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Abstract

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Many studies have documented the negative impact of invasive species on populations, communities, and ecosystems, although most have focused solely on antagonistic rather than mutualistic interactions. For mutualistic interactions, such as pollination, a key to understanding their impacts is how invasive species interact with native species and alter interaction networks. Chapter 1 explores the impacts of invasive species on islands, particularly in regard to plants, pollinators, and how these exotic species attach to existing pollination interaction networks. Island pollination networks differ from mainland counterparts in several important characteristics, including fewer species, more connectance, and increased vulnerability to both invasion and extinction. A progression of invasion has been previously proposed, through which supergeneralist native species facilitate the entry of new exotic species, then are eventually replaced by a few supergeneralist invader species that ultimately dominate the interaction networks. As a result, highly-linked exotic supergeneralists become central nodes in the networks, thus altering network topology and community structure and functioning. Here, I evaluate the evidence for (1) native supergeneralists that provide attachment points for exotic species, (2) exotic supergeneralists that are potentially replacing the function of native species, and (3) the consequences for the replacement of native species with exotics. Both native and exotic supergeneralist species are found on islands, which may therefore represent different points along the invasion trajectory, with consequent concerns for future conservation.

Chapter 2 utilizes a long-term series of observed floral visitations to break apart the potential differences between plants and pollinators as invaders of a community. When plants are introduced into a new environment, their reproductive success can be limited by the lack of a suitable pollinator. If there is no suitable native pollinator, the success of exotic plants may depend on the presence of exotic pollinators, a situation mirrored for exotic plant visitors. Yet, rarely are the distinct roles for native and non-native species of both plants and pollinators examined in the same community. This study examines the role of exotic plants and insects in floral visitation networks in Hawaii, in simple ecological communities with a depauperate native pollinator fauna. On the island of Hawaii, in sites that differed with respect to the presence of exotic plants, floral visitors were observed and quantified across multiple years and seasons.

Where exotic plants were present, exotic insects were observed to visit both native and exotic plant species, while native insects rarely utilized exotic plant resources. Additionally, the majority of floral visitors comprised exotic bees and syrphid flies. In contrast, where the vegetation was dominated by native plants, native bees were major visitors. Thus, the impact of exotic plants and insect visitors on visitation networks was non-symmetrical. Exotic plants relied upon exotic insect taxa, while exotic insect taxa were able to utilize both native and exotic plants. This study demonstrates that the role of mutualistic interactions on the success and impact of invasive species cannot be predicted by looking at isolated interactions, but must also consider the context of the interactions.

Chapter 3 evaluates how these floral visitation networks vary over time. Pollination systems provide important ecosystem services in both natural and managed ecosystems, but their future ecological stability is uncertain as a result of global change, including the impacts of invasive species, habitat loss, and a changing climate. Understanding how these systems vary naturally through time, including intra-annually, can provide critical context for evaluating future change, as well as elucidating the complexity of interspecific interactions in the community. This study examines temporal variation in floral visitation networks in a tropical system in Hawaii characterized by both native and non-native pollinators and plants, and less seasonal variation than in temperate regions. The three most common floral visitors exhibited unique seasonal visitation patterns. In the presence of only native plant species, both the exotic honeybee *Apis mellifera* and the endemic *Hylaeus* bees had similar seasonal variation in floral foraging. However, when the vegetation was a mix of native and exotic species, *Apis* visitation tracked the peak blooming of exotic plants while *Hylaeus* only visited native plants, leading to seasonal variation in resource partitioning. In contrast, visitation by the invasive yellowjacket *Vespula pensylvanica* consistently peaked during the fall, unrelated to plant blooming cycles. Thus, even in a system with minimal seasonal climate variation, there were marked differences in the patterns of pollination interactions between seasons, suggesting that intra-annual variation must be considered in predictions for stability of pollination networks in a changing world.

Finally, Chapter 4 reviews and assesses the range of conservation threats to these Hawaiian pollination systems. Pollination interactions worldwide are facing a wide variety of threats, including habitat loss/change, agricultural intensification, pesticide/herbicide use, invasive species, parasites/disease, and global climate change. Pollination networks in Hawaii are of special concern, because of the unique nature of Hawaii's terrestrial biota, including both plants and pollinators. As the sites from this study were located within a protected national park, the most likely sources for their endangerment are exotic/invasive species, the introduction and spread of parasites/disease, and the slow but potentially devastating effects of climate change. Hawaiian ecosystems, and these sites in particular, are additionally subject to the changes and hazards associated with a zone of active geologic activity. In this chapter, I address specifically both the rising global threats of parasites/disease and climate change and the unique local dangers of active volcanoes for Hawaiian pollination interactions. The variety and magnitude of potential effects provide a wealth of opportunities for future research utilizing existing network data to evaluate how these factors operate both independently and interactively to create change.

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Chapter 1: Alien Takeover: Invasions of island pollination systems

Abstract

Many studies have documented the negative impact of invasive species on populations, communities, and ecosystems, although most have focused solely on antagonistic rather than mutualistic interactions. For mutualistic interactions, such as pollination, a key to understanding their impacts is how invasive species interact with native species and alter interaction networks. In this process, a progression of invasion has been proposed, through which supergeneralist native species facilitate the entry of new exotic species, then are eventually replaced by a few supergeneralist invader species that ultimately dominate the interaction networks (Aizen, Morales et al. 2008; Traveset and Richardson 2014). As a result, highly-linked exotic supergeneralists become central nodes in the networks, thus altering network topology and community structure and functioning. This review examines this concept with a focus on pollination interaction networks on islands, which differ from mainland counterparts in several important characteristics, including fewer species, more connectance, and increased vulnerability to both invasion and extinction. Here, I evaluate the evidence for (1) native supergeneralists that provide attachment points for exotic species, (2) exotic supergeneralists that are potentially replacing the function of native species, and (3) the consequences for the replacement of native species with exotics. Both native and exotic supergeneralist species are found on islands, which may therefore represent different points along the invasion trajectory, with consequent concerns for future conservation.

Introduction: Invasive species on islands

Invasive and exotic species are major conservation concerns for modern ecosystems (Soule 1990; Mack, Simberloff et al. 2000). Island ecosystems are particularly susceptible to invasion (Lonsdale 1999) and have often been held up as an example for the potentially devastating effects of invasive species (Simberloff 1995; Simberloff 2000; Denslow 2003) (but see (Guo and Ricklefs 2010)). These effects have occurred across trophic levels and via many different mechanisms, all leading to ecosystem transformation. Many examples illustrate this effect. One ornamental tree species (*Miconia calvescens*) was introduced to French Polynesia in 1937 and has outcompeted native trees to the extent that it now covers two thirds of Tahiti in monotypic stands (Meyer and Florence 1996). In Guam, the brown tree snake has extirpated the majority of native forest vertebrates (Fritts and Rodda 1998). Invasive rat species are voracious omnivores and have left a trail of extinctions and other detrimental effects across multiple island ecosystems (Harper and Bunbury 2015), including many Pacific islands (Drake and Hunt 2009; Meyer and Butaud 2009), the Galapagos (Clark 1981; Harris 2009), and the Canaries (Nogales, Rodriguez-Luengo et al. 2006). The frequent co-occurrence of domestic cats has not successfully controlled these invasive rats, and instead feral cats on islands have caused at least 14% of worldwide extinctions of birds, reptiles, and mammals through both direct predation and indirect effects via disease or competition (Medina, Bonnaud et al. 2011; Medina, Bonnaud et al. 2014). Removing the cats themselves can then lead to devastating trophic cascades as exotic herbivores are then released from predation pressure (Bergstrom, Lucieer et al. 2009). Exotic plant species, particularly grasses, have altered the fire regime in parts of Hawaii, introducing fire in regions without fire-adapted native species and hastening the takeover of exotic plant species (Hughes, Vitousek et al. 1991).

The impacts of invasive species are more severe on islands with increased endemism (Berglund, Järemo et al. 2009) and on those with more exotic species (Walsh, Venter et al. 2012), highlighting both the acute danger to the most unique island ecosystems and the need to understand how exotic species establish and naturalize. Given the above significant and drastic effects of invasive species on islands, research and theory about invasive species have long been dominated by discussions about their negative interactions with other species. However, recent investigations have delved into the potential role of mutualistic interactions with invasive species (Traveset and Richardson 2006; Traveset and Richardson 2014). Organisms are rarely wholly independent of other species, and are instead part of a complex network of interspecific interactions. Newly-arrived species form new relationships with species that are already present. In the context of mutualisms, this frequently takes the form of new pollination interactions.

With fewer, and unrepresentative species, compared to continental regions, island pollination networks are potentially more vulnerable than mainland systems due to the reduced redundancy. Islands have smaller networks with greater connectance (greater proportion of species connected to each other through pollination interactions) compared to mainland networks (Trøjelsgaard and Olesen 2013) and thus changes in interactions are more likely to have ripple effects throughout the network onto other species. Since adding exotic species to the network could be expected to have greater effects than in mainland systems, it is critical to determine how novel species invade island networks and attach to the existing island networks. Simply, a new plant or pollinator entering a system can either attach to a native species or an exotic species. Olesen et al. (Olesen, Eskildsen et al. 2002) proposed that successful naturalization of exotic species might thus be attributable to either endemic supergeneralists that were able to further broaden their range to exotic species, or else to invader complexes whereby non-native species primarily interact with each other. The term “supergeneralist” is used loosely in the literature, but here refers to a species that interacts with a wide range of potential partners spanning a significant proportion of the available flora or fauna.

It has been proposed that in interaction networks there is a progression of invasion, by which these original, supergeneralist native species that facilitated the entry of exotic species are ultimately replaced by a few supergeneralist invader species that eventually dominate the network (Aizen, Morales et al. 2008; Traveset and Richardson 2014). This progression seems particularly likely to occur on islands, with the potential for particularly strong effects. As many native island species are expected to be subject to continuing reductions and extinctions, this could lead to the need for replacement ecosystem services. These replacement services could theoretically be provided by exotic supergeneralists, as reduced redundancy and increased generalization in island systems make it more likely that an exotic species could potentially replace lost function. These exotic supergeneralists could therefore infiltrate and eventually dominate pollination networks, replacing either endemic supergeneralists or a suite of endemic species. As islands are important sources of worldwide beta diversity (Myers, Mittermeier et al. 2000), the potential increased role of exotic supergeneralists will contribute to increasing global biotic homogenization.

The rise of exotic supergeneralists can lead to increasing facilitation of new exotic species, and thus the development of exotic-exotic interactions forming invader complexes. Invader complexes where invasive species primarily interact with each other in synergistic mutualistic interactions could also potentially form the basis of an invasional meltdown, in which a series of cascading effects lead to major ecosystem change (Simberloff and Von Holle 1999; Simberloff 2006). Indeed, perhaps the most well-documented example of an invasional meltdown is from an oceanic island. On Christmas Island in the Indian Ocean, the dominant herbivore has historically been the native land crab *Gecarcoidea natalis*. The invasive yellow crazy ants, *Anoplolepis gracilipes*, were accidentally introduced to the island, but their populations only began to explode with the later introduction of non-native scale insects. The ants and scale insects form a strong mutualistic partnership, with the ants protecting the scales against predators and the scales providing the ants with abundant carbohydrates through their honeydew. This partnership tipped off an invasional meltdown. Excess honeydew led to sooty mold on tree leaves, causing dieback and opening forest light gaps. Ants killed the land crabs (later feeding on their carcasses for protein), which removed herbivore pressure on seedlings and allowed many new species to flourish in the newly opened light gaps (O'Dowd, Green et al. 2003; Green, O'Dowd et al. 2011). The end result was a complete transformation of the island ecosystem. While such transformations have not yet been documented with pollination networks, the vulnerability of island ecosystems and the prevalence of both invasive pollinators and invasive plant species indicate the possibility of similar future events. Even in the absence of true invasional meltdown, once an invasive species becomes established and integrated into an ecosystem, control or eradication becomes correspondingly more complicated (Zavaleta, Hobbs et al. 2001; Bergstrom, Lucieer et al. 2009), so it is critically important to understand how exotic species become established in the first place.

Island pollination systems (natural state)

Theory: Generalized and depauperate

Compared to mainland systems, islands systems are relatively depauperate, lacking in many of the groups commonly found in mainland systems (Cox, Elmqvist et al. 1991; Paulay 1994). Many remote oceanic islands completely lack native social insects, such as the honeybees and bumblebees that dominate pollinator interactions in many mainland systems, and have a restricted suite of other pollinator species. For example, the Galapagos islands have a single species of native bees (Chamorro, Heleno et al. 2012), and the Hawaiian islands have a single monophyletic genus of native solitary bees and only two butterfly species (one of which is not a pollinator) (Chapter 2, and references therein).

A new plant arriving on an island is unlikely to have arrived together with a viable population of its pollinators. Thus, under “Baker’s Law”, it is more likely for plants with generalized pollination syndromes to successfully colonize new habitats (Baker 1955; Baker 1967). The broader the range of potential pollinators, the more likely it would be that there is an existing species able to perform essential pollination services for a newly arrived plant. While not codified under a specific “law”, the colonization of floral visitors might logically be expected to follow a similar pattern. Floral visitors/potential pollinators that are able to utilize a wider range of flowers in their diet are more likely to find one or more suitable partners upon arrival than a more specialized forager. While some species subsequently develop increased specialization (e.g. Wilson’s taxon cycle (Wilson 1961; Ricklefs and Bermingham 2002)) we expect that both plants and pollinators on islands would follow a pattern of broad generalization, with at least some species that could be classified as “supergeneralists”.

Data: Results from studies (general, broad-scale)

What do we know from studies of actual island pollination systems?

Most studies of plant-pollinator interactions revolve around pairwise interactions, and islands are no exception. Perhaps the most famous examples of island pollination systems revolve around co-evolution for high degrees of specialization – the pairing of honeycreepers and lobelioids in Hawaii (Lammers and Freeman 1986; Lunau 2004) and the apparently perfect match between the orchid *Angraecum sesquipedale* and pollinator moth *Xanthopan morganii praedicta* in Madagascar (Arditti, Elliott et al. 2012). However, these cases are notable precisely for their exceptional nature, and we must examine the broader picture (i.e. pollination networks) to better understand island pollination systems as a whole.

Studies on island pollination networks have revealed several distinct differences from mainland systems. A 2013 meta-analysis of pollination networks world-wide found smaller networks with higher connectance and temperature in islands compared to mainland networks (Trøjelsgaard and Olesen 2013). In other words, island networks generally contain fewer species and these species fulfill more of the potential species interaction pairs – islands are indeed relatively depauperate and there is more generalization among island species interactions. Island plants have lower linkage levels (i.e., fewer connections per species) than mainland plants, and therefore have been described as being more “specialized” than mainland species (Olesen and Jordano 2002). However, in this case, “specialized” simply refers to the fact that island plant species currently interact with relatively few pollinator species compared to mainland counterparts, and does not necessarily reflect any adaptations that would restrict pollination by additional species added to the network. Due to the smaller overall size of island networks, these “specialized” plants may in fact interact with a greater *proportion* of the available floral visitors than “generalized” mainland species.

In an extreme example of a depauperate island pollination network, observations in the Juan Fernandez islands of Chile found that floral visitors were “rare to uncommon”, with perhaps 9% of plant species being pollinated by two native hummingbirds, and (with the possible exception of one plant species) “there is no certainty that any of the species are truly insect pollinated”(Bernardello, Anderson et al. 2001). In one study covering 300 hours of floral observations of 25 endemic plant species over 3 field seasons, only 23 total native insect floral visits were recorded, with one nonnative ant species also contributing visitation near the single human-populated area (Anderson, Bernardello et al. 2001). Instead, most plant species have reduced or inconspicuous flowers and apparently rely on self-compatibility or wind-pollination for reproduction (Anderson, Bernardello et al. 2001; Bernardello, Anderson et al. 2001).

Invading islands: How do new exotic species become incorporated?

The first step in understanding the progression of plant/pollinator invasion on islands is to determine how a new exotic species is able to attach to the existing pollination network. Is there evidence for the types of native supergeneralists that are found in mainland systems? Do these native supergeneralists actually interact with exotic species and thus facilitate their incorporation into the pollination network? Or, do new exotic species primarily attach to existing exotic species, forming invader complexes?

1. Evidence for native/endemic supergeneralists

Overall, there is significant evidence for the existence of native supergeneralist species on islands, for both plants and pollinators.

Plants

Within the plant-pollinator mutualism, there is evidence that both endemic plants and endemic pollinators on islands may be highly generalized in their interactions. On the plant side of the equation, three native plant species on the Galapagos Islands are each associated with more than 40 different pollinator species: *Croton scouleri* (73 visitors)*, Cordia leucophlyctis* (59)*,* and *Lantana peduncularis* (45) (Traveset, Heleno et al. 2013). (But see McMullen 1993, a more limited study that recorded only a few visitors to each of those species).

In Hawaii, the common native tree *Metrosideros polymorpha* has open inflorescences with large amounts of easily accessible pollen and nectar, which allows a wide variety of floral visitors to utilize those resources. Its flowers are visited by a wide range of actual or potential pollinator species, including: Native birds (*Himatione sanguine*, *Hemignathus virens*, and *Vestiaria coccinea*, all Fringillidae) (Carpenter 1976; Koch and Sahli 2013) and *Hylaeus* bees (Magnacca 2007; Lach 2008; Hanna, Foote et al. 2014), as well as invasive species such as ants (*Pheidole megacephala*, *Linepithema humile*, *Anoplolepis gracilipes*) (Lach 2005; Lach 2008), honeybees (*Apis mellifera* (Lach 2008; Hanna, Foote et al. 2013)), yellowjackets (*Vespula* *pensylvanica* (Hanna, Foote et al. 2013; Hanna, Foote et al. 2014)), and Japanese white-eyes (*Zosterops japonica* (Carpenter 1976)). Additional examples of native plant species that receive a broad range of floral visitors are provided in Chapter 2.

Similarly, *Echium wildpretii* is an endemic plant in the Canary Islands that has a high nectar content (Kraemer and Schmitt 1997) and relatively open flowers. While it appears to have typical bird-pollination characteristics and is most effectively visited by a native bee (*Anthophora alluaudi*) (Kraemer and Schmitt 1997), it has also been recorded as being heavily utilized by unspecified non-native hymenoptera – nectar levels were depleted compared to areas with only native hymenoptera (Dupont, Hansen et al. 2003; Dupont 2004). *Echium* flowers are also utilized by a range of other insect species such as the Canarian bumblebee (*Bombus terrestris canariensis*), an endemic wasp (*Ancistrocerus haematodes*), and a cosmopolitan hawkmoth (*Macroglossum stellatarum* (Kraemer and Schmitt 1997)).

Pollinators

Depauperate island systems, particularly those where extinctions are already occurring, are more likely to rely upon keystone species for pollination services (Power, Tilman et al. 1996). These keystone species are the endemic supergeneralists, which may have always fulfilled that role or are simply the last remainders of a more diverse former fauna.

Perhaps the most frequently cited example of an island endemic supergeneralist pollinator is the Galapagos carpenter bee, *Xylocopa darwini*. It is the only bee species native to the Galapagos archipelago, and is thus perhaps unsurprisingly involved in a wide range of pollination interactions. It is considered to be the most important pollinator of the islands, visiting flowers with a wide range of floral morphologies (Chamorro, Heleno et al. 2012). In the first compilation of observations, Linsley et al. (1966) listed 60 flowering plant species that it was known to visit, including many non-natives (Linsley, Rick et al. 1966). McMullen (1993) increased the recorded visitation by *X. darwini* to 79 plant species, of which 17 were non-native, and noted that "the more recent arrivals to the Galapagos Islands are favored as sources of pollen and nectar"(McMullen 1993). A limited pollination network study determined that *X. darwini* visited 11 of the 12 observed flowering plant species (Philipp, Bocher et al. 2006). Finally, a recent and comprehensive pollination network study in the Galapagos concurred with the supergeneralist polylectic nature of *X. darwini*, including usage of exotic plant species, although specific taxon breakdowns were not provided and only 3 exotic plant species were observed for floral visitors (Traveset, Heleno et al. 2013). Traveset at el. (2013) also suggested the endemic lycaenid butterfly *Leptotes parrhasioides* as a supergeneralist pollinator, using a criterion of greater than 20 network links (plant species visited). It is unclear if any of those links were to exotic plant species, however the review by McMullen (1993) included 4 exotic species among the 11 then known to be visited by *L. parrhasioides*.

On Aldabra, two floral visitor species were observed to visit an unusually high number of plant species: the sunbird *Nectarinia sovimanga* and the beetle *Mausoleopsis aldabrensis*

(Woodell 1979). Of the 73 plant species that were in flower at the time of the study, the sunbird was recorded on the flowers of 27 species, 10 of which were introduced. During the same time period, *M. aldabrensis* was observed on 39 species including 10 that were introduced. As with nearly all pollination network studies, however, these observations are based on floral visitation rather than effective pollination. In particular, Woodell questioned the potential efficacy of the sunbird as a pollinator noting that it frequently moved between (rather than within) species and that few of the flowers appear to have adaptations to bird-pollination. In contrast, Woodell noted striking floral constancy in *M. aldabrensis* and that "large amounts of pollen" adhered to their legs and bodies, which together indicates a strong probability of effective pollen transfer between flowers.

Across islands of the South Pacific, flying foxes (*Pteropus* spp.) are critical native keystone species for seed dispersal and also play major roles in floral visitation/pollination (Cox, Elmqvist et al. 1991; McConkey and Drake 2015). In many Pacific island systems, they may be serving as native supergeneralists for pollination interactions. In the Palau islands, *Pteropus* was recorded as visiting 28 species of flowers including multiple introduced species (Wiles, Engbring et al. 1997). In Samoa, *Pteropus* "used" the flowers of >16 species, and 79% of canopy trees depend on them for either pollination or seed dispersal (Banack 1998). *Pteropus* are also the main or sole pollinator for two species that are visited by a diverse assemblage of pollinators in mainland populations – the introduced tree *Ceiba pentandra* (Elmqvist, Cox et al. 1992) and the liana *Freycinetia* (Cox 1984). These interactions demonstrate how new plant species may attach to pollination networks via a native supergeneralist pollinator.

On some islands, the endemic supergeneralist is, unusually, a reptile (Olesen and Valido 2003). Endemic geckos in the genus *Phelsuma* have been reported as important pollinators across multiple islands in the Indian Ocean. In one study on Ile aux Aigrettes in Mauritius, *Phelsuma ornata* was observed to visited 10/14 plant species, including 3 exotic plant species (Olesen, Eskildsen et al. 2002). Nyhagen et al. (2001) add one more endemic plant species to that list (Nyhagen, Kragelund et al. 2001), and include additional references to the importance of *Phelsuma* as a pollinator on Round Island (Mauritius) and the Seychelles. On the Balearic Islands, the endemic lizard *Podarcis lilfordi* is an important pollinator for the native shrub *Euphorbia dendroides* (Traveset and Saez 1997), and may pollinate more than 23 other plant species (Olesen and Valido 2003).

The Hawaiian Islands have a single, monophyletic genus of native bees. However, unlike *Xylocopa darwini* in the Galapagos, *Hylaeus* bees in Hawaii almost exclusively utilize native plant species even when exotic species are available (Chapter 2)(Magnacca 2007; Wilson, Sidhu et al. 2010). As they visit a variety of different native plant species across a range of different floral morphologies (Chapter 2), *Hylaeus* bees as a group may thus represent an example of an island endemic supergeneralist that nonetheless does *not* serve as an attachment point for new plant species. Similarly, on some of the Ogasawara (Bonin) islands of Japan, unspecified "endemic small bees" visited nearly all of the endemic plant species (20 of 24), but were observed on only 25% (3 of 12) of exotic species (Abe, Wada et al. 2011).

Broadly, the evidence suggests that many island systems do indeed have native supergeneralist plants and pollinators that can facilitate the attachment of new exotic species to the existing pollination network. However, the definite preference of endemic bees for native plant species in both Hawaii and the Ogasawara (Bonin) islands illustrates that just establishing that a native species is a supergeneralist is insufficient to prove that it will expand its diet to include exotic species.

2. *Evidence for invader complexes*

The alternative to the attachment of new exotic species to native supergeneralists is that these new species preferentially attach to established exotic species, potentially forming an invader complex of interacting exotic species. In contrast to the well-supported evidence for endemic/native supergeneralists in island pollination networks, the evidence for invader complexes seems to be largely conflated with the effect of exotic supergeneralists (but see Chapter 2). Only a few, uncommon exotic-exotic interactions were observed in the Galapagos (Traveset, Heleno et al. 2013). For the Azorean island Flores and the Mauritian Ile aux Aigrettes, observations of plant-pollinator interactions included fewer pairs of exotic-exotic species interactions than expected (Olesen, Eskildsen et al. 2002). On islands where exotic-exotic interactions were common or dominant, the frequency and strength of these interactions is largely driven by an exotic supergeneralist rather than a suite of exotic species. In the Ogasawara (Bonin) Islands, honeybees utilize both native and exotic plant species, but demonstrate a preference for exotic plant species, particularly during times of the year with reduced native flower bloom (Kato, Shibata et al. 1999; Abe, Wada et al. 2011). In the Flores and Ile aux Aigrettes study, while there were fewer types of exotic-exotic species-pair interactions than expected, the data nonetheless indicate the potentially important role of exotic pollinators when interaction frequency is taken into account. Honeybees were the dominant floral visitor for three of the five exotic plant species on Ile aux Aigrettes, possibly indicating a facilitative role for their success.

While exotic honeybees were also the dominant supergeneralist pollinator species in Hawaii, there are also a number of other exotic flower-visiting species that contributed to the significantly greater than expected number of exotic-exotic interactions, including ants, syrphid flies, and yellowjacket wasps (Chapter 2). Thus, this suite of exotic flower visitors interacting with a suite of exotic plant species may constitute a true invader complex.

Progression of invasions over time

Does exotic species attachment on islands proceed from initial dependence on native supergeneralists to the eventual rise of exotic supergeneralists?

1. *Native supergeneralists -> invader complexes/exotic supergeneralists*

The contrast between the relative importance of native supergeneralists versus invader complexes/exotic supergeneralists for the attachment of new exotic species may not be mutually exclusive, but rather represent different points along the invasion trajectory. Aizen et al. (2008) proposed that over the course of an invasion, "links [are] transferred from generalist native species to super-generalist alien species" (Aizen, Morales et al. 2008). This progression is simple to envision with island ecosystems. A pristine island environment containing only native species would naturally lack invader complexes. Specialist pairs of plants and their pollinators are highly unlikely to be simultaneously introduced (except through specific human intervention). Some new exotic plant species may be able to entirely self-pollinate or clonally reproduce. Likewise it is possible that species that may serve as occasional pollinators in their native area may not include nectar or pollen in their diet in their introduced area (and thus not serve any role in pollen transfer). However, these species are not considered here because within the island context they do not connect to other species within the pollination network. The first true exotic additions to the pollination network would therefore of necessity need to be able to attach to existing native species. At this early stage of invasion, the most likely attachment point is a generalized species that already accepts a wide range of partners. In one mainland example, the exotic *Impatiens glandulifera* was facilitated in its invasion by a suite of generalist native pollinators that eventually allowed *Impatiens* to dominate the local pollen-transport networks (Lopezaraiza-Mikel, Hayes et al. 2007). In the Galapagos, exotic plants are not generalists themselves, but primarily attach to generalist pollinators (such as the supergeneralist endemic bee *Xylocopa darwini*) (Traveset, Heleno et al. 2013).

As the number of exotic species in the network begins to increase, the possibility of exotic-exotic attachment likewise increases, particularly as invasive plant species tend to be more generalized than native species (Albrecht, Padrón et al. 2014). At this point, the identity of the established exotic species becomes important. If the existing exotic species are relatively specialized or exist in low frequency, then new exotic species may then still be more likely to rely upon native supergeneralists to establish themselves. If, however, the existing exotic species include plants or pollinators that are plentiful and highly generalized themselves, then the likelihood of invader alliances is greatly increased (e.g., Chapter 2). This stage in the invasion sequence might therefore represent a turning point between the early importance of endemic supergeneralists to the later importance of invader complexes in determining the attachment of new species to pollination networks. These new complexes are thus not structured around endemic supergeneralists, but exotic supergeneralists.

2. Evidence for exotic supergeneralists

Exotic supergeneralists already play a major role in some island pollination networks. The most common example of an exotic supergeneralist is the European honeybee, *Apis mellifera*, which is well-known for its broad foraging range everywhere it is established. Thus, it is unsurprising that on islands where honeybees have been introduced and successfully naturalized, they are likewise highly polylectic in their foraging preferences (Kato, Shibata et al. 1999; Dupont 2004; Kato and Kawakita 2004; Abe, Wada et al. 2011). On the Ogasawara

(Bonin) islands of Japan, honeybees visited 62.1% of the plant species, including 28/38 exotic species, 22/30 native, and 32/64 endemic (Abe, Wada et al. 2011). On Ile aux Aigrettes in Mauritius, honeybees visited a greater proportion of the flora (12/14) than any other pollinator and accounted for more than four times as many individual visits as the next most common floral visitor (Olesen, Eskildsen et al. 2002).

On the Galapagos Islands, the most recent pollination network studies have posited three potential exotic supergeneralist pollinators: *Hemiargus ramon* (Lycaenidae), *Polistes versicolor* (Vespidae), and *Pseudodoros clavatus* (Syrphidae) (Traveset, Heleno et al. 2013). On two of the studied islands, the pollinators with the highest linkage levels (i.e., that visit the most plant species) are exotic species. It is not known, however, how effective these species are at actually effecting pollen transfer. In particular, the authors posit that *Polistes versicolor*, despite being a prolific floral visitor, is unlikely to play a major role in successful pollination.

The relative role of native versus exotic supergeneralists is perhaps most pronounced in Hawaii. Since the native *Hylaeus* bees may be supergeneralist pollinators that are nonetheless not “welcoming” to exotic plant species, honeybees may be serving an important role as supergeneralists for both native and non-native plant species (Chapter 2). The invasive Japanese white-eye, *Zosterops japonicus*, may also fill that exotic supergeneralist role for bird-pollinated plants. It is now the most common bird in Hawaii, and has successfully naturalized across all surveyed forests across a breadth of climate and vegetation (Scott, Mountainspring et al. 1986). *Zosterops* has been recorded visiting and at least potentially pollinating a variety of flowers including the native species *Metrosideros polymorpha* (Carpenter 1976), *Vaccinium calycinum* (Waring, Loope et al. 1993), *Clermontia* spp. (Lammers, Weller et al. 1987; Aslan, Zavaleta et al. 2014), and *Freycinetia arborea* (Cox 1983).

The lack of long-term time series of invasions in progress makes it impossible to be certain whether (or how often) invasions of pollination systems actually follow the pattern of initial facilitation by native supergeneralists then takeover by exotic supergeneralists. However, the components of that progression do exist on islands, so it remains plausible. Future researchers should revisit these pollination systems and look for shifts in linkage distribution from native to exotic species.

Reasons for concern

If island pollination networks are indeed following a progression from native supergeneralists to invader complexes/exotic supergeneralists, then it might seem that ecosystem function is being essentially preserved and thus there is less reason for conservation concern. However, there are a number of reasons why this is not the case.

1. *Biotic homogenization*

On the broadest level, the replacement of endemic species with exotic species (even if ecosystem function is maintained) leads to increasing global homogenization through lowered beta diversity (McKinney and Lockwood 1999; Sax and Gaines 2003; Clavel, Julliard et al. 2011). This process of biotic homogenization has already been recorded in island ecosystems for both plants (Castro, Munoz et al. 2007; Castro, Daehler et al. 2010) and insects (Shaw, Spear et al. 2010).

On a local level, the shift towards exotic supergeneralists can cause the restructuring of a pollination network from containing many diffuse interactions to being dominated by one or a few strong interactors (nodes). Abe (2011) recorded significantly fewer visitor groups (i.e. less visitor diversity) to plants in areas where honeybees were dominant. This loss of diversity in an already depauperate fauna increases the vulnerability of these ecosystems, as biodiversity provides a level of "insurance" against changing conditions (Yachi and Loreau 1999; Loreau, Naeem et al. 2001). With just a few strong interactors, the loss of even one of those species would have a much greater effect on the community.

2. *Exotic species can outcompete native species*

Exotic species that have naturalized into island systems and provide pollination services can also have negative competitive effects on remaining native species. Japanese white eyes *(Zosterops japonicus)* are highly generalized and overlap the ecological niches of several native bird species in Hawaii. Negative correlations between the populations of *Zosterops* and the endemic elepaio (*Chaseimpis sandwichensis*) and i'iwi (*Vestiaria coccinea*) demonstrate the role of exploitative resource competition for insects and nectar, respectively, with the greater densities of *Zosterops* indicating that it is successfully outcompeting those native birds (Mountainspring and Scott 1985). Additionally, in areas with large *Zosterops* populations, the juveniles of eight native bird species were stunted in size and had reduced survival (Freed and Cann 2009). Thus, while *Zosterops* is generalized enough to visit and potentially pollinate a wide range of flowering plants, the ability of *Zosterops* to outcompete native birds (many of which serve as important pollinators to native plants) may nevertheless hasten the transition to an exotic-dominated landscape. Alarmingly, projects to restore native forests may themselves trigger increased population growth in *Zosterops*, which then expand into contiguous habitats (Freed and Cann 2012).

The eusocial structure of honeybee colonies leads to dense populations, efficient foraging (via worker communication), and high resource consumption of both pollen and nectar. In contrast, many native bees or other pollinators are solitary and thus exist in lower population densities and exert less demand for resources. This difference has led many researchers and conservation workers to posit that honeybees (or similarly social bumblebees) should outcompete native species through indirect resource competition (or to a lesser extent, direct aggressive interactions at flowers) (Donovan 1980; Sugden and Pyke 1991; Roubik 2001; Roubik and Wolda 2001; Roubik and Villanueva-Gutierrez 2009; Howlett and Donovan 2010). However, actual effects of competition between honeybees and native pollinators have been difficult to prove. Native bee populations are normally highly variable in space and time, so long-term trends are needed in order to show a true decline (Roubik 2001; Williams, Minckley et al. 2001). Assigning the cause of that decline to competition from honeybees or other non-native pollinators is even more difficult. On the island of Mauritius, honeybees were shown to compete with endemic bird species for the nectar resources of two endemic tree species, however the lack of control sites without honeybees rendered it impossible to determine if that resource competition was having any detrimental effect (Hansen, Olesen et al. 2002). In Hawaii, eusocial ants (Junker, Bleil et al. 2010) and *Vespula* wasps (Hanna, Foote et al. 2014) have been shown to drain the nectar resources of *Metrosideros* flowers, but the actual impact of this resource depletion on the populations of legitimate pollinators is unknown. The aggressive behavior of ants (Lach 2008) and *Vespula* wasps (Hanna, Foote et al. 2014) also deters other floral visitors, which can result in lowered reproductive success for *Metrosideros* (Hanna, Foote et al. 2013).

The relative role of exotic plants in competing with natives for pollination services is more complicated (Bjerknes, Totland et al. 2007; Morales and Traveset 2009). Exotic plants that produce copious rewards can attract pollinators away from native species, thus outcompeting them for pollination service (Chittka and Schürkens 2001). However, the attractiveness of these flowers may also increase the number of pollinators in an area, which can increase the floral visitation to other species via a “magnet species” effect (Laverty 1992). Research on the Balearic Islands have found mixed effects, depending on both the native species involved (Moragues and Traveset 2005) and the spatial scale. Attractive exotic species increased pollinators in the wider area (benefiting native plants), but in close proximity pollinators prefer the exotic flowers (Jakobsson, Padron et al. 2009) with the strength of effect varying by pollinator guild (Albrecht, Ramis et al. 2016). Exotic plant species that have native congeners can also endanger natives through cross-visitation and/or hybridization (e.g *Carpobrotus* in the Balearic Islands (Jakobsson, Padron et al. 2008) and *Rubus* in Hawaii (Randell, Howarth et al. 2004)).

3. *Due to the extinction or reduction of native pollinators and plants, replacement service may be needed. However, true replacement function is not guaranteed*

Both island plants and pollinators have been subject to extinctions and range reductions in recent history, which both opens up new niche space (which can be appropriated by invaders) and can necessitate the replacement of mutualist partners in order to maintain ecosystem functions. In this context, the establishment of new exotic supergeneralist partners might seem beneficial and even critical to the continued existence of native species. However, the recent history of extinctions and “replacements” of pollinators and plants on islands has shown that these new partners may not be providing a full “rescue effect” of replacement function.

a. *Native pollinator extinctions and need for replacement*

Many native pollinator species on islands are extinct or endangered, although the consequent effects on the local flora are not always known. Worldwide, there are very few known examples where the extinction of a plant species can be conclusively traced to the loss of their pollinator (Bond 1994). However, this may be the result of a lack of data rather than lack of occurrence, and island ecosystems are likely to be at higher threat for reciprocal extinction (Cox and Elmqvist 2000).

In Hawaii, multiple pollination groups have been subject to repeated extinction and endangerment. Of the native insect pollinators, 52 species of *Hylaeus* bees and 26 species of moths are now extinct (Cox and Elmqvist 2000). Seven more *Hylaeus* species were placed on the U.S. Fish & Wildlife Endangered Species list in 2016 (Ollerton 2017), and many others are rare or threatened (Magnacca 2007). The native avifauna is also highly threatened, with both multiple past extinctions (Olson and James 1982) and expected increased future conservation concerns due to disease and climate change (Paxton, Camp et al. 2016). Thirty-one species of Campanulaceae in Hawaii are thought to already be extinct due at least partially to the loss of their bird pollinators (Cox and Elmqvist 2000), while other plant species have been able to switch to exotic pollinators (Cox 1983) or rely on self-pollination (Cory, Pender et al. 2015).

Across the South Pacific and the Indian Ocean, the native supergeneralist flying foxes (*Pteropus* spp.) are likewise under threat (Vincenot, Florens et al. 2017). They have long been a component of the diet of local peoples, however the advent of new hunting practices and modern economics has led to overhunting in recent times (Bräutigam and Elmqvist 1990). As at least some groups of local hunters believe that the supply of *Pteropus* is infinite (Brooke and Tschapka 2002), unsustainable hunting practice are likely to continue. On other islands, *Pteropus* are considered vermin by local governments and these threatened endemic species are therefore subject to massive population culls (Vincenot, Florens et al. 2017). The detrimental effects of hunting are magnified after tropical cyclones, when food resources for bats decrease and hunting increases (Craig, Trail et al. 1994; Pierson, Elmqvist et al. 1996; McConkey, Drake et al. 2004; Esselstyn, Amar et al. 2006). As tropical cyclone destructiveness is linked to global warming (Emanuel 2005; Knutson, McBride et al. 2010), we can expect increased disruption of *Pteropus* populations in the future. Given the critical importance of *Pteropus* for both pollination and seed dispersal on these islands (McConkey and Drake 2015; Vincenot, Florens et al. 2017), their endangerment and extinction will undoubtedly have negative effects on the local flora unless replacement service can be provided.

