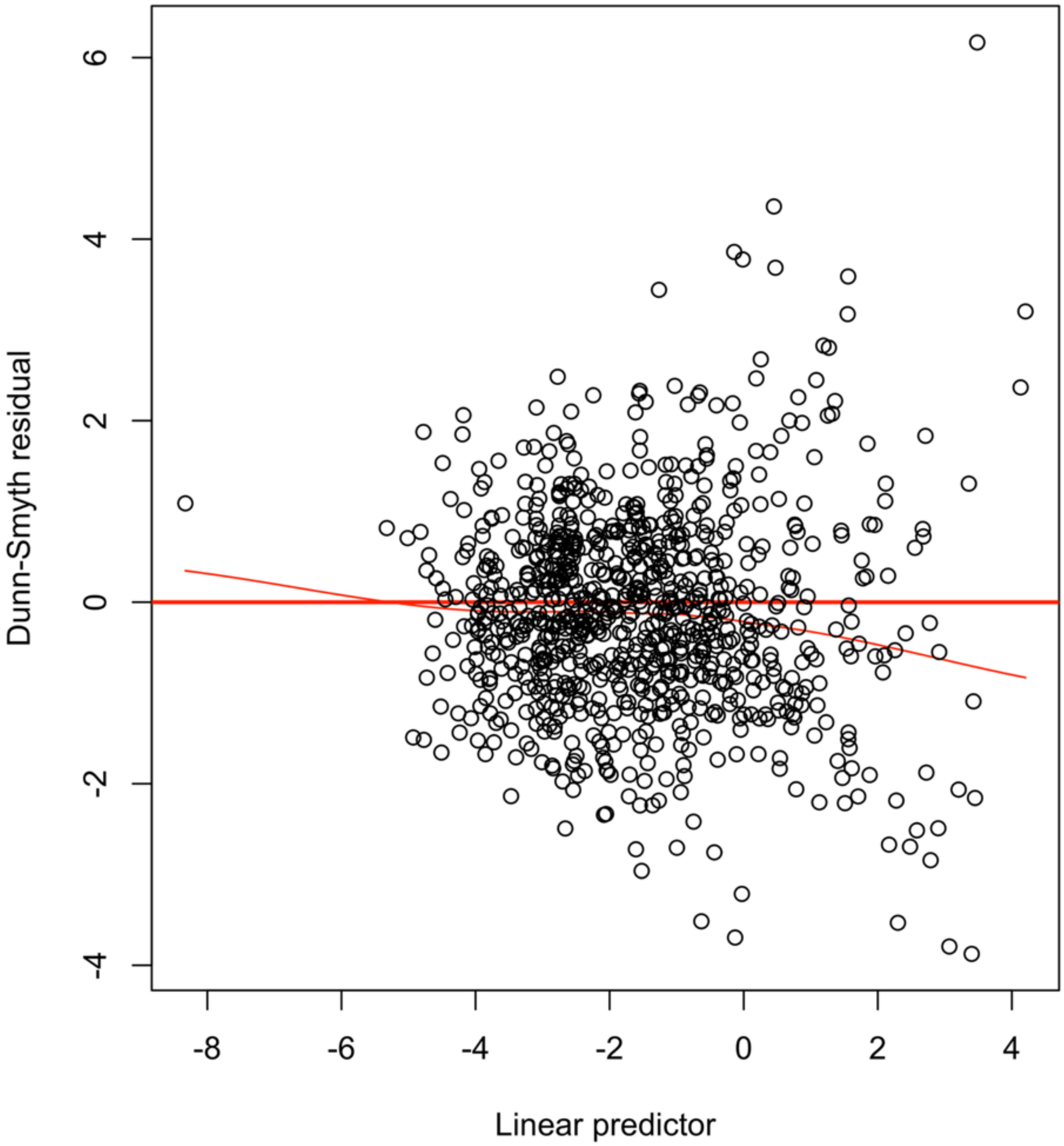

Figure S 13: Residuals from the traitGLM model with negative binomial distribution and LASSO shrinkage.

Appendix S 5:

Methods:

Data was collected according to the methods described in chapter II. Only Hemiptera samples collected in 2014 on Hawaiʻi Island were used for this analysis. Due to limitations on the leaf traits data and LiDAR data, both of which were only sampled on Hawaiʻi Island, I was not able to include Hemiptera assemblages from Maui, Molokaʻi and Kauaʻi.

Leaf traits were measured as described in chapter II. LiDAR data was collected and forest structure metrics were calculated as described in chapter II.

A list of species present was compiled and Hemiptera traits were added based upon direct measurement (body size) or the literature. Where possible, data at the species level was used, however for poorly described species I based trait information on the nearest taxonomic level for which information was available, no coarser than at the family level (See Table S 15 for Hemiptera trait information and sources). Body size was calculated by taking the mean body size for a species across all samples.

Hemiptera morphology was photographed using a Canon microscope camera on a dissection microscope, with specimens carefully placed with the relevant body part perpendicular to the microscope table. When necessary specimens were pinned in place to maintain the correct position. Canon software was used to take measurements on the photos, and photos were saved for reference purposes. I measured body size, wing length, wing width, rostrum length, and pro-, meso- and meta-tibia and femur length. For each species, at least 5 specimens from different sites were measured (where possible), and the mean measurement was calculated. Species level means were used across all sites (i.e. not taking into account intraspecific variation). Ratios were then calculated for each metric of interest, including wing size proportionate to body, wind aspect, rostrum length proportionate to body, profemur as a function of metafemur and metatibia as a function of metafemur.

All statistics were executed using R (R Core Team 2017).

I calculated functional diversity based on all mentioned morphological ratios, absolute body size, feeding guild, location of the nymph and degree of specialization. Functional diversity was calculated using the package 'FD' in R (Laliberté and Legendre 2010). I generated a null expectation for functional diversity by randomizing traits across species, and running 999 iterations to calculate null values. I then used the observed and null values to calculate standardized effect size, as such correcting for any effects of richness on functional richness.

Structural equation models were generated using the package 'pieceSEM' in R (Package et al. 2016). Richness and abundance were modeled as negative binomial distributions, while functional dispersion, and tree height were modeled as a gaussian distribution. All models had a random effect for site. The best model also included a correlation term for maximum tree height and understory density, maximum tree height and height entropy, and substrate age and volcano. I compared AICs to come to the best model, visually assessed model residuals, and calculated global goodness of fit with Fisher's C. I did not use a model including both canopy structural variables and all leaf traits due to the high number of predictors relative to observations, and the high number of links between predictors.

The relationship between forest structural measures and functional and taxonomic richness and dispersion were also modeled independently. I used a linear mixed effects model with site as random effect and substrate age, maximum tree height and height for 25% of returns as predictors, and visually inspected model residuals (Figure S 5.1).

Table S 16: SEM output for model including leaf traits

Hill 1		
	Coefficient Estimate	P *value*
Age	0.1543	0.7833
Volcano		0.9002
Hemiptera abundance	-0.0027	0.0062**
Foliar nitrogen	-0.1736	0.2581
Foliar phosphorus	0.1584	0.2276
Seed presence	-0.1609	0.1002
Specific leaf area	-0.2331	0.1580
Functional Dispersion		
Age	-0.0343	0.8719
Volcano		
Foliar nitrogen	-0.1731	0.2910
Foliar phosphorus	-0.3494	0.0100**
Seed presence	0.1332	0.2811
Specific leaf area	0.0585	0.7489
Abundance		
Age	0.2329	0.6624
Volcano		
Hemiptera abundance		
Foliar nitrogen	0.8629	0.0000***
Foliar phosphorus	-0.1402	0.0053**
Seed presence	-0.3041	0.0000***
Specific leaf area	0.1795	0.0000***

Table S 17: SEM output for model including LiDAR forest structure metrics

Hill 1		
	Coefficient Estimate	P *value*
Age	0.0774	0.5781
Volcano		
Hemiptera abundance	-0.0023	0.0121*
Max tree height	0.0143	0.7210
Entropy	0.1659	0.3080
Cumulative 25%	-0.1289	0.2110
Functional Dispersion		
Age	0.2836	0.1784
Volcano		
Hemiptera abundance	0.0005	0.5525
Max tree height	0.1104	0.0342*
Entropy	-0.3393	0.1136
Cumulative 25%	-0.3119	0.0309*
Abundance		
Age	0.3010	0.5264
Volcano		
Max tree height	-0.0153	0.8561
Cumulative 25%	0.4002	0.1425
entropy	-0.0066	0.9866

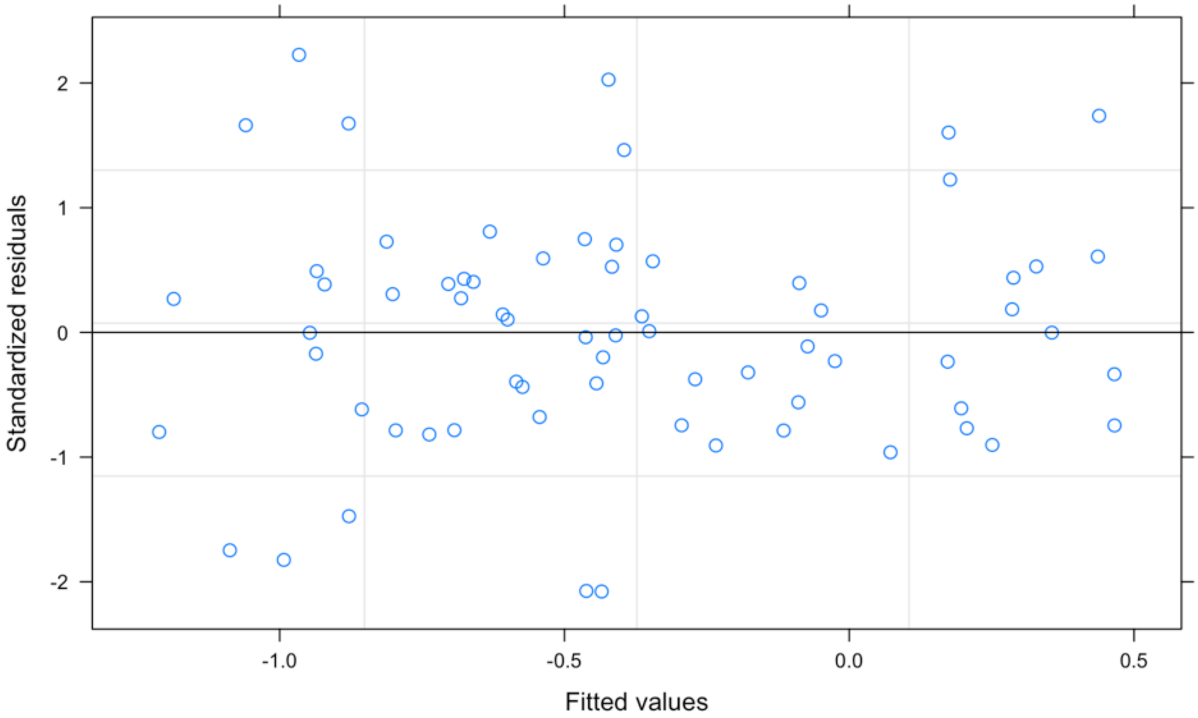

Figure S 14: Model residuals for linear mixed effect model of functional dispersion as a function of height for 25% of LiDAR returns.

Bibliography

Adler, P. B., A. Fajardo, A. R. Kleinhesselink, and N. J. B. Kraft. 2013. Trait-based tests of coexistence mechanisms. Ecology Letters 16:1294–306.

Adler, P. B., J. HilleRisLambers, and J. M. Levine. 2007. A niche for neutrality. Ecology Letters 10:95–104.

Agrawal, A. A. 2005. Natural selection on common milkweed (Asclepias syriaca) by a community of specialized insect herbivores. Evolutionary Ecology Research 7:651–667.

Agrawal, A. A., and M. Fishbein. 2006. Plant Defense Syndromes. Ecology 87.

Amada, G., Y. Onoda, T. Ichie, and K. Kitayama. 2017. Influence of leaf trichomes on boundary layer conductance and gas-exchange characteristics in Metrosideros polymorpha (Myrtaceae). Biotropica 49:482–492.