Endangered island plant species are under significant threat from multiple sources including habitat destruction, invasive herbivores, and seed predators, and the loss or reduction of their pollinators may be one more nail in the proverbial coffin. The charismatic Hawaiian lobelioid *Brighamia insignis* has been reduced to a single individual in the wild (Walsh 2015), mostly due to the detrimental effects of introduced pigs and rats. However, it is also mostly self-incompatible and may have been pollinated by an endemic hawkmoth (*Tinostoma smaragditis*, the fabulous green sphinx moth)(Walsh 2015), which is now so rare that decades have elapsed between individual collections (Heddle, Wood et al. 2000). Similarly, the now-extinct *Paschalococos disperta* palm of Easter Island, while primarily endangered through overexploitation by local peoples, may have also relied on pollination services from a native parrot that was driven to extinction by the introduced Polynesian rat (Cox and Elmqvist 2000). Fortunately, extensive conservation efforts have so far managed to preserve *Brighamia* through botanical gardens and outplantings, but floral visitation in the Hawaiian collections remains very rare (Walsh 2015). Without an adequate replacement pollinator, *Brighamia* will remain practically extinct in the wild, even if all other conservation concerns are addressed.

b. *Native plant extinctions and need for replacement*

Overall, recorded native plant extinctions on islands are relatively rare compared to the dire fate of many native island bird species (many of which serve some pollination function) (Sax, Gaines et al. 2002). While the introduction of new faunal species has correlated with declines in comparable fauna, the introduction of new plant species has generally resulted in increased local plant diversity instead of consequent extinctions, at least over the short term (Sax and Gaines 2003; Stohlgren, Barnett et al. 2008). Thus, less is known about native plant extinctions and their consequent effects on their pollinators.

Shifts in pollinator interactions can lead to evolutionary change: The extinction and/or endangerment of lobelioid species in Hawaii led to a change in bill morphology for their presumed co-evolved native pollinator (Smith, Freed et al. 1995). The long, curved corollas of lobelioid flowers required a long curved bill to reach their nectar resources. Compared to older specimens predating the extinction/endangerment of the lobelioids, modern i'iwi birds (*Vestiaria coccinea*) have shorter bills reflecting their shift to feeding on the open flowers of *Metrosideros polymorpha* (Smith, Freed et al. 1995). These shorter bills thus have a more generalized morphology, and may potentially indicate a shift from specialization to increased generalization as a result of the loss of their co-evolved mutualist. In a large study of 21 plant-hummingbird quantitative pollination networks, shorter-billed hummingbirds were shown to be more generalist in their preferences and to be more likely to utilize exotic species than longer-billed hummingbirds (Maruyama, Vizentin-Bugoni et al. 2016). Over evolutionary time-spans, island pollinators may thus be able to compensate for the loss of native partners through increased generalization to include exotic species. This could create new native supergeneralists, rather than necessarily leading towards favoring new exotic supergeneralists. Either case, however, would potentially facilitate increased future plant invasion.

However, Hawaiian island pollinators may not have a long evolutionary time span to adapt their behavior or physiology. More than 100 known plant species are extinct, and 366 more species are currently listed as endangered or threatened (http://dlnr.hawaii.gov/ecosystems/rare-plants/). In particular, *Metrosideros polymorpha* trees on the Big Island of Hawaii are currently threatened by an invasive fungus that causes rapid plant mortality (Keith, Hughes et al. 2015; Mortenson, Hughes et al. 2016; Stone 2017)(Chapter 4). As these trees are important pollinator resources, the loss of significant portions of their population will undoubtedly have downstream effects on species that rely on their pollen and/nectar.

c. Replacement by exotic species may work for some island species but not for others

Given that island populations are vulnerable to extinctions, how effective are exotic species at providing important replacement ecosystem services? If a new, exotic pollinator is able to adequately replace the function of an endangered or extinct native pollinator, then it could be considered beneficial to that ecosystem. A recent review of native and non-native vertebrate pollinators (including both island and mainland systems) found that non-native pollinators were less effective than native counterparts, but that they could provide at least some replacement services where the native vertebrate pollinators had been extirpated (Aslan, Zavaleta et al. 2012).

A number of Hawaiian bird species had/have close pollinator relationships with native plant species, such as the honeycreepers with lobelioid plants (Lunau 2004). In the wake of these native bird extinctions/extirpations, other bird species (primarily the supergeneralist *Zosterops japonicus*, Japanese white-eye) have provided pollination service to native Hawaiian plants. *Zosterops* may be an effective pollinator for *Freycinetia arborea*, which was once presumably pollinated by a range of extinct Hawaiian bird species (Cox 1983). It has also been recorded as the primary visitor for the native *Scaevola procera* and *S. glabra*, with visitation behavior that was “conducive to pollination”(Elmore 2008). A related species, *Zosterops lateralis*, has provided “rescue” pollination service for three plant species in New Zealand that have lost their endemic pollinator species (Pattemore and Wilcove 2012). *Zosterops japonicus* has likewise also been credited with providing replacement seed dispersal services in the Bonin Islands (Kawakami, Mizusawa et al. 2009). However, this “rescue effect” is not universally effective. In studies of three *Clermontia* species (lobelioids), only two were effectively visited by *Zosterops* while one species received zero floral visitation (Lammers, Weller et al. 1987; Aslan, Hart et al. 2014; Aslan, Zavaleta et al. 2014). In a separate study of rare Hawaiian native plant species, *Zosterops* was observed to visit the lobelioids *Cyanea pinnatifida* and *Cyanea superba*, but was considered more likely to be functioning as a nectar robber than as a potential pollinator (Gardener and Daehler 2006). Additionally, as mentioned above, resource competition with *Zosterops* may also be lowering the populations of remaining native bird species that *are* effective pollinators of native plants (Freed and Cann 2009; Freed and Cann 2014). Thus, while it is possible for this non-native species to at least partially or potentially compensate for the loss of native pollination services, it is unlikely to be a truly effective replacement overall in this ecosystem. Similarly, introduced birds have been shown to be ineffective at replacing native avian seed dispersers in Hawaii (Chimera and Drake 2010; Wu, Delparte et al. 2014) (but see (Foster and Robinson 2007)).

On Mauritius, the rare *Nesocodon mauritianus* (Campanulaceae) is one of three endemic plant species to produce red nectar, which attracts the native supergeneralist *Phelsuma* geckos (Hansen, Beer et al. 2006). However, where *Phelsuma* is absent, the flowers are visited almost solely by the exotic red-whiskered bulbul *Pycnonotus jocosus* (Olesen, Ronsted et al. 1998). While some of these floral visitations occur in a way that might facilitate cross-pollination (inserting the head inside the flower to access nectar), approximately 90% of the observed interactions involved nectar robbing or floral destruction (Olesen, Ronsted et al. 1998). Thus, while the bulbul may provide some degree of rescue pollinator service, it is clearly inefficient and inferior. Furthermore, the omnivorous and generalist bulbuls contribute to the propagation and invasion into native forests of exotic plant species through seed dispersal (Linnebjerg, Hansen et al. 2009).

In New Zealand, native short-tongued bees were able to partially replace pollination service to two ornithophilous plants after loss of their native pollinator (Robertson, Ladley et al. 2005). In Hawaii, both native (short-tongued *Hylaeus* bees) and exotic (European honeybees, *Apis mellifera*) insect species visit ornithophilous *Metrosideros* trees, which have suffered a reduction in their native avifaunal partners (Chapter 2)(Junker, Bleil et al. 2010; Hanna, Foote et al. 2013). It has even been speculated that the variability and open morphology of *Metrosideros* flowers are adaptations to specifically promote insect pollination in the event of the failure of bird pollination (Carpenter 1976). However, differences in floral visitation behavior may affect the relative pollination effectiveness of the native *Hylaeus* versus the exotic *Apis*. *Hylaeus*, which forage almost solely on pollen on *Metrosideros*, were not observed to contact stigmas and effect pollen transfer, while *Apis* forages on both nectar and pollen and successfully transferred pollen (Junker, Bleil et al. 2010). Thus, the exotic *Apis* may be providing at least partial replacement pollination services for *Metrosideros* trees (Hanna, Foote et al. 2013).

As a counter example, differential usage of native ohelo (*Vaccinium reticulatum*) flowers by honeybees versus native *Hylaeus* bees due to differences in head size and tongue length could potentially lead to opposite differences in pollination effectiveness (Chapter 2). Ohelo flowers are urn-shaped, and during floral visitation the smaller (and shorter-tongued) *Hylaeus* bees fit their entire bodies inside the flower and contact the floral reproductive organs. The larger heads of honeybees cannot fit inside these flowers, but they can reach the nectar with their longer tongues. With this feeding pattern, it is unlikely that they contact the anthers or styles in a way that would facilitate cross-pollination (personal observation, personal communication from Heather Sahli). Thus, honeybees are likely not able to serve as effective replacement pollinators for this plant.

Overall, there is a distinct and unsurprising pattern for the relationships where exotic species are able to provide replacement pollinator services – replacement pollinators are most effective when the native flowers have a generalized morphology and accessible rewards. Specialized flowers with restrictive morphology such as lobelioids and ohelo may be utilized by exotic pollinators, but only as nectar robbers rather than as mutualists. While Baker's Law predicts that many island native flowers follow a generalized pattern, it is the most unique and morphologically-distinct species that would be expected to suffer the most when pollination networks become dominated by exotic supergeneralists.

4. *Potential for invasional meltdown*

If the invasion sequence does indeed proceed from endemic supergeneralists to invader complexes/exotic supergeneralists, it might seem that the logical next step could be an invasional meltdown (described above). As exotic-exotic interactions increase and form a larger and larger proportion of interactions, should we expect to see a tipping point where runaway mutualistic interactions lead to a transformation of the island ecosystem?

In Australia, non-native honeybees and the highly invasive plant *Lantana camara* have been observed to exhibit synergistic interactions where copious *Lantana* floral resources fuels the success and growth of honeybee colonies, and readily available and effective honeybee pollination facilitates the success and expansion of *Lantana* invasion (Goulson and Derwent 2004). However, pollination interactions are usually more diffuse and generalized than classic examples of invasional meltdown. Honeybees, the most common invasive pollinator, feed on and pollinate multiple other species (including potentially many native species), so runaway synergistic effects are generally less likely to occur than with other types of interspecific interactions. However, their role can be combined with the effects of other exotic species in the ecosystem. On the Ogasawara (Bonin) islands of Japan, an invasive predatory anole (*Anolis carolinensis*) has decimated the native insect population, preferentially consuming native pollinator species over the introduced European honeybees (Abe, Makino et al. 2008). On islands with these invasive anoles, the pollinator fauna is now dominated by European honeybees, which preferentially visit exotic plant species, leading to high fruit set for exotic species and significant pollen limitation for native plant species (Abe, Wada et al. 2011). Over time, the combined impact of the preference of the exotic predator for native pollinator species and the preference of the exotic pollinator for exotic plant species facilitates the transformation of the island ecosystem to one dominated by exotic species.

Non-native pollinators can also have major ecosystem effects through their other interspecific interactions. *Zosterops* has been implicated in potential invasional meltdown through its facilitative seed-dispersal relationship with the invasive firetree, *Myrica faya* (Woodward, Vitousek et al. 1990)(but see (Larosa, Smith et al. 1985)), which leads to positive effects on other exotic species and downstream detrimental effects on both native pollinator bird species and the potentially supergeneralist native tree *Metrosideros polymorpha* (Vitousek, Walker et al. 1987; Aplet 1990; Woodward, Vitousek et al. 1990; Walker and Vitousek 1991).

Conclusion

Invasive species on islands are widely known to have devastating effects through negative interactions, but even putatively mutualist interactions can threaten native ecosystems. Many island communities have native supergeneralist species that facilitate the attachment of new exotic species. Some of these new exotic species will themselves be supergeneralists, which can lead to the redistribution of links away from native species to center around exotic species. This redistribution of links is especially probable in already depauperate and vulnerable island systems that are undergoing additional species extinctions. While these exotic supergeneralists can theoretically provide replacement ecosystem functions for extinct or endangered native species, in practice the “rescue effect” is only effective for some species-pairs. In order to actually track the progression of invasive species and linkages in island pollination systems, long-term studies of broad-scale pollination networks are critical. In some island systems, it may be too late, as exotic supergeneralists already occupy a central role in pollination networks.

Chapter 2: Asymmetric attachment of pollinators and plants determine entry of invasive species in Hawaii

Abstract

A key mechanism explaining the success of invasive species is escape from antagonistic interactions. However, the potential role of mutualistic interactions involving non-native species has only recently begun to be explored. When plants are introduced into a new environment, their reproductive success can be limited by the lack of a suitable pollinator. If there is no suitable native pollinator, the success of exotic plants may depend on the presence of exotic pollinators, a situation mirrored for exotic plant visitors. Yet, rarely are the distinct roles for native and non-native species of both plants and pollinators examined in the same community. This study examines the role of non-native plants and insects in floral visitation networks in Hawaii, in simple ecological communities with a depauperate native pollinator fauna. On the island of Hawaii, in sites that differed with respect to the presence of non-native plants, floral visitors were observed and quantified across multiple years and seasons. Where non-native plants were present, non-native insects were observed to visit both native and non-native plant species, while native insects rarely utilized non-native plant resources. Additionally, the majority of floral visitors comprised non-native bees and syrphid flies. In contrast, where the vegetation was dominated by native plants, native bees were major visitors. Thus, the impact of exotic plants and insect visitors on visitation networks was non-symmetrical. Non-native plants relied upon non-native insect taxa, while non-native insect taxa were able to utilize both native and non-native plants. This study demonstrates that the role of mutualistic interactions on the success and impact of invasive species cannot be predicted by looking at isolated interactions, but must also consider the context of the interactions.

Introduction

The standard paradigm for the success of non-native species in new habitats is that they are able to naturalize and flourish because they have escaped from their natural enemies (Wolfe 2002; Torchin, Lafferty et al. 2003; Torchin and Mitchell 2004). This “enemy release” approach underlies modern attempts at biological control (Keane and Crawley 2002), in which undesired exotic species are targeted with natural enemies from their home region. However, the important role of mutualisms and other positive interactions for facilitating species invasion has lately become more apparent (Traveset and Richardson 2014), with the failure of some potential invasions credited to “mutualist release” (Zenni and Nuñez 2013), a condition where incoming species lack a required mutualist partner. The benefit of mutualisms in the success of some invasive species has been particularly well-documented in island systems. In Hawaii, for example, Japanese white-eyes (*Zosterops japonicus*) feed on the berries of the invasive *Morella faya* tree and serve as major seed dispersers (Woodward, Vitousek et al. 1990). As *M. faya* is a nitrogen-fixer and the volcanic soils of Hawaii are nitrogen poor, the nitrogen enrichment of *M. faya* facilitates the presence of a variety of exotic plants that would otherwise be nitrogen-limited (Vitousek, Walker et al. 1987; Vitousek and Walker 1989). The presence of *M. faya* also increases the local population of exotic earthworms, which allows for further nitrogen enrichment of the soil (Aplet 1990). On Christmas Island, the exotic yellow-legged crazy ant, *Anoplolepis gracilipes*, was naturalized for decades before the introduction of exotic honeydew-secreting scale insects facilitated the formation of dense ant supercolonies (O'Dowd, Green et al. 2003; Green, O'Dowd et al. 2011). The mutualism between the ants and scale insects has had synergistic and cascading effects resulting in a near-total transformation of the local ecosystem, a process that has been described as an invasional meltdown (O'Dowd, Green et al. 2003; Green, O'Dowd et al. 2011). In another example, two non-native frugivorous bird species in French Polynesia are major seed dispersers for the invasive plant *Miconia calvescens*, but are not effective seed dispersers for native plant species (Spotswood, Meyer et al. 2012). Similarly, one study in Hawaii found that even in forests dominated by native trees, more than 92% of the dispersed seeds were from non-native plant species, primarily dispersed by non-native birds (Chimera and Drake 2010). In both of these islands systems, the mutualism between non-native species coupled with the failure of seed dispersal for native plants are expected to strongly shift the balance towards dominance of non-native species.

One potentially critical mutualism for the successful naturalization and invasion of plants into new habitats is pollination. It has been estimated that over 87% percent of wild plants require or benefit from cross-pollination (Ollerton, Winfree et al. 2011). In some areas, new exotic plant species are able to integrate into the local pollination network through the actions of native “super generalists” (Olesen, Eskildsen et al. 2002). These super generalist pollinators will visit most of the available flowering species, whether native or exotic, so new exotic species are able to readily obtain pollination services (Chapter 1). If there is no suitable native pollinator, then exotic plants may require, or greatly benefit from, the presence of exotic pollinators. A growing body of literature suggests that this is not uncommon. In Australia, the spread of the noxious weed *Lantana camara* has been linked with the presence of the non-native European honeybee (Goulson and Derwent 2004). Non-native fig trees in Florida were unable to reproduce until the introduction of their mutualist pollinating fig wasps (Nadel, Frank et al. 1992). A newly introduced orchid bee in Florida eliminates the pollen limitation previously faced by the invasive *Solanum torvum* (Liu and Pemberton 2009).

Hawaii presents an ideal location to examine the pollination interactions between native and non-native species for three main reasons. (1) Many communities are characterized by a wide variety of exotic naturalized plant and insect species. (2) A high proportion of plant species require outcrossing for successful reproduction and Hawaii is notable for the unusually high prevalence of dioecy among native plant species. While “Baker’s Law” suggests that plants that successfully establish after long-distance dispersal should be self-compatible or apomictic (Baker 1955; Stebbins 1957; Baker 1967), it has been estimated that 14.7% to 27.5% of Hawaiian native plant species are dioecious (Carlquist 1966; Sakai, Wagner et al. 1995) and therefore require some form of pollen transfer between individuals. This proportion of dioecy is among the highest known among native floras, and far exceeds the dioecious proportion in mainland regions such as California (3%), or other comparable isolated island floras such as the Galapagos (3%) or Reunion (4%) (Baker and Cox 1984). While some of these dioecious species are specialized for wind pollination and thus do not require animal pollinators, there is still an unusually high proportion of plants which must rely upon other species for pollen transfer. Additionally, the silversword alliance, one of the most species-rich native plant groups in Hawaii, features a fully-functional self-incompatibility system in most species, which also enforces outcrossing (Carr, Powell et al. 1986).

(3) Finally, the available native pollinator fauna is highly depauperate compared to mainland communities, and limited even in comparison to many other island ecosystems. While Hawaii is known for the spectacular adaptive radiation of flower-visiting honeycreepers, many of those species are now extinct or severely reduced in numbers and/or extent (Carlquist 1965). There is also only a single native bat species (*Lasiurus cinereus semotus*), which feeds on insects rather than flowers or floral resources (Jacobs 1999). Hawaii is strikingly limited in the major insect groups frequently considered to play a major role in pollination. There are no native syrphid flies (hoverflies), and no native social insects. There are only two native butterfly species: *Udara blackburni* (Lycaenidae) and *Vanessa tameamea* (Nymphalidae), and *Vanessa tameamea* feeds primarily on acacia sap rather than floral nectar (Tabashnik, Perreira et al. 1992). The native bees of Hawaii are composed of a single monophyletic lineage of *Hylaeus* (Colletidae) comprising 60 species. The genus has been recently revised (Daly and Magnacca 2003), and combined molecular and biogeographic analysis suggests that the genus has been in Hawaii for less than 700,000 years (Magnacca and Danforth 2006; Magnacca and Danforth 2007). Many aspects of the ecology of *Hylaeus* remain to be investigated. In particular, these bees are believed to be important pollinators of native plants (Magnacca 2007), but their pollination ecology is largely unknown.

The pollination ecology of Hawaiian plants is surprisingly understudied compared to the mainland, particularly considering the attention devoted to native plant conservation. The floral visitors and potential pollinators of many species remain unknown. The most well-studied system is the association between two adaptive radiations: lobelioids and honeycreepers, where distinctive matching morphologies between flower curvature and bill shape are thought to promote species-specific pairings (Lunau 2004)

Hylaeus bees have been anecdotally observed as generally ignoring exotic plants for floral visitation (Magnacca 2005). In one review, out of the 75 plant species that *Hylaeus* has been collected from, only 14 were non-native (Daly and Magnacca 2003). However, as it was not specified where on the plant the specimen was collected, these records do not necessarily reflect floral visitation and may simply reflect the vicinity of where the individual was collected. More recently, a molecular analysis of the pollen stored in the crops of 21 *Hylaeus* individuals from Maui and the Big Island found only pollen from native plant species (Wilson, Sidhu et al. 2010). This consistent preference suggests that exotic plant species may need to rely majorly or solely on generalist pollinators such as the introduced European honey bee (Memmott and Waser 2002). This observation also suggests that although *Hylaeus* may be a relatively recent radiation in Hawaii, there has been sufficient time for the evolution of pollination interactions. Honey bees in other locations have previously been observed to visit and pollinate exotic plants that are ignored or unsuccessfully visited by native pollinators (Hanley and Goulson 2003). In several cases, a synergistic effect between invasive honey bees and invasive plants has been suggested (Barthell, Randall et al. 2001; Goulson and Derwent 2004). Thus, the presence of exotic honey bees in Hawaii may facilitate the invasion of exotic plant species not pollinated by native bees, and the invasive plants may benefit the honey bees in turn.

The long-term effects of species invasion have only recently begun to be considered (Strayer, Eviner et al. 2006), so although honey bees have long been established on the Hawaiian Islands, they may still be exerting strong community-level effects on both native and exotic species. In Australia, for example, the presence of commercial *Apis mellifera* colonies has been shown to reduce the fecundity of native *Hylaeus* (Paini and Roberts 2005). While the population density of feral honey bee colonies is lower than for commercial colonies, it is still possible that similar effects may exist between naturalized *Apis mellifera* and *Hylaeus* in Hawaii. Furthermore, if honey bees and exotic plant species are indeed facilitating each other's presence and spread, then the effect of honey bees may be increasing with the rising numbers of newly-introduced plants. As more and more resources are devoted towards combating invasive species, it becomes increasingly important that we determine the role of pollinators in facilitating plant invasions.

Invasive bees may also be actively disrupting native reproductive mutualisms (Traveset and Richardson 2006). Since eusocial honey bees are highly active and proficient foragers, there is a strong possibility that they may have detrimental effects on the solitary *Hylaeus* through resource competition (Kato, Shibata et al. 1999). Honey bees may also be less efficient or effective pollinators of native plants than *Hylaeus*, or they may increase levels of selfing or hybridization (Traveset and Richardson 2006). Thus, an important additional goal of this study is to elucidate the role of *Hylaeus* as native plant pollinators and the potential for disruption from honey bees, which would have important consequences for conservation planning.

The replacement of unavailable or extinct native pollinators with exotic pollinators has been observed in multiple instances (Dick 2001; Pattemore and Wilcove 2012). In Hawaii, the extinction of several endemic bird species left the dioecious vine *Freycinetia arborea* without likely pollinators for 15-20 years before the introduction and spread of the Japanese white-eye *Zosterops japonicus* (Cox 1983). Similarly, *Apis mellifera* may be at least partially compensating for the loss of those bird pollinators for the endemic tree *Metrosideros polymorpha* (Hanna, Foote et al. 2013). In a more complex scenario, a tiny native bee in New Zealand has been unexpectedly shown to be able to increase the reproductive success of a native mistletoe with a restrictive bird-triggered pollination system (Kelly, Ladley et al. 1996). The populations of the native birds have been severely reduced, so the actions of these tiny bees are necessary to "open" the flowers to cross-pollination by invasive wasps and honeybees (Kelly, Ladley et al. 1996). Thus, it is also possible that introduced species may serve as "rescue" pollinators in lieu of missing native species, and thus may be important for native plant conservation in the future.

Here, we consider the interactions between native and exotic insect floral visitors and native and exotic flowering plants from four viewpoints (Figure 1). Firstly (1), do native insect species incorporate exotic species into their foraging? Are they able to take advantage of these new floral resources? (2) Do exotic insect species utilize both native and non-native floral resources? Or do they form compartments of exotic-exotic interactions? (3) How strongly do native plants depend on visitation by native insects? Is there potential for rescue pollination by exotic species in the event of native pollinator loss? (4) How do exotic plants attach to the floral visitation networks? Are there native "super generalists" that could facilitate their reproduction or must they rely on the presence of exotic pollinators? To address these questions, I constructed complete floral visitation networks for two ecological communities on the Big Island of Hawaii. One area was populated with both native and exotic floral visitors but only native plants, and a second area contained both native and exotic floral visitors and native and exotic plants.

Methods

Study Sites:

This study was conducted at Hawaii Volcanoes National Park on the Big Island of Hawaii (Figure 2). Sites were chosen based on accessibility and species composition. Certain species were targeted due to diversity of floral shape, local endemicity, or relevance to well-known systems. The site with only native plant species (Hilina Pali) was chosen for its relatively high species diversity (Table 1). This was the only site in the native plant area containing *Dubautia ciliolata* (a close relative of the famed Hawaiian silverswords), *Vaccinium reticulatum* (which has a restrictive floral shape and has been reputed to be "buzz-pollinated" by native bees), and *Scaevola kilauae* (a highly localized endemic relative of a widespread Polynesian littoral species). The site with mixed species (Byron Ledge) was the only site in the park that had a high diversity of native and non-native herbaceous and shrubby species, including many of the same native species as in the native site (Table 2). It also had both local species of *Dubautia* (*D. ciliolata* and *D. scabra*) alongside putative *Dubautia* hybrids.

Floral Network Observations:

Observations were conducted between 8AM and 4:30PM during periods of fair weather – no precipitation, maximum wind gusts below 20mph, and at least partial sunshine (<80% cloud cover). The Hilina Pali native site was observed during the summer and fall of 2007, spring and summer of 2008, and continuously (as weather permitted) from spring 2009 to summer 2010. The Byron Ledge mixed plant site was added in the summer of 2008, and then continuously observed from spring 2009 to summer 2010. Weather conditions were recorded with a Kestrel 3000 portable weather station at the beginning and end of daily observations. Temperature and humidity were measured in nearby shade. To measure wind speed, the Kestrel was held up at arm's length for 30 seconds, and the average and maximum windspeed were recorded for that time span (as in (McCall and Primack 1992)). Cloud cover was estimated to the nearest 10%. Weather conditions were recorded each time at the same place in each site.

Plant species were observed in a random order (observation order created via random number generator). Observed individuals were chosen haphazardly from among flowering individuals of that species that were safely observable (away from lava cracks, deep potholes, etc.). Whenever possible, individuals were chosen that did not require trampling or otherwise disturbing the other vegetation. Each individual plant was observed for 10 minutes through Pentax Papilio close-focus binoculars from a distance of 2-4 feet. For each insect visitor (no non-insect visitors were observed), I recorded visitor identity (to the lowest taxonomic level possible), the number of flowers (or flower heads, for compound flowers) visited, the total time spent visiting flowers within the observation area, and additional notes about behavior (pollen vs. nectar collecting, position on the flower, interactions with other insects, etc.). Insects that could not be field-identified were photographed or collected as voucher specimens whenever possible. The number of observed flowers and the total number of flowers on each plant were also recorded. For very large plants, I counted all of the flowers on a quarter of the plant and multiplied by 4 to estimate the total flowers.

A total of 2,398 10-minute observation sessions were completed, over a total of 42,389 flowers. 6,541 flower visits were recorded from 2,583 individual floral visitors. Quantitative floral interaction networks were plotted using the BIPARTITE package in R (Dormann, Gruber et al. 2008). Dependence of plant species on floral visitors was calculated as the proportion of total floral visits to that plant that were performed by each floral visitor (Jordano 1987; Bascompte and Jordano 2007). Dependence scores can serve as a proxy for the strength of plant-pollinator interactions, regardless of the per-visit effectiveness of the putative pollinator (Vazquez, Morris et al. 2005). Visitation rates were calculated as the number of visits per floral unit per hour. Due to the extreme non-normality of visitation rate data, non-parametric Kruskal-Wallis tests were used to determine differences in visitation rate.

Results

Interaction Networks

Field identifications of many of the flower-visiting insects were resolvable to species for a few common or charismatic species such as the honey bee, *Apis mellifera*, and the native butterfly *Udara blackburni*. Others were identified to genus, including all of the native *Hylaeus*. The remaining insect visitors were identified to the lowest possible taxonomic level or were grouped into morphospecies whenever possible. This level of taxonomic resolution is common for observation-based floral visitation networks (e.g. (Koch and Sahli 2013)).

In the Hilina Pali native site, a total of 25 different insect groups were observed visiting flowers. Most of the visitors were non-native, with *Apis mellifera* representing 17.5% (268/1533) of the total overall visits. The only known native insects were *Hylaeus* bees, representing 19.4% (297/1533) of the total overall visits. The simplified qualitative network shows that non-native insect species will visit and utilize the full series of native plant species available on site (Figure 3A). *Hylaeus* bees made up the largest component of native insect visitors, and were observed visiting the flowers of every plant species. The compiled, total quantitative interaction network shows similar patterns (Figure 4A).

At the Byron Ledge mixed site in the simplified qualitative network, the non-native insect visitors are shown to interact with nearly all plant species regardless of origin (Figure 3B). The native insect visitors, with the *Hylaeus* bees as the most oligolectic components, were mostly observed on native plant species, although isolated visits were recorded to the non-native *Ageratina* sp., *Bidens pilosa*, *Polygonum capitatum*, *Rubus argutus*, and *Hypochaeris radicata*. The quantitative network shows that native insect-exotic plant interactions were relatively rare, with only 14 interactions of that type recorded out of 1424 total observed interactions (Figure 4B). There were significantly more exotic-exotic interactions and fewer native-exotic interactions than expected (χ^2, $p<0.0001$).

Species Dependence

At the Hilina Pali native site, dependence scores for the plant species on the three major floral visitor groups (*Apis mellifera*, *Hylaeus*, and syrphid flies) show no clear pattern (Figure 5A). Some species (e.g., *Dodonaea viscosa*, *Vaccinium reticulatum*) received almost zero visitation from *Apis mellifera* and Syrphidae, one species was dominated by *Apis mellifera*, and the remaining species showing a relatively balanced dependence between the three groups. At the Byron Ledge mixed site, for the same three major floral visitor groups, a distinct pattern emerges between the native and non-native plant species (Figure 5B). With the exception of the *Dubautia* species, the native plants all had high dependence scores for *Hylaeus*. In contrast, every non-native plant species strongly depended on the two non-native groups.

Visitation Rate

At the Hilina Pali native site (Figure 6A), visitation rates by non-native insects were significantly higher for *Metrosideros polymorpha* and *Scaevola kilaueae*. Visitation rates by native insects were significantly higher for *Dodonaea viscosa* and *Vaccinium reticulatum*. There was no significant difference between native/non-native visitation rates for *Dubautia ciliolata*, *Leptecophylla tameiameiae*, *Osteomeles anthyllidifolia*, and *Wikstroemia phillyreifolia*.

At the Byron Ledge mixed site (Figure 6B), non-native insect visitation rates were significantly higher for 10 plant species, including all 7 exotic plant species. For the remaining 5 plant species, there was no significant difference in visitation rates between native and non-native species.

Discussion

Overall, the impact of exotic plants and insect visitors on visitation networks was non-symmetrical. Where non-native plants were present, non-native insects were observed to visit both native and non-native plant species, while native insects rarely utilized non-native plant resources. Additionally, the majority of floral visitors comprised non-native bees and syrphid flies. In contrast, where the vegetation was dominated by native plants, native bees were major visitors. Non-native plants relied upon non-native insect taxa, while non-native insect taxa were able to utilize both native and non-native plants.

The preference of *Hylaeus* for native plant species over non-native plants accords with previous observations. As *Hylaeus* was observed to visit nearly all of the native plant species at both sites, they can be described as endemic supergeneralist floral visitors, at least at the generic level (there may be greater specialization at the species level which could not be observed in this study). These endemic supergeneralists are relatively common in island pollination networks (see examples in Chapter 1). However, unlike most island endemic supergeneralists, which are posited to serve as the incorporation point for non-native species (Olesen, Eskildsen et al. 2002), *Hylaeus* mostly avoids non-native plants. This result also contrasts with mainland studies, which have shown that native bees will utilize floral resources from non-native plants, even if they do not prefer them (Williams, Cariveau et al. 2011). As *Hylaeus* comprise the majority of the native pollinator fauna in Hawaii, non-native plant species arriving on the islands cannot depend on attaching to pollinator networks through native species links. The opposite scenario is true for non-native pollinator species. Non-native insects were able to freely utilize the floral resources of native plant species, integrating into pollination networks by attaching via both native and non-native links. *Metrosideros polymorpha*, a native tree with copious and easily accessible floral resources, was a particularly important resource for non-native social insects, which have high resource demands (e.g. honeybees, yellowjackets, and ants).

Interactions between non-native species were significantly overrepresented in the mixed system. Non-native floral visitors such as honeybees, syrphid flies, and yellowjackets preferentially visited non-native plant species, creating an “invader complex” (Olesen, Eskildsen et al. 2002) for facilitating the reproductive success of non-native plants. This association between non-native species was also observed in the Ogasawara (Bonin) Islands of Japan, where non-native honeybees were shown to prefer non-native plants (Abe, Wada et al. 2011). Other island systems reported the opposite interaction, with significantly fewer alien-alien interactions than expected (Olesen, Eskildsen et al. 2002) . The distinction between these two groups may rest on the presence/absence of supergeneralist endemic pollinators that will utilize non-native plant species. Both the Ogasawara (Bonin) Islands and Hawaii lacked endemic supergeneralist pollinators linked to non-native plants, which enforced the creation of links between non-native species. In the presence of endemic supergeneralists that are much less tied to the native flora, such as the carpenter bee *Xylocopa darwini* in the Galapagos (Linsley, Rick et al. 1966; McMullen 1993; Traveset, Heleno et al. 2013), non-native plants primarily attach to native pollinators (and vice versa) and thus create mixed links.

While the conclusions from this study are based on only two study sites, this level of replication is common in floral visitation networks, likely due to the time and effort required for floral observations. Many published network studies are based either on a single site (e.g. (Memmott 1999; Dupont, Hansen et al. 2003; Lundgren and Olesen 2005)) or one site per treatment (e.g. (Kaiser-Bunbury, Memmott et al. 2009; Koch and Sahli 2013)), and/or are compiled from a single season or less (see examples in Chapter 3). For this study, the decision was made to sacrifice spatial replication for increased temporal breadth.

Missing and forbidden network links

Within a species interaction network, there are inevitably linkages between species that were not observed. These instances of zero interactions fall under two groupings, deemed “missing” and “forbidden” links (Olesen, Bascompte et al. 2011). Missing links are those that are unobserved due to sampling constraints – increasing the sampling time or other parameters would theoretically result in that interaction eventually being observed. This is equivalent to the “sampling zeros” used in statistical models. Forbidden links are those that would never be observed, even under infinite sampling, because the interaction is impossible due to morphological or temporal constraints. This is equivalent to statistical “structural zeros”. Differentiating between the two with real-world data can be difficult, but the observed floral visitation networks here likely contain both types of unobserved linkages.

Missing links

The overall visitation rates to *Dodonaea viscosa* and *Coprosma ernodeoides* were very low, and were essentially zero for female flowers. However, despite being dioecious, *Dodonaea viscosa* and *Coprosma ernodeoides* likely do not require, or perhaps even benefit from, floral visitation by insects. Both *Dodonaea* and *Coprosma* have adaptations for wind-pollination. *Coprosma* flowers are elevated above the prostrate vegetative body and have exposed anthers and styles with no petals, sepals, or attractive coloration. The styles are long and feathery, which aid in their ability to trap wind-borne pollen grains. *Dodonaea* flowers likewise lack attractive petals and sepals, although the staminate flowers are generally brightly colored. The pistillate flowers are reduced to bare styles with no discernible rewards or attractants. Since the staminate flowers of both *Dodonaea* and *Coprosma* offer easily accessible pollen rewards, they do serve as potential nutrient resources for pollen-gathering floral visitors. Thus, increased observation time might lead to the observation of more floral visitors. Since these floral visitors almost certainly would not then visit unrewarding female flowers, however, this is an instance of floral predation (even parasitism) rather than mutualism.

Very few insects were observed on the flowers of *Wikstroemia phillyreifolia*. In previous research on Hawaiian *Wikstroemia*, only a few thrips and a single *Apis mellifera* were observed to visit the flowers (Mayer 1990). Similarly, in 1000 minutes of observation in this study over a total of 1,172 flowers, the only recorded floral visitors were four *Apis mellifera*, one *Hylaeus*, and one small unidentified fly (Figure 7). The small, tubular flowers are also unlikely to be visited by birds or other vertebrates. This near-complete lack of observed visitation is particularly interesting, as most Hawaiian *Wikstroemia* are dioecious and the tubular floral morphology is not conducive to pollen transfer by wind. Furthermore, the pollen itself is sticky and produced in low quantity (Mayer and Charlesworth 1992), which likewise does not favor non-biological pollen transport. The pollinators of *Wikstroemia* outside of Hawaii are also unknown (Mayer 1990). Nectar analysis suggests that the sugars are suitable for generalist pollinators (Mayer 1990), however it appears that the flowers are nevertheless unattractive, at least to diurnal floral visitors. As no floral observations were carried out at night, it is possible that small moths or other nocturnal insects may be the primary floral visitors and pollinators. Thus, since *Wikstroemia* requires cross-pollination for fertilization, and yet no visitation was observed in a day-limited sampling regime, it is likely that the lack of observed visitation represents "sampling zeros" or missing links. To elucidate the true floral visitors and/or pollinators for this species, nocturnal investigations should be carried out in future studies. It is also possible that the natural pollinator is no longer present in Hawaii, so studies of reproductive success (e.g. seed set) should also be performed to determine if *Wikstroemia* is now pollen-limited.

No floral visitation by birds was observed during this study. However, the floral observation methods, which required the observer to be close to the observed flowers, likely precluded any bird visitation to those flowers. Most of the plant species have relatively small flowers, are close to the ground, and do not offer significant nectar rewards, which together makes it unlikely that they would be of interest to birds. The one exception is *Metrosideros* (ohia), which has large red flowers and produces copious nectar. Several different bird species have been observed to visit ohia flowers, and birds have traditionally served as the primary pollen-transfer agents (Carpenter 1976). However, due to the precarious status of many Hawaiian birds, insect visitors, particularly native or exotic bees, may be the more important visitors in future years. Recent studies have indicated that *Apis mellifera* and, to a lesser extent, *Hylaeus* bees are now likely the main floral visitors and pollinators for *Metrosideros* (Junker, Bleil et al. 2010; Hanna, Foote et al. 2013; Koch and Sahli 2013).

Forbidden links

Forbidden links in floral visitation networks can derive from two origins. There may be temporal mismatches between flowering times and floral visitor availability, which will be addressed in the next chapter. Flowers may also have restrictive morphologies that require visitors to possess the requisite traits to access floral resources. Perhaps the most famous example of this type of restriction is the extreme length of the nectar spur of the orchid *Angraecum sesquipedale*, which requires the extremely long proboscis of the sphinx moth *Xanthopan morgani* to reach it (Arditti, Elliott et al. 2012). In Hawaii, the curved shapes of many flowers in the lobelioid group are thought to result from co-evolution with the beak shapes of endemic honeycreepers (Lunau 2004). However, the open floral morphology of most of the plant species in the study sites renders this type of forbidden link unlikely. The main exception may be *Vaccinium reticulatum*, which has a campanulate (urn-shaped) flower with a restricted corolla opening. While the width of this opening may vary for different populations, at these study sites native *Hylaeus* bees were able to enter the flower fully while the heads of the non-native *Apis mellifera* were too large to breach the opening (Figure 8). However, the longer proboscis of *Apis* may permit honey bees to reach the nectar resources nonetheless. The stigma and anthers of *Vaccinium* do not extend beyond the corolla, and *Apis* is unlikely to come into significant contact with either. The ability of *Apis* to effectively cross-pollinate *Vaccinium* has not been studied, but may be expected to be lower than that of *Hylaeus* due to this difference in floral visitation behavior. Furthermore, *Hylaeus* has been observed to engage in "buzzing" behavior within *Vaccinium* flowers, which facilitates the release of pollen from the anthers (Heather Sahli, personal communication). Thus, even though *Apis* was observed (albeit rarely) visiting *Vaccinium* flowers, the *Apis-Vaccinium* interaction may translate into an actual forbidden link for effective cross pollination. The native plant *Scaevola kilauae*, found only at the Hilina Pali native site, is also recorded as having flowers with a deep corolla. However, this measurement is deceptive as *Scaevola* flowers, commonly known as "half-flowers", are actually completely open along one side and present no morphological restrictions to access (Figure 9).