Anderson, M. J., T. O. Crist, A. L. Freestone, and N. J. Sanders. 2011. Navigating the multiple meanings of beta diversity: a roadmap for the practicing ecologist. Ecology Letters 14:19–28.

Anderson, M. J., K. E. Ellingsen, and B. H. McArdle. 2006. Multivariate dispersion as a measure of beta diversity. Ecology Letters 9:683–693.

Arnan, X., J. Bosch, L. Comas, M. Gracia, and J. Retana. 2011. Habitat determinants of abundance, structure and composition of flying Hymenoptera communities in mountain old-growth forests. Insect Conservation and Diversity 4:200–211.

Asner, G., K. Carlson, and R. Martin. 2005. Substrate age and precipitation effects on Hawaiian forest canopies from spaceborne imaging spectroscopy. Remote Sensing of Environment 98:457–467.

Asner, G. P., D. E. Knapp, J. Boardman, R. O. Green, T. Kennedy-Bowdoin, M. Eastwood, R. E. Martin, C. Anderson, and C. B. Field. 2012. Carnegie Airborne Observatory-2: Increasing science data dimensionality via high-fidelity multi-sensor fusion. Remote Sensing of Environment 124:454–465.

Asner, G. P., R. E. Martin, L. M. Keith, W. P. Heller, M. A. Hughes, N. R. Vaughn, R. F. Hughes, and C. Balzotti. 2018. A spectral mapping signature for the Rapid Ohia Death (ROD) pathogen in Hawaiian forests. Remote Sensing 10.

Auffret, A. G., E. Aggemyr, J. Plue, and S. A. O. Cousins. 2017. Spatial scale and specialization affect how biogeography and functional traits predict long-term patterns of community turnover. Functional Ecology 31:436–443.

Austin, A. T. 2002. Differential effects of precipitation on production and decomposition along a rainfall gradient in Hawaii. Ecology 83:328–338.

Austin, A. T., and P. M. Vitousek. 1998. Nutrient dynamics on a precipitation gradient in Hawai'i. Oecologia 113:519–529.

Baldwin, B. G., and M. J. Sanderson. 1998. Age and rate of diversification of the Hawaiian silversword alliance (Compositae). Proceedings of the National Academy of Sciences 95:9402–6.

Baldwin, B. G., and W. L. Wagner. 2010. Hawaiian angiosperm radiations of North American origin. Annals of Botany 105:849–879.

Bangert, R. K., R. J. Turek, G. D. Martinsen, G. M. Wimp, J. K. Bailey, and T. G. Whitham. 2005. Benefits of conservation of plant genetic diversity to arthropod diversity. Conservation Biology 19:379–390.

Barbour, M. A., M. A. Rodriguez-Cabal, E. T. Wu, R. Julkunen-Tiitto, C. E. Ritland, A. E. Miscampbell, E. S. Jules, and G. M. Crutsinger. 2015. Multiple plant traits shape the genetic basis of herbivore community assembly. Functional Ecology 29:995–1006.

Barnes, I., A. Fourie, M. J. Wingfield, T. C. Harrington, D. L. McNew, L. S. Sugiyama, B. C. Luiz, W. P. Heller, and L. M. Keith. 2018. New Ceratocystis species associated with rapid death of Metrosideros polymorpha in Hawai`i . Persoonia - Molecular Phylogeny and Evolution of Fungi 40:154–181.

Bartomeus, I., D. P. Cariveau, T. Harrison, and R. Winfree. 2018. On the inconsistency of pollinator species traits for predicting either response to land-use change or functional contribution. Oikos 127:306–315.

Bartoń, K. 2018. MuMIn: Multi-Model Inference. R package version 1.40.4.

Barton, P. S., S. A. Cunningham, B. C. T. Macdonald, S. McIntyre, D. B. Lindenmayer, and A. D. Manning. 2013. Species traits predict assemblage dynamics at ephemeral resource patches created by carrion. PloS one 8:e53961.

Barton, P. S., H. Gibb, A. D. Manning, D. B. Lindenmayer, and S. A. Cunningham. 2011. Morphological traits as predictors of diet and microhabitat use in a diverse beetle assemblage. Biological Journal of the Linnean Society 102:301–310.

Baselga, A. 2010a. Multiplicative partition of true diversity yields independent alpha and beta components; additive partition does not. Ecology 91:1974–1981.

Baselga, A. 2010b. Partitioning the turnover and nestedness components of beta diversity:134–143.

Basset, Y., P. M. Hammond, H. Barrios, J. D. Holloway, and S. E. 2003. Miller. 2003. Vertical stratification of arthropod assemblages. Page *in* Y. Basset, V. Novotny, M. S.E., and R. L. Kitching, editors. Arthropods of tropical forests: spatio-temporal dynamics and resource use in the canopy.

Basset, Y., J. Lepš, and V. Novotný. 2001. Habitat and successional status of plants in relation to the communities of their leaf-chewing herbivores in Papua New Guinea. Journal of Ecology 89:186–199.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

Beltrán, E., A. Valiente-Banuet, and M. Verdú. 2012. Trait divergence and indirect interactions allow facilitation of congeneric species. Annals of botany.

Bender, D. J., L. Tischendorf, and L. Fahrig. 2003. Using patch isolation metrics to predict animal movement in binary landscapes. Landscape Ecology 18:17–39.

Bennett, G. M., and P. M. O'Grady. 2012. Host-plants shape insect diversity: Phylogeny, origin, and species diversity of native Hawaiian leafhoppers (Cicadellidae: Nesophrosyne). Molecular Phylogenetics and Evolution 65:705–717.

Bennett, G. M., and P. M. O'Grady. 2013. Historical biogeography and ecological opportunity in the adaptive radiation of native Hawaiian leafhoppers (Cicadellidae: Nesophrosyne). Journal of Biogeography 40:1512–1523.

Berggren, Å., A. Carlson, and O. Kindvall. 2001. The effect of landscape composition on colonization success, growth rate and dispersal in introduced bush-crickets Metrioptera roeseli. Journal of Animal Ecology 70:663–670.

Bezemer, T. M., and T. H. Jones. 1998. Plant-insect herbivore interactions in elevated atmospheric CO2 : Quantitative analyses and guild effects. Oikos 82:212–222.

Bodin, O., and S. Saura. 2010. Ranking individual habitat patches as connectivity providers: Integrating network analysis and patch removal experiments. Ecological Modelling 221:2393–2405.

Bolnick, D. I., P. Amarasekare, M. S. Araújo, R. Bürger, J. M. Levine, M. Novak, V. H. W. Rudolf, S. J. Schreiber, M. C. Urban, and D. A. Vasseur. 2011. Why intraspecific trait variation matters in community ecology. Trends in Ecology & Evolution 26:183–192.

Bonte, D., T. Hovestadt, and H. J. Poethke. 2010. Evolution of dispersal polymorphism and local adaptation of dispersal distance in spatially structured landscapes. Oikos 119:560–566.

Borges, P. A. V., and V. K. Brown. 1999. Effect of island geological age on the arthropod species richness of Azorean pastures. Biological Journal of the Linnean Society 66:373–410.

ter Braak, C. J. F., P. R. Peres-Neto, and S. Dray. 2017. A critical issue in model-based inference for studying trait-based community assembly and a solution. PeerJ 5:e2885.

Brooks, D. R., J. Storkey, S. J. Clark, L. G. Firbank, S. Petit, and I. P. Woiwod. 2012. Trophic links between functional groups of arable plants and beetles are stable at a national scale. Journal of Animal Ecology 81:4–13.

Brousseau, P. M., D. Gravel, and I. T. Handa. 2018. On the development of a predictive functional trait approach for studying terrestrial arthropods. Journal of Animal Ecology 87:1209–1220.

Brown, A. M., D. I. Warton, N. R. Andrew, M. Binns, G. Cassis, and H. Gibb. 2014. The fourth-corner solution - using predictive models to understand how species traits interact with the environment. Methods in Ecology and Evolution 5:344–352.

Cagnolo, L., Graciela Valladares, A. Salvo, M. Cabido, and M. Zak. 2009. Habitat fragmentation and species loss across three interacting trophic levels : Effects of life-history and food-web traits. Conservation Biology 23:1167–1175.

Calabrese, J. M., and W. F. Fagan. 2004. A comparison-shopper's guide to connectivity metrics. Frontiers in Ecology and the Environment 2:529–536.

Carroll, S. P., and C. Boyd. 1992. Host race radiation in the soapberry bug: natural history with the history. Evolution 46:1052–1069.

Carroll, S. P., A. P. Hendry, D. N. Reznick, and C. W. Fox. 2007. Evolution on ecological time-scales. Functional Ecology 21:387–393.

Carson, H. L., and D. A. Clague. 1995. Geology and biogeography of the Hawaiian Islands. Pages 14–29 *in* W. L. Wagner and V. A. Funk, editors. Hawaiian Biogeography: Evolution on a Hot Spot Archipelago. Smithsonian Institution Press.

Cavender-Bares, J., K. H. Kozak, P. V. A. Fine, and S. W. Kembel. 2009. The merging of community ecology and phylogenetic biology. Ecology Letters 12:693–715.

Chadwick, O. A., L. A. Derry, P. M. Vitousek, B. J. Huebert, and L. O. Hedin. 1999. Changing sources of nutrients during four million years of ecosystem development. Nature 397:491–497.

Chao, A., R. K. Colwell, N. J. Gotelli, T. C. Hsieh, E. L. Sander, K. H. Ma, R. K. Colwell, and A. M. Ellison. 2014. Rarefaction and extrapolation with Hill numbers : A framework for sampling and estimation in species diversity studies. Ecological Monographs 84:45–67.

Chapin, F. S., L. R. Walker, C. L. Fastie, and L. C. Sharman. 1994. Mechanisms of primary succession following deglaciation at Glacier Bay, Alaska. Ecological Monographs 64:149–175.

Chase, J. M., N. J. B. Kraft, K. G. Smith, M. Vellend, and B. D. Inouye. 2011. Using null models to disentangle variation in community dissimilarity from variation in alpha -diversity. Ecosphere 2:1–11.

Chase, J. M., B. J. McGill, D. J. McGlinn, F. May, S. A. Blowes, X. Xiao, T. M. Knight, O. Purschke, and N. J. Gotelli. 2018. Embracing scale-dependence to achieve a deeper understanding of biodiversity and its change across communities. Ecology Letters 21:1737–1751.

Chase, J. M. N., and J. A. Myers. 2011. Disentangling the importance of ecological niches from stochastic processes across scales. Philosophical Transactions of the Royal Society B: Biological Sciences 366:2351–63.

Clague, D. A., and G. B. Dalrymple. 1987. The Hawaiian-Emperor volcanic chain: Part I Geologic evolution. Pages 5–100 Volcanism in Hawaii.

Clements, F. E. 1916. Plant Succession: An Analysis of the Development of Vegetation. Carnegie Institute of Washington, Washington D.C.

Clesceri, L. S., A. E. Greenberg, and A. D. Eaton. 1998. Standard methods for the examination of water and wastewater. Page (L. S. Clesceri, A. E. Greenberg, and A. D. Eaton, Eds.). American Public Health Association, New York.

Collinge, S. K. 2000. Effects of Grassland Fragmentation on Insect Species Loss, Colonization, and Movement Patterns. Ecology 81:2211–2226.

Condit, R., N. Pitman, E. G. Leigh Jr., J. Chave, J. Terborgh, R. B. Foster, P. Nunez, S. Aguilar, R. Valencia, G. Villa, H. C. Muller-Landau, E. Losos, and S. P. Hubbell. 2002. Beta-diversity in tropical forest trees. Science 295:666–669.

Connell, J. H., and R. O. Slatyer. 1977. Mechanisms of Succession in Natural Communities and Their Role in Community Stability and Organization. The American Naturalist 111:1119–1144.

Cook, W. M., K. T. Lane, B. L. Foster, and R. D. Holt. 2002. Island theory, matrix effects and species richness patterns in habitat fragments. Ecology Letters 5:619–623.

Cordell, S., G. Goldstein, D. Mueller-Dombois, D. Webb, and P. M. Vitousek. 1998. Physiological and morphological variation in Metrosideros polymorpha, a dominant Hawaiian tree species, along an altitudinal gradient: The role of phenotypic plasticity. Oecologia 113:188–196.