The general lack of morphologically-driven forbidden links in the floral visitation network contrasts with previous work on seed dispersal systems in Hawaii. Introduced birds have been shown to feed on and disperse the seeds of multiple native Hawaiian plant species (Foster and Robinson 2007). However, one study on the seed dispersal network of a dry forest community on East Maui found that exotic bird visitors rarely dispersed the seeds of native trees, possibly due to the generally larger size of the native tree fruits (Chimera and Drake 2010). As the exotic bird species were generally small, with concomitantly small beak sizes, they were able to swallow the small fruits of the exotic trees whole, while only serving as "fruit predators" on the larger native tree fruits (Chimera and Drake 2010). Thus, in this dry forest community, the exotic fruit dispersers are promoting the reproduction and spread of exotic plant species to the exclusion of native species. This differs from my observed floral visitation network, which showed that exotic floral visitors do utilize native floral resources, and mainly visit them in ways consistent with potential pollen transfer and effective pollination.

Competition between native and non-native species

Direct competition

Aggressive interactions were only occasionally observed between floral visitors, most commonly between syrphid flies on *Hypochaeris* flowers. Approaching syrphids would frequently either chase off or be chased off by the current occupant of the flower. No aggressive interactions were observed between native and non-native bees. *Hylaeus* and *Apis* were often observed visiting neighboring flowers, and on a few occasions even shared the same inflorescence without apparent hostility. This lack of between-bee interference competition has been previously documented for bumblebees and "wild bees" in Maine (Heinrich 1976)and *Apis* and native bees in the neotropics (Roubik 2009), although stingless bees are known to fiercely defend their feeding territories (Johnson and Hubbell 1974).

The presence of ants (all exotic) in *Vaccinium reticulatum* has been shown to deter floral parasitism by the caterpillars of the introduced plume moth, but their role in affecting floral visitation of *Vaccinium* by other species is still unknown (Bleil, Bluethgen et al. 2011). Bleil, et al. did not observe any floral visitors to *Vaccinium* aside from ants and caterpillars over the course of their investigation from March to May 2009. On one occasion, I observed ants behaving aggressively towards a *Vespula* wasp drinking nectar from a *Metrosideros* flower, but otherwise any potential ant deterrence did not appear to be the result of direct interaction. Previous studies on interference competition between ants and other floral visitors on ohia flowers have demonstrated that different ant species will compete for nectar (Lach 2005) and that *Hylaeus* bees (but not *Apis mellifera*) will avoid inflorescences containing African big-headed ants, *Pheidole megacephala* (Lach 2008). This preference for *Hylaeus* bees to avoid flowers with predatory ants accords with previous research showing that the presence of predators on flowers will reduce both the visit frequency and duration of potential pollinators (Suttle 2003). While I did not observe any predation of pollinators by ants, ants are known to predate upon *Hylaeus* and may have major effects on their populations (Cole, Medeiros et al. 1992; Hanna, Foote et al. 2014). *Vespula* are also known predators for *Hylaeus* and *Apis* (Wilson, Mullen et al. 2009; Koch and Sahli 2013), and previous work by Hanna et al. (2014) recorded *Vespula* regularly chasing off both *Hylaeus* and *Apis* from *Metrosideros* flowers.

Indirect competition

Competition between native and non-native floral visitors may also be indirect, via exploitation of shared resources. Multiple ant species utilize *Metrosideros* nectar, and their foraging periods overlap with peak visitation times for both birds and other insects (Lach 2005). *Metrosideros* flowers visited by ants are generally completely drained of nectar (Junker, Bleil et al. 2010), a reduced state that was not observed even under heavy visitation by other insect visitors (personal observation). *Vaccinium* flowers visited by ants are likewise drained of nectar (Bleil, Bluethgen et al. 2011). *Vespula* can also cause significant drawdown of nectar resources in *Metrosideros* (Hanna, Foote et al. 2014). Although no birds were observed in this study, *Metrosideros* is known to be a major floral resource for nectarivorous birds and the availability of its nectar has been tied to the population density and/or reproductive fitness of native bird species (Ralph and Fancy 1995; Berlin, Simon et al. 2001). Thus, exploitative competition by ants and *Vespula* may have negative effects on legitimate pollinators.

However, nectar is not the only available floral resource. In *Metrosideros* flowers, nectar and pollen are spatially separated, and *Hylaeus* bees were observed foraging on pollen at the tips of the anthers at the same time as ants foraged for nectar at the inflorescence base. This separation of desired floral resources may permit continued coexistence between visitors (Junker, Bleil et al. 2010). Similarly, introduced honey bees in Brazil forage on staminate *Clusia arrudae* flowers for pollen, while not affecting the resins sought by the native pollinator, *Eufriesea nigrohirta* (Apidae) (do Carmo, Franceschinelli et al. 2004). As the anthers and stigmas of *Metrosideros* are both located well above the nectar sources in the inflorescences, the potential pollination ability of *Hylaeus* bees would be unaffected by ant activity in the absence of aggressive interactions.

At the native plant site, there was a sharp differentiation between resource use by *Hylaeus* versus *Apis* on *Metrosideros*, perhaps indicating some degree of resource partitioning to reduce competition (Figure 10). Nearly all *Hylaeus* visits to *Metrosideros* were for pollen collection, while nearly all *Apis* visits to *Metrosideros* were for nectar collection. Unsurprisingly, all *Vespula* visits were for nectar only, as was the sole visit recorded from an ant. This difference in resource use was not observed between *Hylaeus* and *Apis* at the mixed site, although the results in that case are complicated by the relatively low visitation of *Apis* on *Metrosideros* and the increased presence of *Hylaeus* males. Of the 12 observations of nectar-feeding behavior from *Hylaeus*, 5 were from putative males. Since they do not provision nests, male *Hylaeus* bees do not collect pollen and thus will only forage for nectar. Females forage for both nectar and pollen. Only putative females were observed on *Metrosideros* flowers at the native site.

Notable interactions

Dubautia species and hybridization

Within the Byron Ledge mixed site, two of the native plant species are *Dubautia ciliolata* and *Dubautia scabra*, which are closely related members of the silversword alliance (Carlquist, Baldwin et al. 2003). The silversword alliance is one of the best known adaptive radiations of plants in Hawaii, ranging from small Kauai bog shrubs to the spectacular silverswords found at the summits of Maui and the Big Island. *Dubautia scabra* is common in the Byron Ledge mixed site, occurring in nearly a third of the surveyed quadrats, while *D. ciliolata* is rare with only scattered individuals. There is also a large patch of putative hybrids between the two species, which have intermediate floral and vegetative characteristics. At least six species of floral visitors were observed on both *D. scabra* and *D. ciliolata*, indicating potential cross-pollinators for hybridization (Figure 11, Table 3). Additionally, while *Apis mellifera* was not observed on *D. ciliolata* flowers at the mixed site, it was seen to visit *D. ciliolata* at the native site, where *D. ciliolata* was more common. Thus, it is possible that this interaction occurs at this site as well, and was simply not captured during timed observations. *Apis mellifera* was also observed moving directly between *D. scabra* and the putative hybrid in a single foraging bout, indicating the possibility of continued gene transfer amongst these species after hybridization (Figure 12). Previous molecular data on hybridization between *D. scabra* and *D. ciliolata* showed backcrossing only between the hybrid and *D. ciliolata* (never *D. scabra*) (Caraway, Carr et al. 2001). However, the sample size in that study was relatively low (19 hybrid individuals from a single population) and no reason was given to preclude hybrid-*D. scabra* backcrosses, so gene flow may indeed occur in that direction in nature as well. *Dubautia scabra* and *D. ciliolata* generally occur on different substrate types, which limits gene flow through selection against hybrids (Robichaux, Carr et al. 1990). At the Byron Ledge mixed site, both species are found on the same substrate, which may thus permit more extensive gene flow and hybridization.

Unusual floral visitors

Not all of the recorded floral visitors are from typically flower-associating groups, but that does not mean that their potential for pollen transfer should be automatically discounted. Katydids comprised ~7% of the visitors to *Osteomeles anthyllidifolia*, and averaged 179 seconds per flower and 2.5 flowers per visit (Figure 13). The native cricket *Trigonidium* was also observed visiting the flowers of *Dubautia scabra* in a manner conducive to potential pollen transfer (Figure 14). While katydids and crickets are not generally considered among the insects capable of effecting efficient pollen transfer, the role of Orthoptera as pollinators has recently begun to be explored (Micheneau, Fournel et al. 2010). On Mauritius and Reunion, the only floral visitors to the orchid *Angraecum cadetti* are from an undescribed cricket species, which is apparently effective at both pollen removal and deposition (Micheneau, Fournel et al. 2010). Visitation time per flower was long (16.5s) compared to birds or hawkmoths (Micheneau, Fournel et al. 2010), which accords with the relatively long visitation time for the katydids on *Osteomeles* (179s/flower vs. 10.8s/flower for *Hylaeus* and 4.8s/flower for *Apis mellifera*). Perhaps one key feature of that observed cricket-orchid mutualism is that it occurs on the islands of Mauritius and Reunion. Island pollination systems, perhaps owing to the generally depauperate status of “standard” pollinators due to isolation from source populations, often feature pollinators that would be considered unusual in mainland areas. Lizards have been shown to be effective (and even important) pollinators in New Zealand (Whitaker 1987), Mauritius (Nyhagen, Kragelund et al. 2001), the Balearic Islands (Traveset and Saez 1997), and other island systems (Olesen and Valido 2003). In Madagascar, home of the previously mentioned *Xanthopan-Angraecum* pollination interaction, ruffled lemurs (*Varecia variegata*) have been shown to be crucial pollinators for the traveler’s tree, *Ravenala madagascariensis* (Kress, Schatz et al. 1994). As another invertebrate example, cockroaches (*Amazonina platystyla*ta) have been shown to have a specialized pollination mutualism with *Clusia aff. sellowiana* on an inselberg (isolated island-like area) in French Guiana (Vlasáková, Kalinová et al. 2008). Unusual pollination systems are also not limited to endemic, potentially co-evolved systems. On Samoa, the sole pollinator of the introduced tree *Ceiba pentandra* is the native Pacific flying fox, *Pteropus tonganus*, whereas *Ceiba* is visited by a diverse assemblage of vertebrates and invertebrates in its native range (Elmqvist, Cox et al. 1992).

Conservation Implications

In many regions around the world, the decline of both feral and managed *Apis mellifera* colonies are a source of concern, both due to potential effects on reproduction of wild plants and the already acknowledged negative effects on the ability of managed colonies to keep up with demand for crop pollination (Watanabe 1994). In light of these existing and predicted declines, a significant amount of research has been aimed at discovering and encouraging alternative pollinators. In the U.S. mainland, a major focus of this research is on the potential of native bees as pollinators of crops such as watermelon (Winfree, Williams et al. 2007) and tomato (Greenleaf and Kremen 2006; Winfree, Williams et al. 2008). However, in Hawaii this scenario is unlikely due to the unsuitability of the native *Hylaeus* as a managed pollinator for agriculture. While specifically agricultural crops were not included in this study, the apparent reluctance of the native pollinators to utilize exotic plant species means they are unlikely to serve as effective pollinators for exotic crops.

Instead, here we must consider the opposite role – the idea of the exotic *Apis mellifera* as a rescue pollinator for native plants as the native pollinators decline. Of the 60 endemic species of *Hylaeus* in Hawaii, 10 have no recent sightings or collections and are potentially extinct, 10 are very rare, 7 are found in restricted or endangered habitats, and 5 more are locally extirpated from islands of their past range (Magnacca 2007). Seven species have been officially designated as endangered species by the U.S. Fish and Wildlife Service (Ollerton 2017). Overall, more than half of the known species are of current conservation concern, and more may become endangered in the future due to increasing habitat loss from development and negative effects from invasive ants (Cole, Medeiros et al. 1992; Lach 2008) and yellowjackets (Gambino, Medeiros et al. 1987; Hanna, Foote et al. 2014). Therefore, in contrast to mainland agriculture's need to use native bees to sustain pollination services due to honeybee decline (Winfree, Williams et al. 2007), Hawaii may instead require the continued presence of feral honey bee colonies to sustain pollination of native plants previously visited by *Hylaeus* species.

The degree to which feral honey bee colonies are able to replace lost ecosystem function will depend on multiple factors requiring further investigation for the Hawaiian flora. First, it is unknown how many native plant species actually require or benefit from cross-pollination. Tests for self-incompatibility have been carried out only for certain charismatic groups such as the silversword alliance (Carr, Powell et al. 1986). Appearances alone may be deceiving, as some visibly hermaphroditic species have been found to be functionally dioecious ("cryptic dioecy") (Mayer and Charlesworth 1991), while others may be self-compatible but not autogamous, or may have increased fitness or fecundity when cross-pollinated (Husband and Schemske 1996). Secondly, while honey bees are often considered to be broadly effective and efficient floral visitors they may not be as effective as native bees (Westerkamp 1991; Garibaldi, Steffan-Dewenter et al. 2013) and may not utilize floral resources in the same way (Brittain, Kremen et al. 2013). Further research is necessary to investigate these differences for the Hawaiian flora in order to translate floral visitation by honeybees into a measure of effective pollination. Finally, feral honey bee colonies in Hawaii are themselves vulnerable to decline (Martin, Highfield et al. 2012). Thus, even if honeybees are able to partially compensate for the loss of native pollinators in Hawaii, wild pollination services will remain a conservation concern in the future.

Chapter 2: Figures and Tables

Figure 1: Diagram of potential pollination interactions between native and non-native species in Hawaii

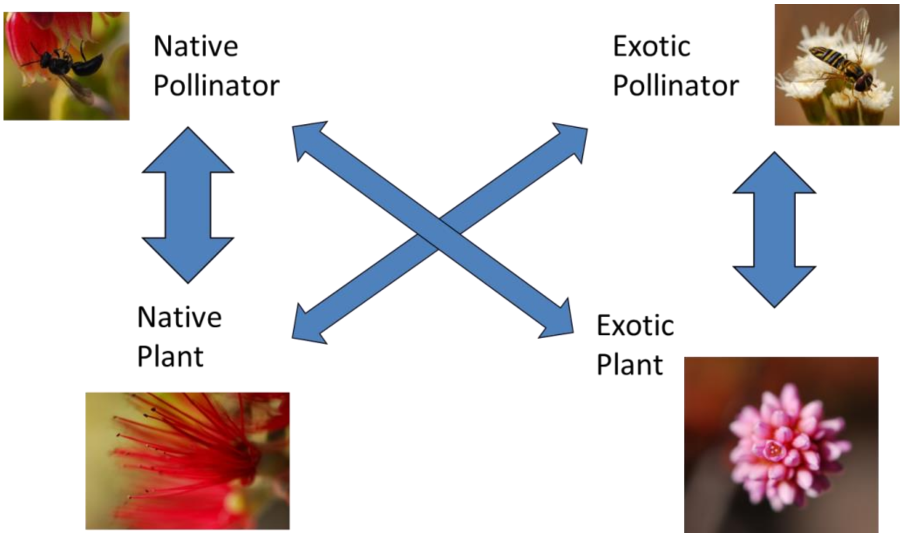


Figure 2: Location of study sites: (A) Hilina Pali native site, (B) Byron Ledge mixed site

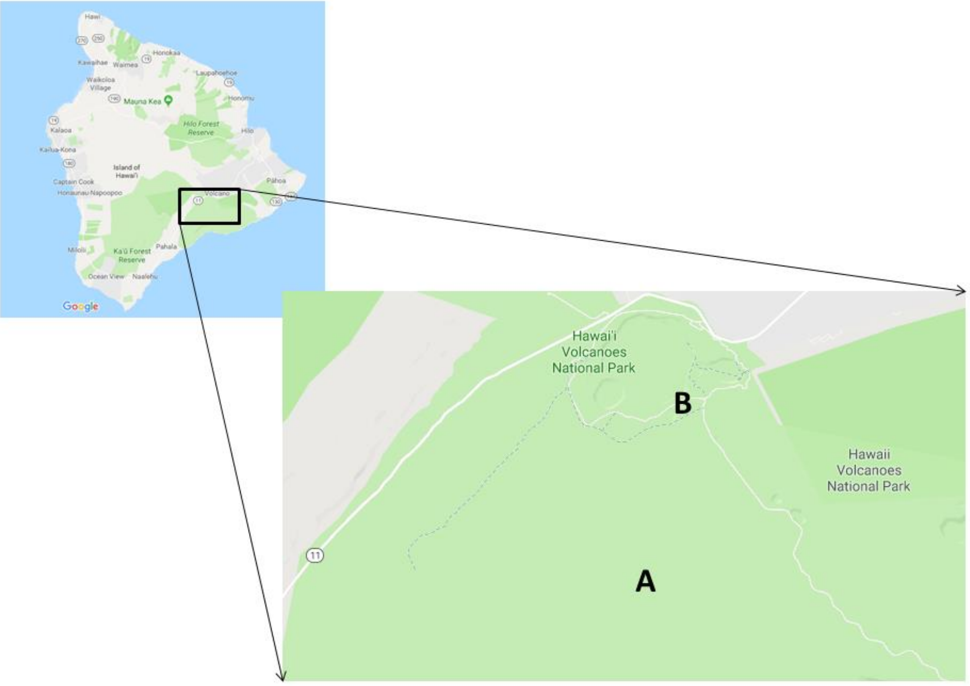


Table 1: Plant species at the Hilina Pali site characterized by native plant species. All information from Wagner et al (1999) unless otherwise indicated.

Species	**Family**	**Native /Exotic**	**Breeding system**	**Flower color**	**Corolla depth**	**Native to**	**Other references**	**Common name**	**Other**	**Wagner et al. (1999) pg #**
Dodonaea viscosa	Sapindaceae	Native	Dioecious, some perfect	pink-red (M), yellow (F)	Open	Pantropical		a'ali'i		1227
Dubautia ciliolata	Asteraceae	Native	Self-compatible	Yellow	4-6mm	Hawaii	Carr, Powell, et al.		"Flowering primarily June-November"	295
Metrosideros polymorpha	Myrtaceae	Native	Red flowers partially self-compatible	Red	Open	All main islands except Niihau and Kahoolawe	Carpenter	ohia lehua		967
Osteomeles anthyllidifolia	Rosaceae	Native	?	White	Open	Cook Islands, Tonga, Hawaii		ulei		1104
Scaevola kilaueae	Goodeniaceae	Native	?	White & purple	20-25mm	Kilauea & Kau area on Hawaii		naupaka kuahiwi		786
Leptecophylla tameiameiae	Epacridaceae	Native	Mixed	White	2.5-4.5mm	All main islands except Niihau and Kahoolawe	Carlquist	pukiawe	"Flowers perfect or unisexual". Genus recently renamed from *Styphelia*	590
Vaccinium reticulatum	Ericaceae	Native	"Self-pollinates"	Red	8-12mm	Common on Maui, Hawaii. Rare on Kauai, Oahu, Molokai	Vander Kloet	ohelo	"flowering and fruiting throughout the year, but flowering is most prolific from April to September"	593
Wikstroemia phillyreifolia	Thymelaeaceae	Native	Cryptically dioecious	Yellow	Calyx 5-11mm	Hawaii	Mayer	akia		1288

Table 2: Plant species at the Byron Ledge site, characterized by mixed native/exotic plant species. All information from Wagner et al (1999) unless otherwise indicated.

Species	**Family**	**Native /Exotic**	**Breeding system**	**Flower color**	**Corolla depth**	**Other references**	**Common name**	**Other**	**Native to**	**Wagner et al (1999) pg #**
Ageratina riparia	Asteraceae	**Exotic**	?	White	3-3.5mm		pamakani		Mexico and West Indies	255
Anemone hupehensis	Ranunculaceae	**Exotic**	?	White	Open		Japanese anemone		China	1087
Arundina graminifolia	Orchidaceae	**Exotic**	?	White, pink, purple	4-5cm		Bamboo orchid		Asia, India, Melanesia, some Pacific islands	1471
Bidens pilosa	Asteraceae	**Exotic**		Yellow	2-3mm	Jepson eFlora	ki		Tropical America	279
Coprosma ernodeoides	Rubiaceae	Native	Dioecious	yellow (M), white (F)	8-9mm (M), 5-6mm (F)		kukaenene		Hawaii & East Maui	1125
Dodonaea viscosa	Sapindaceae	Native	Dioecious, some perfect	pink-red (M), yellow (F)	Open		a'ali'i		Pantropical	1227
Dubautia ciliolata	Asteraceae	Native	Self-compatible	Yellow	4-6mm	Carr, Powell et al.		"Flowering primarily June-November"	Hawaii	295
Dubautia hybrid	Asteraceae	Native		Yellow					Hawaii	
Dubautia scabra	Asteraceae	Native		White	3.5-4mm	Carr, Powell et al.		"Flowering throughout the year"	Molokai, Lanai, Maui, Hawaii	307
Epilobium billardierianum	Onagraceae	**Exotic**	?	Purple	?				Australia, New Zealand, Chatham Islands	995
Hedychium gardnerianum	Zingiberaceae	**Exotic**	?	Yellow	5-5.5cm		Kahili ginger		Himalayas	1623

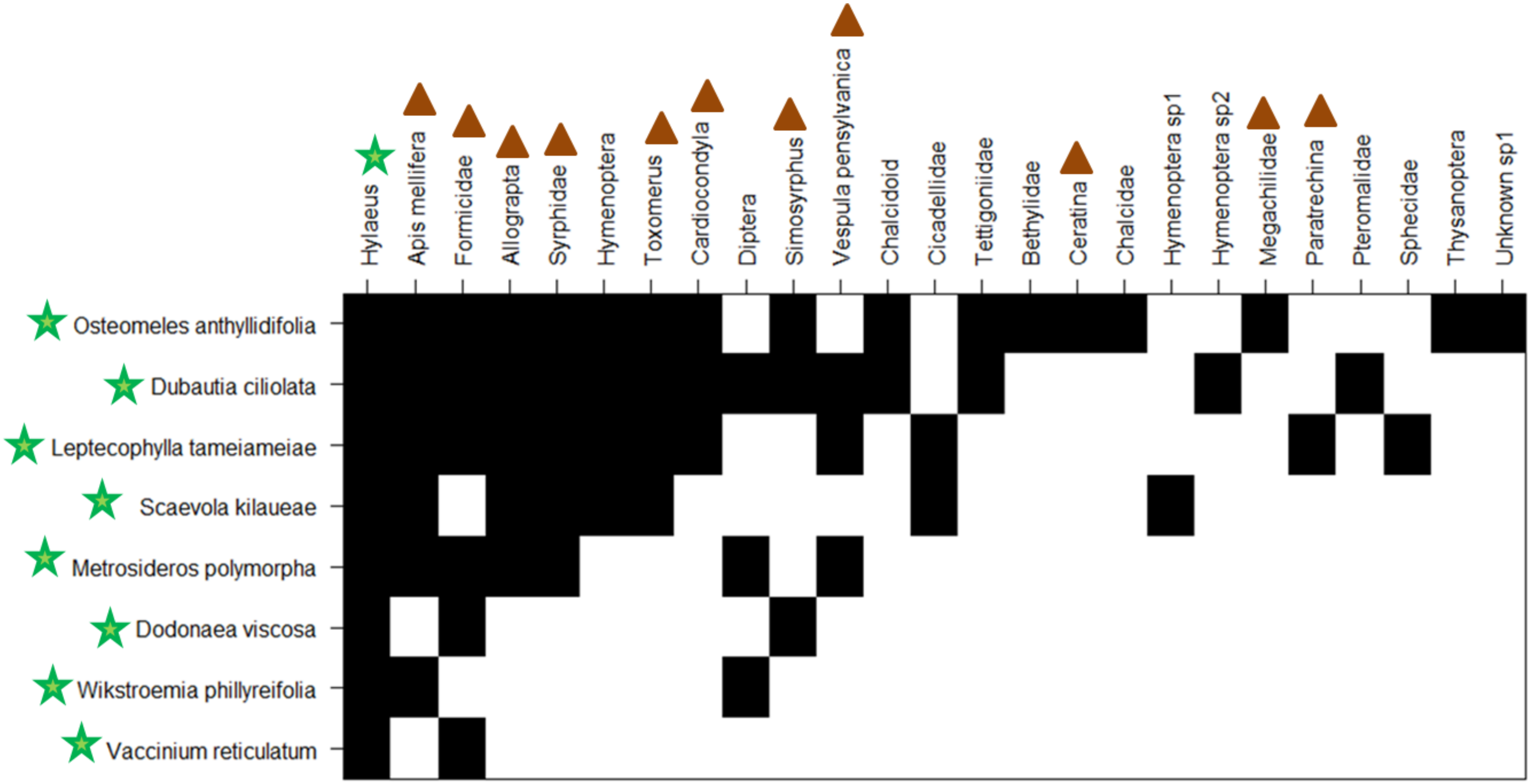
Hypochoeris radicata	Asteraceae	**Exotic**	?	Yellow	?		Hairy cat's ear	Sometimes spelled Hypoch**a**eris radicata	Eurasia	327
Metrosideros polymorpha	Myrtaceae	Native	Red flowers partially self-compatible	Red	Open	Carpenter	ohia lehua		All main islands except Niihau and Kahoolawe	967
Polygonum capitatum	Polygonaceae	**Exotic**	?	Pink	2-3mm	Jepson eFlora		Also known as *Persicaria capitata*	Himalayas and Western China	1063
Rubus argutus	Rosaceae	**Exotic**		White	Open		Prickly Florida blackberry		Central and eastern US	1107
Rubus ellipticus	Rosaceae	**Exotic**		White	Open		Yellow Himalayan raspberry		Tropical and subtropical India	1107
Styphelia tameiameiae	Epacridaceae	Native	Mixed	White	2.5-4.5mm	Carlquist	pukiawe	"Flowers perfect or unisexual"	All main islands except Niihau and Kahoolawe	590
Vaccinium reticulatum	Ericaceae	Native	"Self-pollinates"	Red	8-12mm	Vander Kloet	ohelo	"flowering and fruiting throughout the year, but flowering is most prolific from April to September"	Common on Maui, Hawaii. Rare on Kauai, Oahu, Molokai	593

Table references (combined):

(Carlquist 1970; Carpenter 1976; Carr, Powell et al. 1986; Mayer 1994; Vander Kloet 1996; Wagner, Herbst et al. 1999)

Figure 3: Presence-absence interaction network for (A) Hilina Pali native site, and (B) Byron Ledge mixed site, each arranged to maximize nestedness. Rows are plants, columns are floral visitors. Native taxa are indicated with green stars, and exotic species with brown triangles. Taxa without symbols have unknown evolutionary origin. The most generalized taxa are at the top and left.

A. Hilina Pali native site



B. Byron Ledge mixed site

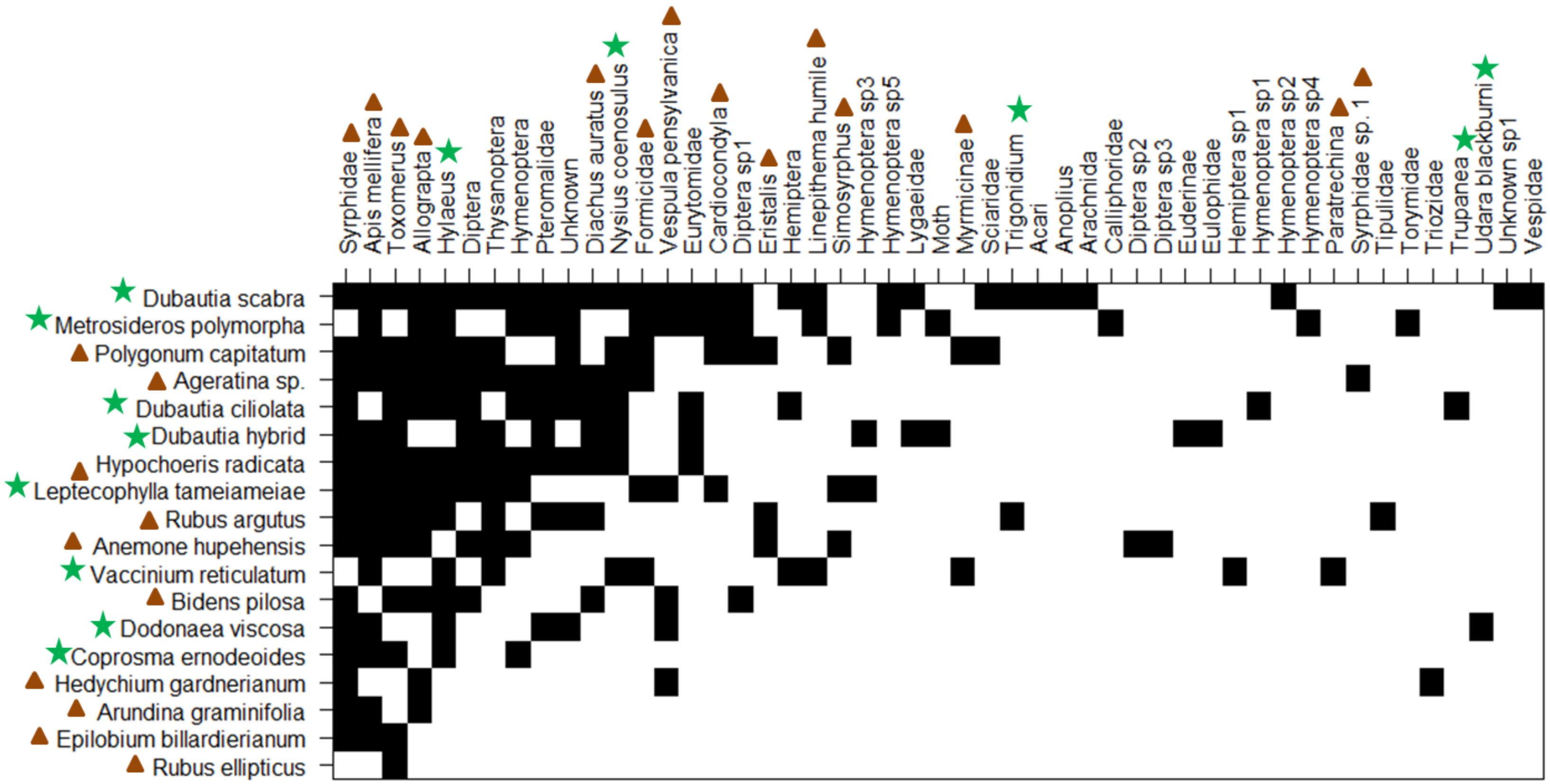
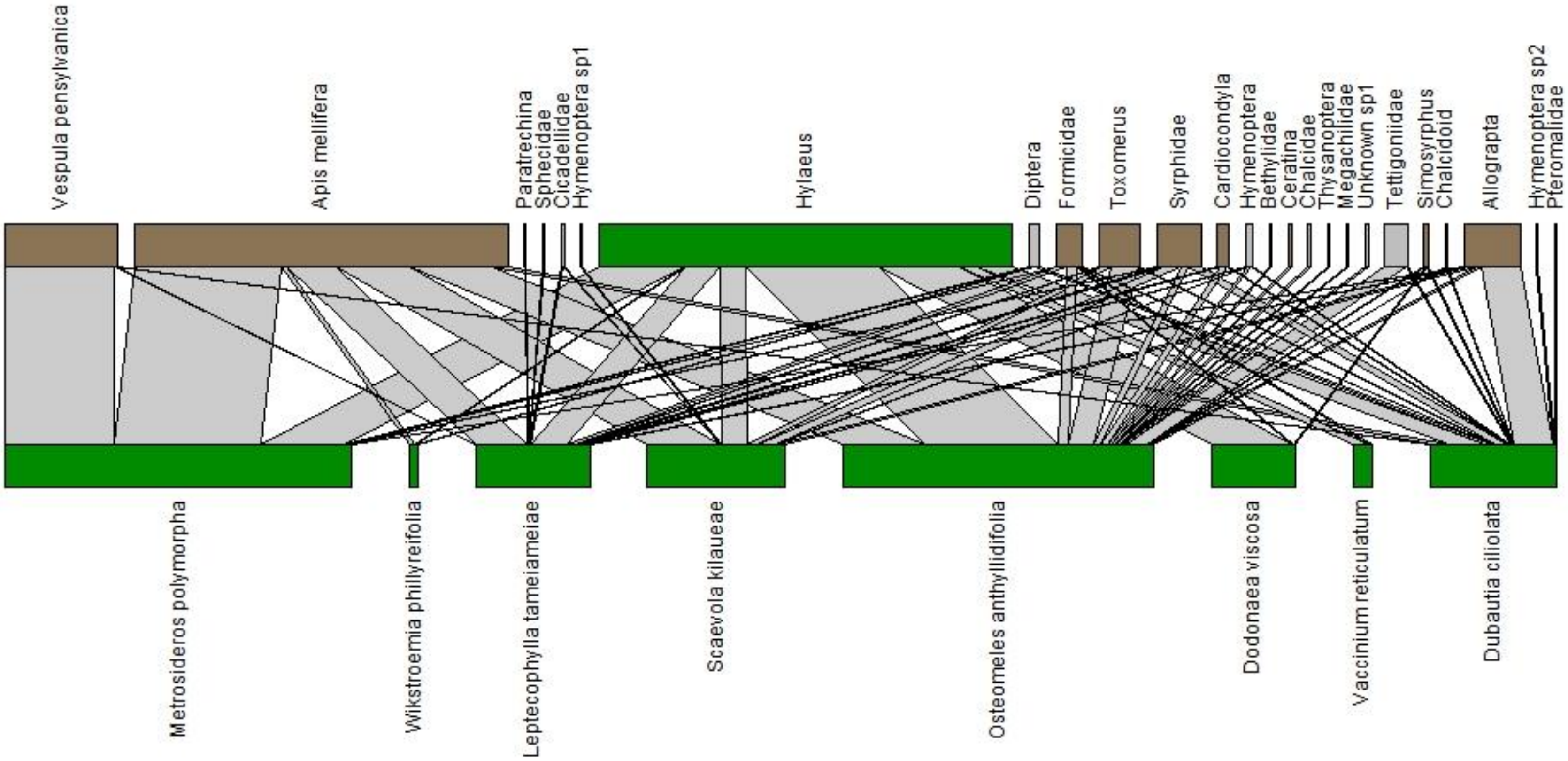


Figure 4: Quantitative floral visitation network for the for (A) Hilina Pali native site, and (A) Byron Ledge mixed site. Native taxa are in green, non-native taxa are brown, and taxa of unknown evolutionary origin are in grey.

A. Hilina Pali Native site



B. Byron Ledge mixed site

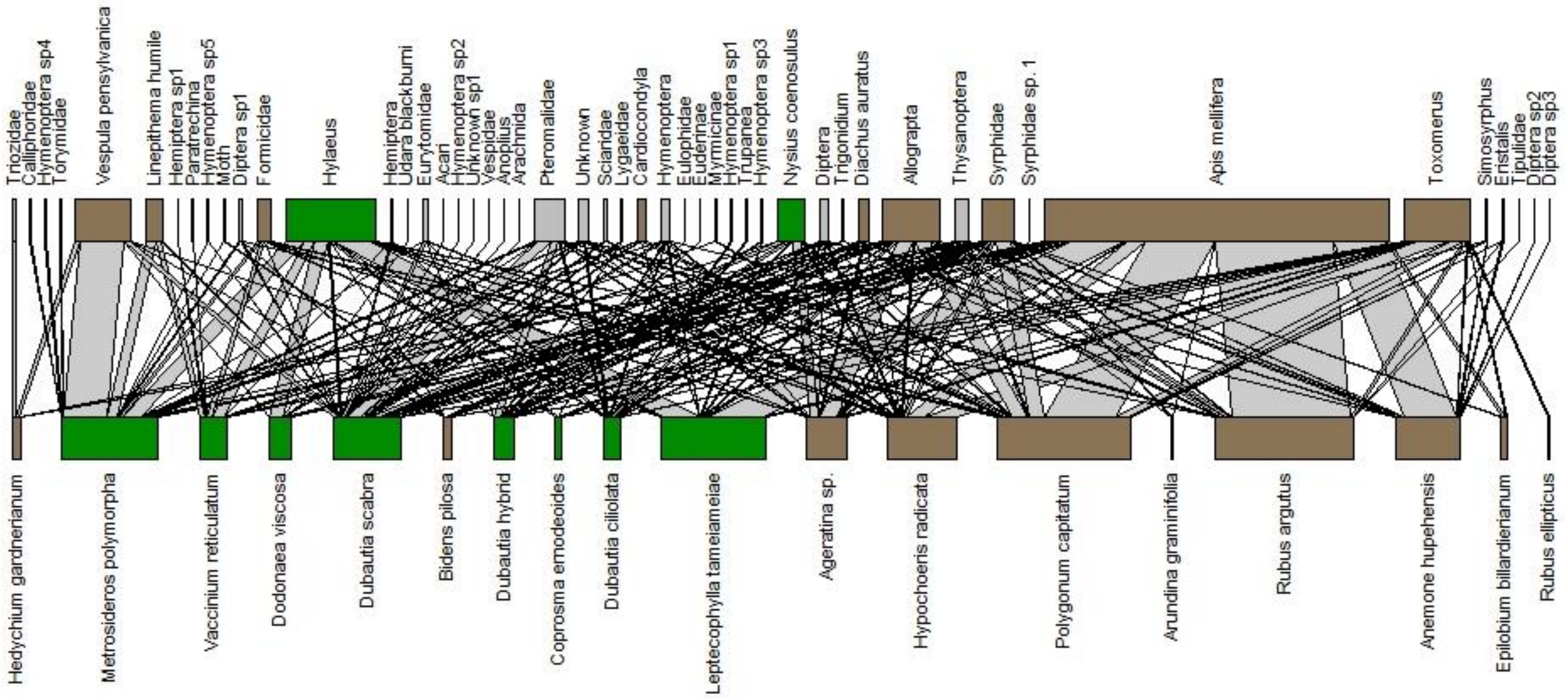
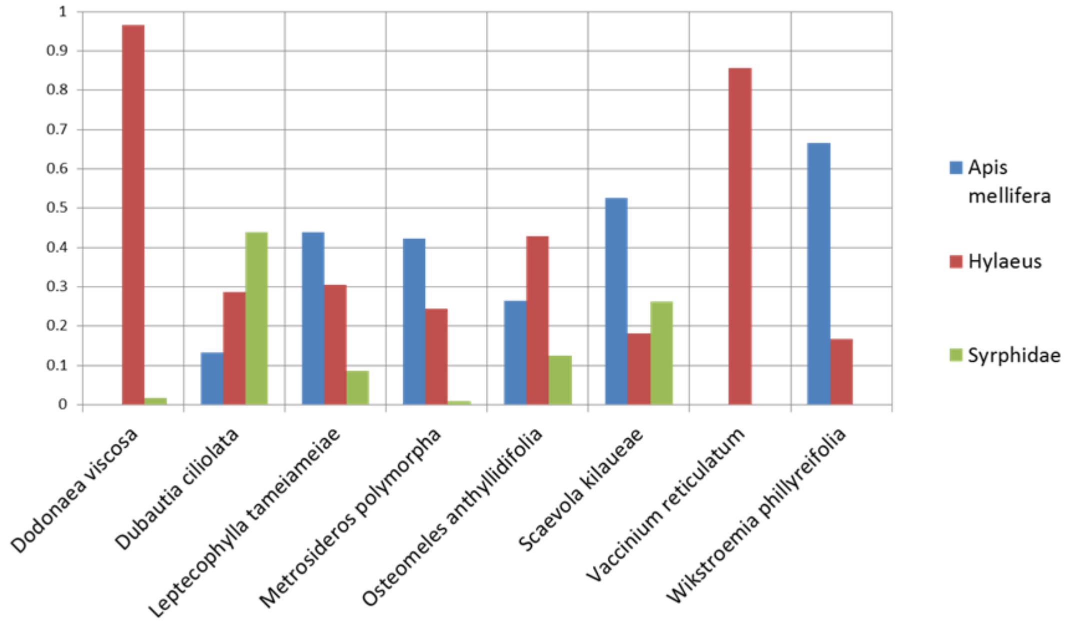


Figure 5: Plant dependence on insect groups for (A) the Hilina Pali native site and (B) Byron Ledge mixed site.