Cornelissen, J. H. C., S. Lavorel, E. Garnier, S. Díaz, N. Buchmann, D. E. Gurvich, P. B. Reich, H. Ter Steege, H. D. Morgan, M. G. A. Van Der Heijden, J. G. Pausas, and H. Poorter. 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. Australian Journal of Botany 51:335.

Cornwell, W. K., R. Bhaskar, L. Sack, S. Cordell, and C. K. Lunch. 2007. Adjustment of structure and function of Hawaiian Metrosideros polymorpha at high vs. low precipitation. Functional Ecology 21:1063–1071.

Cottenie, K. 2005. Integrating environmental and spatial processes in ecological community dynamics. Ecology Letters 8:1175–1182.

Cottenie, K., E. Michels, N. Nuytten, and L. D. E. Meester. 2003. Zooplankton metacommunity structure: regional vs local processes in highly interconnected ponds. Ecology 84:991–1000.

Cowie, R. H., and B. S. Holland. 2008. Molecular biogeography and diversification of the endemic terrestrial fauna of the Hawaiian Islands. Philosophical Transactions of the Royal Society B: Biological Sciences 363:3363–3376.

Crews, T. E., K. Kitayama, J. H. Fownes, R. H. Riley, D. A. Herbert, D. Mueller-Dombois, and P. M. Vitousek. 1995. Changes in Soil Phosphorus Fractions and Ecosystem Dynamics Across a Long Chronosequence in Hawaii. Ecology 76:1407–1424.

Crutsinger, G. M., M. D. Collins, J. a Fordyce, Z. Gompert, C. C. Nice, and N. J. Sanders. 2006. Plant genotypic diversity predicts community structure and governs an ecosystem process. Science 313:966–968.

Curtis, J. T. 1956. The modification of mid-latitude grasslands and forests by man. Pages 721–736 *in* W. L. J. Thomas, editor. Man's Role in Changing the Face of the Earth. University of Chicago Press, Chicago, Illinois.

Dawson, J. W., and L. Stemmermann. 1999. Metrosideros Banks ex Gaertn. Pages 964–970 *in* W. L. Wagner, D. R. Herbst, and S. H. Sohmer, editors. Manual of the flowering plants of Hawai'i. Bernice P. Bishop Museum Press, Honolulu, Hawai'i.

Denno, R. F., G. K. Roderick, M. A. Peterson, A. F. Huberty, H. G. Döbel, M. D. Eubanks, J. E. Losey, and G. a. Langellotto. 1996. Habitat persistence underlies intraspecific variation in the dispersal strategies of planthoppers. Ecological Monographs 66:389–408.

Diaz, S., M. Cabido, and F. Casanoves. 1998. Plant functional traits and environmental filters at a regional scale. Journal of Vegetation Science 9:113–122.

Díaz, S., I. Noy-Meir, and M. Cabido. 2001. Can grazing of herbaceous plants be predicted from simple vegetative traits? Journal of Applied Ecology 38:497–508.

Didham, R. K., V. Kapos, and R. M. Ewers. 2012. Rethinking the conceptual foundations of habitat fragmentation research. Oikos 121:161–170.

Dinnage, R. 2009. Disturbance Alters the Phylogenetic Composition and Structure of Plant Communities in an Old Field System 4.

Dornelas, M., N. J. Gotelli, B. J. McGill, H. Shimadzu, F. Moyes, C. Sievers, and A. E. Magurran. 2014. Assemblage Time Series Reveal Biodiversity Change but Not Systematic Loss. Science 344:296–300.

Drakare, S., J. J. Lennon, and H. Hillebrand. 2006. The imprint of the geographical, evolutionary and ecological context on species – area relationships. Ecology Letters 9:215–227.

Drake, D. R., and D. Mueller-Dombois. 1993. Population Development of Rain Forest Trees on a Chronosequence of Hawaiian Lava Flows. Ecology 74:1012–1019.

Dray, S., P. Choler, S. Dolédec, P. R. Peres-Neto, W. Thuiller, S. Pavoine, and C. J.

F. Ter Braak. 2014. Combining the fourth-corner and the RLQ methods for assessing trait responses to environmental variation. Ecology 95:14–21.

Dray, S., and P. Legendre. 2008. Testing the species traits–environment relationships: the fourth-corner problem revisited. Ecology 89:3400–3412.

Eber, S. 2004. Bottom-up density regulation in the holly leaf-miner Phytomyza ilicis. Journal of Animal Ecology 73:948–958.

Edwards, C., J. Read, and G. Sanson. 2000. Characterising sclerophylly: Some mechanical properties of leaves from heath and forest. Oecologia 123:158–167.

Ehleringer, J. R., and H. A. Mooney. 1978. Leaf hairs. Quantum 200:183–200.

Emerson, B. C., and N. Kolm. 2005. Species Diversity Can Drive Speciation. Nature 434:1015–1017.

Emerson, B. C., and N. Kolm. 2007. Species diversity can drive speciation: Reply. Ecology 88:2135–2138.

ESRI. 2012. ArcGIS Release 10.1. Environmental Systems Research Institute (ESRI), Redlands, CA.

Ewers, R. M., and R. K. Didham. 2006. Confounding factors in the detection of species responses to habitat fragmentation. Biological Reviews 81:117–142.

Eycott, A. E., G. B. Stewart, L. M. Buyung-Ali, D. E. Bowler, K. Watts, and A. S. Pullin. 2012. A meta-analysis on the impact of different matrix structures on species movement rates. Landscape Ecology 27:1263–1278.

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution, and Systematics 34:487–515.

Fahrig, L. 2017. Ecological responses to habitat fragmentation per se. Annual Review of Ecology, Evolution, and Systematics 48:1–23.

Fahrig, L., V. Arroyo-Rodríguez, J. R. Bennett, V. Boucher-Lalonde, E. Cazetta, D. J. Currie, F. Eigenbrod, A. T. Ford, S. P. Harrison, J. A. G. Jaeger, N. Koper, A. E. Martin, J.-L. Martin, J. P. Metzger, P. Morrison, J. R. Rhodes, D. A. Saunders, D. Simberloff, A. C. Smith, L. Tischendorf, M. Vellend, and J. I. Watling. 2019. Is habitat fragmentation bad for biodiversity? Biological Conservation 230:179–186.

Farnon Ellwood, M. D., A. Manica, and W. A. Foster. 2009. Stochastic and deterministic processes jointly structure tropical arthropod communities. Ecology Letters 12:277–284.

Feeny, P. 1976. Plant apparency and chemical defense. Pages 1–40 *in* J. W. Wallace and R. L. Mansell, editors. Recent Advances in Phytochemistry. Plenum Press, New York, NY.

Fenton, M. B. 2008. The structure of aerial-feeding bat faunas as indicated by ears and wing elements. Canadian Journal of Zoology 50:287–296.

Ferraz, G., G. J. Russell, P. C. Stouffer, R. O. Bierregaard, S. L. Pimm, and T. E. Lovejoy. 2003. Rates of species loss from Amazonian forest fragments. Proceedings of the National Academy of Sciences 100:14069–14073.

Findley, J. S. 1973. Phenetic packing as a measure of faunal diversity. The American Naturalist 107:580–584.

Flaspohler, D. J., C. P. Giardina, G. P. Asner, P. Hart, J. Price, C. K. Lyons, and X. Castaneda. 2010. Long-term effects of fragmentation and fragment properties on bird species richness in Hawaiian forests. Biological Conservation 143:280–288.

Fletcher, R. J. J., R. K. Didham, C. Banks-Leite, J. Barlow, R. M. Ewers, J. Rosindell, R. D. Holt, A. Gonzalez, R. Pardini, E. I. Damschen, F. P. L. Melo, L. Ries, J. A. Prevedello, T. Tscharntke, W. F. Laurance, T. Lovejoy, and N. M. Haddad. 2018. Is habitat fragmentation good for biodiversity ? Biological Conservation 226:9–15.

Forbes, A. E., and J. M. N. Chase. 2002. The role of habitat connectivity and landscape geometry in experimental zooplankton metacommunities. Oikos 96:433–440.

Forister, M. L., V. Novotny, A. K. Panorska, L. Baje, Y. Basset, P. T. Butterill, L. Cizek, P. D. Coley, F. Dem, I. R. Diniz, P. Drozd, M. Fox, A. E. Glassmire, R. Hazen, J. Hrcek, J. P. Jahner, O. Kaman, T. J. Kozubowski, T. a Kursar, O. T. Lewis, J. Lill, R. J. Marquis, S. E. Miller, H. C. Morais, M. Murakami, H. Nickel, N. a Pardikes, R. E. Ricklefs, M. S. Singer, A. M. Smilanich, J. O. Stireman, S. Villamarín-Cortez, S. Vodka, M. Volf, D. L. Wagner, T. Walla, G. D. Weiblen, and L. a Dyer. 2014. The global distribution of diet breadth in insect herbivores. Proceedings of the National Academy of Sciences of the United States of America.

Fountain-Jones, N. M., S. C. Baker, and G. J. Jordan. 2015. Moving beyond the guild concept : developing a practical functional trait framework. Ecological Entomology 40:1–13.

Funk, J. L., and H. L. Throop. 2010. Enemy release and plant invasion: Patterns of defensive traits and leaf damage in Hawaii. Oecologia 162:815–823.

Funk, V. A., and W. L. Wagner. 1995. Biogeographic patterns in the Hawaiian Islands. Page Hawaiian Biogeography: Evolution on a Hot Spot Archipelago. Smithsonian Institution Press, Washington D.C.

Gaiman, Neil. 2001. American Gods. Harper Collins, London, UK.

Gavenda, R. 1992. Hawaiian Quaternary paleoenvironments: A review of geological, pedological, and botanical evidence. Pacific Science 46:295–307.

Gibb, H., and D. F. Hochuli. 2002. Habitat fragmentation in an urban environment : large and small fragments support different arthropod assemblages. Biological Conservation 106:91–100.

Gibb, H., and C. L. Parr. 2013. Does Structural Complexity Determine the Morphology of Assemblages? An Experimental Test on Three Continents. PLoS ONE 8:1–7.

Gilbert, F., A. Gonzalez, and I. Evans-Freke. 1998. Corridors maintain species richness in the fragmented landscapes of a microecosystem. Proceedings of the Royal Society B: Biological Sciences 265:577–582.

Gillespie, R. 2004a. Community assembly through adaptive radiation in Hawaiian spiders. Science 303:356–359.

Gillespie, R. G. 2002. Biogeography of spiders on remote oceanic islands of the Pacific: archipelagoes as stepping stones? Journal of Biogeography 29:655–662.

Gillespie, R. G. 2004b. Community assembly through adaptive radiation in Hawaiian spiders. Science 303:356–359.

Gobbi, M., M. Caccianiga, B. Cerabolini, F. Bernardi, a. Luzzaro, and S. Pierce. 2010. Plant adaptive responses during primary succession are associated with functional adaptations in ground beetles on deglaciated terrain. Community

Ecology 11:223–231.

Gossner, M. M., N. K. Simons, R. Achtziger, T. Blick, W. H. O. Dorow, F. Dziock, F. Köhler, W. Rabitsch, and W. W. Weisser. 2015. A summary of eight traits of Coleoptera, Hemiptera, Orthoptera and Araneae, occurring in grasslands in Germany. Scientific Data 2:150013.

Gotelli, N. J., and R. K. Colwell. 2001. Quantifying biodiversity: Procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters 4:379–391.

Gotelli, N. J., G. R. Graves, and C. Rahbek. 2010. Macroecological signals of species interactions in the Danish avifauna. Proceedings of the National Academy of Sciences 107:5030–5035.

Gravel, D., C. D. Canham, M. Beaudet, and C. Messier. 2006. Reconciling niche and neutrality: the continuum hypothesis. Ecology Letters 9:399–409.

Grove, S. J. 2002. The influence of forest management history on the integrity of the saproxylic beetle fauna in an Australian lowland tropical rainforest. Biological Conservation 104:149–171.

Grubb, P. J. 1986. Sclerophylls, pachyphylls and pycnophylls: the nature and significance of hard leaf surfaces. Pages 137–150 *in* B. E. Juniper and T. R. E. Southwood, editors. Insects and the Plant Surface. Edward Arnold, London, UK.

Gruner, D. S. 2003. Regressions of length and width to predict arthropod biomass in the Hawaiian Islands. Pacific Science 57:325–336.

Gruner, D. S. 2004. Attenuation of top-down and bottom-up forces in a complex terrestrial community. Ecology 85:3010–3022.

Gruner, D. S. 2005. Biotic resistance to an invasive spider conferred by generalist insectivorous birds on Hawai'i Island. Biological Invasions 7:541–546.

Gruner, D. S. 2007. Geological age, ecosystem development, and local resource constraints on arthropod community structure in the Hawaiian Islands. Biological Journal of the Linnean Society 90:551–570.

Gruner, D. S., N. J. Gotelli, J. P. Price, and R. H. Cowie. 2008. Does species richness drive speciation? A reassessment with the Hawaiian biota. Ecography 31:080304020349105.

Gruner, D. S., A. D. Taylor, and R. E. Forkner. 2005. The effects of foliar pubescence and nutrient enrichment on arthropod communities of Metrosideros polymorpha (Myrtaceae). Ecological Entomology 30:428–443.

Haddad, N. M., L. A. Brudvig, J. Clobert, K. F. Davies, A. Gonzalez, R. D. Holt, T. E. Lovejoy, J. O. Sexton, M. P. Austin, C. D. Collins, W. M. Cook, E. I. Damschen, R. M. Ewers, B. L. Foster, C. N. Jenkins, A. J. King, W. F. Laurance, D. J. Levey, C. R. Margules, B. A. Melbourne, A. O. Nicholls, J. L. Orrock, D.-X. Song, and J. R. Townshend. 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. Science Advances 1:1–9.

Haddad, N. M., A. Gonzalez, L. A. Brudvig, M. A. Burt, D. J. Levey, and E. I. Damschen. 2017a. Experimental evidence does not support the Habitat Amount Hypothesis. Ecography 40:48–55.

Haddad, N. M., and W. M. Hicks. 2000. Host Pubescence and the Behavior and Performance of the Butterfly. Science:299–303.

Haddad, N. M., R. D. Holt, R. J. J. Fletcher, M. Loreau, and J. Clobert. 2017b.

Connecting models, data, and concepts to understand fragmentation's ecosystem-wide effects. Ecography 40:1–8.

Haila, Y. 2002. A conceptual genealogy of fragmentation research: from island biogeography to landscape ecology. Ecological Applications 12:321–334.

Hanley, M. E., B. B. Lamont, M. M. Fairbanks, and C. M. Rafferty. 2007. Plant structural traits and their role in anti-herbivore defence. Perspectives in Plant Ecology, Evolution and Systematics 8:157–178.

Hanski, I. 1994. A practical model of metapopulation dynamics. Journal of Animal Ecology 63:151–162.

Hardy, N. B., and S. P. Otto. 2014. Specialization and generalization in the diversification of phytophagous insects: tests of the musical chairs and oscillation hypotheses. Proceedings of the Royal Society B: Biological Sciences 281.

Harrell, J. C., and E. P. Holzapfel. 1966. Trapping of air-borne insects on ships in the Pacific, part 6. Pacific Insects 8:33–42.

Harris, A. J. L., S. K. Rowland, N. Villeneuve, and T. Thordarson. 2017. Pāhoehoe, ʻaʻā, and block lava: an illustrated history of the nomenclature. Bulletin of Volcanology 79.

Harrison, S., S. J. Ross, and J. H. Lawton. 1992. Beta diversity on geographic gradients in Britain. Journal of Animal Ecology 61:151–158.

Harvey, J. A., N. M. van Dam, C. E. Raaijmakers, J. M. Bullock, and R. Gols. 2011. Tri-trophic effects of inter- and intra-population variation in defence chemistry of wild cabbage (Brassica oleracea). Oecologia 166:421–431.

Hastie, T., R. Tibshirani, and J. Friedman. 2009. The elements of statistical learning: Data mining, inference and prediction. 2nd edn. Springer, New York, New York.

Hawkins, B. A., H. V Cornell, and M. E. Hochberg. 1997. Predators, parasitoids, and pathogens as mortality agents in phytophagous insect populations. Ecology 78:2145–2152.

Haynes, K. J., T. Diekötter, and T. O. Crist. 2007. Resource complementation and the response of an insect herbivore to habitat area and fragmentation. Oecologia 153:511–520.

Hedin, L. O. . P. M. V. P. a. M. 2003. Nutrient Losses Over Four Million Years of Tropical Forest Development. Ecology 84:2231–2255.

Heller, W. P., and L. M. Keith. 2018. Real-time PCR assays to detect and distinguish the Rapid ʻŌhiʻa Death pathogens Ceratocystis lukuohia and C. huliohia. Phytopathology 108:1395–1401.

Helmus, M. R., W. B. Keller, M. J. Paterson, N. D. Yan, C. H. Cannon, and J. A. Rusak. 2010. Communities contain closely related species during ecosystem disturbance. Ecology Letters 13:162–174.

Henle, K., K. F. Davies, M. Kleyer, C. Margules, and J. Settele. 2004. Predictors of species sensitivity to fragmentation. Biodiversity and Conservation 13:207–251.

Herbert, D. A., J. H. Fownes, and P. M. Vitousek. 1999. Hurricane Damage to a Hawaiian Forest: Nutrient Supply Rate Affects Resistance and Resilience. Ecology 80:908–920.

Hersch-Green, E. I., N. E. Turley, and M. T. J. Johnson. 2011. Community genetics: What have we accomplished and where should we be going? Philosophical

Transactions of the Royal Society B: Biological Sciences 366:1453–1460.

Heyborne, W. H., J. C. Miller, and G. L. Parsons. 2003. Ground dwelling beetles and forest vegetation change over a 17-year-period, in western Oregon, USA. Forest Ecology and Management 179:123–134.

Hill, M. O. 1973. Diversity and evenness: A unifying notation and its consequences. Ecology 54:427–432.

Holt, R. D., J. H. Lawton, G. A. Polis, and N. D. Martinez. 1999. Trophic rank and the species-area relationship. Ecology 80:1495–1504.

Holzapfel, E. P., and J. C. Harrell. 1968. Transoceanic dispersal studies of insects. Pacific Insects 10:115–153.

Homburg, K., N. Homburg, F. S. C. H. Af, A. Schuldt, and T. Assmann. 2013a. Carabids.org – a dynamic online database of ground beetle species traits (Coleoptera , Carabidae). Insect Conservation and Diversity.

Homburg, K., A. Schuldt, C. Drees, and T. Assmann. 2013b. Broad-scale geographic patterns in body size and hind wing development of western Palaearctic carabid beetles (Coleoptera : Carabidae). Ecography 36:166–177.

Hoof, J., L. Sack, D. T. Webb, and E. T. Nilsen. 2008. Contrasting structure and function of pubescent and glabrous varieties of Hawaiian Metrosideros polymorpha (Myrtaceae) at high elevation. Biotropica 40:113–118.

Hormiga, G., M. Arnedo, and R. G. Gillespie. 2003. Speciation on a conveyor belt: sequential colonization of the hawaiian islands by Orsonwelles spiders (Araneae, Linyphiidae). Systematic biology 52:70–88.

Horn, H. S., and R. H. MacArthur. 1972. Competition among Fugitive Species in a Harlequin Environment. Ecology 53:749–752.

Hotchkiss, S., and J. O. Juvik. 1999. A late-quaternary pollen record from Ka'au Crater, O'ahu, Hawai'i. Quaternary Research 52:115–128.

Hotchkiss, S., P. M. Vitousek, O. A. Chadwick, and J. Price. 2000. Climate Cycles , Geomorphological Change , and the Interpretation of Soil and Ecosystem Development:522–533.

Howard, M. M., A. Kalske, and A. Kessler. 2018. Eco-evolutionary processes affecting plant–herbivore interactions during early community succession. Oecologia 187:547–559.

Howarth, F. G. 1987. Evolutionary ecology of aeolian and subterranean habitats in Hawaii. Trends in Ecology and Evolution 2:220–223.

Howarth, F. G. 1990. Hawaii terrestrial arthropods: An overview. Bishop Museum Occasional Papers 30:4–26.

Hsieh, T. C., K. H. Ma, and A. Chao. 2016. iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). Methods in Ecology and Evolution 7:1451–1456.

Hubbell, S. P. 2001. The Unified Neutral Theory of Biodiversity and Biogeography. Princeton University Press.

Huffaker, C. B. 1958. Experimental studes on predation: dispersion factors and predatory-prey oscillations. Hilgardia 27:343–383.

Hughes, A. R., B. D. Inouye, M. T. J. Johnson, N. Underwood, and M. Vellend. 2008. Ecological consequences of genetic diversity. Ecology Letters 11:609–623.

Hulcr, J., R. a Beaver, W. Puranasakul, S. a Dole, and S. Sonthichai. 2008. A comparison of bark and ambrosia beetle communities in two forest types in northern Thailand (Coleoptera: Curculionidae: Scolytinae and Platypodinae). Environmental entomology 37:1461–1470.

Hutchinson, G. E. 1959. Homage to Santa Rosalia or Why are there so many kinds of animals? The American Naturalist 93:145–159.

Iddles, T. L., J. Read, and G. D. Sanson. 2003. The potential contribution of biomechanical properties to anti-herbivore defence in seedlings of six Australian rainforest trees. Australian Journal of Botany 51:119.

Inoue, T. 2003. Chronosequential change in a butterfly community after clear-cutting of deciduous forests in a cool temperate region of central Japan. Entomological Science 6:151–163.

James, S. a, C. F. Puttock, U. F. Service, and R. P. Adams. 2004. Morphological and genetic variation within Metrosideros polymorpha (Myrtaceae) on Hawai‘i. New Zealand Journal of Botany 42:263–270.

Jamil, T., W. a. Ozinga, M. Kleyer, and C. J. F. ter Braak. 2013. Selecting traits that explain species-environment relationships: a generalized linear mixed model approach. Journal of Vegetation Science 24:988–1000.

Janssen, P., M. Fuhr, E. Cateau, B. Nusillard, and C. Bouget. 2017. Forest continuity acts congruently with stand maturity in structuring the functional composition of saproxylic beetles. Biological Conservation 205:1–10.

Jeffries, J. M., R. J. Marquis, and R. E. Forkner. 2006. Forest age influences oak insect herbivore community structure, richness, and density. Ecological Applications 16:901–912.

Joel, G., G. Aplet, and P. M. Vitousek. 1994. Leaf Morphology Along Environmental Gradients in Hawaiian Metrosideros Polymorpha. Biotropica 26:17–22.

Johnson, E. A., and K. Miyanishi. 2008. Testing the assumptions of chronosequences in succession. Ecology Letters 11:419–431.

Johnson, M. T. J. 2008. Bottom-up effects of plant genotype on aphids, ants, and predators. Ecology 89:145–154.

Johnson, M. T. J., and A. A. Agrawal. 2005. Plant genotype and environment interact to shape a diverse arthropod community on evening primrose (Oenothera biennis). Ecology 86:874–885.

Johnson, M. T. J., M. J. Lajeunesse, and A. A. Agrawal. 2006. Additive and interactive effects of plant genotypic diversity on arthropod communities and plant fitness. Ecology Letters 9:24–34.

Jones, N. T., R. M. Germain, T. N. Grainger, A. Hall, L. Baldwin, and B. Gilbert. 2015. Dispersal mode mediates the effect of patch size and patch connectivity on metacommunity diversity. Journal of Ecology 103:935–944.

Jordan, G. J., R. A. Dillon, and P. H. Weston. 2005. Solar radiation as a factor in the evolution of scleromorphic leaf anatomy in Proteaceae. American Journal of Botany 92:789–796.

Jost, L. 2006. Entropy and diversity. Oikos 113:363–375.

Jost, L., P. Devries, T. Walla, H. Greeney, A. Chao, and C. Ricotta. 2010. Partitioning diversity for conservation analyses. Diversity and Distributions 16:65–76.

Jung, V., C. Violle, C. Mondy, L. Hoffmann, and S. Muller. 2010. Intraspecific variability and trait-based community assembly. Journal of Ecology 98:1134–

1140.