A.



B.

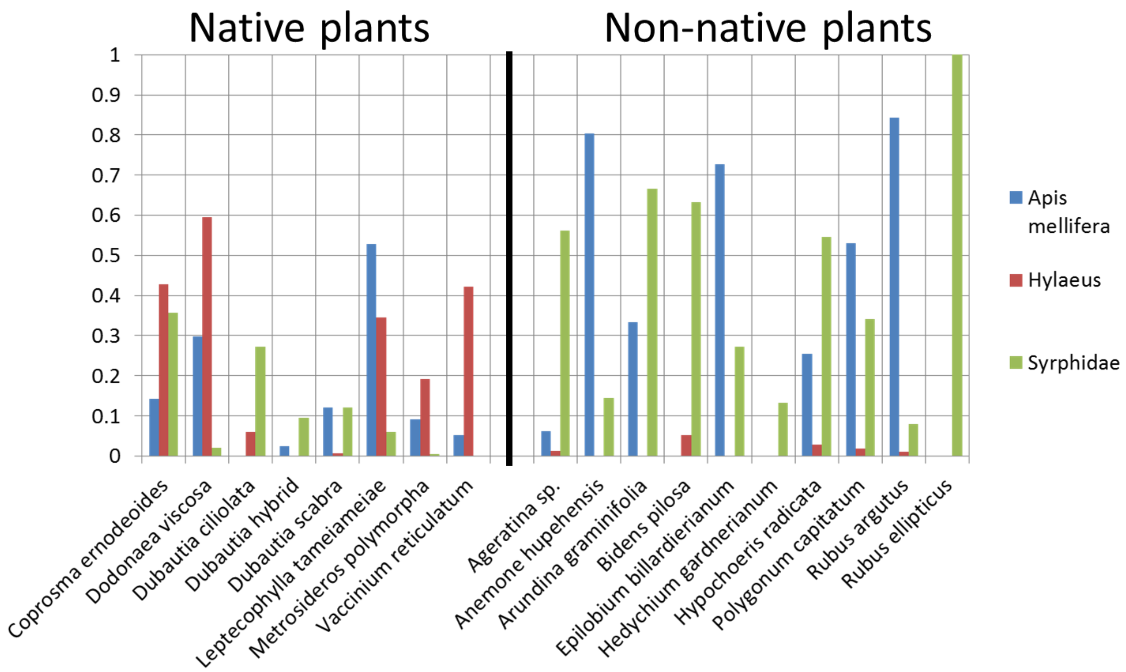
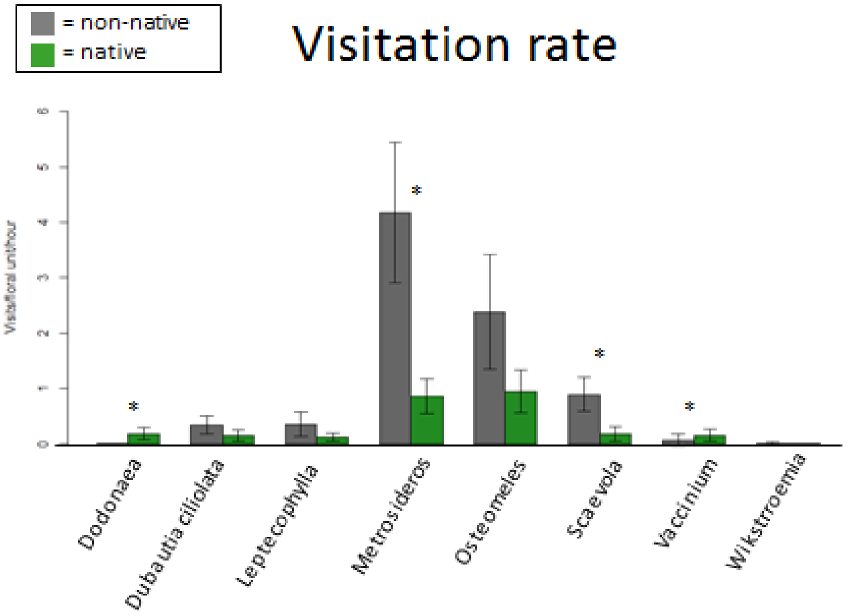


Figure 6: Visitation rates at (A) Hilina Pali native site, and (B) Byron Ledge mixed site. Starred comparisons are significant at $p<0.05$

A.



B.

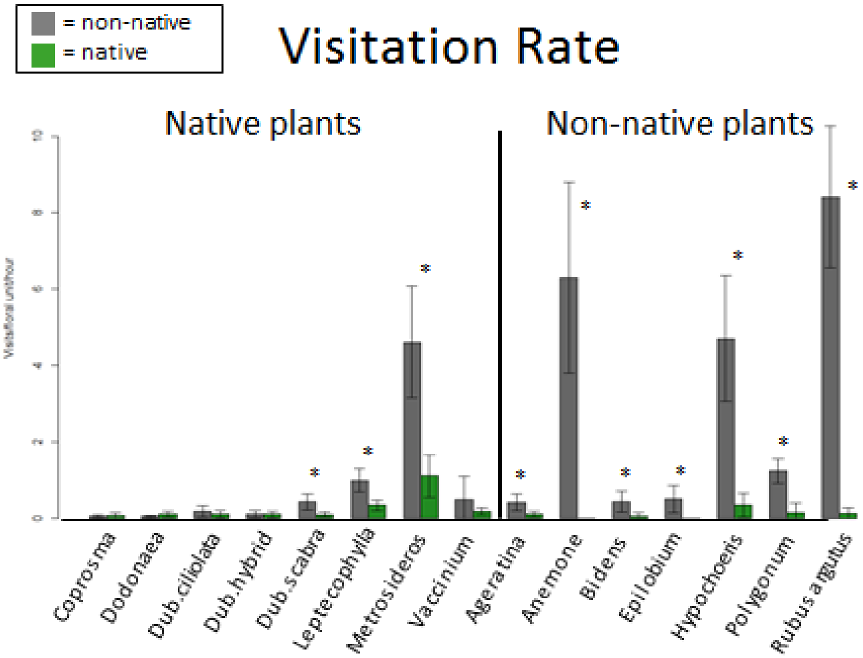


Figure 7: Honeybee visitation to *Wikstroemia phillyreifolia*. Floral visitation was very rarely observed, but not forbidden by morphological constraints.

Figure 8: Comparison of (A) *Apis* vs. (B) *Hylaeus* vs. (C) Formicidae visitation to *Vaccinium*:

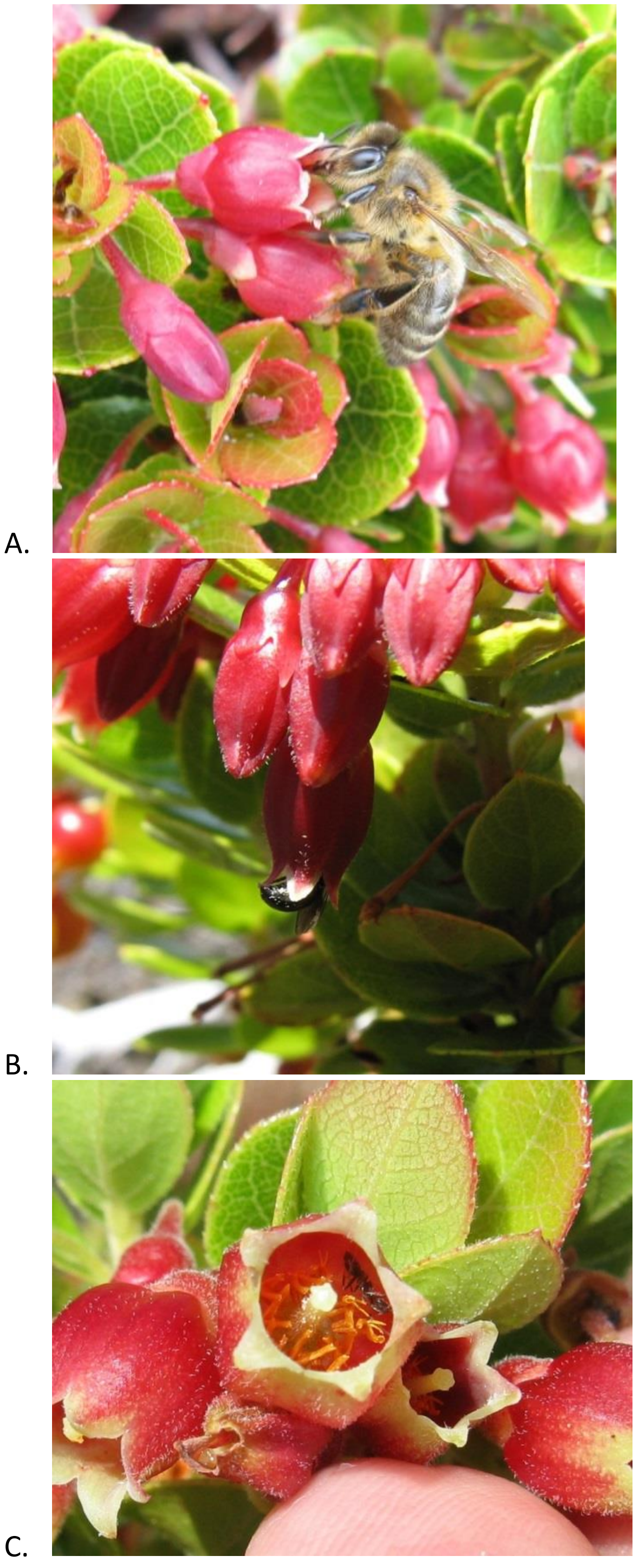


Figure 9: *Scaevola kilaueae* flower. Note that despite having a deep corolla, the flower is asymmetrical and openly accessible along one side. Some insects visited from the base, others from the top.

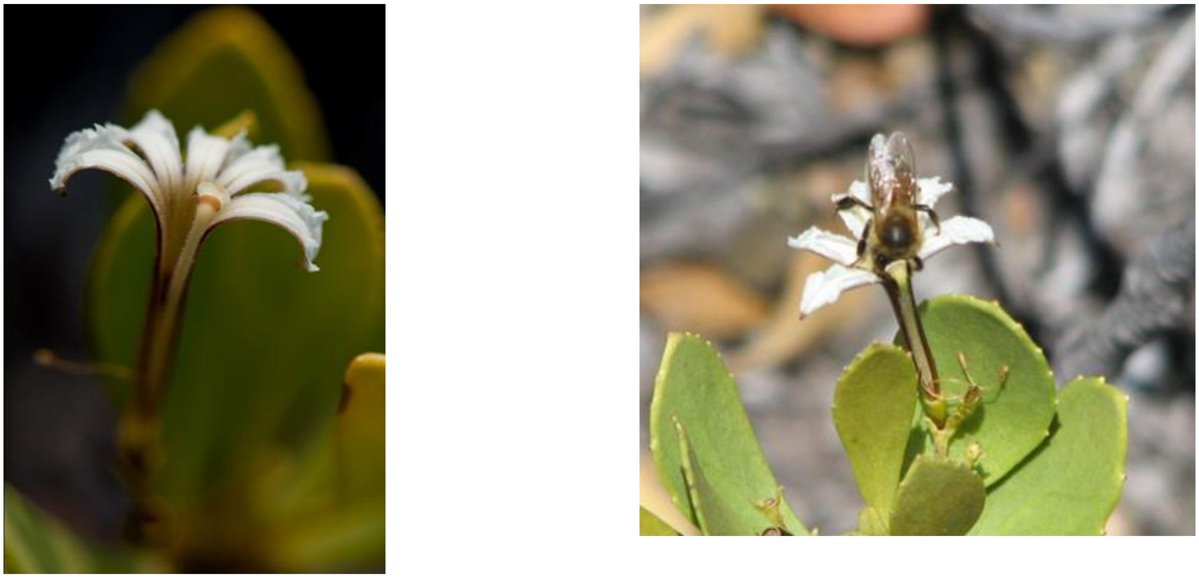


Figure 10: Comparison of different floral visitors to *Metrosideros polymorpha.* (A) Pollen harvesting by *Hylaeus*. (B) Nectar harvesting by ants. (C) Nectar harvesting by *Vespula* with no contact to reproductive organs. (D) Nectar harvesting by *Vespula* with contact to stigmas and anthers. (E) Nectar harvesting by *Apis* with no contact to reproductive organs. (F) Floral visitation by *Apis* with contact to reproductive organs.


A.
D.
B.
E.
C.
F.

Figure 11: Routes for pollen transfer among *Dubautia* at mixed site. 1: Between *Dubautia ciliolata* and *Dubautia scabra*. 2: Between *Dubautia ciliolata* and putative hybrid. 3: Between *Dubautia scabra* and putative hybrid

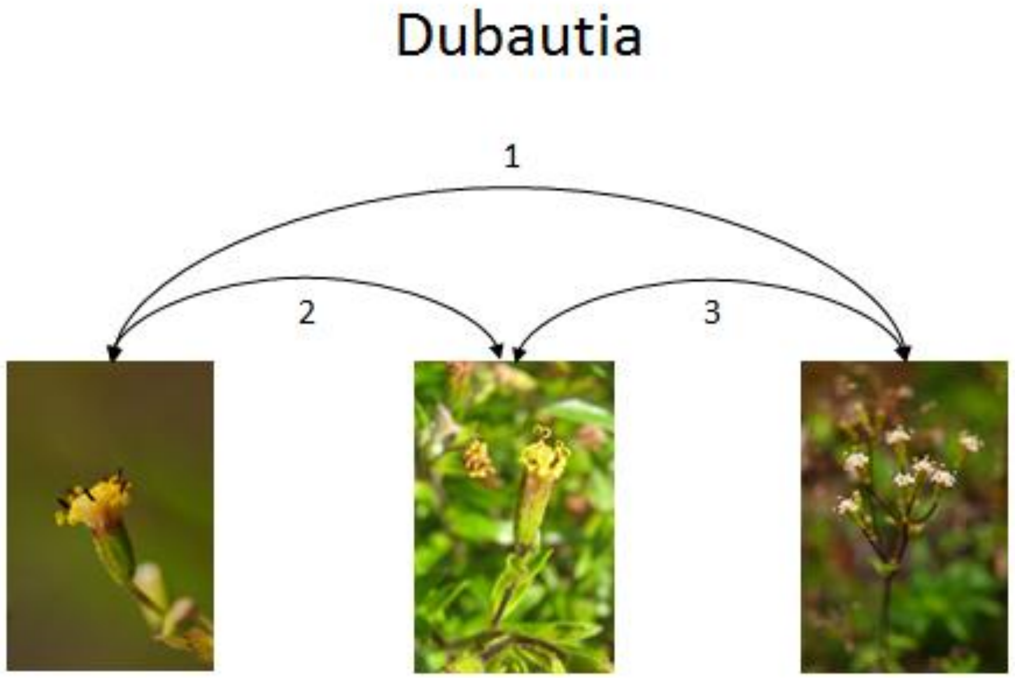


Table 3: Overlap in floral visitors to different *Dubautia* species (plus hybrid) at the mixed site. Includes incidental observations outside of formal observation periods.

1: *D. ciliolata* and *D. scabra*	**2: *D. ciliolata* and hybrid**	**3: *D. scabra* and hybrid**	**Shared among all *Dubautia***
Allograpta	*Diachus auratus*	*Allograpta*	*Diachus auratus*
Diachus auratus	*Nysius coenosulus*	*Apis mellifera*	*Nysius coenosulus*
Hylaeus	Pteromalidae	*Diachus auratus*	Pteromalidae
Nysius coenosulus	Syrphidae	*Hylaeus*	Syrphidae
Pteromalidae	*Toxomerus*	*Nysius coenosulus*	*Toxomerus*
Syrphidae		Pteromalidae	
Toxomerus		Syrphidae	
		Toxomerus	

Figure 12: (A) *Apis mellifera* on *Dubautia* hybrid (B) *Apis mellifera* on *Dubautia scabra*. *Apis mellifera* were observed moving directly between *D. scabra* and the putative hybrid.

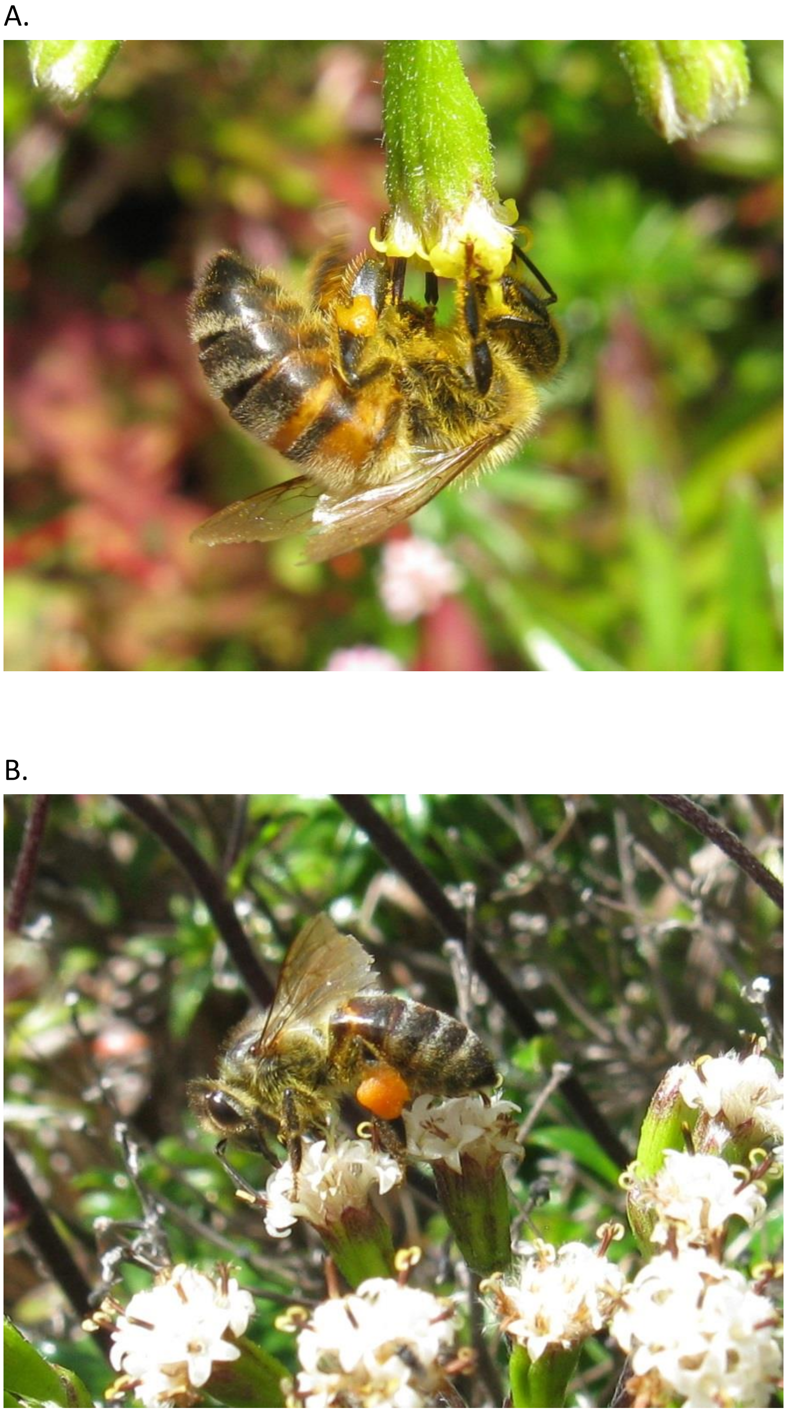


Figure 13: Tettigoniidae (Orthoptera) on ulei, *Osteomeles anthyllidifolia*

Figure 14: Pollen on native *Trigonidium* (Orthoptera) visiting *Dubautia scabra*:

Chapter 3: Temporal Variation in Floral Visitation Networks in Hawaii

Abstract

Pollination systems provide important ecosystem services in both natural and managed ecosystems, but their future ecological stability is uncertain as a result of global change, including the impacts of invasive species, habitat loss, and a changing climate. Understanding how these systems vary naturally through time, including intra-annually, can provide critical context for evaluating future change, as well as elucidating the complexity of interspecific interactions in the community. This study examines temporal variation in floral visitation networks in a tropical system in Hawaii characterized by both native and non-native pollinators and plants, and less seasonal variation than in temperate regions. The three most common floral visitors exhibited unique seasonal visitation patterns. In the presence of only native plant species, both the exotic honeybee *Apis mellifera* and the endemic *Hylaeus* bees had similar seasonal variation in floral foraging. However, when the vegetation was a mix of native and exotic species, *Apis* visitation tracked the peak blooming of exotic plants while *Hylaeus* only visited native plants, leading to seasonal variation in resource partitioning. In contrast, visitation by the invasive yellowjacket *Vespula pensylvanica* consistently peaked during the fall, unrelated to plant blooming cycles. Thus, even in a system with minimal seasonal climate variation, there were marked differences in the patterns of pollination interactions between seasons, suggesting that intra-annual variation must be considered in predictions for stability of pollination networks in a changing world.

Introduction

Worldwide, more than 87% of flowering plants rely on pollination services from other organisms, mostly insects (Ollerton, Winfree et al. 2011), with vast economic benefits of upwards of $100 billion/year (Costanza, d'Arge et al. 1997). However, since the majority of that valuation comes from agriculture, economics alone are insufficient for appreciating the critical importance of pollination services in maintaining natural ecosystems. These services are currently under global threat from habitat loss/alteration, invasive species, agricultural intensification, and a changing climate (Kearns, Inouye et al. 1998; Potts, Biesmeijer et al. 2010; González-Varo, Biesmeijer et al. 2013). In the face of these threats, it has become increasingly important to study and understand natural pollination systems, in order to evaluate the impacts of these incipient and ongoing pressures. While the majority of wild pollination studies have examined pairwise interactions, recent work bolstered by network theory has examined ecosystem-wide food webs (Thompson, Brose et al. 2012), and broad-scale mutualistic interaction networks (Chapter 2).

Due to the intense time commitments of compiling observational interaction data, many of these plant-pollinator interaction networks are compiled over relatively short time periods. Most surveys encompass a single season of observation or less, e.g. (Memmott 1999; Dupont, Hansen et al. 2003; Lundgren and Olesen 2005; Freed and Cann 2009; Kaiser-Bunbury, Memmott et al. 2009; Valdovinos, Ramos-Jiliberto et al. 2009). Studies which aim to describe the plant-pollinator network of an area may rely on data spanning as few as 5 consecutive days of observation (Philipp, Bocher et al. 2006), which therefore captures only a fleeting snapshot of existing relationships. Thus, both the intra-annual and inter-annual temporal stability of pollination systems remains understudied, in an era when understanding impacts of global environmental change is critical. Sampling completeness also has methodological consequences, affecting a variety of frequently cited network metrics (Nielsen and Bascompte 2007; Rivera-Hutinel, Bustamante et al. 2012), so a reliance on under-sampled data can have noticeable effects on the conclusions to be drawn from resulting interaction networks. Even when networks incorporate extensive visitation records compiled over multiple seasons or years, they frequently combine all of the data together for network presentation and analysis e.g. (Memmott and Waser 2002; Abe 2006). This lumping of data can potentially obscure a range of temporal variation in interactions, which can have real ecological implications (Figure 1). See Basilio et al. 2006 for further examples of how cumulative network data can be misleading (Basilio, Medan et al. 2006).

There is ample evidence that both plant and pollinator components of these networks are subject to temporal variation. Species may be present in the interaction network during particular times, and absent in others. Floral resources are known to vary over time (e.g. (Maruyama, Vizentin-Bugoni et al. 2016)) in addition to the expected seasonality of blooming periods. Bee faunas, which comprise a large proportion of most pollinator networks, are known to be highly temporally variable and include many rare species which may appear only with increased sampling effort (Roubik 2001; Williams, Minckley et al. 2001). The diversity and abundance of pollinators overall has likewise been shown to be highly temporally variable for single plant species (Herrera 1988; Hughes, Vitousek et al. 1991; Cane and Payne 1993; Fritts and Rodda 1998), which indicates likely pollinator variability for the greater interaction network. Even if a species is present in the study area, it does not necessarily follow that the species will be a part of the interaction network. Not all floral visitors are dependent on floral resources – omnivorous species may only sporadically utilize pollen or nectar as food sources. In order to be a participant in a temporally described network, a species must both be available and observed to be actively interacting with other species during that specific time period.

The *interactions* between plants and pollinators themselves may also change over time. As different plants have peak flowering at different times during the year, a pollinator may shift from one plant species to another. In the Ogasawara Islands of Japan, exotic honey bees were observed to frequent native flower species when they were in bloom, but relied on exotic plant species during winter and spring when native bloom was low (Kato, Shibata et al. 1999). On a longer time-scale, a study of Central European plant-pollinator interactions showed that exotic plant species accrued a greater diversity of insect visitors the longer that species had been naturalized in an area (Pysek, Jarosik et al. 2011). The strengths of these interactions are also subject to temporal variability. A pollinator might visit a plant more frequently during a season when it is the dominant flowering species, and less frequently once other choices are available.

The few studies that have examined the temporal variability in plant/pollinator interaction networks have all found high levels of variability. Petanidou et al. (2008) surveyed plant-pollinator interactions in a scrub community in Greece over four years, finding that less than 5% of the species interactions were consistently observed across all four years (Petanidou, Kallimanis et al. 2008). In a two-year study in Greenland, there was high species turnover between years, and an even higher turnover of linkages between species (Olesen, Bascompte et al. 2008). In a California montane meadow community, only 35.7% of the plants and 18.1% of the pollinator species interacted with the same partner across the three summers of the study (Alarcon, Waser et al. 2008). In this latter case, the general network topology was consistent between the first and third summers, while the second summer was distinct in species composition and lower in floral abundance, perhaps due to drought conditions in that year. Even though the basic structure of the network was similar between the first and third years, the identity of the interactions still showed significant variability. Thus, in each study that examined between-year variation, floral visitation networks were not consistent from year-to-year. Studies examining variation within a single year or flowering season have likewise found that plant-pollinator interaction networks are constantly changing. For a woody coastal community in Argentina, plant-pollinator interactions fell into three distinct assemblages divided by season (Basilio, Medan et al. 2006). Even within the very short flowering season of the high Arctic, there were two distinct plant-pollinator interaction communities (early and late season) (Lundgren and Olesen 2005). Unsurprisingly, studies on intra-annual variation thus far have generally focused on ecosystems that have strong seasonal climates. However, the potential for important variation in tropical climates should not be ignored, particularly as tropical ecosystems (and particularly tropical islands) make up the majority of biodiversity hotspots for conservation (Myers, Mittermeier et al. 2000).

Few studies have attempted to combine analysis of both inter- and intra-annual variation in plant-pollinator interaction networks (Olesen, Bascompte et al. 2008). These analyses were based solely on qualitative data, which only incorporates the presence or absence of observed interactions. The frequency of interactions is also crucial for determining the actual ecological effect of these potentially mutualistic interactions (Vazquez, Morris et al. 2005). Overall pollinator efficacy is the result of both pollinator quality and quantity (Herrera 1987; Herrera 1989), the latter of which is missing from most existing temporally-quantified plant-pollinator networks.

To better understand both intra-annual and inter-annual temporal variation in pollination systems, visitation networks were studied in a set of habitats on the Big Island of Hawaii over multiple seasons and years. The study was designed to address three main goals: 1) to understand temporal variation in a tropical climate that is not subject to the great shifts in temperature or day length characteristic of temperate zones, 2) to reveal visitation patterns for both exotic (*Apis mellifera* bees and *Vespula pensylvanica* wasps) and native floral visitors (*Hylaeus* bees), and 3) to establish a baseline for floral visitation networks that can be used for future comparative studies in the face of current and future global change.

Methods

Locations:

This study was conducted in two sites at Hawaii Volcanoes National Park on the Big Island of Hawaii (Figure 2). Sites were chosen based on accessibility and species composition, especially relative abundance of native and introduced plants. Particular species were targeted for diversity of floral shape, local endemicity, or relevance to well-known systems. For the site with only native plant species (Hilina Pali), the site was chosen for its relatively high species diversity – it was the only site in the area containing *Dubautia ciliolata* (a close relative of the famed Hawaiian silverswords), *Vaccinium reticulatum* (which has a restrictive floral shape and has been reputed to be "buzzed" by native bees (Heather Sahli, pers. comm.)), and *Scaevola kilauae* (a highly localized endemic relative of a widespread Polynesian littoral species). For the site with mixed species (Byron Ledge), it was the only site in the park that had a high diversity of native and non-native herbaceous and shrubby species, including many of the same native species as in the native site. It also had both local species of *Dubautia* (*D. ciliolata* and *D. scabra*) and a patch of putative *Dubautia* hybrids. Complete lists of plant species are available in Chapter 2.

Observations:

Observations were conducted between 8AM and 4:30PM during periods of fair weather – no precipitation, maximum wind gusts below 20mph, and at least partial sunshine (<80% cloud cover). Weather conditions were recorded with a Kestrel 3000 pocket weather station at the beginning and end of daily observations. Temperature and humidity were measured in nearby shade. To measure wind speed, the Kestrel was held up at arm's length for 30 seconds, and the average and maximum windspeed was recorded for that time span (as in (McCall and Primack 1992). Cloud cover was estimated to the nearest 10%. Weather conditions were recorded each time at the same place in each site. Climate measurements were compared using ANOVA and pairwise t-tests in R.

Species were observed in a random order (observation order created in Microsoft Excel via random number generator). Observed individuals were chosen haphazardly from among flowering individuals of that species that were safely observable (away from lava cracks, deep potholes, etc.). Whenever possible, individuals were chosen that did not require trampling or otherwise disturbing the other vegetation. Each individual plant was observed for 10 minutes through Pentax Papilio close-focus binoculars from 2-4 feet away. During that time, I remained as still as possible to avoid disturbing potential visitors. For each insect visitor (no non-insect visitors were observed), I recorded visitor identity to the lowest taxonomic level possible, the number of flowers (or flower heads, for compound flowers) visited, the total time spent visiting flowers within the observation area, and notes about behavior (pollen vs nectar collecting, position on the flower, interactions with other insects, etc.). Insects that could not be field-identified were photographed or collected as voucher specimens when possible. The number of observed flowers and the total number flowers on the plant were also recorded. For very large plants, I counted all of the flowers on a quarter of the plant and multiplied by 4 to estimate the total number of flowers.

Due to heavy cloud cover and frequent rainfall during the months of December-February, observations were divided only into Spring, Summer, and Fall data collection periods. The native site was observed during the summer and fall of 2007, spring and summer of 2008, and continuously (as weather permitted) from spring 2009 to summer 2010. The mixed plant site was added in the summer of 2008, and then continuously observed from spring 2009 to summer 2010. A total of 2,398 10-minute observation sessions were completed, over a total of 42,389 flowers. 6,541 flower visits were recorded from 2,583 individual floral visitors.

Vegetation surveys

Plant surveys were conducted in July 2009, November 2009, and March 2010. At the Byron Ledge mixed plant site, five parallel 70m transects were established at 10m intervals, and 1m quadrats were placed every ten meters along each transect for a total of 40 quadrats. Due to the sparseness of vegetation at the Hilina Pali native plant site, eight parallel 90m transects were used, for a total of 80 quadrats. Within each quadrat, I recorded the percent cover, number of individuals, and number of flowers for each species.

Data analysis

Quantitative floral interaction networks were plotted using the BIPARTITE package in R (Dormann, Gruber et al. 2008; Team 2014). Climate data was compared in R with ANOVA. Due to the extreme non-normality of visitation rate data, non-parametric Kruskal-Wallis tests were used to examine for differences in visitation rate between seasons and years.

Results

Climate data

The spring of 2009 was unusually cold (Bleil, Bluethgen et al. 2011) and rainy when compared to longer-term data. Since no observation sessions were performed when it was overcast or precipitating, the weather conditions limited the number of days available for data collection. Overall, during the spring observation sessions, the temperature averaged 4.7 degrees cooler than the summer and fall (Figure 3A, $p<0.0001$), and the Byron Ledge mixed site also averaged 2.7 degrees cooler than the Hilina Pali native site (Figure 3B, $p<0.0001$), but there was no interaction between site and season ($p=0.92$).

Vegetation surveys

The vegetation at the Hilina Pali native site was dominated by unidentified grasses (which were not observed blooming at any time) (52.5% of quadrats), *Leptecophylla tameiameiae* (47.5%), and *Dodonaea viscosa* (34%) (Table 1A). All other species were present in only 1 or 2 quadrats. The Byron Ledge mixed site has higher species diversity and higher evenness than in the mixed site (Table 1B). Seven flowering plant species were relatively rare at the site and were not captured in the quadrats. One flowering plant species, *Vaccinium calycinum*, was represented at the site by a single, small individual that was never recorded flowering and was thus not included in any floral visitation data.

Table 2 shows the seasonal variation in available flowers in the surveyed quadrats at each site. Due to the extreme patchiness of the vegetation at both sites, the floral surveys are more indicative of intra-annual changes in flowering of those specific patches rather than a perfect representation of the available resources at each site. For example, no *Rubus argutus* flowers were ever recorded within a quadrat in the Byron Ledge mixed area, despite copious flowering and visitation during the spring months. Similarly, no *Metrosideros* flowers were recorded within a quadrat in the Hilina Pali native site (and only 12 flowers of *Metrosideros* were captured in the Byron Ledge mixed site), yet it was a major target for floral visitors at both sites.

Temporal variation in interaction networks

There was no significant difference in overall visitation rates between years at the native site (p=0.437) or at the mixed site (p=0.08). At both sites, nearly all flowering plant species were consistently found during each year of observation, though not all were consistently recorded as participating in the network in all time periods. *Vaccinium reticulatum* was present at the Hilina Pali native site every summer, but no visits were recorded in the summer of 2009. However, as *Vaccinium* is a relatively uncommon plant within that site, and never received high visitation in any year or season, it is entirely possible that visits were simply unobserved during that summer (representing temporal "missing links"). In the Byron Ledge mixed site, individuals of *Epilobium billiardianum* and *Arundina graminifolia* were not found during the first year of observation, although both remained rare in subsequent years and consequently were not major network components at any time. For all species in both sites, seasonal flowering patterns were consistent from year to year (pers. obs.).

In the Hilina Pali native plant site, the only plant species with a limited flowering time was *Osteomeles anthyllidifolia*, which peaked in the spring, rarely flowered during the summer, and had limited flowering during the fall months. This variation in flowering was strongly reflected in the observed interaction networks for this area. During the spring months, insect visitation to *Osteomeles* dominates the network (Figure 4A). Sixty two percent (62.0%, 168/271) of all visits to plants during this period were to *Osteomeles*, including 63.3% (88/139) of all visits by *Hylaeus* and 62.8% (49/78) of all visits by *Apis*. In the summer, very few floral visitations were recorded, with an increase beginning in the fall as flowers increased. There were a few other similarities in seasonal variation between *Apis* and *Hylaeus* (Figure 4 B,C). Both visited *Dubautia ciliolata* almost exclusively during the summer (*Apis* 12 summer visits/12 total visits, *Hylaeus* 24 summer/26 total), and utilized *Scaevola kilauae* more in the summer and fall. The one major difference is for *Dodonaea viscosa*, which was favored by *Hylaeus* in summer and fall but not visited at all in this site by *Apis*. Overall, the visitation patterns for both *Hylaeus* and *Apis* showed similar seasonal variations, mostly driven by seasonal changes in visitation to match the flowering of *Osteomeles*.

In the Byron Ledge mixed plant site, it was the non-native plants that generally displayed more pronounced seasonality in flowering, although most of them produced at least some flowers year-round. *Rubus argutus* flowering peaked in the spring, which corresponded with an increased prominence within the overall visitation network. *Anemone hupehensis* flowered only during the summer, during which time they were highly attractive to non-native insects. Bamboo orchid, *Arundina graminifolia*, and kahili ginger, *Hedychium gardnerianum*, also flowered only during the summer months, although they were relatively rare in the site and had little impact on general visitation patterns. *Ageratina* flowering peaked in the spring months, however there were always at least some flowers available and visitation remained largely consistent between seasons. *Apis* floral visitation tracked the flowering of both *Rubus* and *Anemone* (Figure 5). While *Apis* favored *Rubus* and visited the flowers even when they were rare, during the spring peak blooming period 71.2% (72/101) of all visits to plants were to *Rubus*. In the summer, the only time *Anemone* was in bloom, *Apis* also strongly incorporated *Anemone* into their foraging, representing 25.5% (106/415) of their visits to plants. However, despite *Rubus* and *Anemone* being clearly attractive to *Apis*, to the extent that seasonal visitation patterns by *Apis* matched their peak blooming period, those flowers were rarely visited by *Hylaeus* (zero visits to *Anemone*, 3 visits to *Rubus*) (Figure 5C).

At both sites, overall floral visitation rates were significantly higher during the fall season (Hilina Pali native site $p<0.0001$, Byron Ledge mixed site $p<0.0001$). These increases in overall visitation rates were driven by the sharply increased fall visitation rate of *Vespula pensylvanica* (Figure 6), particularly for *Metrosideros polymorpha* (Figure 7). *Vespula* was nearly always recorded on *Metrosideros polymorpha* (Byron Ledge mixed site 80% of visits to plants (92/115), Hilina Pali native site 88.9% (78/81)), and had significantly higher visitation rates during the fall at both sites (Hilina Pali native site $p<0.0001$, Byron Ledge mixed site $p <0.0001$). In contrast, the visitation rate for *Apis* on *Metrosideros* did not vary significantly between seasons at either site. *Hylaeus* visitation rates for *Metrosideros* were significantly higher in the spring at the Hilina Pali native site ($p=0.0017$), but did not vary between seasons at the Byron Ledge mixed site.

The full, temporally-resolved quantitative interaction networks are presented in Appendix 1.

Discussion

Overall, the Hawaiian pollination networks observed in this study displayed much more variation within years than between years. The consistency between years may be attributable to being relatively small, generalized networks where there are simply not as many transitory species moving in and out of the system. These types of small, highly linked networks are typical for island ecosystems (Trøjelsgaard and Olesen 2013). Instead of inter-annual variation, these networks displayed patterns of seasonal variation despite a relatively consistent climate throughout the year -- temperature varied only by a few degrees, with somewhat cooler spring temperatures, and increased rain noted during the winter months. The winter rains may have obscured even stronger seasonal variation, as they precluded pollinator observations and the winter season was thus excluded from analysis. Most flowering species in both sites produced flowers throughout the year, with the exception of several exotic plants in the Byron Ledge mixed site that had strictly limited flowering seasons. The plants that bloomed year-round generally had seasonal peaks in flowering, however, which often corresponded to increased visitation and thus a greater presence in the network. The major floral visitors were all likewise observed throughout the year, with distinct seasonal variation in their foraging.