Juvik, S. P., and J. O. Juvik. 1998. Atlas of Hawai‘i. Third edition. University of Hawaii Press, Honolulu, Hawai’i.

Kattge, J., S. Díaz, S. Lavorel, I. C. Prentice, P. Leadley, G. Bönisch, E. Garnier, M. Westoby, P. B. Reich, I. J. Wright, J. H. C. Cornelissen, C. Violle, S. P. Harrison, P. M. Van Bodegom, M. Reichstein, B. J. Enquist, N. A. Soudzilovskaia, D. D. Ackerly, M. Anand, O. Atkin, M. Bahn, T. R. Baker, D. Baldocchi, R. Bekker, C. C. Blanco, B. Blonder, W. J. Bond, R. Bradstock, D. E. Bunker, F. Casanoves, J. Cavender-Bares, J. Q. Chambers, F. S. Chapin, J. Chave, D. Coomes, W. K. Cornwell, J. M. Craine, B. H. Dobrin, L. Duarte, W. Durka, J. Elser, G. Esser, M. Estiarte, W. F. Fagan, J. Fang, F. Fernández-Méndez, A. Fidelis, B. Finegan, O. Flores, H. Ford, D. Frank, G. T. Freschet, N. M. Fyllas, R. V. Gallagher, W. A. Green, A. G. Gutierrez, T. Hickler, S. I. Higgins, J. G. Hodgson, A. Jalili, S. Jansen, C. A. Joly, A. J. Kerkhoff, D. Kirkup, K. Kitajima, M. Kleyer, S. Klotz, J. M. H. Knops, K. Kramer, I. Kühn, H. Kurokawa, D. Laughlin, T. D. Lee, M. Leishman, F. Lens, T. Lenz, S. L. Lewis, J. Lloyd, J. Llusià, F. Louault, S. Ma, M. D. Mahecha, P. Manning, T. Massad, B. E. Medlyn, J. Messier, A. T. Moles, S. C. Müller, K. Nadrowski, S. Naeem, Ü. Niinemets, S. Nöllert, A. Nüske, R. Ogaya, J. Oleksyn, V. G. Onipchenko, Y. Onoda, J. Ordoñez, G. Overbeck, W. A. Ozinga, S. Patiño, S. Paula, J. G. Pausas, J. Peñuelas, O. L. Phillips, V. Pillar, H. Poorter, L. Poorter, P. Poschlod, A. Prinzing, R. Proulx, A. Rammig, S. Reinsch, B. Reu, L. Sack, B. Salgado-Negret, J. Sardans, S. Shiodera, B. Shipley, A. Siefert, E. Sosinski, J. F. Soussana, E. Swaine, N. Swenson, K. Thompson, P. Thornton, M. Waldram, E. Weiher, M. White, S. White, S. J. Wright, B. Yguel, S. Zaehle, A. E. Zanne, and C. Wirth. 2011. TRY - a global database of plant traits. Global Change Biology 17:2905–2935.

Keddy, P. A. 1992. Assembly and response rules: two goals for predictive community ecology. Journal of Vegetation Science 3:157–164.

Keith, L. M., R. F. Hughes, L. S. Sugiyama, W. P. Heller, B. C. Bushe, and J. B. Friday. 2015. First Report of Ceratocystis Wilt on `Ohia (Metrosideros polymorpha). Plant Disease 99:1276–1277.

Keitt, T. H., D. L. Urban, and B. T. Milne. 1997. Detecting critical scales in fragmented landscapes. Conservation Ecology 1:1–19.

Kennedy, C. M., P. P. Marra, W. F. Fagan, and M. C. Neel. 2010. Landscape matrix and species traits mediate responses of Neotropical resident birds to forest fragmentation in Jamaica. Ecological Monographs 80:651–669.

Kitayama, K., and D. Mueller-Dombois. 1995. Vegetation changes along gradients of long-term soil development in the Hawaiian montane rainforest zone. Vegetation 120:1–20.

Kitching, R. L. 2013. Niches and neutrality: Community ecology for entomologists. Australian Journal of Entomology 52:1–7.

Kleyer, M., R. M. Bekker, I. C. Knevel, J. P. Bakker, K. Thompson, M. Sonnenschein, P. Poschlod, J. M. van Groenendael, L. Klimeš, J. Klimešová, S. Klotz, G. M. Rusch, M. Hermy, D. Adriaens, G. Boedeltje, B. Bossuyt, A. Dannemann, P. Endels, L. Götzenberger, J. G. Hodgson, A.-K. Jackel, I. Kühn,

D. Kunzmann, W. A. Ozinga, C. Römermann, M. Stadler, J. Schlegelmilch, H. J. Steendam, O. Tackenberg, B. Wilmann, J. H. C. Cornelissen, O. Eriksson, E. Garnier, and B. Peco. 2008. The LEDA Traitbase: a database of life-history traits of the Northwest European flora. Journal of Ecology 96:1266–1274.

Kneitel, J. M., and J. M. Chase. 2004. Trade-offs in community ecology: linking spatial scales and species coexistence. Ecology Letters 7:69–80.

Knowlton, J. L., D. J. Flaspohler, E. H. Paxton, T. Fukami, C. P. Giardina, D. S. Gruner, and E. E. W. Rankin. 2017. Movements of four native Hawaiian birds across a naturally fragmented landscape. Journal of Avian Biology 48:921–931.

Kraft, N. J. B., L. S. Comita, J. M. Chase, N. J. Sanders, N. G. Swenson, T. O. Crist, J. C. Stegen, M. Vellend, B. Boyle, M. J. Anderson, H. V Cornell, K. F. Davies, A. L. Freestone, B. D. Inouye, S. P. Harrison, and J. A. Myers. 2011. Disentangling the Drivers of Diversity Along Latitudinal and Elevational Gradients. Science 333:1755–1758.

Kraft, N. J. B., R. Valencia, and D. D. Ackerly. 2008. Functional Traits and Niche-Based Tree Community Assembly in an Amazonian Forest. Science 322:580–582.

Kupfer, J. A., G. P. Malanson, and S. B. Franklin. 2006. Not seeing the ocean for the islands: The mediating influence of matrix-based processes on forest fragmentation effects. Global Ecology and Biogeography 15:8–20.

Laliberté, E., and P. Legendre. 2010. A distance-based framework for measuring functional diversity from multiple traits. Ecology 91:299–305.

Larsen, S., J. M. Chase, I. Durance, and S. J. Ormerod. 2018. Lifting the veil: richness measurements fail to detect systematic biodiversity change over three decades. Ecology 99:1316–1326.

Lassau, S. a, D. F. Hochuli, G. Cassis, and C. a M. Reid. 2005. Effects of habitat complexity on forest beetle diversity: do functional groups respond consistently? Diversity & Distributions 11:73–82.

Lavorel, S., and E. Garnier. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisting the Holy Grail. Functional Ecology 16:545–556.

Lawton, J. H. 1983. Plant architecture and the diversity of phytophagous insects. Annual Review of Entomology 28:23–39.

Lawton, J. H., and D. R. Strong. 1981. Community Patterns and Competition in Folivorous Insects. The American Naturalist 118:317–338.

Legendre, P., R. Galzin, and M. L. Harmelin-Vivien. 1997. Relating Behavior To Habitat: Solutions To The Fourth-Corner Problem. Ecology 78:547–562.

Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, R. D. Holt, J. B. Shurin, R. Law, D. Tilman, M. Loreau, and A. Gonzalez. 2004. The metacommunity concept: A framework for multi-scale community ecology. Ecology Letters 7:601–613.

Levin, D. A. 1973. The role of trichomes in plant defense. The Quarterly Review of Biology 48:3–15.

Lewinsohn, T. M., V. Novotny, and Y. Basset. 2005. Insects on Plants: Diversity of Herbivore Assemblages Revisited. Annual Review of Ecology, Evolution, and Systematics 36:597–620.

Lewinsohn, T. M., and T. Roslin. 2008. Four ways towards tropical herbivore megadiversity. Ecology Letters 11:398–416.

Liakopoulos, G., S. Stavrianakou, and G. Karabourniotis. 2006. Trichome layers versus dehaired lamina of Olea europaea leaves: Differences in flavonoid distribution, UV-absorbing capacity, and wax yield. Environmental and Experimental Botany 55:294–304.

Löbel, S., L. Mair, N. Lönnell, B. Schröder, and T. Snäll. 2018. Biological traits explain bryophyte species distributions and responses to forest fragmentation and climatic variation. Journal of Ecology 106:1700–1713.

Losos, J. B., P. H. Harvey, A. J. Leigh Brown, J. M. Smith, and S. Nee. 1996. Community evolution in Greater Antillean Anolis lizards: Phylogenetic patterns and experimental tests. New uses for new phylogenies 349:308–321.

Maaß, S., M. Maraun, S. Scheu, M. C. Rillig, and T. Caruso. 2015. Environmental filtering vs. resource-based niche partitioning in diverse soil animal assemblages. Soil Biology and Biochemistry 85:145–152.

MacArthur, R. H. 1958. Population Ecology of Some Warblers of Northeastern Coniferous Forests. Ecology 39:599–619.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press.

Maddox, G. . D., and R. B. Boot. 1990. Structure of the encounter between goldenrod (Solidago altissima) and its diverse insect fauna. Ecology 71:2115–2124.

Martinsen, G. D., and T. G. Whitham. 1994. More birds nest in hybrid cottonwood trees. The Wilson Bulletin 106:474–481.

Mattson, W. J. 1980. Herbivory in relation to plant nitrogen content. Annual Review of Ecological Systems 11:119–61.

McGill, B. J. 2010. Matters of Scale. Science 328:575–576.

McGill, B. J. 2015. Steering the trait bandwagon.

McGill, B. J., M. Dornelas, N. J. Gotelli, and A. E. Magurran. 2015. Fifteen forms of biodiversity trend in the anthropocene. Trends in Ecology and Evolution 30:104–113.

McGill, B. J., B. J. Enquist, E. Weiher, and M. Westoby. 2006. Rebuilding community ecology from functional traits. Trends in Ecology & Evolution 21:178–85.

McGuinness, K. A. 1984. Species-area curves. Biological Reviews 59:423–440.

Mcpeek, M. A. 1996. Linking Local Species Interactions to Rates of Speciation in Communities. Ecology 77:1355–1366.

Medeiros, M. J., D. Davis, F. G. Howarth, and R. G. Gillespie. 2009. Evolution of cave living in Hawaiian Schrankia (Lepidoptera: Noctuidae) with description of a remarkable new cave species. Zoological Journal of the Linnean Society 156:114–139.

Medeiros, M. J., and R. G. Gillespie. 2011. Biogeography and the evolution of flightlessness in a radiation of Hawaiian moths (Xyloryctidae: Thyrocopa). Journal of Biogeography 38:101–111.

Messier, J., B. J. McGill, and M. J. Lechowicz. 2010. How do traits vary across ecological scales? A case for trait-based ecology. Ecology letters 13:838–48.

Messing, R. H., M. N. Tremblay, E. B. Mondor, R. G. Foottit, and K. S. Pike. 2007.

Invasive aphids attack native Hawaiian plants. Biological Invasions 9:601–607.

Meyer, W. M., and N. W. Yeung. 2011. Trophic relationships among terrestrial molluscs in a Hawaiian rain forest: analysis of carbon and nitrogen isotopes. Journal of Tropical Ecology 27:441–445.

Miller, J. E. D., E. I. Damschen, and A. R. Ives. 2018. Functional traits and community composition : A comparison among community- - weighted means , weighted correlations , and multilevel models 2018:1–11.

Miller, R. O. 1998. High-temperature oxidation: Dry Ashing. Page *in* Y. P. Kalra, editor. Handbook of Reference Methods for Plant Analysis. CRC, Florida.

Mittelbach, G. G., and D. W. Schemske. 2015. Ecological and evolutionary perspectives on community assembly. Trends in Ecology & Evolution 30:241–247.

Moilanen, A., and I. Hanski. 1998. Metapopulation Dynamics: Effects of Habitat Quality and Landscape Structure. Ecology 79.

Moilanen, A., and M. Nieminen. 2002. Simple connectivity measure in spatial ecology. Ecology 83:1131–1145.

Moles, A. T., B. Peco, I. R. Wallis, W. J. Foley, A. G. B. Poore, E. W. Seabloom, P. A. Vesk, A. J. Bisigato, L. Cella-Pizarro, C. J. Clark, P. S. Cohen, W. K. Cornwell, W. Edwards, R. Ejrnæs, T. Gonzales-Ojeda, B. J. Graae, G. Hay, F. C. Lumbwe, B. Magaña-Rodríguez, B. D. Moore, P. L. Peri, J. R. Poulsen, J. C. Stegen, R. Veldtman, H. von Zeipel, N. R. Andrew, S. L. Boulter, E. T. Borer, J. H. C. Cornelissen, A. G. Farji-Brener, J. L. Degabriel, E. Jurado, L. A. Kyhn, B. Low, C. P. H. Mulder, K. Reardon-Smith, J. Rodríguez-Velázquez, A. De Fortier, Z. Zheng, P. G. Blendinger, B. J. Enquist, J. M. Facelli, T. Knight, J. D. Majer, M. Martínez-Ramos, P. Mcquillan, and F. K. C. Hui. 2013. Correlations between physical and chemical defences in plants: Tradeoffs, syndromes, or just many different ways to skin a herbivorous cat? New Phytologist 198:252–263.

Mondor, E. B., M. N. Tremblay, and R. H. Messing. 2007. Morphological and ecological traits promoting aphid colonization of the Hawaiian Islands. Biological Invasions 9:87–100.

Moretti, M., T. C. Dias, F. De Bello, F. Altermatt, J. R. Bell, B. Fournier, S. L. Chown, F. M. Azc, P. Sousa, J. Ellers, M. P. Berg, A. T. C. Dias, F. De Bello, F. Altermatt, S. L. Chown, M. Francisco, J. R. Bell, B. Fournier, M. Hedde, J. Hortal, S. Ibanez, and E. Öckinger. 2016. Handbook of protocols for standardized measurement of terrestrial invertebrate functional traits. Functional Ecology.

Morrison, K. R., and E. A. Stacy. 2014. Intraspecific divergence and evolution of a life-history trade-off along a successional gradient in Hawaii's Metrosideros polymorpha. Journal of Evolutionary Biology 27:1192–1204.

Mortenson, L. A., R. F. Hughes, J. B. Friday, L. M. Keith, J. M. Barbosa, N. J. Friday, Z. Liu, and T. G. Sowards. 2016. Forest Ecology and Management Assessing spatial distribution , stand impacts and rate of Ceratocystis fimbriata induced ' o ¯ hi ' a (Metrosideros polymorpha) mortality in a tropical wet forest , Hawai ' i Island , USA 377:83–92.

Mouquet, N., and M. Loreau. 2003. Community patterns in source-sink metacommunities. The American Naturalist 162:544–557.

Mueller-Dombois, D. 1987. Forest Dynamics in Hawaii. Trends in Ecology and Evolution 2:216–220.

Mueller, M. C. 2015. Islands within islands: The effects of habitat fragmentation, novel community interactions, and climate on Hawaiian Drosophila populations. University of Hawai'i at Hilo.

Müller, J., R. Brandl, M. Brändle, B. Förster, B. C. de Araujo, M. M. Gossner, A. Ladas, M. Wagner, M. Maraun, P. Schall, S. Schmidt, M. Heurich, S. Thorn, and S. Seibold. 2018. LiDAR-derived canopy structure supports the more-individuals hypothesis for arthropod diversity in temperate forests. Oikos 127:814–824.

Myers, J. A., J. M. Chase, I. Jiménez, P. M. Jørgensen, A. Araujo-Murakami, N. Paniagua-Zambrana, and R. Seidel. 2013. Beta-diversity in temperate and tropical forests reflects dissimilar mechanisms of community assembly. Ecology Letters 16:151–157.

Neall, V. E., and S. a Trewick. 2008. The age and origin of the Pacific islands: a geological overview. Philosophical transactions of the Royal Society of London. Series B, Biological sciences 363:3293–3308.

Neel, M. C., H. R. H. R. Tumas, and B. W. B. W. Marsden. 2014. Representing connectivity: quantifying effective habitat availability based on area and connectivity for conservation status assessment and recovery. PeerJ 2.

Nielsen, K. B., R. Kjøller, H. H. Bruun, T. K. Schnoor, and S. Rosendahl. 2016. Colonization of new land by arbuscular mycorrhizal fungi. Fungal Ecology 20:22–29.

Nogueira-Filho, S. L. G., S. S. C. Nogueira, and J. M. V Fragoso. 2009. Ecological impacts of feral pigs in the Hawaiian Islands. Biodiversity and Conservation 18:3677–3683.

van Noordwijk, C. G. E., W. Verberk, H. Turin, T. Heijerman, K. Alders, W. Dekoninck, K. Hannig, E. Regan, S. Mccormack, M. J. F. Brown, E. Remke, H. Siepel, M. P. Berg, and D. Bonte. 2015. Species–area relationships are modulated by trophic rank , habitat affinity , and dispersal ability. Ecology 96:518–531.

Norden, N., S. G. Letcher, V. Boukili, and N. G. Swenson. 2012. Demographic drivers of successional changes in phylogenetic structure across life-history stages in plant communities. Ecology 93:70–82.

Norros, V., R. Penttilä, M. Suominen, and O. Ovaskainen. 2012. Dispersal may limit the occurrence of specialist wood decay fungi already at small spatial scales. Oikos 121:961–974.

Novotny, V. 2009. Beta diversity of plant-insect food webs in tropical forests: A conceptual framework. Insect Conservation and Diversity 2:5–9.

Novotny, V., S. E. Miller, J. Hulcr, R. A. I. Drew, Y. Basset, M. Janda, G. P. Setliff, K. Darrow, A. J. A. Stewart, J. Auga, B. Isua, K. Molem, M. Manumbor, E. Tamtiai, M. Mogia, and G. D. Weiblen. 2007. Low beta diversity of herbivorous insects in tropical forests. Nature 448:692–695.

Novotný, V., and G. D. Weiblen. 2005. From communities to continents: beta diversity of herbivorous insects. Annales Zoologici Fennici 42:463–475.

Öckinger, E., R. Lindborg, N. E. Sjödin, and R. Bommarco. 2012. Landscape matrix modifies richness of plants and insects in grassland fragments. Ecography 35:259–267.

Oksanen, J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, E. Szoecs, and H. Wagner. 2018. vegan: Community Ecology Package.

Orrock, J. L., and J. I. Watling. 2010. Local community size mediates ecological drift and competition in metacommunities. Proceedings of the Royal Society B: Biological Sciences 277:2185–2191.

Package, T., T. Piecewise, S. Equation, and A. J. Lefcheck. 2016. Package ' piecewiseSEM .' Methods in Ecology and Evolution:Version 1.1.

Pakeman, R. J., and J. Stockan. 2013. Using plant functional traits as a link between land use and bee foraging abundance. Acta Oecologica 50:32–39.

Pakeman, R. J., and J. A. Stockan. 2014. Drivers of carabid functional diversity: abiotic environment , plant functional traits, or plant functional diversity? 95:1213–1224.

Pascual-Hortal, L., and S. Saura. 2006. Comparison and development of new graph-based landscape connectivity indices: towards the priorization of habitat patches and corridors for conservation. Landscape Ecology 21:959–967.

Patiño, J., R. J. Whittaker, P. A. V Borges, J. M. Fernández-Palacios, C. Ah-Peng, M. B. Araújo, S. P. Ávila, P. Cardoso, J. Cornuault, E. J. de Boer, L. de Nascimento, A. Gil, A. González-Castro, D. S. Gruner, R. Heleno, J. Hortal, J. C. Illera, C. N. Kaiser-Bunbury, T. J. Matthews, A. Papadopoulou, N. Pettorelli, J. P. Price, A. M. C. Santos, M. J. Steinbauer, K. A. Triantis, L. M. Valente, P. Vargas, P. Weigelt, and B. C. Emerson. 2017. A roadmap for island biology: 50 fundamental questions after 50 years of The Theory of Island Biogeography. Journal of Biogeography 44:963–983.

Peck, S. 1994. Aerial Dispersal of Insects Between and to Islands in the Galápagos Archipelago, Ecuador. Annals of the Entomological Society of America 87:218–224.

Peeters, P. J., G. Sanson, and J. Read. 2007. Leaf biomechanical properties and the densities of herbivorous insect guilds. Functional Ecology 21:246–255.

Peñuelas, J., J. Sardans, J. Llusia, S. M. Owen, J. Silva, and Ü. Niinemets. 2010. Higher allocation to low cost chemical defenses in invasive species of Hawaii. Journal of Chemical Ecology 36:1255–1270.

Percy, D. M. 2017. Making the most of your host: The metrosideros-feeding psyllids (Hemiptera, Psylloidea) of the Hawaiian Islands. ZooKeys 2017:1–163.

Percy, D. M., A. M. Garver, W. L. Wagner, H. F. James, C. W. Cunningham, S. E. Miller, and R. C. Fleischer. 2008. Progressive island colonization and ancient origin of Hawaiian Metrosideros (Myrtaceae). Proceedings. Biological sciences / The Royal Society 275:1479–1490.

Percy, D. M., R. Page, and Q. Cronk. 2004. Plant-Insect Interactions: Double-Dating Associated Insect and Plant Lineages Reveals Asynchronous Radiations. Systematic Biology 53:120–127.

Pereira, H. M., P. W. Leadley, V. Proenca, R. Alkemade, J. P. W. Scharlemann, J. F. Fernandez-Manjarres, M. B. Araujo, P. Balvanera, R. Biggs, W. W. L. Cheung, L. Chini, H. D. Cooper, E. L. Gilman, S. Guenette, G. C. Hurtt, H. P.

Huntington, G. M. Mace, T. Oberdorff, C. Revenga, P. Rodrigues, R. J. Scholes, U. R. Sumaila, and M. Walpole. 2010. Scenarios for global biodiversity in the 21st century. Science 330:1496–1502.

Pereira, H. M., V. M. Proença, and L. Vicente. 2007. Does species diversity really drive speciation? Ecography 30:328–330.

Peres-Neto, P. R., S. Dray, and C. J. F. ter Braak. 2017. Linking trait variation to the environment: critical issues with community-weighted mean correlation resolved by the fourth-corner approach. Ecography 40:806–816.

Pérez-Estrada, L. B., Z. Cano-Santana, and K. Oyama. 2000. Variation in leaf trichomes of Wigandia urens: Environmental factors and physiological consequences. Tree Physiology 20:629–632.

Perry, D. R. 1978. A method of access into the crowns of emergent and canopy trees. Biotropica 10:155–157.

Petchey, O. L., and K. J. Gaston. 2006. Functional diversity: back to basics and looking forward. Ecology letters 9:741–58.

Phillips, H. R. P., J. M. Halley, J. N. Urbina-Cardona, and A. Purvis. 2017. The effect of fragment area on site-level biodiversity. Ecography:1220–1231.

Pickett, S. T. A. 1989. Space-for-time substitutions as an alternative to long- term studies. Pages 110–135 *in* G. E. Likens, editor. Long-term Studies in Ecology. Springer, New York, NY.

Pole, M. 1993. Early miocene flora of the manuherikia group, New Zealand. 7. myrtaceae, including eucalyptus. Journal of the Royal Society of New Zealand 23:313–328.

Polhemus, D. a. 2011. Continuing Studies on the Genus Orthotylus in the Hawaiian Islands (Heteroptera: Miridae), with Descriptions of Thirty-Two New Species. Entomologica Americana 117:37–109.

Polhemus, D. A. 1997. Phylogenetic analysis of the Hawaiian damselfly genus Megalagrion (Odonata: Coenagrionidae): Implications for biogeography, ecology, and conservation biology. Pacific Science 51:395–412.

Pollock, L. J., W. K. Morris, and P. a. Vesk. 2012. The role of functional traits in species distributions revealed through a hierarchical model. Ecography 35:716–725.

Preston, F. W. 1962. The Canonical Distribution of Commonness and Rarity: Part II. Ecology 43:410–432.

Prevedello, J. A., and M. V. Vieira. 2010. Does the type of matrix matter? A quantitative review of the evidence. Biodiversity and Conservation 19:1205–1223.