While the conclusions from this study are based on only two study sites, this level of replication is common in floral visitation networks, likely due to the time and effort required for floral observations. Many published network studies are based either on a single site (e.g. (Memmott 1999; Dupont, Hansen et al. 2003; Lundgren and Olesen 2005)) or one site per treatment (e.g. (Kaiser-Bunbury, Memmott et al. 2009; Koch and Sahli 2013)), and/or are compiled from a single season or less (see Introduction). For this study, the decision was made to sacrifice spatial replication for increased temporal breadth.

Temporal visitation patterns for *Apis*, *Hylaeus,* and *Vespula*

The three major groups of floral visitors displayed different patterns of seasonal variation. In the presence of only native plant species, *Apis* and *Hylaeus* visited mostly the same suite of plant species and displayed similar patterns of seasonal variation in floral visitation. This similarity in temporal variation in floral utilization can potentially maximize the possibility of resource competition between *Apis* and *Hylaeus*. However, when both native and exotic plant species were present, *Apis* tracked the seasonality of desired floral resources regardless of origin, while *Hylaeus* continued to only visit native species. This disparity, coupled with the seasonal variation in bloom of some exotic species, caused *Apis* and *Hylaeus* to have differing patterns of seasonal variation in the presence of mixed native and exotic plant species. The seasonal shifts of *Apis* to follow the peak bloom of exotic species may thus potentially help to relieve resource competition between *Apis* and *Hylaeus*. The divergence of seasonal floral preference patterns could effectively create resource partitioning, which can facilitate the co-existence of otherwise competing species. A different type of resource partitioning has previously been recorded for floral visitors to *Metrosideros* flowers. In *Metrosideros*, the spatial separation of nectar and pollen rewards means that different floral visitors can forage simultaneously for different resources, with *Hylaeus* mostly foraging for pollen and exotic Hymenoptera (e.g. *Apis*, ants) mostly foraging for nectar (Junker, Bleil et al. 2010).

While *Hylaeus* and *Apis* had differing patterns in their seasonal usage of different plant species, *Vespula* displayed a different type of temporal visitation pattern. *Vespula* nearly always visited the same flower species but significantly varied their visitation rate between seasons. The difference in *Vespula* seasonal visitation rates means that studies conducted only during single seasons could strongly under- or over-estimate the effects of *Vespula* on both overall interaction networks and on visitation to particular flowering species that flower throughout the year. In particular, studies on the effects of *Vespula* on *Metrosideros* visitation were primarily conducted during the fall months (e.g. (Wilson and Holway 2010; Hanna, Foote et al. 2014), while *Metrosideros* flowering occurs year-round with peaks from April to June (Ralph and Fancy 1995). Thus, while *Vespula* performs a significant amount of the visitation to *Metrosideros* flowers during the fall months, it may not have a high overall direct effect on reproductive success of *Metrosideros*. However, *Vespula* may have important indirect effects on plants' reproductive success through its heavy predation on potential pollinators. Although birds are thought to be the traditional and most effective pollinators of *Metrosideros* (Lammers and Freeman 1986), more recent studies have indicated that *Apis mellifera*, and to a lesser extent, *Hylaeus* bees, are now likely the main floral visitors and pollinators for *Metrosideros* (Freed and Cann 2009; Junker, Bleil et al. 2010; Hanna, Foote et al. 2013). Both *Apis* and *Hylaeus* are preyed upon by *Vespula* (Wilson and Holway 2010), so the presence of *Vespula* can have grave effects on the local bee populations. Thus, even if the direct effects of *Vespula* on plants' reproductive success may be strongly seasonal in strength, there may be persistent long-term negative indirect effects through predation on pollinators. There may also be indirect effects via resource depletion if populations of *Vespula* become large enough. In New Zealand, invasive *Vespula* wasps (*Vespula germanica* and *Vespula vulgaris*) reduce the available carbohydrate resources in beech forests by greater than 90% during the times of the year when they are active, which has downstream effects on the forest birds and invertebrates (Moller, Tilley et al. 1991; Beggs 2001). While those carbohydrate resources are honeydew rather than nectar, a similar drawdown has been observed for *Metrosideros* in Hawaii (Hanna, Foote et al. 2014), potentially leading to resource competition, shifts in resource use by other floral visitors, and/or increased seasonal restructuring of visitation networks. In the longer term, continued monitoring of *Vespula* populations and plant-visitor interactions will be necessary to determine the exact extent of the effect of *Vespula* on *Metrosideros* reproductive fitness. In particular, if these *Vespula* populations shift from annual to perennial life histories (as has been frequently observed in Hawaii), the magnitude of their detrimental effects will likely increase (Gambino 1991; Wilson, Mullen et al. 2009).

As discussed in Chapter 2, unobserved interactions between species may be the result of either missing links (which are likely to exist, but were simply unobserved) or forbidden links (which would never be observed even with theoretically unlimited observation time). Chapter 2 outlined the possibilities for missing and forbidden links in these interaction networks based on morphological constraints for either the flowers or potential insect floral visitors. Another potential source of constraints on interactions is temporal mismatching.

The current seasonal variation in *Vespula* visitation creates the only potential major phenological forbidden links – interactions that have not been observed and are unlikely to be observed with increased sampling. In both sites, the visitation rates of *Vespula* skyrocketed during the fall months, which accords with the expected peak of activity for annual colonies (Gambino 1991). As *Osteomeles anthyllidifolia* (native site) and *Rubus argutus* (mixed site) both peaked in flowering during the spring, phenological mismatching could create a largely forbidden linkage with *Vespula*. Similarly, the summer flowering of *Anemone*, combined with limited *Vespula* presence during that time period, could be restricting more extensive interactions between the two. No *Vespula* visitation was recorded on *Osteomeles*, *Rubus*, or *Anemone*, during any time period. If the phenologies of these species change (due to climate change or other causes) to create more temporal overlap, interaction rates could potentially increase. However, *Vespula* primarily forages on flowers for nectar (Hanna, Foote et al. 2014), which is not produced by *Osteomeles*, *Rubus*, or *Anemone* in quantities to rival the flowers of the currently favored *Metrosideros*. Thus, it is unlikely that visitation to those species would significantly increase as long as *Metrosideros* flowers were also present.

Within-day variation: missing and forbidden links

Missing or forbidden links due to temporal mismatch can also occur on a within-day basis. Floral visitation on *Wikstroemia phillyreifolia* was distinctly rare compared to other species, particularly considering its copious and conspicuous flowering during part of the year. The lack of visitation probably reflects the existence of missing links, with the majority of visitation likely occurring at night, when no observation sessions were conducted. Since all observations were conducted between 8AM and 4:30PM, only daytime-active visitors were observed. Since *Wikstroemia* may be primarily pollinated by night-flying moths (as discussed in Chapter 2), there was a temporal mismatch between the cohort of observed insects and the actual active-visitation time for those flowers. Night-time observation sessions might uncover these missing interactions, and should be included in any future studies including pollination of this species.

The flowers of *Epilobium* and *Polygonum* close by 4-5PM each day (personal observation), and thus the lists of interaction partners of these species are unlikely to be expanded by night-time observation. For the other flowering species, both native and non-native, the flowers remained open at night. In *Metrosideros*, the peak of nectar production varies both within and between individual plants, although production was significantly higher during the day than at night (Carpenter 1976). Thus, the majority of visitation likely occurs during daytime hours, overlapping the observation periods of this study. However, for most of the observed species it is unknown whether floral rewards or attractants vary throughout the day, and therefore whether these species might remain attractive to visitors during the night-time hours. Future studies could be useful to elucidate the times of reward presentation and exhaustion to determine whether night-time observation would be beneficial for these other species.

While it was not discussed within this chapter, the exact time of day of each observation period was recorded after 2008, with general time periods recorded for prior observations. This time-specific data allows for further refinement of pollination temporal variation to within the day, which has rarely been attempted for plant-pollinator interaction networks. Pollinator visitation patterns vary throughout the day (Herrera 1990; Totland 1994; Hoehn, Tscharntke et al. 2008), tied to both temporal variation in available floral resources and differing activity periods of different floral visitors. Different ant species, which serve as potential nectar competitors, have also been shown to differ in activity patterns during the day on *Metrosideros*

(Lach 2008). Future analyses could utilize this new dataset to further explore the potential partitioning of or competition for floral visitation. Species that visit the same flowers might do so at different times of the day, thus avoiding interaction and competition with each other. Or, an early-active species might exhaust nectar sources before another species is active, thus excluding it from a potential floral resource. Bumblebees in Maine began foraging an hour before the small wild bees, which were left with only small amounts of leftover nectar (Hughes, Vitousek et al. 1991). In one system where some of the flower species close their flowers rapidly after pollination, this shift in floral availability led to different quantitative plant-pollinator networks in the morning vs. the afternoons (Fründ, Dormann et al. 2011). In order to fully quantify within-day dynamics, future observation times should be expanded to include night-time observations. Timing of nectar and pollen production should also be established for each plant species in order to explore potential nectar and pollen drawdown effects for later visitors.

A baseline to measure against anticipated future change

While this study did not find significant inter-annual differences in pollination networks, a confluence of both local and global threats to plants and pollinators (Chapter 4) ensures that changes will happen. On a local, acute level of threat, the study sites are located in a highly geologically active zone that is subject to volcanic eruptions. On a global, long-term level, anthropogenic climate change is expected to alter species phenology, leading to changes in species interactions. The data from this study establish a baseline of both existing interactions and their natural levels of variation, which can be compared against future observations in order to establish how these factors have altered pollination networks.

Volcanic activity and pollination

The most striking long-term event that occurred during this study was an unexpected volcanic eruption. On March 19, 2008, at the beginning of the spring 2008 observation period, there was an explosive pyroclastic eruption in the Halemaumau crater of the Kilauea caldera (Appendix 2). This was the first such eruption in that area since 1924 (and the first Kilauea summit-area eruption since 1982), and was preceded and followed by increased outgassing of emissions such as sulfur dioxide (SO_2), reaching the highest levels recorded since regular measurements started in 1979 (Wilson, Elias et al. 2008; Houghton, Swanson et al. 2011). Elevated sulfur dioxide has been shown to have a range of effects on plants, including foliar damage (Winner and Mooney 1980), decreased flower production (Lechowicz 1987; Clapperton and Reid 1994; Abe and Hasegawa 2008), and general reallocation of plant resources away from reproduction (Lechowicz 1987). Some bee species reduce their flight activity (Ginevan, Lane et al. 1980) or their rate of pollen collection (Hillman and Benton 1972), which could affect pollination interactions. However, the effects of elevated sulfur dioxide on plants and insects have mostly been studied in the context of anthropogenic pollution (but see (Winner and Mooney 1980; Winner and Mooney 1985; Erenler, Orr et al. 2016)), so they are not necessarily transferable to natural volcanic systems which include other pollutant emissions. In particular, volcanic ash is broadly insecticidal and may be especially deadly for floral visitors like bees and

Vespula wasps (Brown and bin Hussain 1981; Cook, Barron et al. 1981; Masciocchi, Pereira et al. 2013).

The continuing summit eruption also had an immediate effect on the floral observation sessions for this study. As increased local levels of sulfur dioxide and other volcanic emissions have been associated with negative human health consequences in the region (pers. obs. and (Longo, Yang et al. 2010; Longo 2013)), no observations were carried out on days when USGS-measured vog (volcanic smog) levels were above "moderate" (>100 on the EPA Air Quality Index, includes both toxic gases and particulate matter). Thus, any acute effects of volcanic air pollution on insect activity or flowering would not have been recorded, although continued/future long-term monitoring could potentially indicate the cumulative effects of elevated volcanic emission levels on plants, pollinators, or their interactions.

Negligible amounts of volcanic ash were observed at the field sites during the course of this study. However, again due to human health risks (e.g. (Lombardo, Ciancio et al. 2013)), no observations were carried out on the rare days when the ash plume was directly over the field sites, so any acute effects may have been missed. Woyke and Gabka (2011) reported decreased flight activity in honeybees on days when a volcanic ash cloud was overhead (Woyke and Gąbka 2011). Subsequent wind or rain may have removed deposited ash before observations resumed. Other newly produced volcanic products such as Pele's hair and Pele's tears were occasionally found on site, but are not expected to have any effect on plants or floral visitors due to their size. As ash was only occasionally produced and prevailing wind patterns usually blew the volcanic plume away from the study sites, volcanic ash is unlikely to have had an effect on pollinators or floral visitation at these sites during this time period. However, the potential effects should be considered and monitored for pollinators and floral visitation for areas of the Big Island that are more directly downwind from the eruption site.

Since the end of the collection of study data at Kilauea, the summit eruption has continued. In May 2018, the eruptive period entered a new, stronger phase, resulting in the long-term closure of most of Hawaii Volcanoes National Park due to ongoing volcanic hazards such as earthquakes, sulfur dioxide gas, volcanic ash, and explosive eruptions and major subsidence in the immediate vicinity of the summit caldera. The greatly increased amplitude of the eruption increases the likelihood that there would be observable effects on plants, pollinators, and plant-pollinator networks, both in the short and long term.

Climate change, phenology, and plant-pollinator interactions

Long-term monitoring has shown an increase over time in mean surface temperatures in Hawaii, only slightly lagging behind global temperature increases (Giambelluca, Diaz et al. 2008). Climate change, particularly global warming, affects species range, distribution, behavior, and physiology (Walther, Post et al. 2002; Parmesan and Yohe 2003; Parmesan 2006), and can influence the impacts of invasive species (Walther, Roques et al. 2009) (but see (Sorte, Ibáñez et al. 2013) who found generally no difference in native and non-native response to climate change for terrestrial species). Climate change can also have effects on interspecific interactions via alterations in species phenology (Settele, Bishop et al. 2016). Asynchronous phenological changes between plants and their pollinators can lead to phenological mismatch, with plant bloom cycles and pollinator activity periods no longer aligning. As a tropical system, Hawaii does not experience the strong seasonal changes of temperate climates. However, the results of this study show that it is not a constant, unchanging system, and does in fact undergo some seasonal patterns of change in the plant-pollinator network. This seasonal variation means that Hawaii is not immune from future phenological effects due to continuing global climate change.

The actual and potential effects of climate change on phenology and plant-pollinator interactions have been the subject of intensive research (e.g. (Hegland, Nielsen et al. 2009; Willmer 2012; Forrest 2015)). In the Mediterranean, the changing phenology of insect-pollinated plants more closely matched climate models than for wind-pollinated plants, implying that precisely those species that most require matching phenologies are also the most vulnerable (Gordo and Sanz 2010). The degree to which pollination interactions will be disrupted by climate change depends necessarily both on the extent of warming and on the unique responses of the species involved. In northeastern North America, climate change has caused the phenology of 10 wild bee species to advance by a mean of 10.4 days – however, this advance has so far has been paralleled by the phenological advance of the local flowering plant species (Bartomeus, Ascher et al. 2011). This matching allows for the potential maintenance of those mutualisms under climate change, although there may be other, unforeseen consequences of delayed phenology for either plants or their pollinators.

Phenological change can be idiosyncratic for different species, however, and other studies have found lesser degrees of matching between partners. Memmott et al. (2007) modeled expected phenological shifts of both plants and pollinators in a large temporally resolved pollination interaction network and found that these decoupled shifts led to both lowered diet breadth (i.e., pollinators interacted with fewer plant species) and reduced floral resources overall for 17-50% of all pollinator species (Memmott, Craze et al. 2007). However, that model assumes that there will be no changes in floral host use by the pollinators, even in periods where they no longer overlap with any species they formerly visited. This complete lack of compensating behavior seems unlikely, and implies that all of the pollinator species are to some degree specialized for the flowering species they currently utilize. This level of specialization is contrary to results from pollination network studies, which have generally found a nested structure whereby generalists interact with specialists and vice versa (Bascompte, Jordano et al. 2003). This nested structure, which was also observed in these Hawaiian networks (Chapter 2), buffers the effects of species loss/extinction (Memmott, Waser et al. 2004; Burgos, Ceva et al. 2007; Tylianakis, Laliberte et al. 2010). A similar buffering effect is expected when, instead of extinction, species are simply moved out of phenological synchronization (Tylianakis, Laliberte et al. 2010). In these Hawaiian networks, there are super-generalist species of both plants and pollinators that are present in the network during all seasons (although quantities may vary). These highly-generalized, always-active species can promote the continuity of both pollination service (for plants) and provision of necessary resources (for pollinators). In other systems, the presence of exotic supergeneralists have been touted as potential buffers against phenological mismatch (González-Varo, Biesmeijer et al. 2013), while Hawaii also has native supergeneralists that can fill that role.

Additionally, if a plant species is capable of floral phenotypic plasticity, it may be able to quickly adjust to accommodating/attracting a completely different set of pollinators. *Nicotiana attenuata*, a wild tobacco with a typically moth-adapted flower found in the American Southwest, is capable of completely and quickly switching its floral phenology to change pollinators from night-flying moths to day-flying hummingbirds (Kessler, Diezel et al. 2010). In this case, the switch is in response to selection for reduced herbivory, but it could also theoretically serve to respond to a loss or mismatch of the moth pollinators. Flowering species that are naturally polymorphic (e.g. *Linanthus* (Schemske and Bierzychudek 2001) or plastic (e.g. scarlet gilia (Paige and Whitham 1985) could likewise be able to adapt quickly to new pollinator regimes. In these Hawaiian pollination networks, we have some evidence for existing and potential variation that could favor easy shifts in floral characteristics. The wide range of naturally occurring variation in *Metrosideros* is reflected in its species epithet *polymorpha*, and there may have already been a shift in pollinators from mostly native birds to mostly *Apis* and *Hylaeus* bees (Hanna, Foote et al. 2013). Hybridization is another possible source of rapidly generated variation in floral type. In the Byron Ledge mixed site there are already a number of putative *Dubautia* hybrids (with intermediate morphology to the parent species), as well as the potential for hybridization between existing *Vaccinium reticulatum* and nearby *Vaccinium calycinum* (Vander Kloet 1996).

On an evolutionary timescale, even highly specialized flowers can shift to a generalized pollination system with selection for better reproductive success in a new ecosystem (Armbruster and Baldwin 1998). This shift may also be possible for pollinator species. Two bumblebee species in the Rocky Mountains, which were previously specialized on flowers with deep corolla tubes, have evolved shorter tongues in a shift towards greater foraging breadth as climate change caused reduced flowering in their ecosystem (Miller-Struttmann, Geib et al. 2015). A similar shift towards more generalized morphology has occurred in Hawaii. The native i'iwi birds (*Vestiaria coccinea*) have long, curved bills which seemed to fit perfectly into the long, curved corollas of the lobeliad *Clermontia arborescens* (Spieth 1966). However, as populations of *Clermontia* precipitously declined, the i'iwi shifted to feeding from the open flowers of *Metrosideros* and have evolved shorter bills as a result (Smith, Freed et al. 1995).

Plants and their pollinators can also respond to climate change in completely different ways beyond differences in advancing phenology. Pyke et al. (2016) found that while plants in Colorado advanced their phenology as expected, their bumblebee pollinators did not (Pyke, Thomson et al. 2016). Instead, the bumblebee species compensated for warming by shifting to higher elevations, a pattern that can eventually lead to <u>both</u> temporal and geographical mismatches. In Hawaii, the mild year-round climate has facilitated the shift of some colonies of invasive *Vespula* wasps from an annual cycle with overwintering to perennially active colonies that continue to grow in population size. These large perennial colonies have consequently larger requirements for both insect prey and floral nectar (Wilson, Mullen et al. 2009), which could combine to devastate existing pollination networks. As climate warming continues, these life history shifts could become more common or expand to higher elevations.

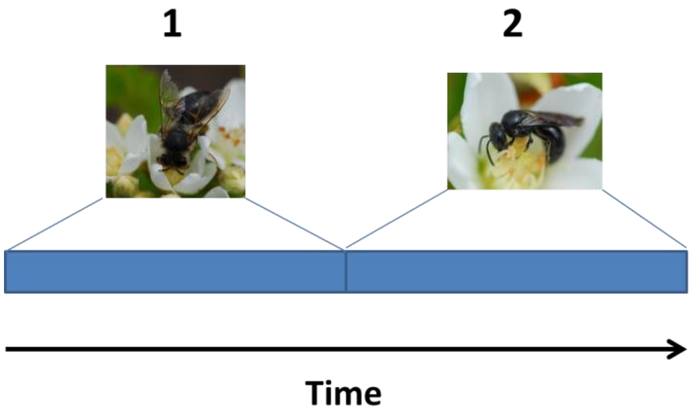
If there are insufficient floral resources due to phenological mismatching, some floral visitors could also potentially shift to non-floral sources of carbohydrates. While observations of *Vespula* behavior were limited in this study to floral nectar foraging, previous researchers have noted a preference for *Vespula* on Maui to obtain carbohydrates through the honeydew produced by the endemic mealybug *Pseudococcus nudus* (Gambino, Medeiros et al. 1987; Gambino, Medeiros et al. 1990), which is also found on the Big Island (Beardsley 1971). *Pseudococcus nudus* has been recorded from both *Leptecophylla tameiameiae* (Gambino, Medeiros et al. 1987; Gambino, Medeiros et al. 1990) and *Dubautia* sp. (Zimmerman 1948), which were common at both sites and featured in the rare floral visits that *Vespula* did not make to *Metrosideros*. Other endemic mealybug species have been recorded from *Metrosideros* (Beardsley 1971), or are noted as major carbohydrate sources for invasive ants (Zimmerman 1948).

Overall, phenological changes are somewhat buffered in Hawaii compared to temperate systems (due to reduced seasonality and the presence of highly generalist species), yet visitation networks differed seasonally, especially with respect to differences by native and non-native pollinators and between sites characterized by more or less native vegetation. In at least some temperate systems, the potential for phenological mismatch can be ameliorated by existing high biodiversity (Bartomeus, Park et al. 2013; Donoso, Stefanescu et al. 2016), aligning with the hypothesis that biodiversity provides “insurance” for changing conditions (Yachi and Loreau 1999; Loreau, Naeem et al. 2001). Given the depauperate nature of Hawaii’s ecosystems relative to the mainland, their relative lack of diversity may thus lead to greater-than-expected mismatch effects. In order to fully understand the impact of climate change, studies must not only track phenological changes for individual species, but also investigate phenological changes in species *interactions* (Walther 2010). Thus, temporally-described interaction networks such as those presented here may become increasingly important in evaluating the effects of future change.

Chapter 3: Figures and Tables

Figure 1: Two visitation scenarios illustrating the importance of temporally qualified interaction networks.

A. Two insect species (1 and 2) are responsible for all of the recorded floral visitation to a particular plant species, sequentially, one after the other. A cumulative quantitative network would suggest that these two insect species compete for floral resources. However, a temporally quantified network reveals the pollinators utilize that flower at different times (e.g. morning/afternoon, spring/summer, drought/rainy).



B. An insect species interacts with both Flower I and Flower II, but sequentially. Flower I and Flower II do not necessarily compete for visitation from this insect – their flowering times might have no overlap. Indeed, Flower I and Flower II might indirectly benefit each other by sustaining the insect populations throughout the year while the other species is not in flower.

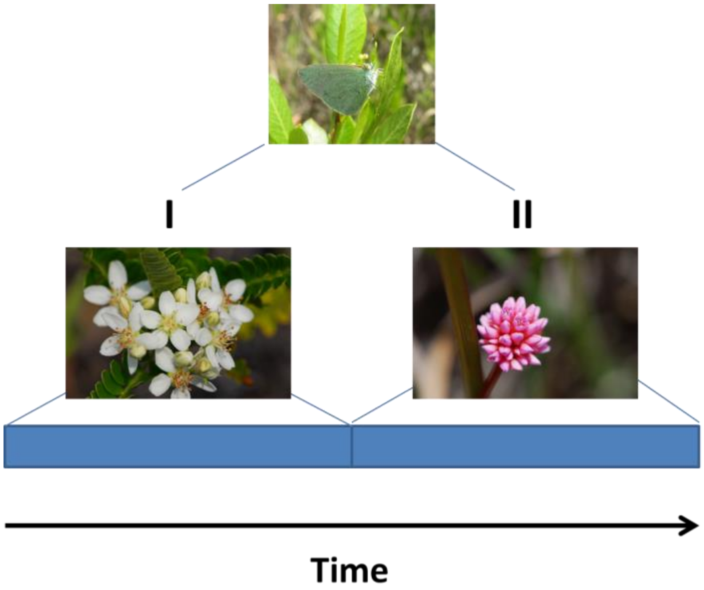


Figure 2: Location of study sites: A) Hilina Pali native site, B) Byron Ledge mixed site

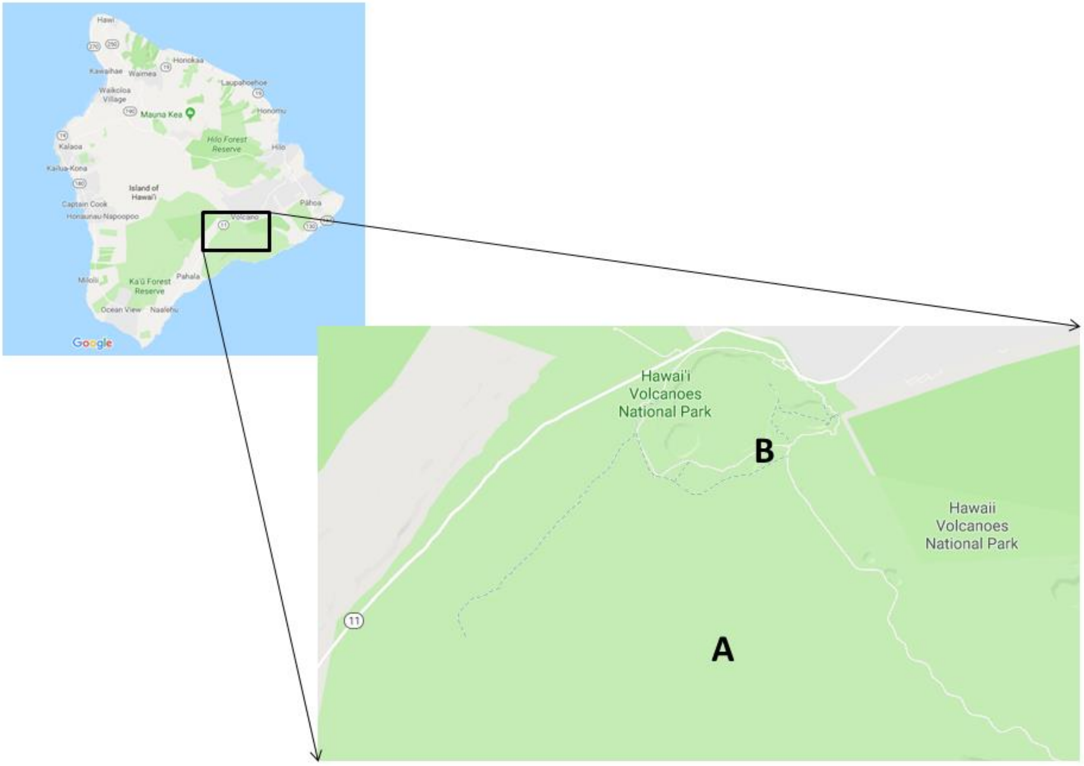
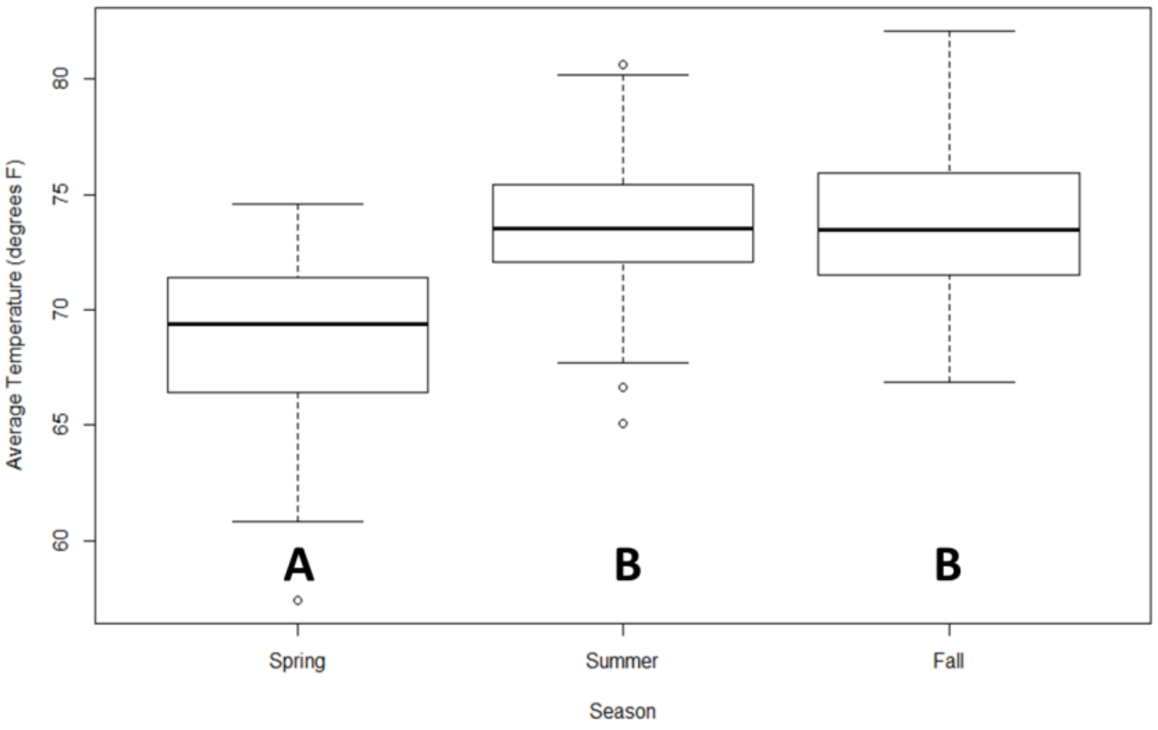


Figure 3: Summary of temperature data for observation sites, (A) by season and (B) by site. Different letters denote statistically significant groups.

A. Temperature data by season



B. Temperature data by site

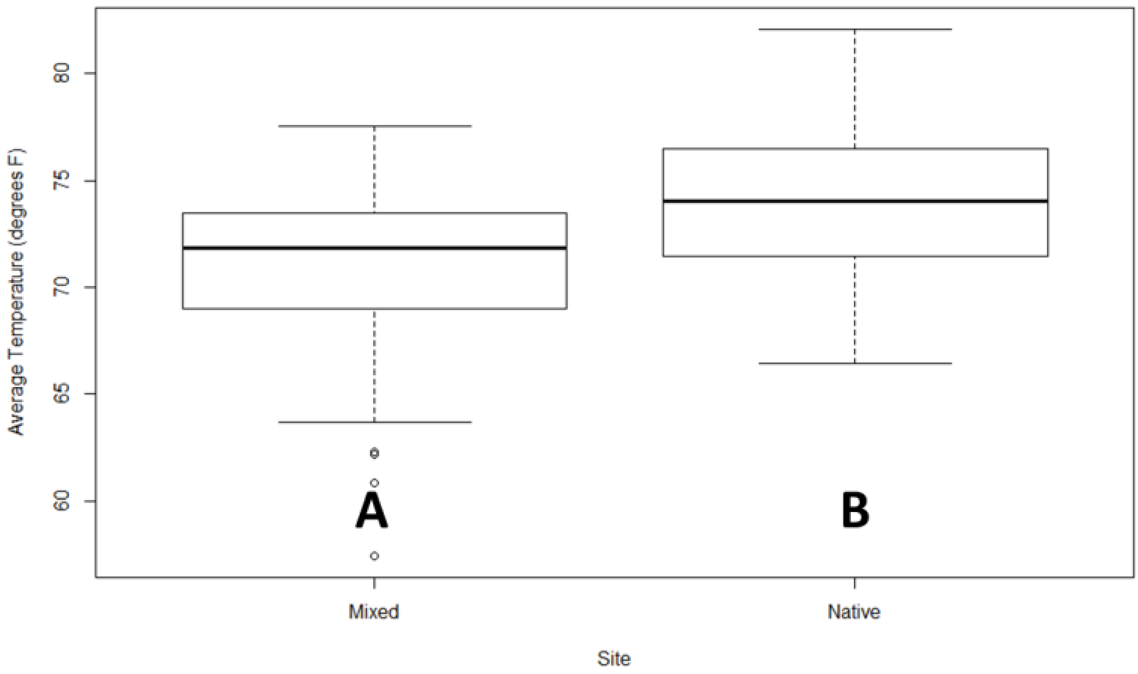


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Table 1: Vegetation survey results. The “# Quadrats” column shows the number of quadrats (out of 80 surveyed) where the listed taxon was recorded (in any survey).

A: Hilina Pali native site

	# Quadrats (80)	Percent
Grasses	42	0.525
Leptecophylla tameiameiae	38	0.475
Dodonaea viscosa	27	0.3375
Osteomeles anthyllidifolia	2	0.025
Metrosideros polymorpha	2	0.025
Vaccinium reticulatum	1	0.0125
Dubautia ciliolata	1	0.0125
Wikstroemia phillyreifolia	1	0.0125
Scaevola kilaueae	1	0.0125

B: Byron Ledge mixed site

	# Quadrats (40)	Percent
Polygonum capitatum	36	0.9
Grasses	35	0.875
Ageratina riparia	25	0.625
Dubautia scabra	13	0.325
Hypochoeris radicata	13	0.325
Psilotum sp.	10	0.25
Rubus argutus	9	0.225
Metrosideros polymorpha	7	0.175
Coprosma ernodeoides	6	0.15
Leptecophylla tameiameiae	5	0.125
Vaccinium reticulatum	5	0.125
Sadleria cyatheoides	5	0.125
Cibotium sp.	3	0.075
Dodonaea viscosa	2	0.05
Epilobium billardierianum	1	0.025
Vaccinium calycinum	1	0.025
Lycopodiaceae	1	0.025
Anemone hupehensis	0	0
Bidens pilosa	0	0
Dubautia ciliolata	0	0
Dubautia hybrid	0	0
Rubus ellipticus	0	0
Arundina graminifolia	0	0
Hedychium gardnerianum	0	0

Table 2: Seasonal changes in available numbers of flowers (or flower heads) over consecutive vegetation surveys

A: Hilina Pali native site

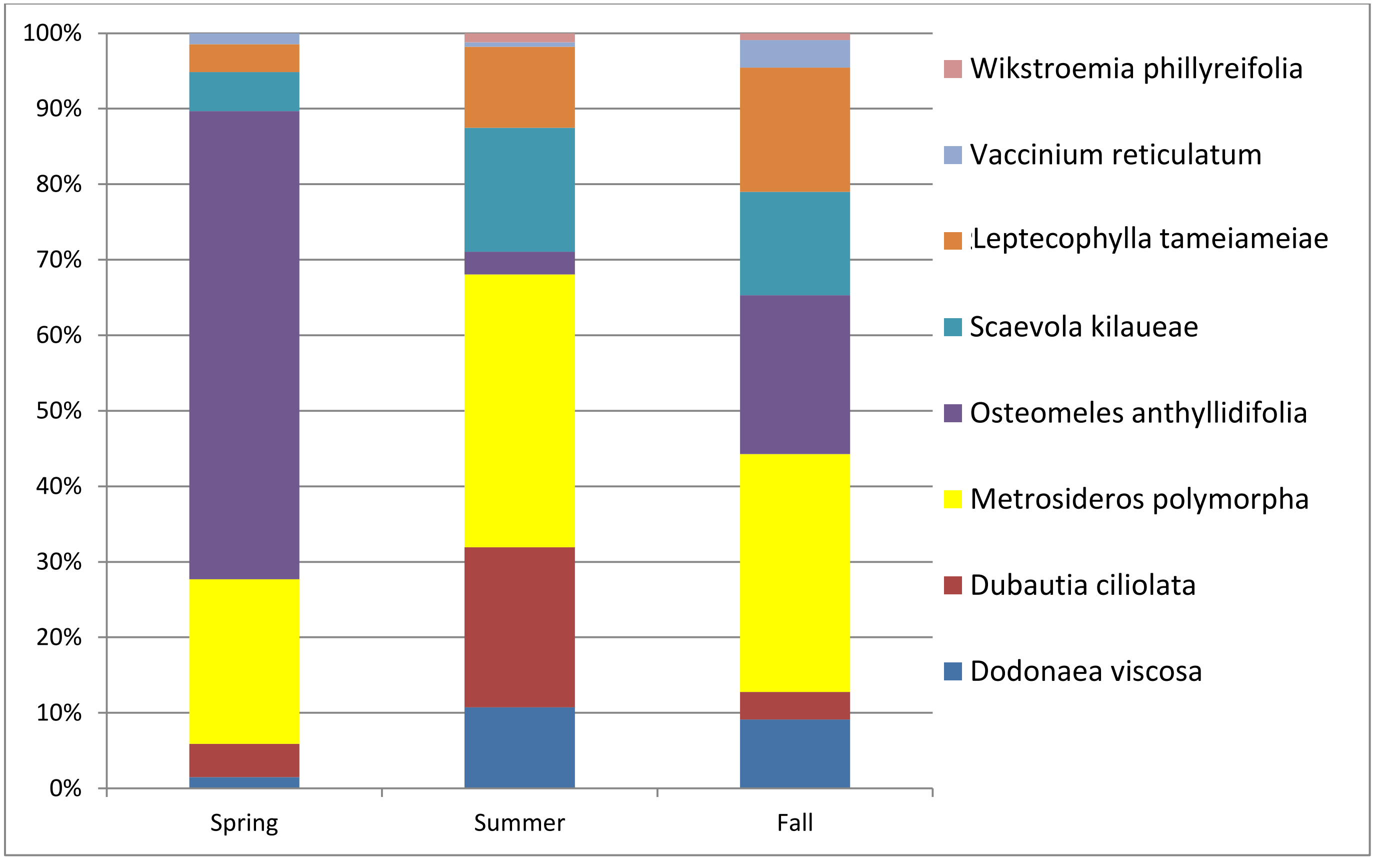
	Fall	Spring	Summer	Total
Dodonaea viscosa	24	19	111	154
Dubautia ciliolata	0	0	0	0
Metrosideros polymorpha	0	0	0	0
Osteomeles anthyllidifolia	4	7	0	11
Scaevola kilaueae	1	0	0	1
Leptecophylla tameiameiae	432	176	367	975
Vaccinium reticulatum	0	0	0	0
Wikstroemia phillyreifolia	209	0	14	223

B: Byron Ledge mixed site

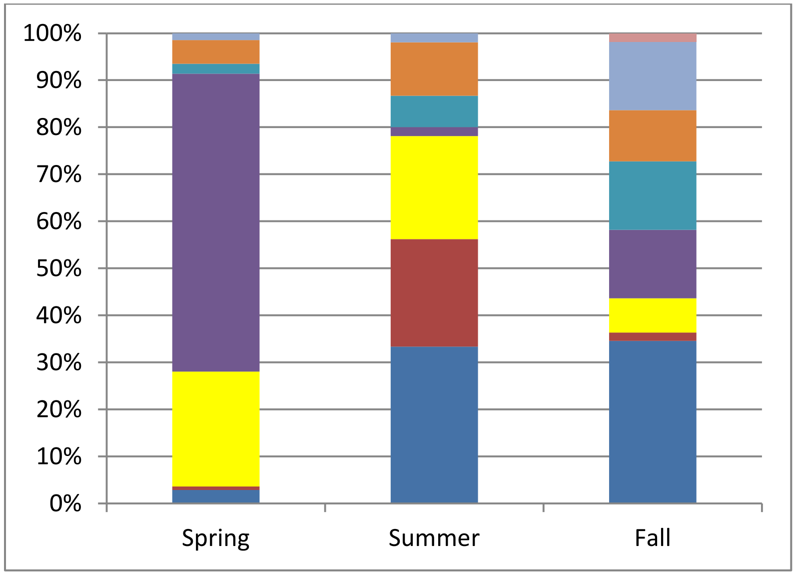
	Fall	Spring	Summer	Total
Ageratina riparia	0	5235	226	5461
Anemone hupehensis	0	0	0	0
Arundina graminifolia	0	0	0	0
Bidens pilosa	0	0	0	0
Coprosma ernodeoides	0	2	182	184
Dodonaea viscosa	94	0	0	94
Dubautia ciliolata	0	0	0	0
Dubautia hybrid	0	0	0	0
Dubautia scabra	364	7	15	386
Epilobium billardierianum	0	0	2	2
Hedychium gardnerianum	0	0	0	0
Hypochoeris radicata	0	0	8	8
Metrosideros polymorpha	0	0	12	12
Polygonum capitatum	1566	306	1396	3268
Rubus argutus	0	0	0	0
Rubus ellipticus	0	0	0	0
Leptecophylla tameiameiae	20	10	74	104
Vaccinium reticulatum	10	1	14	25
Total Flowers	2054	5561	1929	9544

Figure 4: Seasonal variation in floral usage by (A) all insect visitors, (B) *Hylaeus*, and (C) *Apis* at the Hilina Pali native site. Note shifts in proportional usage of *Osteomeles*, which was the only plant with strongly seasonal blooming.