Price, J. P. 2004. Floristic biogeography of the Hawaiian Islands: influences of area, environment and paleogeography. Journal of Biogeography 31:487–500.

Price, J. P., and D. A. Clague. 2002. How old is the Hawaiian biota? Geology and phylogeny suggest recent divergence. Proceedings of the Royal Society B: Biological Sciences 269:2429–2435.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. The American Naturalist 132:652–661.

Purschke, O., B. C. Schmid, M. T. Sykes, P. Poschlod, S. G. Michalski, W. Durka, I. Kühn, M. Winter, and H. C. Prentice. 2013. Contrasting changes in taxonomic, phylogenetic and functional diversity during a long-term succession: insights into assembly processes. Journal of Ecology 101:857–866.

R Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Raunkiær, C. 1934. Life forms of plants and statistical plant geography. Oxford University Press, Oxford, UK.

Rauscher, M. D. 2004. Ecology of host-selection behavior in phytophagous insects. Pages 223–250 *in* R. F. Denno and M. S. McClure, editors. Variable plants and herbivores in natural and managed systems.

Reed, S. C., P. M. Vitousek, and C. C. Cleveland. 2011. Are patterns in nutrient limitation belowground consistent with those aboveground: Results from a 4 million year chronosequence. Biogeochemistry 106:323–336.

Rees, M., R. Condit, M. Crawley, S. Pacala, and D. Tilman. 2001. Long-Term Studies of Vegetation Dynamics. Science 293:650–656.

Renner, I. W., and D. I. Warton. 2013. Equivalence of MAXENT and poisson point process models for species distribution modeling in ecology. Biometrics 69:274–281.

Reusch, T. B. H., A. Ehlers, A. Hammerli, and B. Worm. 2005. Ecosystem recovery after climatic extremes enhanced by genotypic diversity. Proceedings of the National Academy of Sciences 102:2826–2831.

Ricketts, T. H. 2001. The matrix matters: Effective isolation in fragmented landscapes. The American Naturalist 158:87.

Ricklefs, R. E. 1987. Community Diversity: Relative Roles of Local and Regional Processes. Science 235.

Ricklefs, R. E. 2007. History and Diversity: Explorations at the Intersection of Ecology and Evolution. The American Naturalist 170:S56–S70.

Ricklefs, R. E. 2008. Disintegration of the ecological community. The American naturalist 172:741–50.

Ricklefs, R. E., and E. Bermingham. 2007. The Causes of Evolutionary Radiations in Archipelagoes: Passerine Birds in the Lesser Antilles. The American Naturalist 169:285–297.

Ricklefs, R. E., and J. Travis. 1980. A Morphological Approach to the Study of Avian Community Organization. The Auk 97:1769–1779.

Roderick, G. K. 1997. Herbivorous insects and the Hawaiian silversword alliance: coevolution or cospeciation? Pacific Science 51:440–449.

Roderick, G. K., P. J. P. Croucher, A. G. Vandergast, and R. G. Gillespie. 2012. Species Differentiation on a Dynamic Landscape: Shifts in Metapopulation Genetic Structure Using the Chronology of the Hawaiian Archipelago. Evolutionary Biology 39:192–206.

Roderick, G. K., and R. G. Gillespie. 1998. Speciation and phylogeography of Hawaiian terrestrial arthropods. Molecular Ecology 7:519–531.

Roesch Goodman, K., S. C. Welter, and G. K. Roderick. 2012. Genetic divergence is decoupled from ecological diversification in the Hawaiian Nesosydne planthoppers. Evolution 66:2798–2814.

Rohde, K. 1992. Nordic Society Oikos Latitudinal Gradients in Species Diversity : The Search for the Primary. Nordic Society Oikos 65:514–527.

Root, R. B. 1973. Organization of a plant-arthropod association in simple and diverse habitats: the fauna o f collards (Brassica oleracea). Ecological Monographs 43:95–124.

Rosenzweig, M. L. 1995. Species diversity in space and time. Cambridge University Press, New York, NY.

Roussel, J.-R., and D. Auty. 2018. lidR: Airborne LiDAR data manipulation and visualization for forestry applications.

Roy, K., C. P. Ewing, M. A. Hughes, L. Keith, and G. M. Bennett. 2019. Presence and viability of Ceratocystis lukuohia in ambrosia beetle frass from Rapid ʻŌhiʻa Death-affected Metrosideros polymorpha trees on Hawaiʻi Island. Forest Pathology 49:15–18.

Rybicki, J., and I. Hanski. 2013. Species-area relationships and extinctions caused by habitat loss and fragmentation. Ecology Letters 16:27–38.

Sackett, T. E., S. Record, S. Bewick, B. Baiser, J. Nathan, N. J. Sanders, and A. M. Ellison. 2011. Response of macroarthropod assemblages to the loss of hemlock (Tsuga canadensis), a foundation species. Ecosphere 2:art74.

Saint-Germain, M., P. Drapeau, and C. Hébert. 2009. Landscape-Scale Habitat Selection Patterns of <I>Monochamus scutellatus</I> (Coleoptera: Cerambycidae) in a Recently Burned Black Spruce Forest. Environmental Entomology 33:1703–1710.

Saura, S., and L. Rubio. 2010. A common currency for the different ways in which patches and links can contribute to habitat availability and connectivity in the landscape. Ecography 33:523–537.

Saura, S., and J. Torné. 2009. Conefor Sensinode 2.2: A software package for quantifying the importance of habitat patches for landscape connectivity. Environmental Modelling and Software 24:135–139.

Schliep, E. M., A. E. Gelfand, R. M. Mitchell, M. E. Aiello-Lammens, and J. A. Silander. 2018. Assessing the joint behaviour of species traits as filtered by environment. Methods in Ecology and Evolution 9:716–727.

Schmidt, M. H., C. Thies, W. Nentwig, and T. Tscharntke. 2008. Contrasting responses of arable spiders to the landscape matrix at different spatial scales. Journal of Biogeography 35:157–166.

Schoonhoven, L. M., J. J. A. van Loon, and M. Dicke. 2005. Insect-Plant Biology. Oxford University Press, Oxford, UK.

Selling, O. H. 1948. Studies in Hawaiian pollen statistics. Part III. On the late quarternary history of the Hawaiian vegetation. Bishop Museum Special Publication 39.

Shurin, J. B., P. Amarasekare, J. M. Chase, R. D. Holt, M. F. Hoopes, and M. A. Leibold. 2004. Alternative stable states and regional community structure. Journal of Theoretical Biology 227:359–368.

Siefert, A., C. Violle, L. Chalmandrier, C. H. Albert, A. Taudiere, A. Fajardo, L. W. Aarssen, C. Baraloto, M. B. Carlucci, M. V. Cianciaruso, V. de L. Dantas, F. de Bello, D. S. Duarte, Leandro, C. R. Fonseca, G. T. Freschet, S. Gaucherand, N. Gross, K. Hikosaka, B. Jackson, V. Jung, C. Kamiyama, M. Katabuchi, S. W. Kembel, E. Kichenin, N. J. B. Kraft, A. Lagerström, Y. Le Bagousse-Pinguet, Y. Li, N. W. H. Mason, J. Messier, T. Nakashizuka, J. M. Overton, D. A. Peltzer, I.

M. Perez-Ramos, D. Pillar, Valerio, H. C. Prentice, S. Richardson, T. Sasaki, B. Schamp, C. Schob, B. Shipley, M. Sundqvist, M. T. Sykes, M. Vandewalle, and D. A. Wardle. 2015. A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. Ecology Letters 18:1406–1419.

Siemann, E., J. Haarstad, and D. Tilman. 1999. Dynamics of arthropod and plant diversity during old field succession. Ecography 22:406–414.

Silvertown, J. 2004. The ghost of competition past in the phylogeny of island endemic plants. Journal of Ecology 92:168–173.

Simberloff, D. 1976. Experimental zoogeography of islands: Effects of island size. Ecology 57:629–648.

Simberloff, D., and E. O. Wilson. 1969. Experimental zoogeography of islands: The colonization of empty islands. Ecology 50:278–296.

Simberloff, D., E. O. Wilson, and E. Wilson. 1970. Experimental zoogeography of islands: A two-year record of colonization. Ecology 51:934–937.

Simonson, W. D., H. D. Allen, and D. A. Coomes. 2014. Applications of airborne lidar for the assessment of animal species diversity. Methods in Ecology and Evolution 5:719–729.

Singer, M. C. 2004. Oviposition preference: Its definition, measurement and correlates, and its use in assessing risk of host shifts. Proceedings of the XI International Symposium on Biological Control of Weeds:235–244.

Southwood, T. R. E., V. K. Brown, and P. M. Reader. 1979. The relationships of plant and insect diversities in succession. Biological Journal of the Linnean Society 12:327–348.

Stacy, E. A., J. B. Johansen, T. Sakishima, and D. K. Price. 2016. Genetic analysis of an ephemeral intraspecific hybrid zone in the hypervariable tree, Metrosideros polymorpha, on Hawai'i Island. Heredity 117:173–183.

Stacy, E. A., J. B. Johansen, T. Sakishima, D. K. Price, and Y. Pillon. 2014. Incipient radiation within the dominant Hawaiian tree Metrosideros polymorpha. Heredity 113:334–342.

Stacy, E. A., B. Paritosh, M. A. Johnson, and D. K. Price. 2017. Incipient ecological speciation between successional varieties of a dominant tree involves intrinsic postzygotic isolating barriers:2501–2512.

Stam, J. M., A. Kroes, Y. Li, R. Gols, J. J. A. van Loon, E. H. Poelman, and M. Dicke. 2014. Plant interactions with multiple insect herbivores: from community to genes. Annual Review of Plant Biology 65:689–713.

Stamp, N. 2003. Out of the quagmire of plant defense hypotheses. The Quarterly review of biology 78:23–55.

Stamps, J. A., V. V. Krishnan, and M. L. Reid. 2005. Search costs and habitat selection by dispersers. Ecology 86:510–518.

Statzner, B., a G. Hildrew, and V. H. Resh. 2001. Species traits and environmental constraints: entomological research and the history of ecological theory. Annual review of entomology 46:291–316.

Steffan-Dewenter, I., U. Münzenberg, C. Büger, C. Thies, and T. Tscharntke. 2002. Scale-dependent effects of landscape context on three pollinator guilds. Ecology 83:1421–1432.

Steffan-Dewenter, I., and T. Tscharntke. 1997. Early succession of butterfly and plant communities on set-aside fields. Oecologia 109:294–302.

Stegen, J. C., and N. G. Swenson. 2009. Functional trait assembly through ecological and evolutionary time. Theoretical Ecology 2:239–250.

Stein, A., K. Gerstner, and H. Kreft. 2014. Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. Ecology Letters 17:866–880.

Stemmermann, L. 1983. Ecological studies of Hawaiian Metrosideros in a successional context. Pacific Science 37:361–373.

Stemmermann, L., and T. Ihsle. 1993. Replacement of Metrosideros polymorpha, ohia, in Hawaiian dry forest succession. Biotropica 25:36–45.

Sutherland, W. J., R. P. Freckleton, H. C. J. Godfray, S. R. Beissinger, T. Benton, D. D. Cameron, Y. Carmel, D. a. Coomes, T. Coulson, M. C. Emmerson, R. S. Hails, G. C. Hays, D. J. Hodgson, M. J. Hutchings, D. Johnson, J. P. G. Jones, M. J. Keeling, H. Kokko, W. E. Kunin, X. Lambin, O. T. Lewis, Y. Malhi, N. Mieszkowska, E. J. Milner-Gulland, K. Norris, A. B. Phillimore, D. W. Purves, J. M. Reid, D. C. Reuman, K. Thompson, J. M. J. Travis, L. a. Turnbull, D. a. Wardle, and T. Wiegand. 2013. Identification of 100 fundamental ecological questions. Journal of Ecology 101:58–67.

Swenson, N. G. 2014. Functional and Phylogenetic Ecology in R. Springer.

Swenson, N. G., and B. J. Enquist. 2007. Ecological and evolutionary determinants of a key plant functional trait: Wood density and its community-wide variation across latitude and elevation. American Journal of Botany 94:451–459.