A. All insect visitors



B. *Hylaeus* only



C. *Apis* only

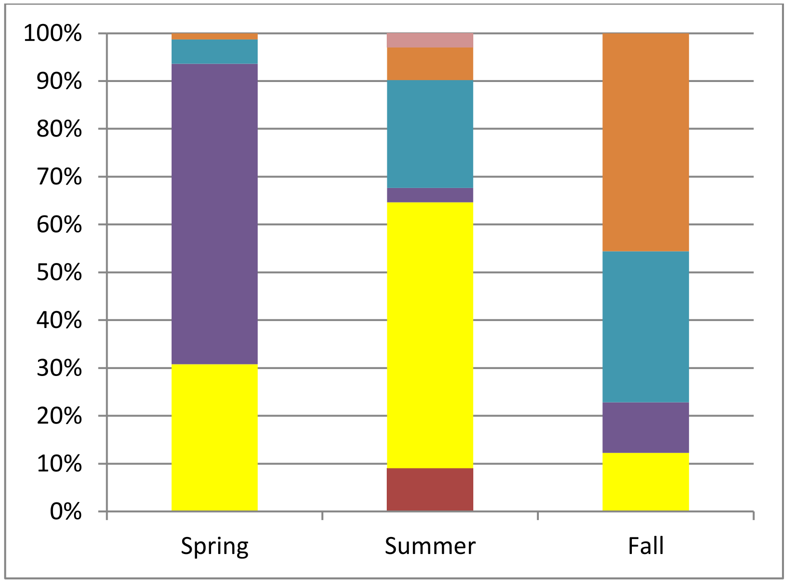
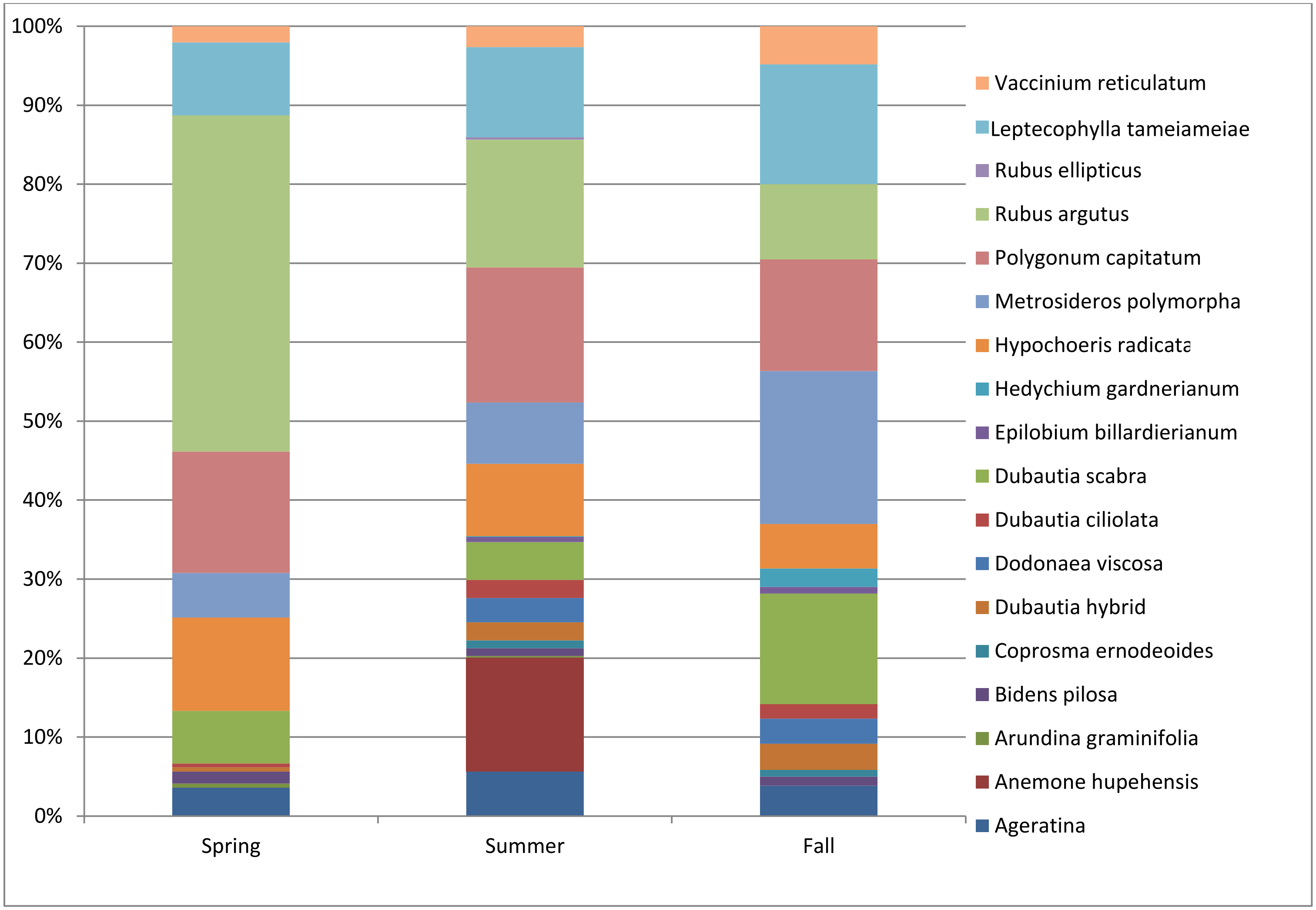
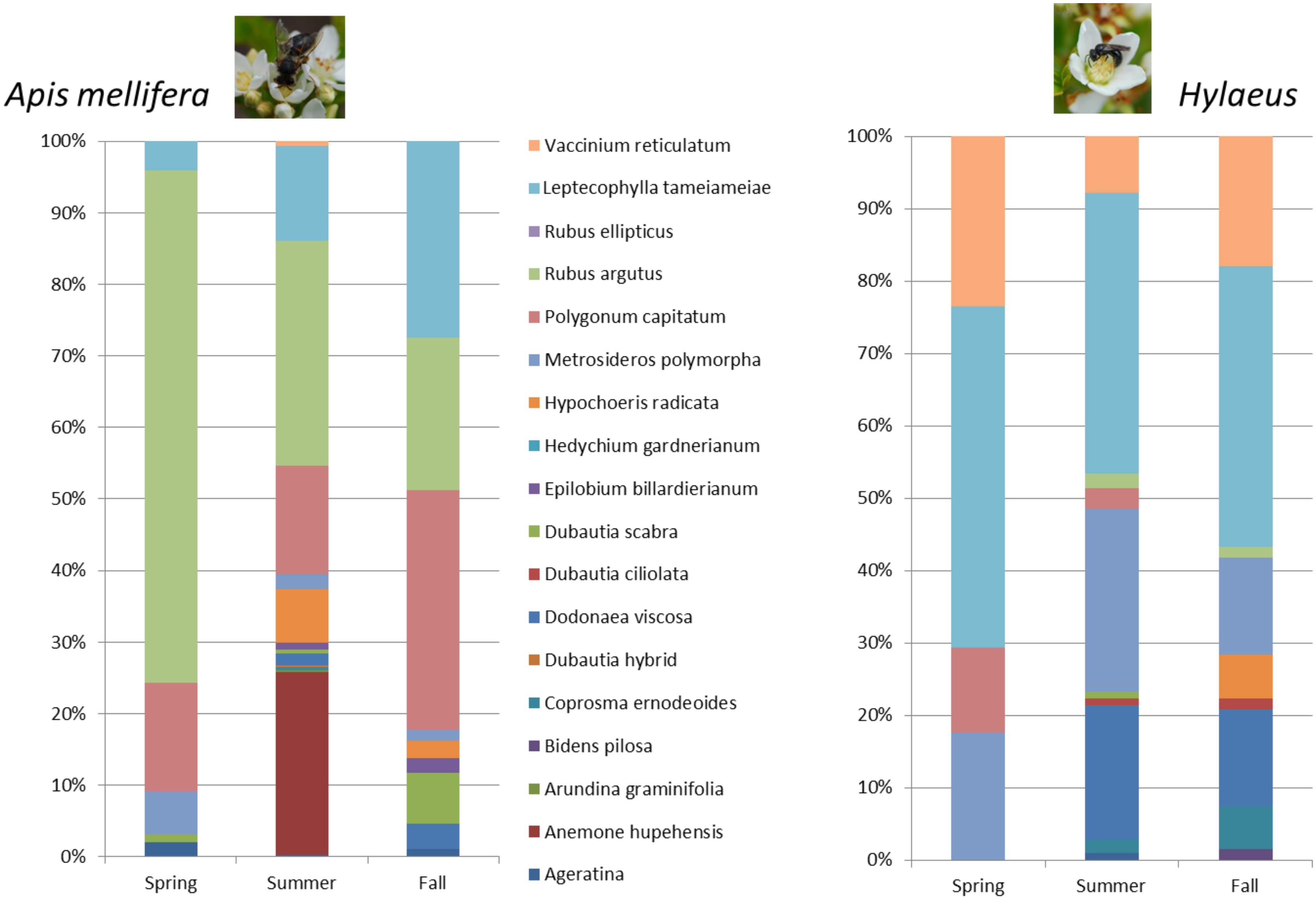


Figure 5: Seasonal variation in floral usage by (A) All insect visitors and (B) *Apis* and *Hylaeus* at the Byron Ledge mixed site. (C) Highlighting specific seasonal differences between *Apis* and *Hylaeus*

A. All insect visitors



B. *Apis* and *Hylaeus* only



C. Highlighting the seasonal variation in visitation to *Rubus argutus* (mainly blooms in the spring) and *Anemone hupehensis* (only blooms in the summer). Both are non-native species and are rarely utilized by *Hylaeus*.

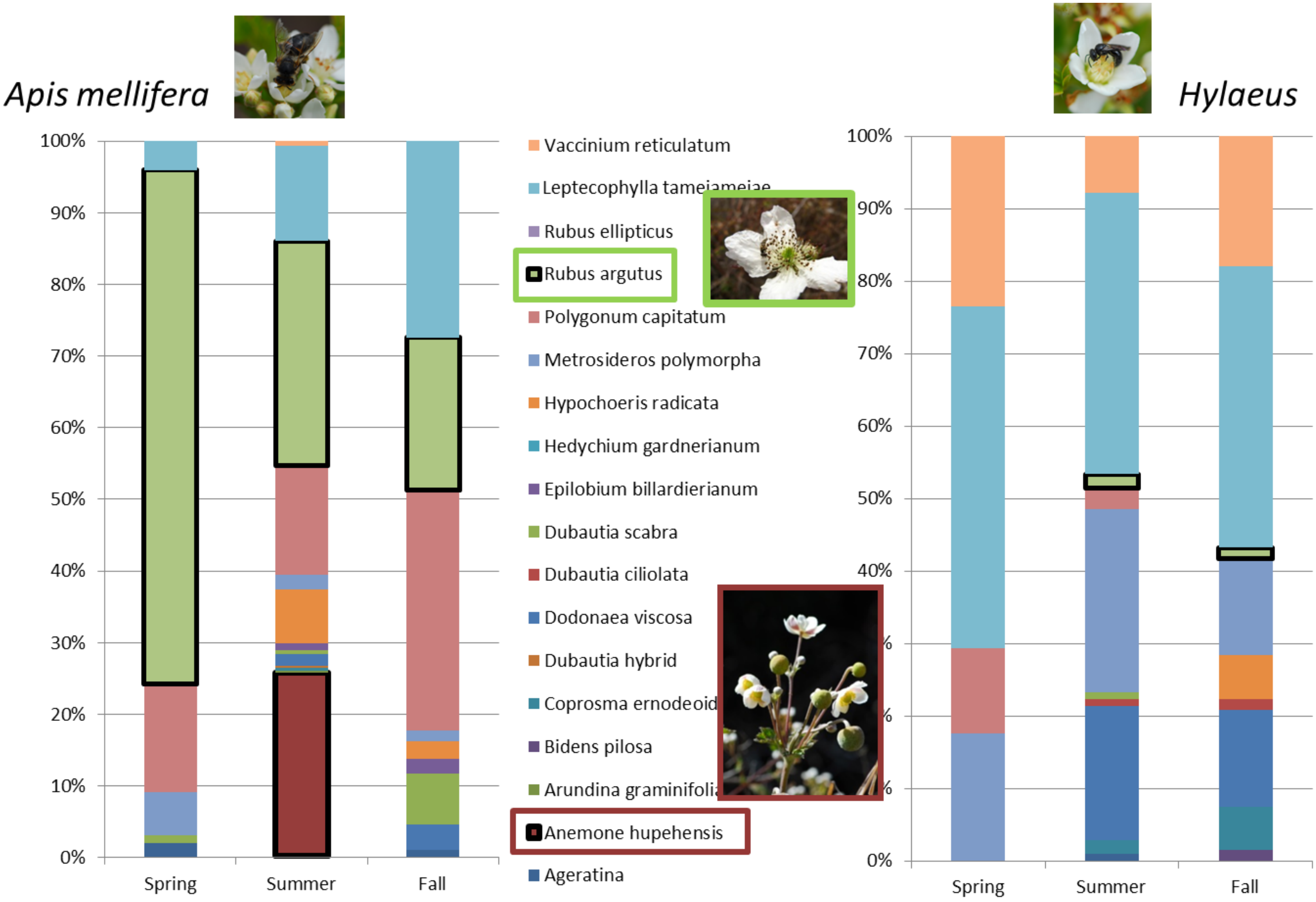
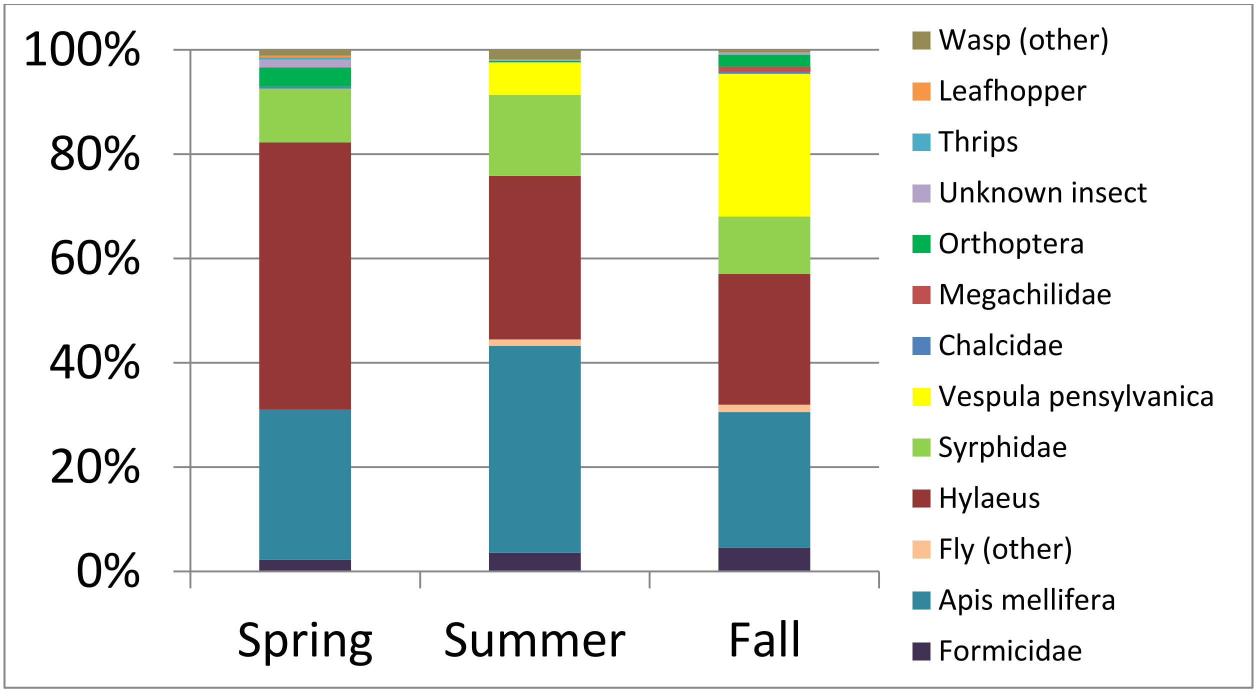


Figure 6: Seasonal variation in visitor identity. Note the increased proportion of *Vespula* visitation during the fall season at both sites.

A. Hilina Pali native site



B. Byron Ledge mixed site

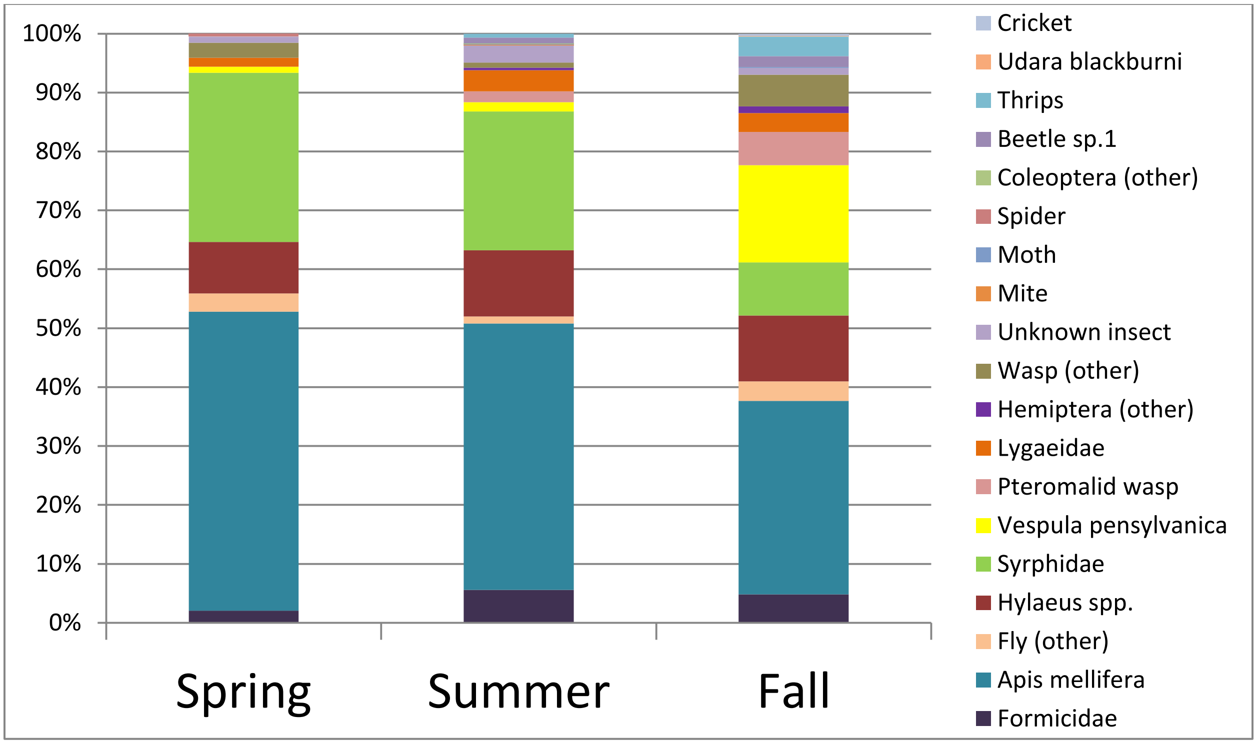
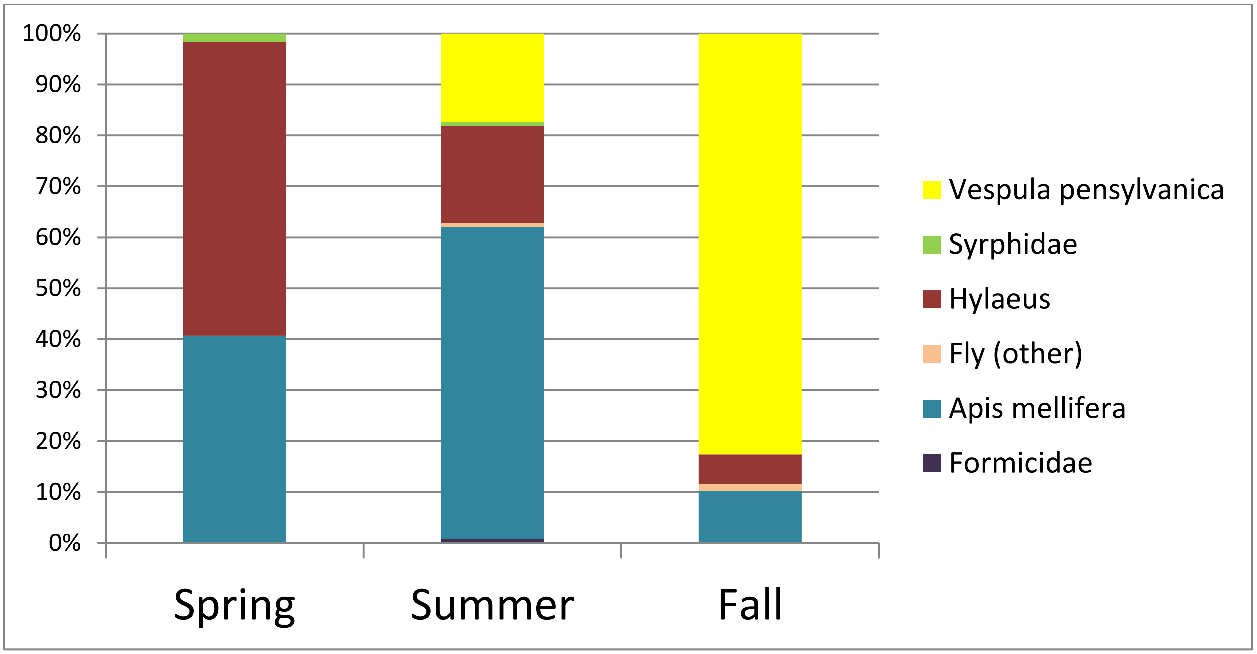
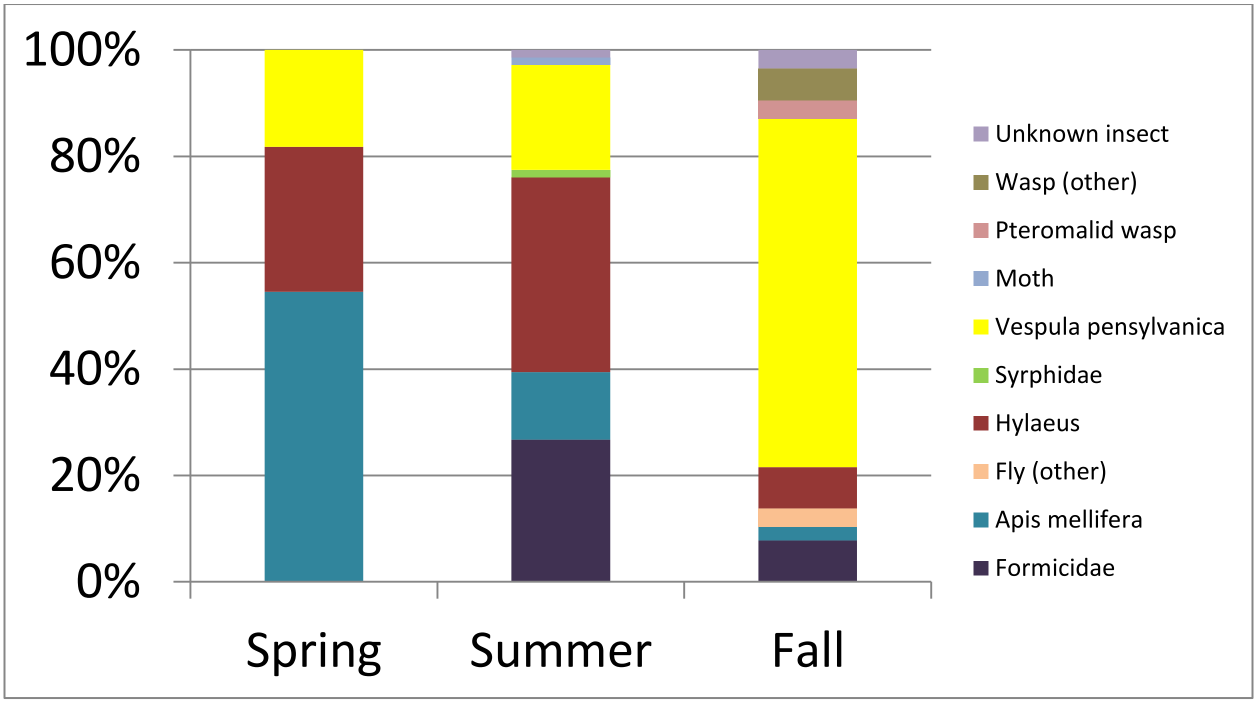


Figure 7: Seasonal variation in floral visitors to *Metrosideros polymorpha*.

A) Hilina Pali native site: Visitation rate for *Apis* was not significantly different between seasons, while *Vespula* was significantly higher in the fall (p<0.0001). *Hylaeus* visitation rate was significantly higher in spring (p=0.0017).



B. Byron Ledge mixed site. Visitation rate for *Apis* and *Hylaeus* was not significantly different between seasons. *Vespula* visitation rate was significantly higher in the fall: p <0.0001



Chapter 4. Emerging conservation concerns for Hawaiian pollination networks

Introduction

Pollination interactions worldwide are facing a wide variety of threats, including habitat loss/change, agricultural intensification, pesticide/herbicide use, invasive species, parasites/disease, and global climate change (Kearns, Inouye et al. 1998; Potts, Biesmeijer et al. 2010; González-Varo, Biesmeijer et al. 2013). Pollination networks in Hawaii are of special concern, because of the unique nature of Hawaii's terrestrial biota, including both plants and pollinators. Here I summarize these issues based on a study of two sites within Hawaii Volcanoes National Park (Chapters 2,3). As the sites from this study were located within a protected national park, the most likely sources for their endangerment are exotic/invasive species, the introduction and spread of parasites/disease, and the slow but potentially devastating effects of climate change (but see (Valenzuela 2018) for a summary of pesticides and agricultural practices pertinent to Hawaiian pollination). Hawaiian ecosystems, and these sites in particular, are additionally subject to the changes and hazards associated with a zone of active geologic activity. Additional information on the effects of exotic and invasive species on visitation networks can be found elsewhere (Chapter 2). In this paper, I address specifically both the rising global threats of parasites/disease and climate change and the unique local dangers of active volcanoes for Hawaiian pollination interactions. The variety and magnitude of potential effects provide a wealth of opportunities for future research utilizing existing network data (Chapter 2,3) to evaluate how these factors operate both independently and interactively to create change.

Emerging Diseases and Parasites

New parasites and diseases can be considered as a subset of invasive species. The spread of both invasive species and parasites/disease are the result of increased global connectivity allowing new species to be transported from their places of origin, and both can have devastating effects on their destination ecosystems (Crowl, Crist et al. 2008). Hawaii has one of the oldest (since 1888) and most comprehensive quarantine systems in the world (Holt 1999), but nevertheless the sheer volume of travelers, imported material, and commercial traffic ensures that some unwanted species slip through. Recent introductions and outbreaks of parasites and disease jeopardize both pollinators and plants in Hawaii, with the most severe and well-documented threats for exotic honeybees (*Apis mellifera*) and the dominant native tree *Metrosideros polymorpha*.

New threats to feral honeybee populations

In Hawaii Volcanoes National Park, honeybees were major network components during all time periods (Chapter 2,3), so any effect on their populations is likely to have strong network ramifications. For a long time, honeybees in Hawaii were spared from the colony collapse disorder (CCD) affecting mainland hives (Martin 2010). Due to favorable climate and the absence of several major honey bee parasites and pathogens (Culliney 2003), Hawaii became a thriving source of honeybee queens for export (Messing 1991; Robson 2012; Szalanski, Tripodi et al. 2016). However, this situation has changed in the past few years, with the recent introductions of the varroa mite (*Varroa destructor*), the small hive beetle (*Aethina tumida*), and multiple pathogens. The varroa mite was first discovered on Oahu in August 2007, and during the next year 65.4% (274/419) of untreated commercial honeybee hives collapsed and feral colonies "disappeared" from urban areas (Martin, Highfield et al. 2012). The varroa mite arrived on the Big Island in January 2009 and had spread throughout the island by November 2010 (Martin, Highfield et al. 2012). The rapid spread of varroa might be aided by the tropical climate, which both allows the mites to reproduce year-round (thus building their populations more quickly) and renders the standard mite-control treatments too toxic to use on Hawaiian honeybees (Martin 2010).

Mites are also vectors for diseases that are likely to contribute to colony collapse. While the varroa mite itself is host-specific to *Apis* spp., the viruses it can carry may infect a much broader range of species. Many wild bee species have been found to carry honey bee viruses, although the effects are not necessarily pathogenic (McMahon, Fürst et al. 2015; Dolezal, Hendrix et al. 2016; Tehel, Brown et al. 2016; Radzevičiūtė, Theodorou et al. 2017). One disease, deformed wing virus (DWV), is so strongly linked to varroa that their association has been described as a mutualistic symbiosis (Di Prisco, Annoscia et al. 2016). DWV has been implicated in CCD and the presence of varroa mites in Hawaii has led to major increases in both infection rates and viral loads in honeybees from mite-affected areas (Martin, Highfield et al. 2012). These high infection rates and viral loads in honeybees can lead to disease spillover into other species. A wide range of insects, including ants (Sebastien, Lester et al. 2015), syrphid flies (Bailes, Deutsch et al. 2018), and beetles (Levitt, Singh et al. 2013) have been found to carry a range of honeybee viruses, with DWV regarded as the most cosmopolitan infection (Gisder and Genersch 2017). In Hawaii, DWV infection has been recorded for three non-native non-*Apis* hymenoptera (*Ceratina smaragdula*, *Polistes aurifer*, and *Polistes exclamens*) in Oahu, while no DMV was recorded in specimens from Maui (which remains varroa-free) (Santamaria, Villalobos et al. 2018). Since the host-specificity of varroa precludes direct disease transmission, it is likely that the virus was transmitted through shared floral resources such as nectar or pollen (Santamaria, Villalobos et al. 2018), which are known to be infective carriers for viral disease (Chen, Evans et al. 2006; Singh, Levitt et al. 2010; Li, Peng et al. 2011) and other parasites/pathogens (Graystock, Goulson et al. 2015). As floral visitation is thus implicated as a primary mode of disease transmission, then all flower-visiting insects are at increased risk of infection and there may be future effects on pollination networks as these diseases become increasingly prevalent.

Israeli acute paralysis virus (IAPV) may also be an emerging threat. As of 2008, Hawaiian honeybees were still reported as free from IAPV (Israeli acute paralysis virus) (Watanabe 2008), which has been found to be strongly correlated with CCD (although not necessarily causal) (Cox-Foster, Conlan et al. 2007). In 2009, Martin et al. (2012) found IAPV in 3 colonies on the Big Island (out of 293 colonies surveyed across Hawaii), and the 2016 USDA APHIS National Honey Bee Survey found IAPV infection in surveyed colonies on both the Big Island and Oahu (https://bip2.beeinformed.org/reports/state_reports/state_report/?year=2016&state=HI). At present it is unknown whether the native *Hylaeus* bees are susceptible to infection by any of these viral diseases, or whether infection would cause any pathogenic effects. Future research is necessary to determine if they are at increased risk from honeybee viruses.

The small hive beetle (*Aethina tumida*)(SHB) is an invasive parasite native to sub-Saharan Africa, and has particularly devastating effects on European honeybees (Neumann, Hoffmann et al. 2010; Neumann, Pettis et al. 2016). As the managed and feral honeybee populations in Hawaii are made up of non-Africanized European honeybees (Messing 1991; Szalanski, Tripodi et al. 2016), they may be particularly vulnerable to infestation by SHB. The SHB was first detected in Hawaii in April 2010 on the Big Island, and is now widespread on both the Big Island and Oahu (Robson 2012). Combined infestation by varroa mites and SHB has been shown to have a negative synergistic effect on thermoregulation in honeybees that is not seen when either species is present alone (Schäfer, Ritter et al. 2011). However, infestation by SHB has also been shown to reduce varroa levels via stimulating hygienic behavior in honeybees (Delaplane, Ellis et al. 2010), so the full effects of interactions between the two parasites are unclear. SHB may also serve as a vector for honeybee viral disease (Eyer, Chen et al. 2009), although the evidence is not as strong as for varroa mites. However, one disease which may be transmitted by SHB is American foulbrood (AFB)(*Paenibacillus larvae*) (Schäfer, Ritter et al. 2010), which was re-discovered in Hawaii in 2016 (http://hdoa.hawaii.gov/blog/main/hawaii-beekeepers-alerted-to-reemergence-of-bee-disease/). This disease had previously devastated the Hawaiian beekeeping industry in the 1930's, but populations had fully recovered and it was no longer present in recent decades (Messing 1991). The re-appearance of foulbrood, particularly in concert with all of the other emerging threats, is potentially a major concern for Hawaiian honeybee colonies.

Altogether, it is clear that Hawaii's honeybee populations (both managed and feral) are facing a perfect storm of threats. Observation data from 2007-2010 did not include any catastrophic collapse of honeybee visitation (Chapters 2,3), but regular follow-up observations should be conducted to detect any current and future effects now that these parasites and disease have continued to spread. One survey of beekeepers found that 55% of all managed colonies were lost on the Big Island in 2010, attributed by the beekeepers to SHB and/or varroa mites (Connor 2011). The effect on feral colonies is unknown. However, honeybees in Hawaii are not necessarily doomed. Hawaii is still free from the parasitic tracheal mite *Acarapis woodi* (Culliney 2003; Martin 2010), which has synergistic effects when combined with varroa (Downey and Winston 2001; Delaplane, Ellis et al. 2010). The protozoan *Nosema ceranae* has been implicated in honeybee colony collapse in Spain (Higes, Martín-Hernández et al. 2009), however there have been no acute effects reported for Hawaiian honeybees despite the state having the highest known prevalence of *Nosema ceranae* in the world (Martin, Hardy et al. 2013). Hawaiian honeybees may also have evolved resistance to American foulbrood after the 1930's outbreak (Eckert 1950), and Finnish researchers have recently claimed to have developed an effective edible vaccine against AFB infection (Salmela and Freitak 2018). Research also continues on evaluating and breeding varroa-resistance into Hawaiian honeybees (Danka, Harris et al. 2010; Danka, Harris et al. 2012). Researchers have also had some success in developing treatments against varroa that are better suited for Hawaii's tropical climate (Martin 2010).

In New Zealand, varroa has been established since 2000 and is believed to have "decimated" feral honey bee populations there (Howlett and Donovan 2010). However, the effect of this decimation on pollination interactions and on other bee species is unknown due to a lack of pre-introduction data (Iwasaki, Barratt et al. 2015). Previous visitation data (Chapter 3) is therefore an important baseline for assessing potential changes in Hawaii as the effects of these parasites and pathogens continue to spread.

In addition to effects on honeybees themselves, downstream effects must be evaluated. Diseases may spread into and affect other hymenoptera, possibly including native species. Floral visitation networks may restructure around reduced honeybee visitation, with consequent effects on pollination and reproductive success for plants and/or increased resource availability for other flower-visiting species. Given the general importance of honeybees in pollinating non-native species, some researchers have even proposed that the reduction of feral honeybee colonies by varroa mites may actually have beneficial ecosystem effects by causing pollen limitation in invasive plant species (Paynter, Main et al. 2010). Likewise, the pathogenic spillover of honeybee viruses such as DWV has been suggested as a possible avenue for biological control of invasive ant species (Sebastien, Lester et al. 2015). The range of the potential effects on floral visitors underscores the importance of continued monitoring for understanding long-term temporal variation in floral visitation networks.

Emerging threats to *Metrosideros*

In addition to the continuing and emerging threat to pollinators in Hawaii, Hawaiian plants are also susceptible to new disease risks. The most well-studied emerging disease threats are for the dominant native forest tree *Metrosideros polymorpha*. On the Big Island of Hawaii, the recent spread of an invasive fungus in *Metrosideros* trees presents the most imminent danger as the disease causes rapid plant mortality, leading to the common name of Rapid Ohia Death (ROD) (Keith, Hughes et al. 2015; Mortenson, Hughes et al. 2016; Stone 2017; Pennisi 2018). While the fungus was initially identified as a type of *Ceratocystis fimbriata*, subsequent phylogenetic analysis showed that there were actually two distinct fungal strains, both new to science: *Ceratocystis lukuohia* (part of the Latin American clade), and *Ceratocystis huliohia* (part of the Asian-Australian clade) (Barnes, Fourie et al. 2018). Dieback of *Metrosideros* stands has been previously documented multiple times over the past century, however previous instances were of even-age stands and were attributed to natural cohort senescence (Mueller-Dombois 1987). Under natural *Metrosideros* cohort dynamics, the senescence of older trees opens up the canopy and releases light constraints on young saplings, which are then able to flourish (Boehmer, Wagner et al. 2013). ROD differs significantly from these previous dieback events by attacking all size-classes, leading to average initial mortality of 39% and subsequent annual mortality of 24-28% in inventoried plots (Mortenson, Hughes et al. 2016). As both mature trees and seedlings/saplings are vulnerable to ROD, natural stand regeneration is therefore disrupted. This consequent widespread *Metrosideros* mortality may then significantly facilitate the success of invasive plant species previously constrained by *Metrosideros* dominance (Zimmerman, Hughes et al. 2008; Mortenson, Hughes et al. 2016). Thus, the threat of ROD is twofold – both for the loss of *Metrosideros* itself (a major ecosystem component), and for the possibility of ecological transformation towards dominance of non-native plant species.

The loss or reduction of *Metrosideros* via ROD is a critical threat to local plant-pollinator interactions. Throughout the course of existing pollination network studies (Chapters 2,3), *Metrosideros* was a significant and consistent component of the plant-pollinator network, and was the only species capable of sustaining bird pollinators (by nectar volume/composition). Thus, any reduction in *Metrosideros* populations will undoubtedly have downstream effects on species that rely on their pollen and/nectar. Any conversion of the ecosystem towards increased non-native plant species will also significantly reshape plant-pollinator interactions, with expected deleterious effects on native pollinators (Chapter 2). While most of the ROD effects will be negative for Hawaiian ecosystems, in the short-term, *Metrosideros* decline may perhaps decrease the spread and success of the invasive *Vespula* yellowjackets, which heavily utilize their flowers as a source of carbohydrates.