Swenson, N. G., J. C. Stegen, S. J. Davies, D. L. Erickson, J. Forero-Montaña, A. H. Hurlbert, W. J. Kress, J. Thompson, M. Uriarte, S. J. Wright, and J. K. Zimmerman. 2012. Temporal turnover in the composition of tropical tree communities: Functional determinism and phylogenetic stochasticity. Ecology 93:490–499.

Swenson, N. G., and M. D. Weiser. 2014. On the packing and filling of functional space in eastern North American tree assemblages. Ecography 2014:1056–1062.

Swenson, N. G., M. D. Weiser, L. Mao, S. Normand, M. Á. Rodríguez, L. Lin, M. Cao, and J.-C. Svenning. 2016. Constancy in Functional Space across a Species Richness Anomaly. The American Naturalist 187:E83–E92.

Swezey, O. H. 1954. Forest Entomology in Hawaii. Bishop Museum Press, Honolulu, Hawai'i.

Tack, A. J. M., O. Ovaskainen, P. Pulkkinen, and T. Roslin. 2010. Spatial location dominates over host plant genotype in structuring an herbivore community Published by : Ecological Society of America Linked references are available on JSTOR for this article : Your use of the JSTOR archive indicates your acceptance of t 91:2660–2672.

Tamme, R., I. Hiiesalu, L. Laanisto, R. Szava-Kovats, and M. Pärtel. 2010. Environmental heterogeneity, species diversity and co-existence at different spatial scales. Journal of Vegetation Science 21:796–801.

Tauber, C. A., M. J. Tauber, and J. G. Giffin. 2007. Flightless Hawaiian Hemerobiidae (Neuroptera): Comparative morphology and biology of a brachypterous species, its macropterous relative and intermediate forms. European Journal of Entomology 104:787–800.

Taylor, P. D., L. Fahrig, K. Henein, and G. Merriam. 1993. Connectivity is a vital element of landscape structure. Oikos 68:571–573.

Tilman, D. 1988. Plant strategies and the dynamics and structure of plant communities. Princeton University Press.

Tilman, D., R. M. May, C. L. Lehman, and M. A. Nowak. 1994. Habitat destruction and the extinction debt. Nature 371:65–66.

Tischendorf, L., and L. Fahrig. 2000. On the usage and measurement of landscape connectivity. Oikos 90:7–19.

Tscharntke, T., and R. Brandl. 2004. Plant-insect interactions in fragmented landscapes. Annual Review of Entomology 49:405–430.

Tscharntke, T., I. Steffan-Dewenter, A. Kruess, and C. Thies. 2002. Characteristics of insect populations on habitat fragments: A mini review. Ecological Research 17:229–239.

Tsujii, Y., Y. Onoda, A. Izuno, Y. Isagi, and K. Kitayama. 2015. A quantitative analysis of phenotypic variations of Metrosideros polymorpha within and across populations along environmental gradients on Mauna Loa, Hawaii. Oecologia.

Tuomisto, H. 2010. A diversity of beta diversities: Straightening up a concept gone awry. Part 2. Quantifying beta diversity and related phenomena. Ecography 33:23–45.

Umaña, M. N., C. Zhang, M. Cao, L. Lin, and N. G. Swenson. 2015. Commonness, rarity, and intraspecific variation in traits and performance in tropical tree seedlings. Ecology Letters 18:1329–1337.

Umetsu, F., J. Paul Metzger, and R. Pardini. 2008. Importance of estimating matrix quality for modeling species distribution in complex tropical landscapes: A test with Atlantic forest small mammals. Ecography 31:359–370.

Urban, D., and T. Keitt. 2001. Landscape connectivity: A graph-theoretic perspective. Ecology 82:1205–1218.

Valiente-Banuet, A., and M. Verdú. 2008. Temporal shifts from facilitation to competition occur between closely related taxa. Journal of Ecology 96:489–494.

Vandergast, A. G., and R. G. Gillespie. 2004. Effects of natural forest fragmentation on a Hawaiian spider community. Environmental Entomology 33:1296–1305.

Vandergast, A. G., R. G. Gillespie, and G. K. Roderick. 2004. Influence of volcanic activity on the population genetic structure of Hawaiian Tetragnatha spiders: Fragmentation, rapid population growth and the potential for accelerated evolution. Molecular Ecology 13:1729–1743.

Vannette, R. L., D. R. Leopold, and T. Fukami. 2016. Forest area and connectivity influence root- associated fungal communities in a fragmented landscape. Ecology 97:2374–2383.

Vaughn, N. R., G. P. Asner, and C. P. Giardina. 2014. Centennial impacts of fragmentation on the canopy structure of tropical montane forest. Ecological Applications 24:1638–1650.

Vellend, M., L. Baeten, I. H. Myers-Smith, S. C. Elmendorf, R. Beauséjour, and C. D. Brown. 2013. Global meta-analysis reveals no net change in local-scale plant biodiversity over time. Proceeding of the National Academy of Sciences of the United State of America 110:19456–19459.

Vellend, M., M. Dornelas, L. Baeten, R. Beausejour, C. Brown, P. de Frenne, S. C.

Elmendorf, N. J. Gotelli, F. Moyes, I. H. Myers-Smith, A. E. Magurran, B. J. McGill, H. Shimadzu, and C. Sievers. 2017. Estimates of local biodiversity change over time stand up to scrutiny. Ecology 98:583–590.

Violle, C., B. J. Enquist, B. J. McGill, L. Jiang, C. H. Albert, C. Hulshof, V. Jung, and J. Messier. 2012. The return of the variance: Intraspecific variability in community ecology. Trends in Ecology and Evolution 27:244–252.

Vitousek, P. M. 1995. The Hawaiian Islands as a model system for ecosystem studies. Pacific Science 49:2–16.

Vitousek, P. M. 1999. Nutrient limitation to nitrogen fixation in young volcanic sites. Ecosystems 2:505–510.

Vitousek, P. M. 2002. Oceanic islands as model systems for ecological studies:573–582.

Vitousek, P. M. 2004. Nutrient Cycling and Limitation: Hawai'i as a model system.

Vitousek, P. M., G. Aplet, D. Turner, and J. J. Lockwood. 1992. The Mauna Loa environmental matrix: foliar and soil nutrients. Oecologia 89:372–382.

Vitousek, P. M., and H. Farrington. 1997. Nutrient limitation and soil development: Experimental test of a biogeochemical theory. Biogeochemistry 37:63–75.

Vitousek, P. M., P. A. Matson, and D. R. Turner. 1988. Elevational and age gradients in hawaiian montane rainforest: foliar and soil nutrients. Oecologia 77:565–570.

Vitousek, P. M., L. R. Walker, L. D. Whiteaker, and P. A. Matson. 1993. Nutrient limitations to plant growth during primary succession in Hawaii Volcanoes National Park. Biogeochemistry 23:197–215.

Volkov, I., J. R. Banavar, S. P. Hubbell, and A. Maritan. 2003. Neutral theory and relative species abundance in ecology. Nature 424:1035–1037.

Walker, L. R., D. A. Wardle, R. D. Bardgett, and B. D. Clarkson. 2010. The use of chronosequences in studies of ecological succession and soil development. Journal of Ecology 98:725–736.

Wallace, J. R. 2012. Imap: Interactive mapping.

Wang, Y., U. Naumann, S. Wright, D. Eddelbuettel, and D. I. Warton. 2017. mvabund: Statistical Methods for Analysing Multivariate Abundance Data.

Wardle, D. a., R. D. Bardgett, L. R. Walker, and K. I. Bonner. 2009. Among- and within-species variation in plant litter decomposition in contrasting long-term chronosequences. Functional Ecology 23:442–453.

Warren, B. H., D. Simberloff, R. E. Ricklefs, R. Aguilée, F. L. Condamine, D. Gravel, H. Morlon, N. Mouquet, J. Rosindell, J. Casquet, E. Conti, J. Cornuault, J. M. Fernández-Palacios, T. Hengl, S. J. Norder, K. F. Rijsdijk, I. Sanmartín, D. Strasberg, K. A. Triantis, L. M. Valente, R. J. Whittaker, R. G. Gillespie, B. C. Emerson, and C. Thébaud. 2014. Islands as model systems in ecology and evolution: prospects fifty years after MacArthur-Wilson. Ecology Letters:n/a-n/a.

Warton, D. I., B. Shipley, and T. Hastie. 2015. CATS regression - a model-based approach to studying trait-based community assembly. Methods in Ecology and Evolution 6:389–398.

Watling, J. I., and M. A. Donnelly. 2006. Fragments as islands: A synthesis of faunal responses to habitat patchiness. Conservation Biology 20:1016–1025.

Webb, C. O., D. D. Ackerly, M. A. Mcpeek, and M. J. Donoghue. 2002. Phylogenies and Community Ecology. Annual Review of Ecology and Systematics 33:475–505.

Weiblen, G. D., C. O. Webb, V. Novotny, Y. Basset, and S. E. Miller. 2006. Phylogenetic Dispersion of Host Use in a Tropical Insect Herbivore Community. Ecology 87:S62–S75.

Whitfeld, T. J. S., V. Novotny, S. E. Miller, J. Hreck, P. Klimes, and G. D. Weiblen. 2012. Predicting tropical insect herbivore abundance from host plant traits and phylogeny. Ecology 93.

Whittaker, R. J., K. a. Triantis, and R. J. Ladle. 2008. A general dynamic theory of oceanic island biogeography. Journal of Biogeography 35:977–994.

Wiens, J. J., and C. H. Graham. 2005. Niche Conservatism: Integrating Evolution, Ecology, and Conservation Biology. Annual Review of Ecology, Evolution, and Systematics 36:519–539.

Wilson, E. E., and D. a. Holway. 2010. Multiple mechanisms underlie displacement of solitary Hawaiian Hymenoptera by an invasive social wasp. Ecology 91:3294–3302.

Wimp, G. M., G. D. Martinsen, K. D. Floate, R. K. Bangert, T. G. Whitham, and T. G. W. Hitham. 2005. Plant genetic determinants of arthropod community structure and diversity. Evolution 59:61–69.

Winegardner, A. K., B. K. Jones, I. S. Y. Ng, T. Siqueira, and K. Cottenie. 2012. The terminology of metacommunity ecology. Trends in Ecology and Evolution 27:253–254.

Wolfe, E. W., and J. Morris. 1996. Geologic map of the Island of Hawaii. Page U.S. Department of the Interior: U.S. Geological Survey. Washington, D.C.

Wright, I. J., P. B. Reich, M. Westoby, D. D. Ackerly, Z. Baruch, F. Bongers, J. Cavender-Bares, T. Chapin, J. H. C. Cornelissen, M. Diemer, J. Flexas, E. Garnier, P. K. Groom, J. Gulias, K. Hikosaka, B. B. Lamont, T. Lee, W. Lee, C. Lusk, J. J. Midgley, M.-L. Navas, U. Niinemets, J. Oleksyn, N. Osada, H. Poorter, P. Poot, L. Prior, V. I. Pyankov, C. Roumet, S. C. Thomas, M. G. Tjoelker, E. J. Veneklaas, and R. Villar. 2004. The worldwide leaf economics spectrum. Nature 428:821–827.

Wright, I. J., and M. Westoby. 2002. Leaves at low versus high rainfall: Coordination of structure, lifespan and physiology. New Phytologist 155:403–416.

Wright, S. D., C. G. Yong, S. R. Wichman, J. W. Dawson, and R. C. Gardner. 2001. Stepping stones to Hawaii: A trans-equatorial dispersal pathway for Metrosideros (Myrtaceae) inferred from nrDNA (ITS + ETS). Journal of Biogeography 28:769–774.

Zellweger, F., T. Roth, H. Bugmann, and K. Bollmann. 2017. Beta diversity of plants, birds and butterflies is closely associated with climate and habitat structure. Global Ecology and Biogeography 26:898–906.

Zerebecki, R. A., G. M. Crutsinger, and A. R. Hughes. 2017. Spartina alterniflora genotypic identity affects plant and consumer responses in an experimental marsh community. Journal of Ecology 105:661–673.

Ziegler, A. C. 2002. Hawaiian natural history, ecology, and evolution. University of Hawaii Press.

Zimmerman, E. C. 1948. Hemiptera. Pages 1–255 Insects of Hawaii.