As of November 2017, ROD was present in Hawaii Volcanoes National Park (including in the vicinity of the Hilina Pali native study site, Chapters 2,3) (https://www.nps.gov/havo/learn/nature/rapid-ohia-death.htm). At that time, no ROD was recorded near the Byron Ledge mixed site (Chapters 2,3), but it remains possible that it will eventually spread to that area as well (if it has not already). Preliminary research on ROD spread and mortality indicates the importance of fencing out feral animals for slowing the spread of the disease (Pennisi 2018), and the area around the Byron Ledge mixed site is currently unfenced. However, recent studies have also shown hopeful signs for avoiding the local extirpation of ohia on the Big Island. Different varieties of *Metrosideros* demonstrate differing levels of resilience in response to infection (with some trees successfully resisting even the most deadly strain), and infection rates have slowed or stagnated in some areas (Pennisi 2018). While continuing research and long-term studies are still clearly needed, particularly with regard to ecosystem-wide and interspecific effects, the original fears of transformative population collapse appear to have partially abated.

While it is the most potentially dangerous, ROD is not the only emerging pathogen to target *Metrosideros*. The rust fungus *Puccinia psidii* was discovered on *Metrosideros* in Oahu in April 2005 and had spread throughout Hawaii by August 2005 (Loope and La Rosa 2008; Loope 2010). While *Puccinia psidii* has a wide host range among Myrtaceae and infects multiple native and non-native species in Hawaii, it has thus far only minimally infected *Metrosideros* despite high spore dispersal pressure from nearby infected species (Loope 2010). However, other strains of *P. psidii* have been shown to be highly virulent on *Metrosideros* (Silva, Andrade et al. 2014), so continued vigilance is necessary both to prevent the accidental introduction of more virulent strains and to monitor changes in virulence of the existing strain.

The root rot *Armillaria gallica* has also been present on the Big Island since at least 2005 in non-native pines, and at least since 2008 in the endemic tree *Sophora chrysophylla* (Kim, Hanna et al. 2010). In 2015, *Armillaria* was found to have spread to *Metrosideros* trees in Kauai, causing root decay and crown-dieback (Kim, Fonseca et al. 2016). While this host shift has not yet been reported on the Big Island, it is likely to occur in the future (if it has not already), particularly given the known wide host range for *Armillaria* species (Brazee and Wick 2009). While the pathogenicity of *Armillaria* alone on host species may vary, it is thought that it may particularly contribute to tree mortality when combined with other stressors such as climate change or co-infection (Brazee and Wick 2009). Thus, given the other emerging threats to *Metrosideros*, there may be significant future risk to populations on the Big Island.

Climate Change

The potential for climate change to affect Hawaiian pollination systems through alterations in phenology have been explored elsewhere (Chapter 3). However, climate change may have a variety of other effects on both plants and pollinators, particularly in regard to shifts in species ranges or distributions and effects on physiology and behavior.

Effects on species ranges/distributions

Generally, species have responded to warming climatic conditions though both poleward latitudinal shifts and upward elevational shifts (Chen, Hill et al. 2011; Parmesan and Hanley 2015). While these distribution changes have been most closely tracked in plants, they have also been seen in insects including bumblebees (Kerr, Pindar et al. 2015) and butterflies (Forister, McCall et al. 2010). For Hawaiian species, given the isolation and relatively small size of each island, latitudinal species range shifts are largely impossible. The median observed latitudinal range shift of 16.9km/decade (Chen, Hill et al. 2011) would quickly shift most species out of even the largest island. Instead, we should expect to see changes in species elevational ranges. In Hawaii, the ranges of many native bird species (including pollinating honeycreeper species) are constrained to cooler high elevations, which serve as refugia against cold-intolerant mosquitos that transmit non-native avian malaria (Atkinson and LaPointe 2009). While some malaria-resistant populations of the honeycreeper amakihi (*Hemignathus virens virens*) have been found, other native honeycreepers likely lack the population sizes and genetic diversity for the evolution of disease resistance (Atkinson and LaPointe 2009). Under increased climate warming models, these high elevation disease refugia are predicted to shrink, greatly reducing the potential ranges for the remaining vulnerable native birds (Fortini, Vorsino et al. 2015; Liao, Atkinson et al. 2017). This “collapse” of the native bird community, attributable to warming and subsequent spread of avian disease, has already been observed on the island of Kauai (Paxton, Camp et al. 2016). Kauai has lower maximum elevations than the Big Island so altitude-based refugia were originally more limited, but as warming proceeds we might expect similar results on higher islands. Diseases and parasites of honeybees may also be affected by climate change. The small hive beetle (SHB) is restricted to warmer temperatures, so it may well follow similar patterns of elevational range expansion in response to climate warming (Le Conte and Navajas 2008).

An additional complicating factor for climate change-based elevational range migration in Hawaii is the presence of the tropical inversion layer. The inversion layer is caused by the collision of cool, dry air from high elevations with warm, moist air from low elevations. This layer creates an upper limit for the development of clouds and precipitation at higher elevations, and thus also effectively serves as the upper boundary for forest habitats. Thus, native birds, which mostly rely on forest habitat, may not be able to continue to expand upwards since their habitat itself is elevation-limited (Atkinson and LaPointe 2009). The exact elevation of the inversion layer varies depending on numerous factors, changing even between nighttime and daytime conditions. However, over the past 40 years of observations there has been no significant upward trend tracking climate warming (Cao, Giambelluca et al. 2007; Longman, Diaz et al. 2015). Instead, the frequency of occurrence of the inversion layer has significantly increased, leading to overall drier conditions at higher elevations (Cao, Giambelluca et al. 2007; Longman, Diaz et al. 2015). These drier conditions have already been implicated in the decline of the endemic Hawaiian silverswords (Krushelnycky, Starr et al. 2016), and will likely limit the upward range shift of lower-elevation species.

Even if native bird populations are able to persist at higher elevations, their range may have shifted away from plant species that rely on them for pollination services. While the ranges of both plants and pollinators are projected to be affected by climate change, the degree and speed of range shifts are not necessarily matched between species (Pyke, Thomson et al. 2016; Settele, Bishop et al. 2016). One 33-year study of bumblebees and associated plant species in Colorado found that while most bumblebee species shifted towards higher elevations in response to climate warming, their associated plant species mostly did not (Pyke, Thomson et al. 2016). Instead, the plant species responded to climate warming by having earlier flowering periods. As the developmental phenology of the bumblebees did not change to compensate, the plants and their pollinators were thus increasingly decoupled in both time and space.

The responses of any individual species to climate warming are highly variable, so further studies are required to determine how Hawaiian plants and pollinators will respond. Chen et al. (2011) found that there was more variation in range shifts within taxonomic groups than between, highlighting that climate effects cannot be generalized to predict how any particular species will respond. Given the uniqueness of the Hawaiian flora and fauna, it may be even less useful to attempt to forecast predicted change based on mainland studies. For example, Chen et al. (2011) found that birds (as a group) had the least elevational shift upwards, however the additional compounding variables of mosquitos and avian malaria in Hawaii are likely to force Hawaiian bird populations to higher altitudes.

Effects on behavior/physiology

Climate change can also cause physiological and behavioral effects in plants and pollinators through a wide range of pathways, including affecting floral resource output or altering insect foraging activity (reviewed in (Scaven and Rafferty 2013)). Behavioral changes in response to warming are likely to differ between taxa. In a study examining watermelon pollination, Rader et al. (2013) found that under warming climate conditions the pollination services of honeybees decreased (due to an increase in cooling behavior over flower visiting), while the pollination services of wild bees increased (Rader, Reilly et al. 2013). These differences in foraging response may be due to differing thermal thresholds – the temperature beyond which bees must switch from foraging to cooling activities. The solitary bee *Anthophora plumipes* was found to increase its pollen and nectar loads (indicative of increased foraging) with higher temperatures up until 24-25°C, after which foraging activity sharply declined (Stone 1994). Stone (1994) also noted similar declines in bumblebee foraging at the same temperature threshold. The effect of temperature on *Hylaeus* is not currently known, but the contrast in body size and hairiness between *Apis* and *Hylaeus* makes it likely that they might have differing responses to temperature. These differences in threshold between *Apis* and *Hylaeus* could lead to shifts in floral visitation proportions as warming increases.

Rising temperatures generally increase insect metabolic rates (requiring increased foraging and resource consumption) while simultaneously affecting insect population growth rates (Deutsch, Tewksbury et al. 2018). For ectotherms such as pollinating insects, tropical species may be <u>more</u> vulnerable to the effects of warming than temperate species, due to a combination of tropical species having narrower thermal tolerances and tropical temperatures already being near their physiological optimum (Deutsch, Tewksbury et al. 2008; Sunday, Bates et al. 2011; Scranton and Amarasekare 2017). Thus, even relatively minor climate warming has a higher likelihood of exceeding tropical species' temperature thresholds. Furthermore, since metabolic rate increases exponentially with temperature (rather than linearly), even minor temperature increases will translate into larger absolute increases in metabolism (Dillon, Wang et al. 2010). A recent model of the effects of climate warming on plant-insect interactions showed that in the tropics the effects of increased resource consumption (due to increased metabolic rate) are offset by their lowered population growth (Deutsch, Tewksbury et al. 2018). While that model was concerned with the negative effects of pest insects on agriculture, similar principles can be applied to mutualistic floral foraging interactions.

Overall, increases in pollinator foraging (and thus pollination services) due to increased metabolic demands are expected to be countered by declines in pollinator populations. In Puerto Rico, an increase of just 2°C in mean maximum temperature has led to declines of 10-60 times in arthropod populations (Lister and Garcia 2018). This decline is robust across all measured taxa, and occurred despite synchronous declines in insectivorous predators, reductions in pesticide use, and increased forest regeneration after economic transition. In the presence of current and future climate warming, Hawaiian insect species are therefore likely to be vulnerable to similar declines even if other conservation measures are implemented. The situation is further complicated by the presence of non-native species (particularly from temperate regions or cosmopolitan distributions), which may have wider thermal tolerances than the native species (Janion-Scheepers, Phillips et al. 2018) or have greater phenotypic plasticity (Chown, Slabber et al. 2007) and thus be more resilient to increased mean temperatures.

There is a robust literature on the effects of climate change on plant growth and physiology (e.g. (Parmesan and Hanley 2015)). For plants, both warming temperatures and rising CO_2 levels are likely to have effects, while only warming was considered for insects (which generally do not directly respond to increased environmental CO_2 alone (Guerenstein and

Hildebrand 2008; Schowalter 2012)). Elevated CO_2 levels have frequently been shown to lead to increased plant growth (e.g. (Jablonski, Wang et al. 2002; DaMatta, Grandis et al. 2010)), however these gains do not occur uniformly across species, and in natural ecosystems plant growth may be limited by other factors (Parmesan and Hanley 2015). The effects of warming and CO_2 are related, with CO_2-enrichment having stronger effects at higher temperatures up to the plant optimum temperature (Polley 2002). However, beyond that threshold, plant performance will decrease regardless of CO_2 level (Polley 2002). While the effects of climate warming on tropical thermal tolerances have been most comprehensively studied in ectotherms, the same vulnerability may also be present in tropical plants and endotherms (DaMatta, Grandis et al. 2010; Araújo, Ferri-Yáñez et al. 2013). If Hawaiian plants are already at their thermal optimum, then rising CO_2 is likely to yield no additional benefit to growth, especially if warming passes that thermal threshold. Limitations in critical soil nutrients may also constrain responses to elevated CO_2 (DaMatta, Grandis et al. 2010; Jin, Tang et al. 2015). The volcanic substrates of Hawaii Volcanoes National Park (the location of the study sites in chapters 2&3) are nitrogen-poor (Vitousek, Walker et al. 1993). Thus, elevating CO_2 could have little overall effect at these study sites, since growth is already nutrient-restricted.

While it has been frequently speculated that climate change would preferentially benefit exotic species (Dukes and Mooney 1999; Walther, Roques et al. 2009; Diez, D'Antonio et al. 2012), a recent meta-analysis found no difference in how native and exotic terrestrial species (mostly plants) respond to climate change (Sorte, Ibáñez et al. 2013). However, the unique conditions in Hawaii may create some differences. Contrary to expectation, exotic species in Hawaii have been shown to outperform native species even under resource-limitation (Funk and Vitousek 2007), so that difference could become exaggerated if those exotic species are less limited by nutrient-poor soils and are thus better able to respond to increased CO_2. Exotic species may also affect nutrient levels themselves – the invasive tree *Myrica faya* is a nitrogen-fixer and substantially increases the available nitrogen for nearby species (Vitousek, Walker et al. 1987; Vitousek and Walker 1989). Since these areas lack native nitrogen fixers, the presence of this exotic species may ameliorate nitrogen restrictions and permit increased growth under elevated CO_2. *Myrica* also inhibits and outperforms *Metrosideros* (Walker and Vitousek 1991), however, so its increasing success could also endanger that major native floral resource and consequently shift pollination networks.

Warming temperatures have a broad range of effects on flowers and floral resources, but different plant species may respond in different directions. While many plants increase flower production in response to higher temperatures (Jablonski, Wang et al. 2002), others reduce flowering or stop flowering altogether (Scaven and Rafferty 2013). Warming may also have effects on scent production from flowers (Cna'ani, Muhlemann et al. 2015; Jamieson, Burkle et al. 2017), nectar production/concentration/composition (Pacini, Nepi et al. 2003; Hoover, Ladley et al. 2012; Takkis, Tscheulin et al. 2018), pollen quantity and composition (Hedhly, Hormaza et al. 2009), and/or flower morphology (Hoover, Ladley et al. 2012). All of these factors can affect the plants' ability to attract and sustain floral visitors. The foraging preferences of bees may also be affected by the temperatures of the flowers themselves, in ways that can vary between co-existing plant species and be unrelated to floral color, morphology, or phylogenetic relationships (Shrestha, Garcia et al. 2018). Overall, compared to the vast literature on the effects of climate change on phenology and species range, there is relatively little research on how climate change affects floral traits. The results we do have so far have been largely idiosyncratic, and often do not include how pollinators react to these changes in floral traits. Thus, it is currently difficult to draw any general conclusions for how climate change is likely to affect floral traits and resulting pollination network interactions in Hawaii.

Volcanic Activity

The Hawaiian islands are volcanic in origin, and the Big Island remains very active geologically. Mauna Loa last erupted in 1984, and Kilauea has seen continuous volcanic activity since 1983, although the location and magnitude of the eruption has varied over time. In the spring of 2008, a new eruptive vent opened at the Kilauea summit and began emitting ash and high levels of sulfur dioxide (SO_2) (Wilson, Elias et al. 2008; Houghton, Swanson et al. 2011). These two pollutants may affect both plant and pollinators in a number of ways.

Sulfur dioxide has been shown to reduce flight activity in some types of small bees (Ginevan, Lane et al. 1980) and have negative effects on brood-rearing and pollen collection in honeybees (Hillman and Benton 1972). However, other bees have been shown to be remarkably tolerant of high sulfur dioxide levels and thrive on the edge of outgassing volcanoes (Erenler, Orr et al. 2016). The effect of sulfur dioxide on either the activity or population health of the native *Hylaeus* bees or other non-honeybee floral visitors in Hawaii is unknown. Detrimental effects of sulfur dioxide have been described for insects including orthoptera (McNary, Milchunas et al. 1981)and *Drosophila* (Ginevan and Lane 1978) under controlled conditions, but positive indirect impacts have been demonstrated for other (generally herbivorous) insects under wild conditions due to pollution effects on host plants (Alstad, Edmunds et al. 1982; Holopainen and Oksanen 1995). As *Hylaeus* and other native insects have an evolutionary history including frequent volcanic eruption and outgassing, it would be interesting for future studies to determine their tolerance for sulfur dioxide pollution under both controlled and wild conditions. Nearly all studies on the effects of sulfur dioxide on insects were evaluating potential effects of anthropogenic, rather than volcanic, air pollution. As volcanic emissions contain more than just sulfur dioxide, these studies therefore provide only a part of the picture. As of 2014, there were no studies that had experimentally examined the effects of a full profile of volcanic gases on insects (Elizalde 2014).

Plant species also differ in their tolerance and response to sulfur dioxide pollution. Some studies have indicated that plants from areas subjected to sulfur dioxide pollution are adapted for increased tolerance (Taylor and Murdy 1975; Ayazloo and Bell 1981; Preston 1993). In the context of this study, we therefore might expect that the native plant species, with an evolutionary history of volcanic eruptions, would be less affected by the increase in volcanic emissions. During a previous eruption in the early 1980’s, mature *Metrosideros* leaves were found to respond by closing stomata to reduce sulfur dioxide uptake and injury, while *Dodonaea* leaves died off but were able to quickly resprout when pollution levels decreased

(Winner and Mooney 1980). In contrast, one study of the invasive *Myrica faya* showed large peaks of leaf fall, which were potentially attributable to exposure to high sulfur dioxide levels, as the population was located near an outgassing vent (Whiteaker and Gardner 1992). However, a broad scale study looking at 20 native and 5 exotic species in the Kilauea area found no systematic difference in sulfur dioxide tolerance between native and exotic species, as measured by foliar injury (Winner and Mooney 1985). Nevertheless, since the most tolerant species were also the most common, there may be long-term filtering/selective effects on community composition where tolerant species are increasingly favored. Thus, the new eruptive vent at the summit may contribute to long-term shifts in the flowering plant community in the surrounding areas.

In addition to direct plant injury, increased sulfur dioxide can cause a number of physiological changes in plants such as decreased growth or changes in emissions of plant volatiles (Alstad, Edmunds et al. 1982). On a short-term level, sulfur dioxide and other air pollutants have been shown to cause shifts in plant resource allocation away from reproduction (Lechowicz 1987). Direct effects of sulfur dioxide on flowering and/or pollination success (via pollen germination, pollen tube growth, etc.) have also been observed in a range of plant species (Varshney and Varshney 1981; Venne, Scholz et al. 1989; Abe and Hasegawa 2008), and could have affected the plants in the study areas. Plants that have evolved tolerance to sulfur dioxide pollution can have higher reproductive success under pollution stress than standard populations (Murdy 1979). However even in tolerant plants, long-term sulfur dioxide pollution can negatively affect the production of flowers/inflorescences, particularly when combined with foliar injury (Clapperton and Reid 1994).

In addition to high levels of sulfur dioxide, the new eruptive vent occasionally produces volcanic ash, which can contaminate nectar and pollen resources and cause internal damage if ingested by floral visitors (Martínez, Masciocchi et al. 2013). *Hylaeus* bees, which store collected pollen internally rather than in external pollen baskets, might be particularly vulnerable to damage from ash-contaminated nectar or pollen. On the other hand, adaptations for internal pollen storage might include some protection from abrasion, as is seen in soil-consuming insects (Morales, Saez et al. 2014). The amount of ash picked up by foraging bees is dependent on both the size of the ash particles and frequency of rainfall (which easily rinses ash from plants) (Brown and Cutright 1981). Martinez et al (2013) experimentally dusted lavender flowers with volcanic ash, and found that visitation rates by honeybees began to recover after only 24 hours following ash introduction, once the bees had learned to recognize the changed appearance of the flowers (Martínez, Masciocchi et al. 2013). However, honeybees do not or cannot detect ash in nectar, and will readily consume ash-contaminated nectar even though it negatively affects survival (Martínez, Masciocchi et al. 2013). Woyke and Gabka (2011) have reported that the presence of a volcanic ash cloud reduces honeybee foraging, however that study is severely limited in scope (only comparing 2 days with ash cloud versus 2 later sunny days) and does not establish if there was a difference between the effects of a volcanic ash cloud versus ordinary cloud cover (Woyke and Gąbka 2011).

Volcanic ash is broadly insecticidal and can have acute negative consequences on many different insect species via its abrasive qualities (Brown and bin Hussain 1981; Cook, Barron et al. 1981; Edwards and Schwartz 1981; Johansen, Eves et al. 1981; Marske, Ivie et al. 2007) or by absorbing moisture and causing fatal dehydration (Philogene 1972; Kuriwada and Reddy 2016). The presence of volcanic ash has also been linked to reduced reproductive performance for crickets (Kuriwada and Reddy 2017). Invasive *Vespula* yellowjackets in Patagonia had high mortality due to volcanic ash from a nearby eruption, which may help to control their population and invasiveness (Masciocchi, Pereira et al. 2013). Similar ash-related devastation to *Vespula pensylvanica* (but not all *Vespula* species) was observed after the eruption of Mount St. Helens, however ant species seemed to be little affected (Akre, Hansen et al. 1981). As *Vespula pensylvanica* is an invasive insect species in Hawaii with numerous deleterious effects on native fauna, any limitation or reduction due to the continuing volcanic eruption would be a benefit to local ecosystems. However, ash also has strong negative effects on *Apis* and other bees (in addition to aforementioned consumption effects), possibly due either to their active foraging movements, which increase the potential for abrasion (Brown and bin Hussain 1981), or to the presence of dense body hair, which traps the abrasive ash and prevents it from being easily washed or blown away (Cook, Barron et al. 1981). Studies on the effects of ash on honeybee behavior have yielded contrasting results on whether it increases or decreases aggressive behavior (Elizalde 2014). Volcanic ash and gas emissions together have also been shown to increase the accumulation of heavy metals in insects near volcanic eruptions although the population-level effects of this are not known (Rodrigues, Cunha et al. 2008).

Due to the unpredictable and often inhospitable nature of volcanoes, very little research has been performed comparing pre- and post-eruption plant-pollinator communities. Sikes and Slowik (2010) surveyed arthropods before and after an eruption on a small Alaskan island and found sharply reduced biodiversity and no plant-associated species 10-12 months post-eruption (Sikes and Slowik 2010). Morales et al (2014) surveyed bumblebees in Chile 4-5 months pre-eruption and 7-8 months post-eruption of the Puyehue Cordon-Caulle volcano complex. After the eruption, bumblebee populations appeared to have dropped by half, with concomitant significant decreases in the pollination of a bumblebee-dependent invasive plant (scotch broom, *Cytisus scoparius*) (Morales, Saez et al. 2014). Kishi et al. (2017) were the first to report on quantitative plant-pollinator networks following a volcanic eruption (on Miyake Island in Japan), and they posited that these interaction networks may be tolerant to volcanic disturbance since network structure was similar between areas that had received ashfall and those that had not (Kishi, Sakura et al. 2017). However their study lacked pre-eruption data, was limited in both extent (along roadsides) and duration (as few as 10 hours per site), and was conducted 12 years after the eruption, so their results may not be broadly applicable.

Since the end of the collection of this set of pollination network data in Hawaii Volcanoes National Park (Chapters 2,3), the summit eruption has continued. In May 2018, the eruptive period entered a new, stronger phase, resulting in the long-term closure of most of the park due to ongoing volcanic hazards such as earthquakes, sulfur dioxide gas, volcanic ash, and explosive eruptions and major subsidence in the immediate vicinity of the summit caldera. The greatly increased amplitude of the eruption increases the likelihood that there would be observable effects on plants, pollinators, and plant-pollinator networks, both in the short and long term. While parts of the park were reopened in late September 2018, including the area around the mixed site, large sections of the park remain closed due to major damage and/or continuing hazards from volcanic activity. Both study sites are at the edge of the currently closed zone, and thus were/are likely subject to continuing effects from the eruption. Future research can be compared with existing network data (Chapters 2,3) to establish how the eruption has affected or restructured interaction networks.

Conclusion

Overall, it is clear that pollination systems in Hawaii are and will continue to be subjected to challenges along multiple fronts. Historical data on pollination networks were compiled during a critical nexus of time for Hawaiian pollination networks (Chapter 2, 3). In particular, these data represent a time before the introduction of new, deadly parasites and diseases for both plants and pollinators, in the midst of continuing species invasions and advancing climate change, and at the onset of a new phase of increased volcanic eruptive activity. Each of these elements can have profound effects on shaping plant and pollinator communities as well as the interactions between them. These factors also need to be broadly considered in a holistic framework, as synergies between drivers can lead to new or greater effects (Brook, Sodhi et al. 2008; González-Varo, Biesmeijer et al. 2013). Continued monitoring and research will be critical to tracking and understanding how pollination networks are affected and transformed under all of these interacting aspects of change.

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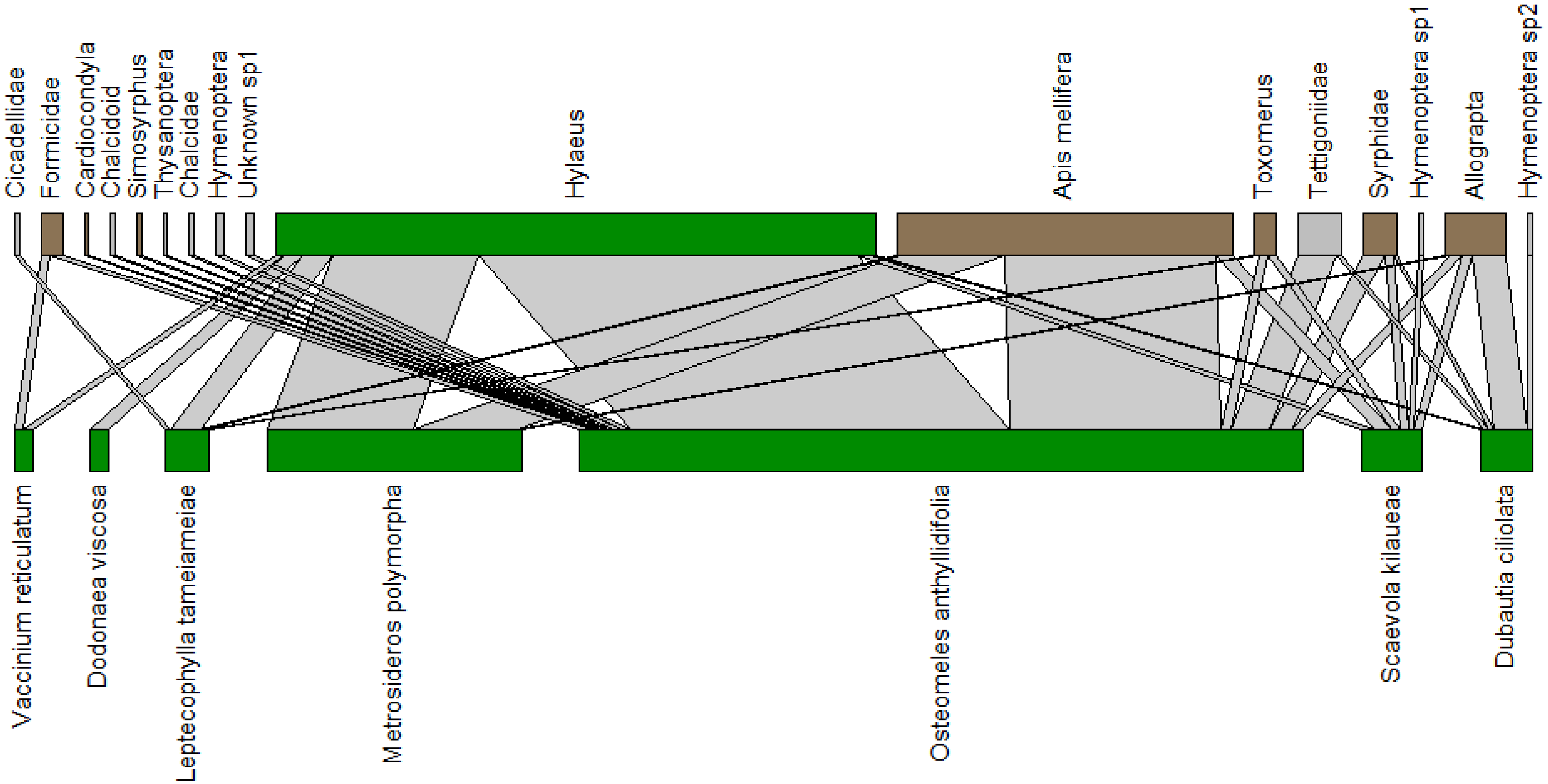
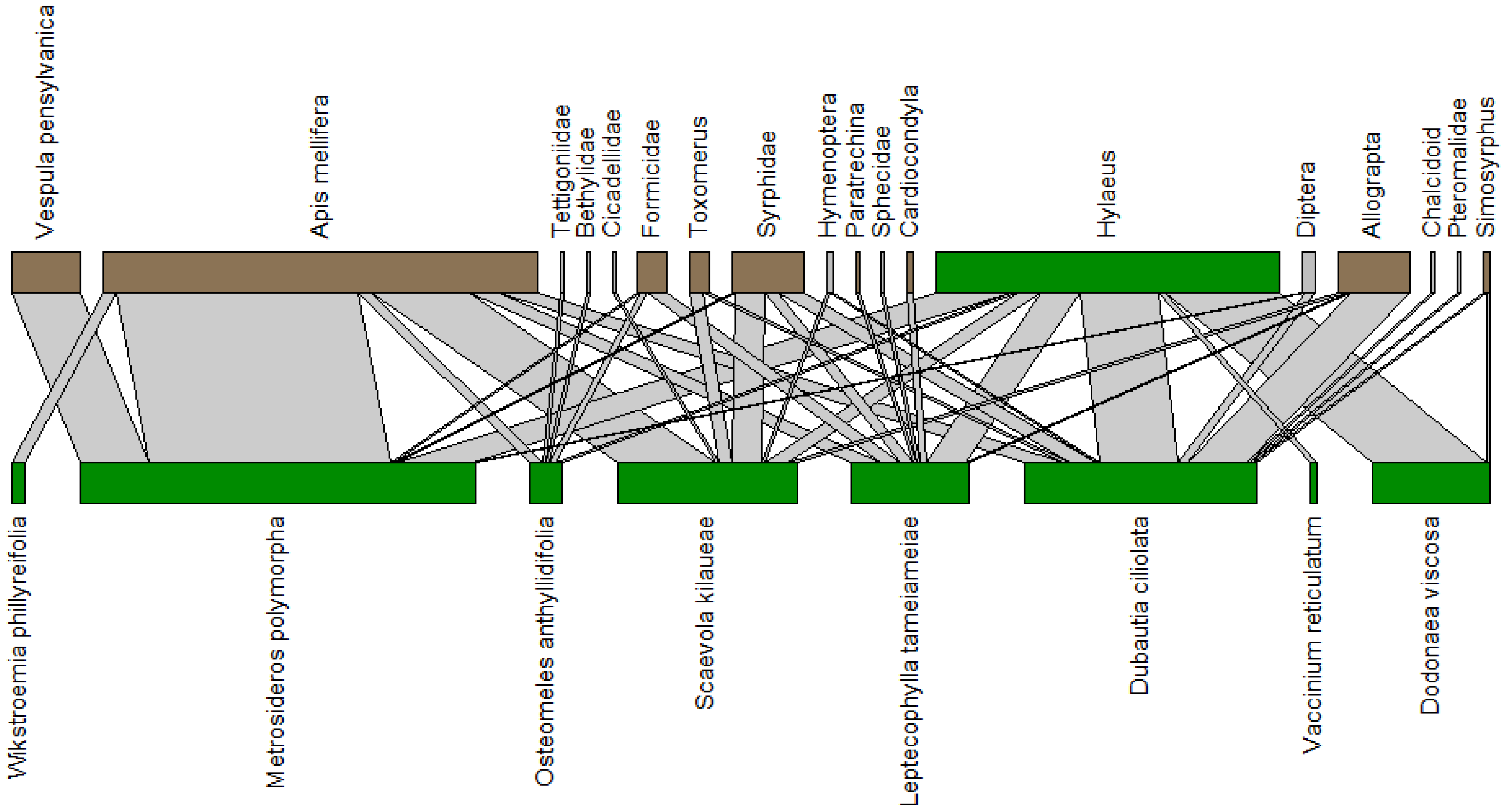
Appendix 1: Temporally described visitation networks. In each network, brown species are exotic, green are native.

Figure 1: Comparing networks across three seasons (combined) at the Hilina Pali native plant site (combined seasonal variation):

A. Spring only (2008, 2009, 2010):



B. Summer only (2007, 2008, 2009):



C. Fall only (2007, 2009):

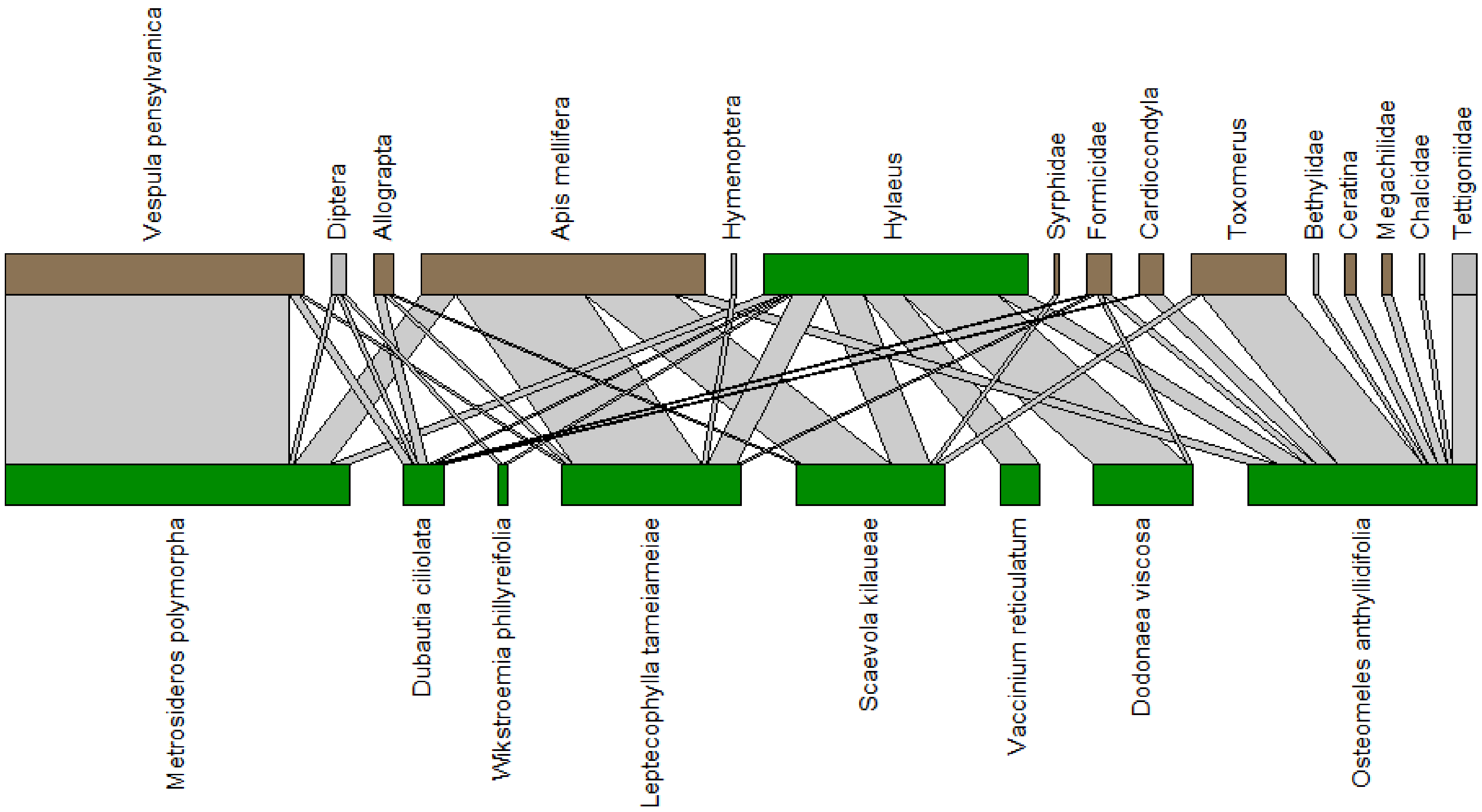
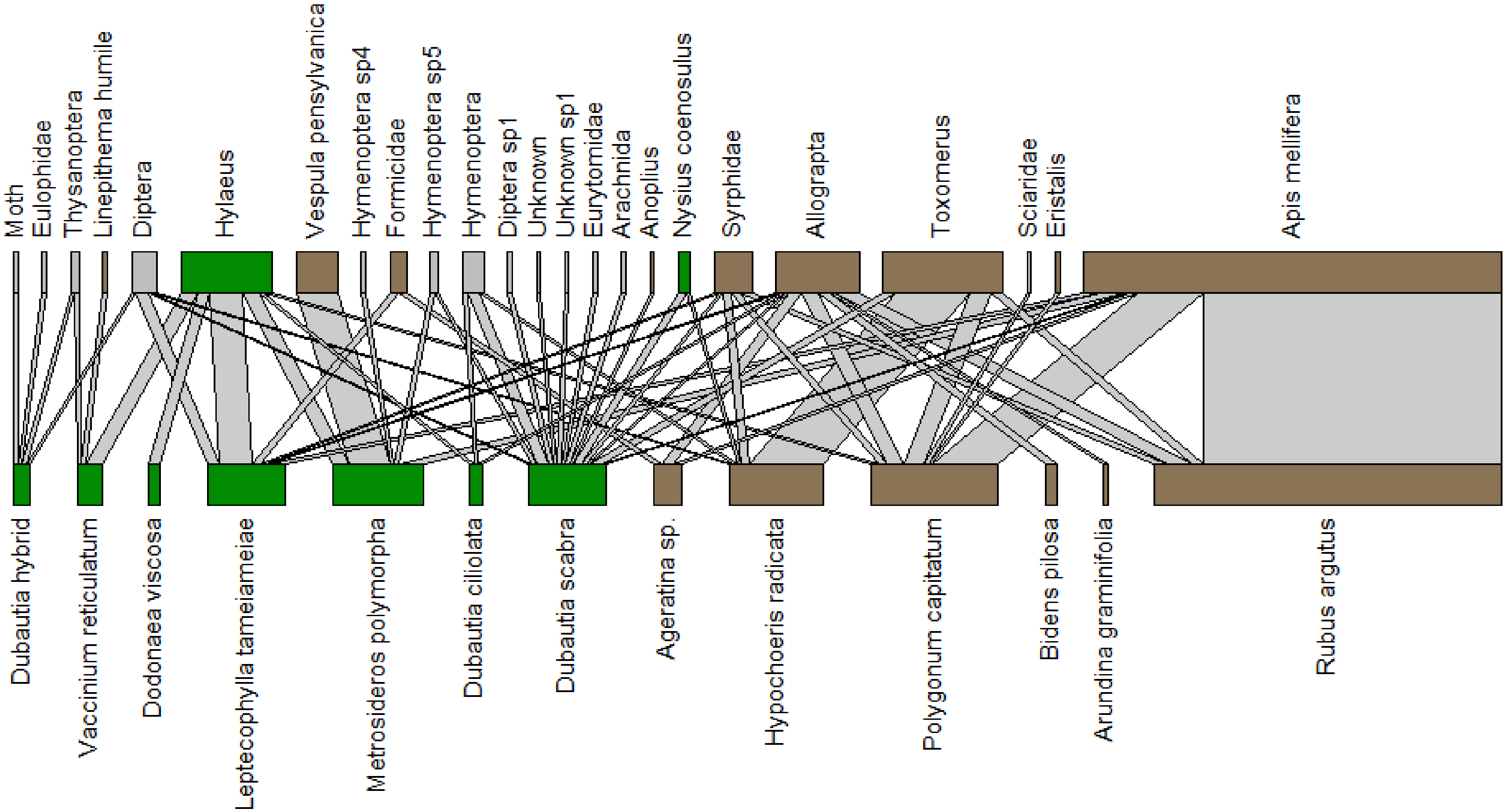
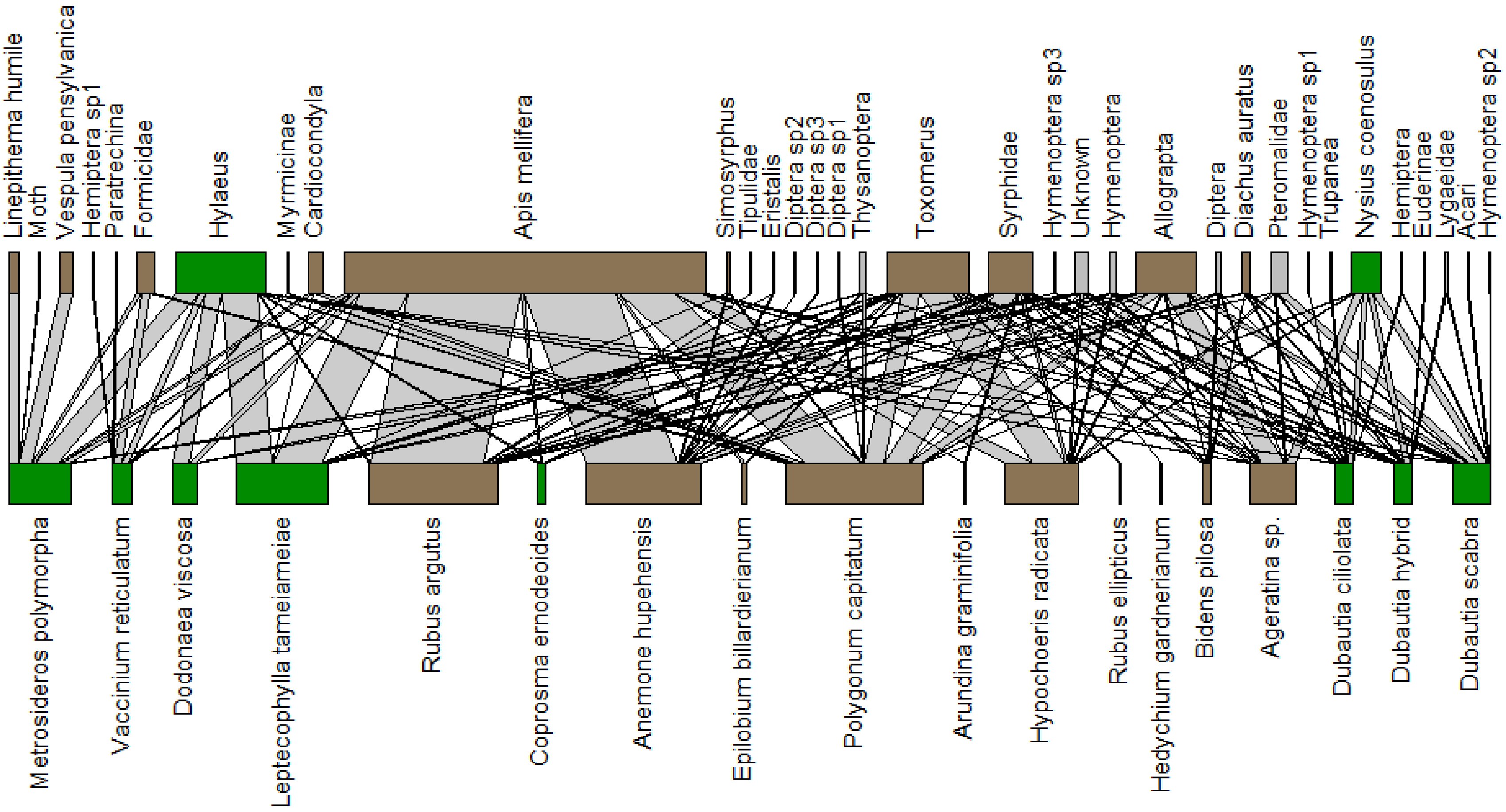


Figure 2: Comparing networks across three seasons (combined) at the Byron Ledge mixed plant site (brown is exotic, green is native) (combined seasonal variation):

A. Spring (2009, 2010):



B. Summer (2008, 2009, 2010):



C. Fall (2009 only):

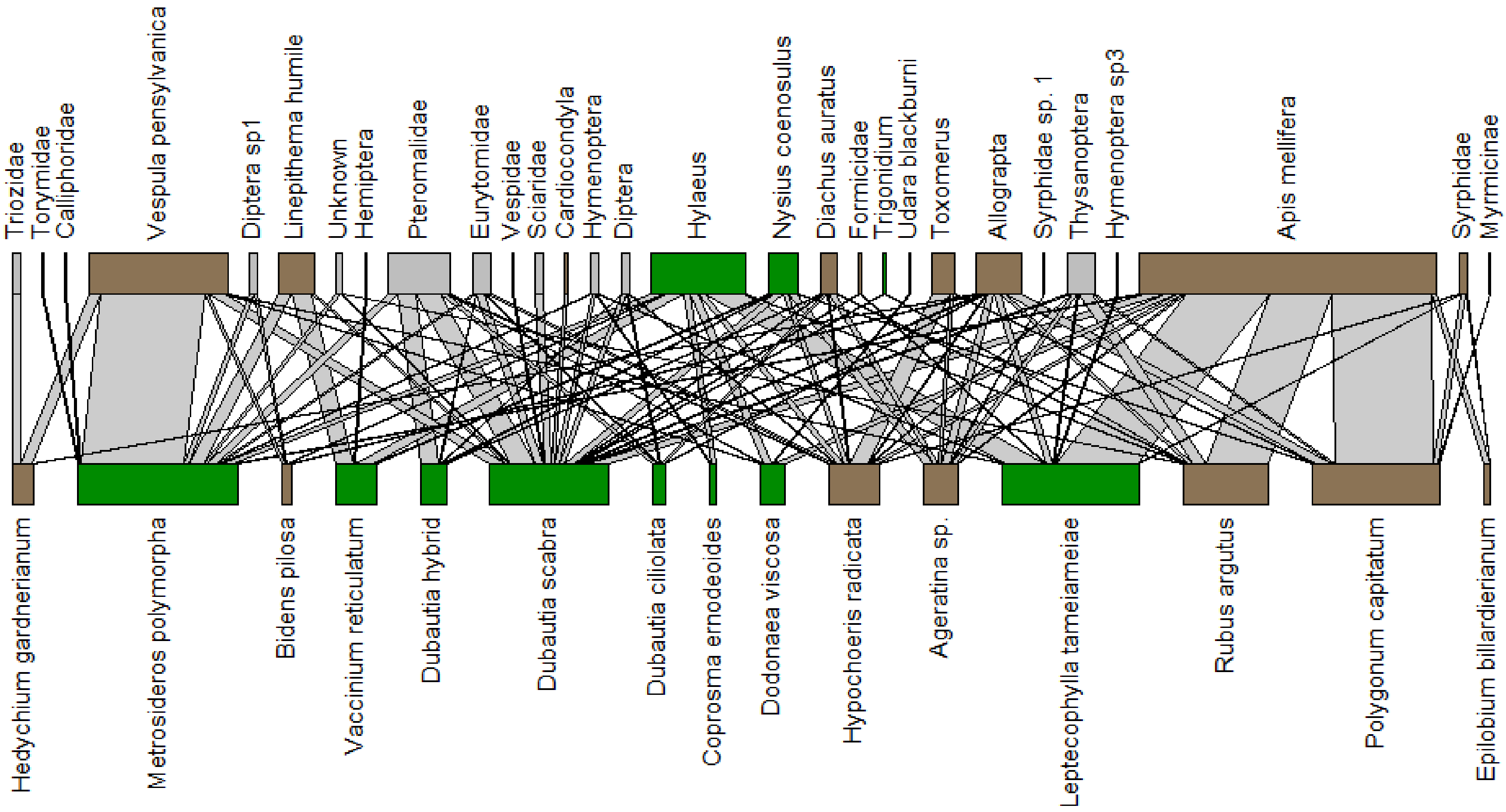
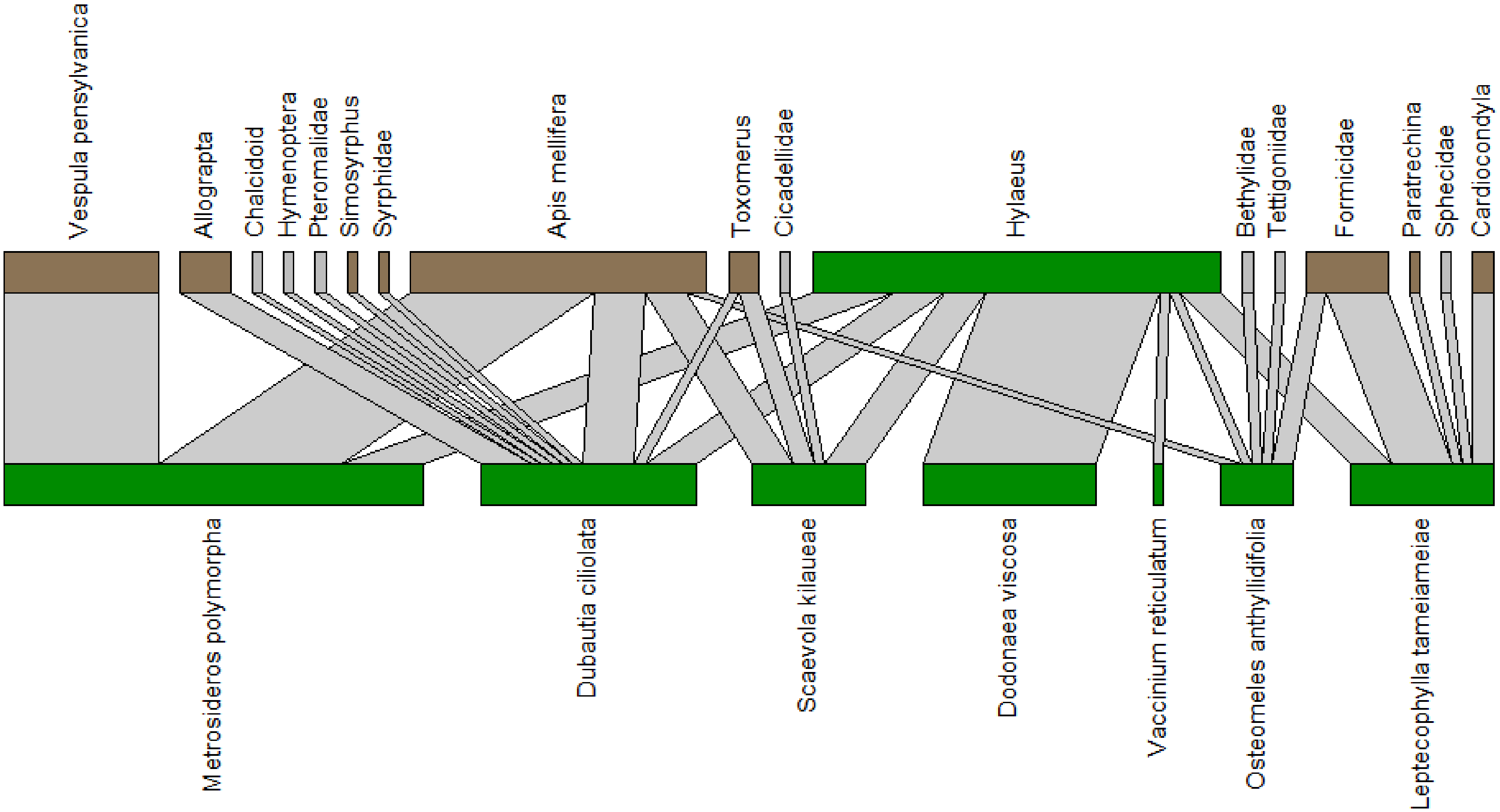
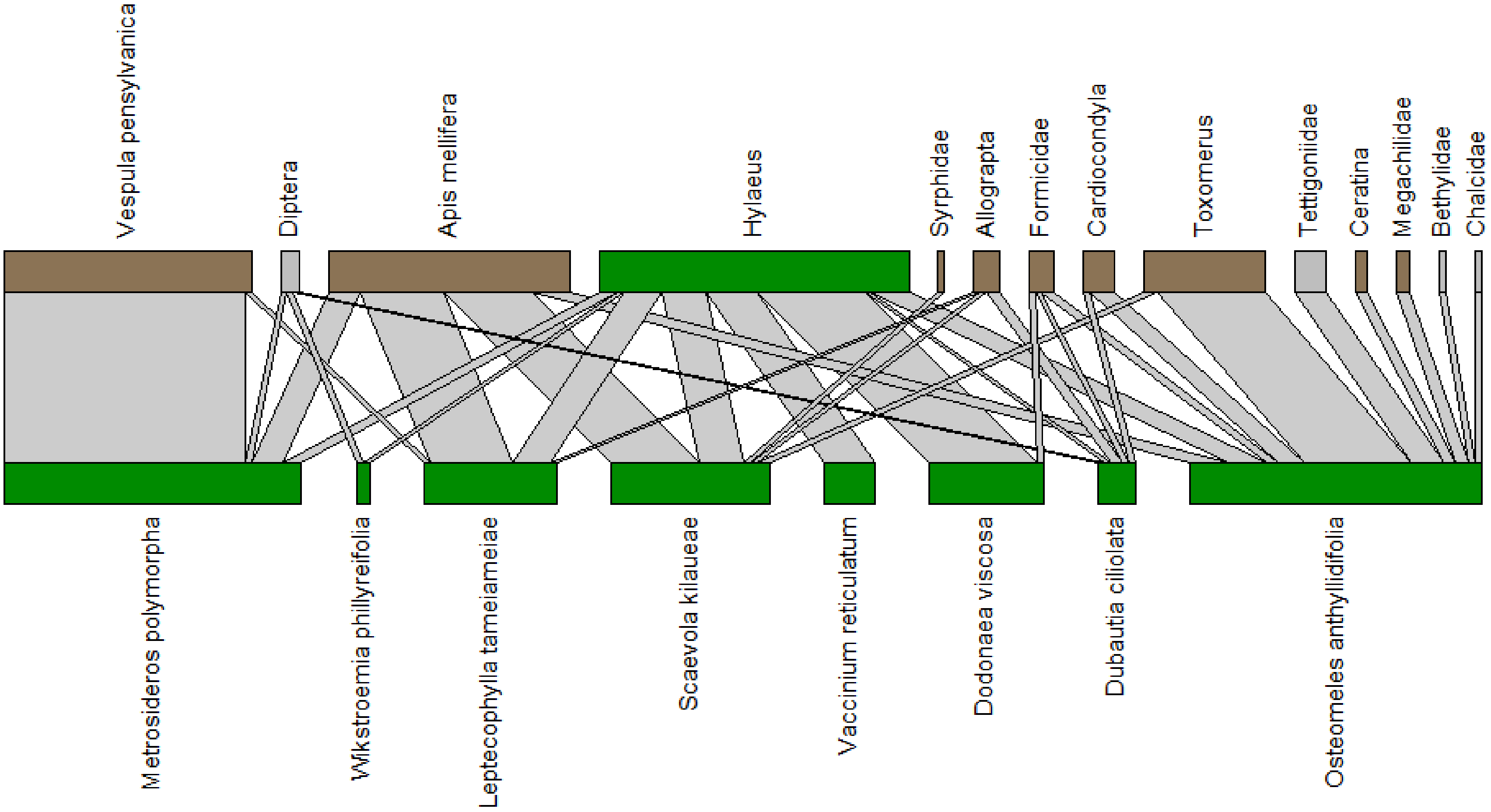


Figure 3: Comparing networks across three consecutive seasons at the Hilina Pali native plant site (Seasonal variation):

A. 2009 Summer



B. 2009 Fall


Vespula pensylvanica
Diptera
Apis mellifera
Hylaeus
Syrphidae
Allograpta
Formicidae
Cardiocondyla
Toxomerus
Tettigoniidae
Ceratina
Megachilidae
Bethylidae
Chalcidae
Metrosideros polymorpha
Wikstroemia phillyreifolia
Leptecophylla tameiameiae
Scaevola kilaueae
Vaccinium reticulatum
Dodonaea viscosa
Dubautia ciliolata
Osteomeles anthyllidifolia

C. 2010 Spring

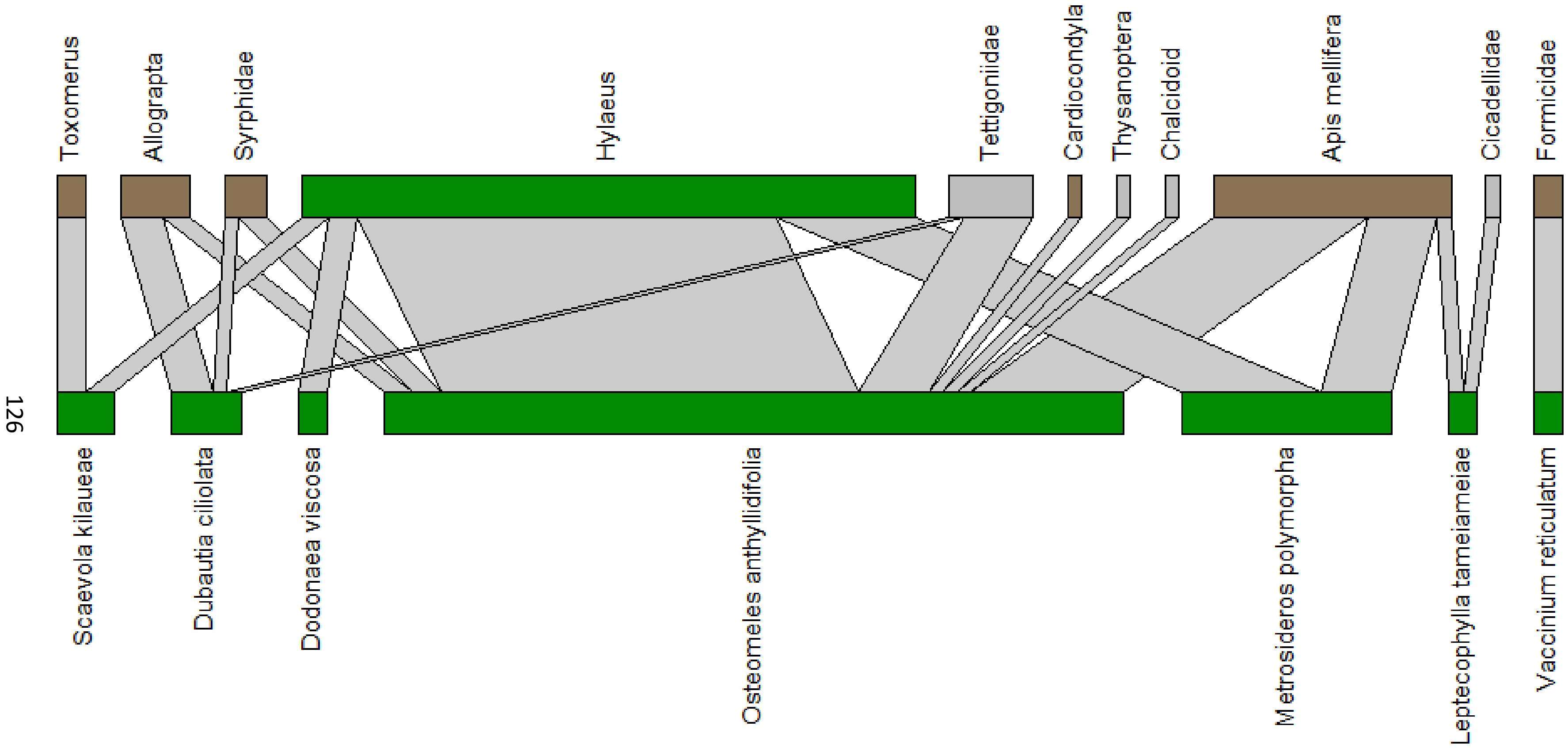
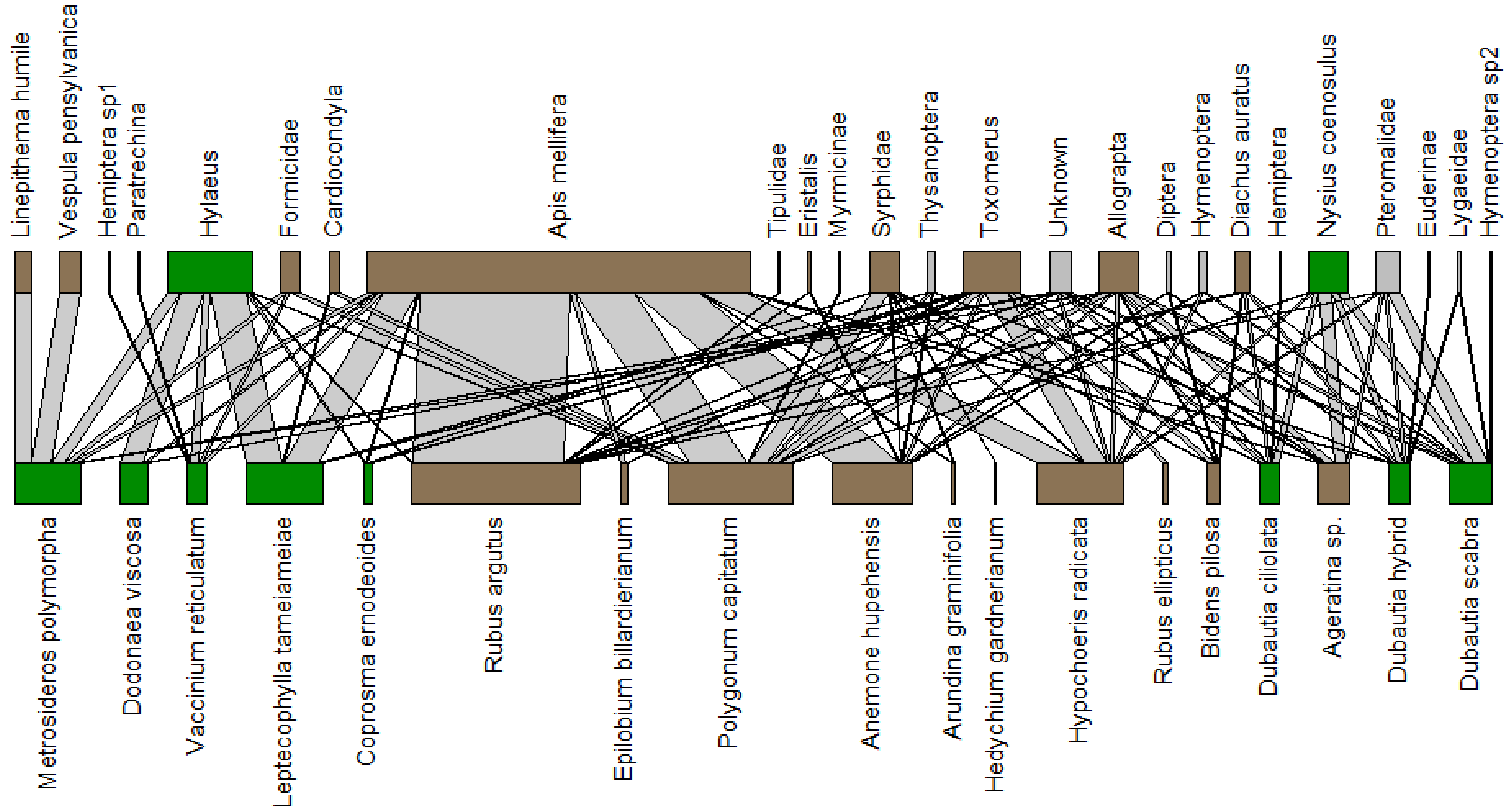
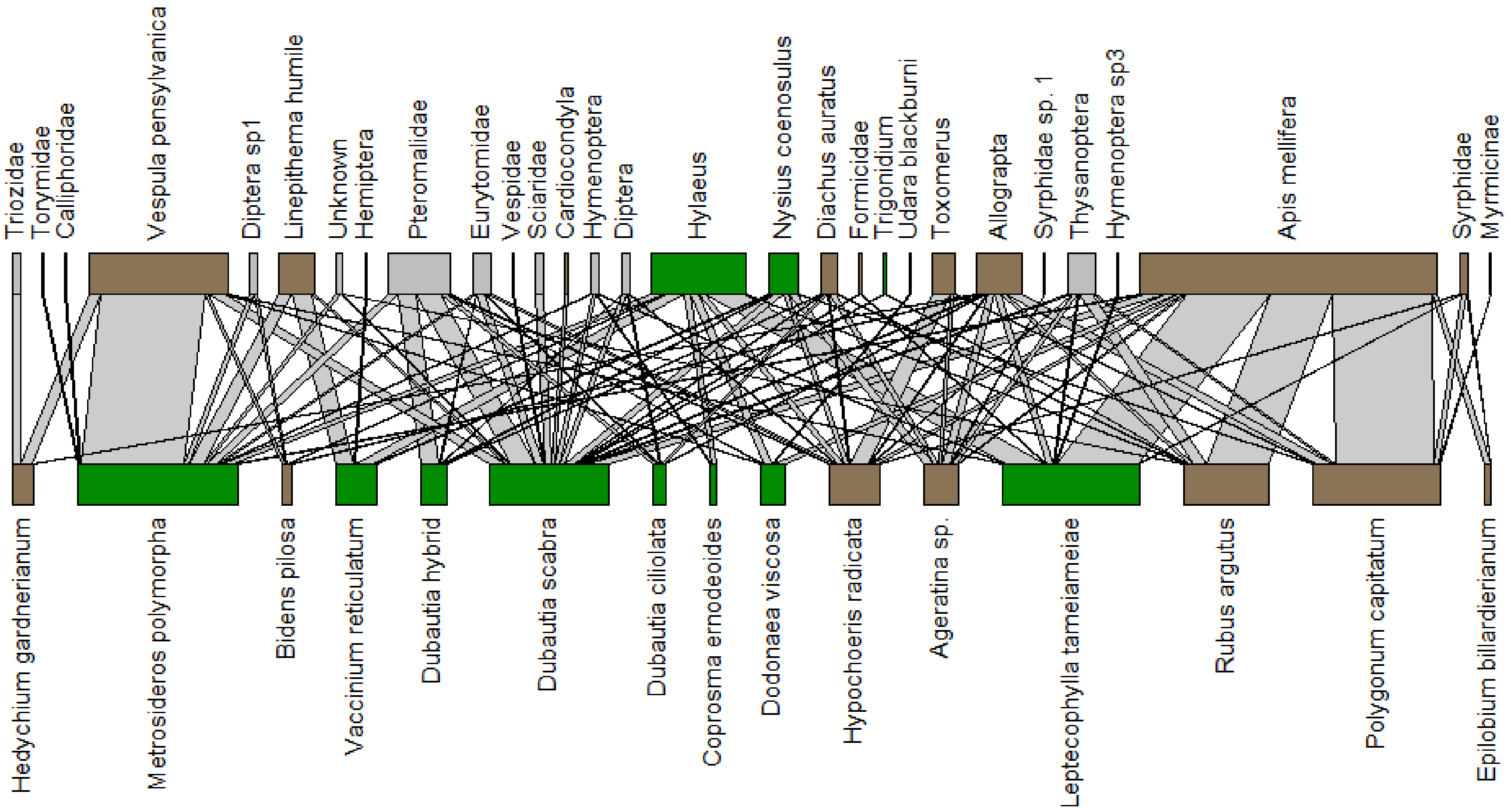


Figure 4: Comparing networks across three consecutive seasons at the Byron Ledge mixed plant site (Seasonal variation):

A. 2009 Summer



B. 2009 Fall


Triozidae
Torymidae
Calliphoridae
Vespula pensylvanica
Diptera sp1
Linepithema humile
Unknown
Hemiptera
Pteromalidae
Eurytomidae
Vespidae
Sciaridae
Cardiocondyla
Hymenoptera
Diptera
Hylaeus
Nysius coenosulus
Diachus auratus
Formicidae
Trigonidium
Udara blackburni
Toxomerus
Allograpta
Syrphidae sp. 1
Thysanoptera
Hymenoptera sp3
Apis mellifera
Syrphidae
Myrmicinae
Hedychium gardnerianum
Metrosideros polymorpha
Bidens pilosa
Vaccinium reticulatum
Dubautia hybrid
Dubautia scabra
Dubautia ciliolata
Coprosma ernodeoides
Dodonaea viscosa
Hypochoeris radicata
Ageratina sp.
Leptecophylla tameiameiae
Rubus argutus
Polygonum capitatum
Epilobium billardierianum

C. 2010 Spring

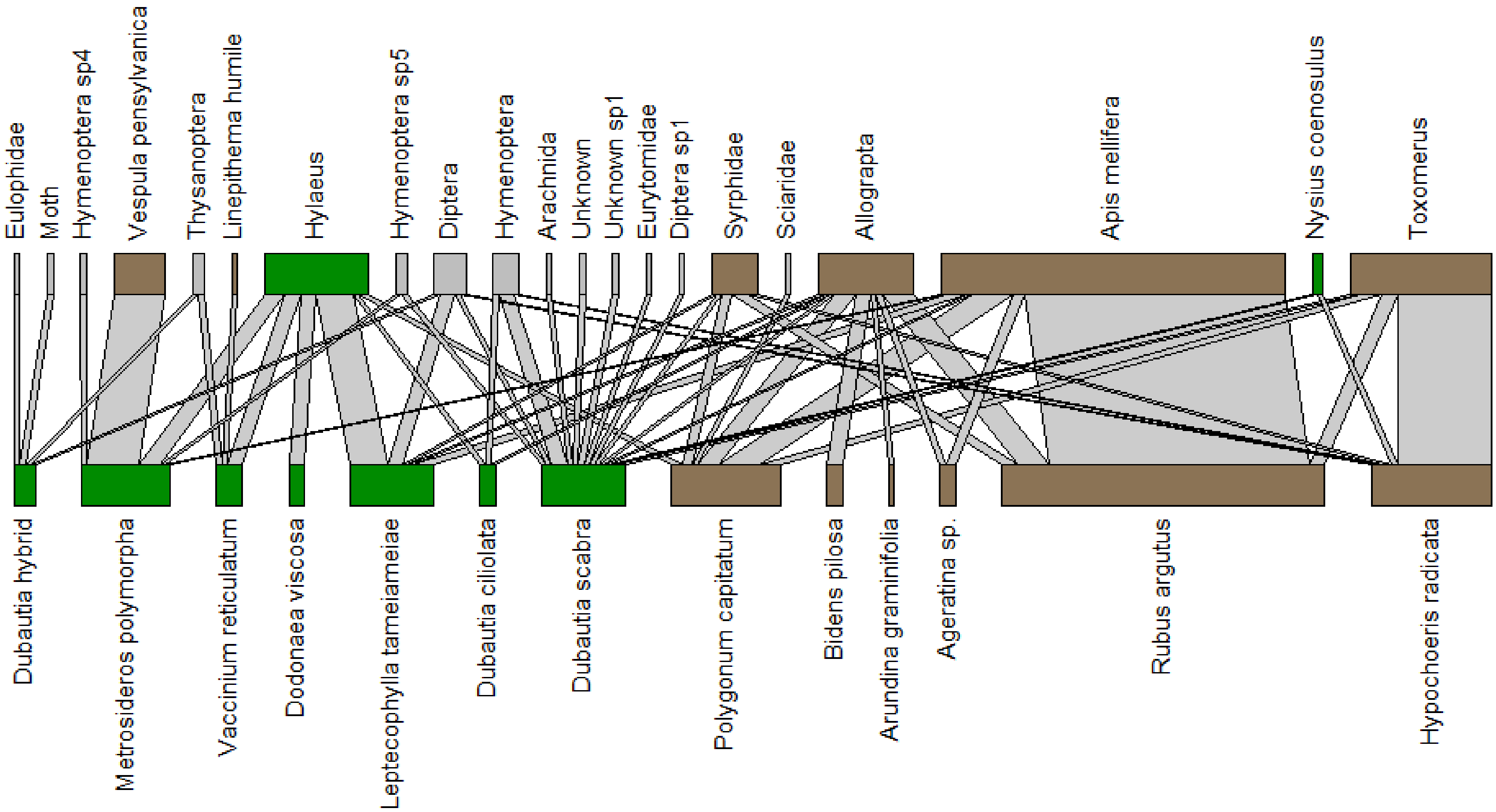
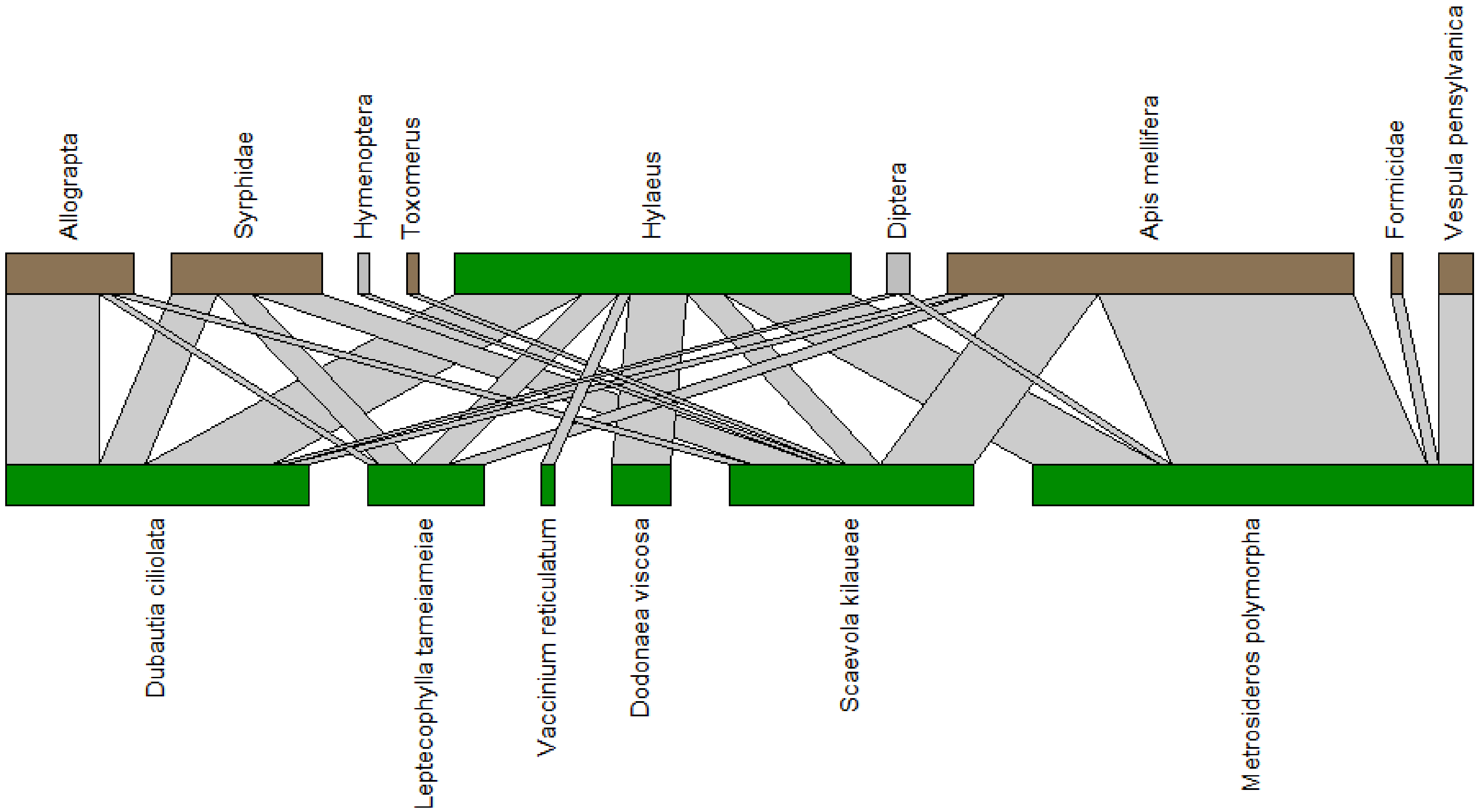
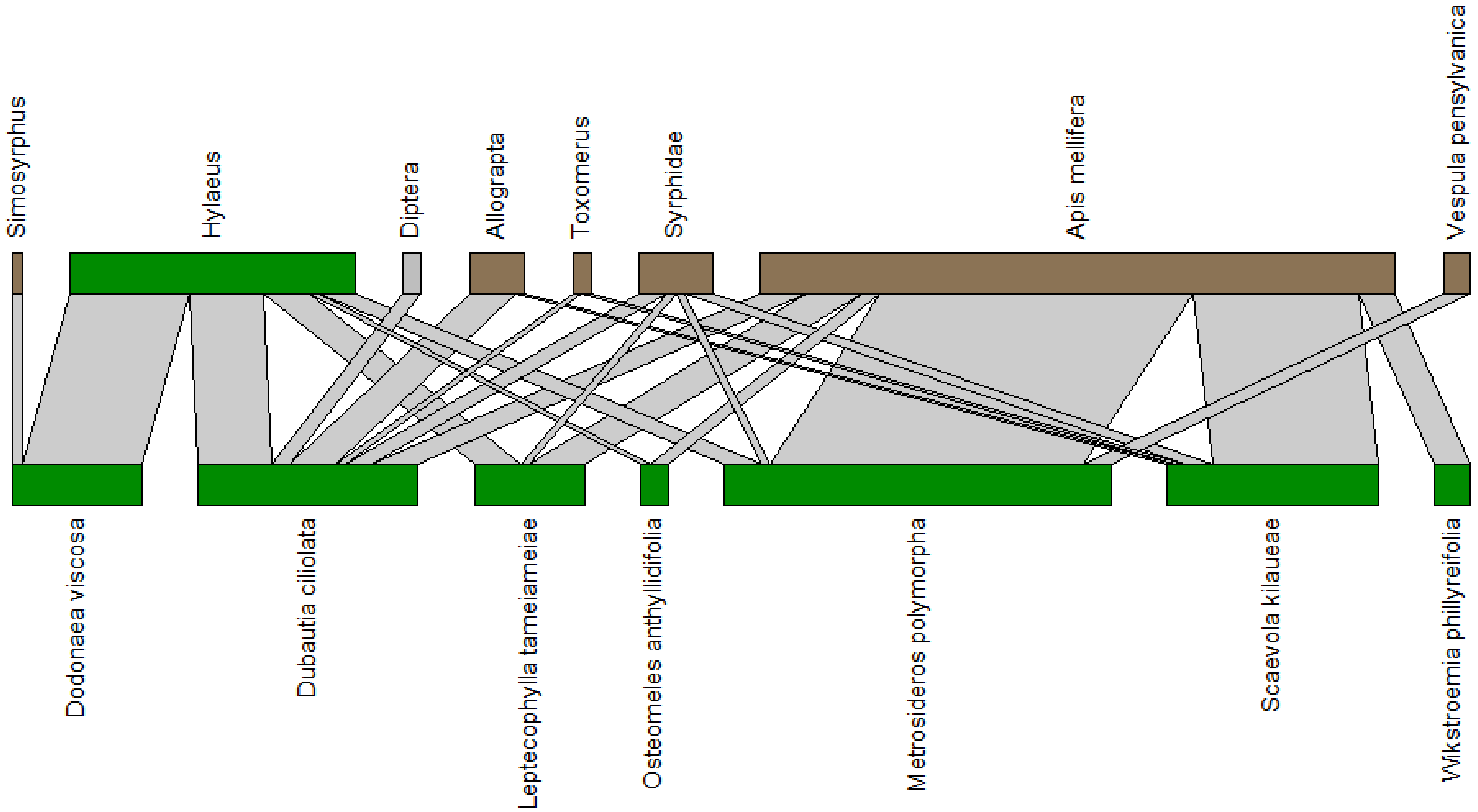


Figure 5: Comparing networks across three summers at the Hilina Pali native plant site (Inter-annual variation):

A. Summer 2007



B. Summer 2008



C. Summer 2009

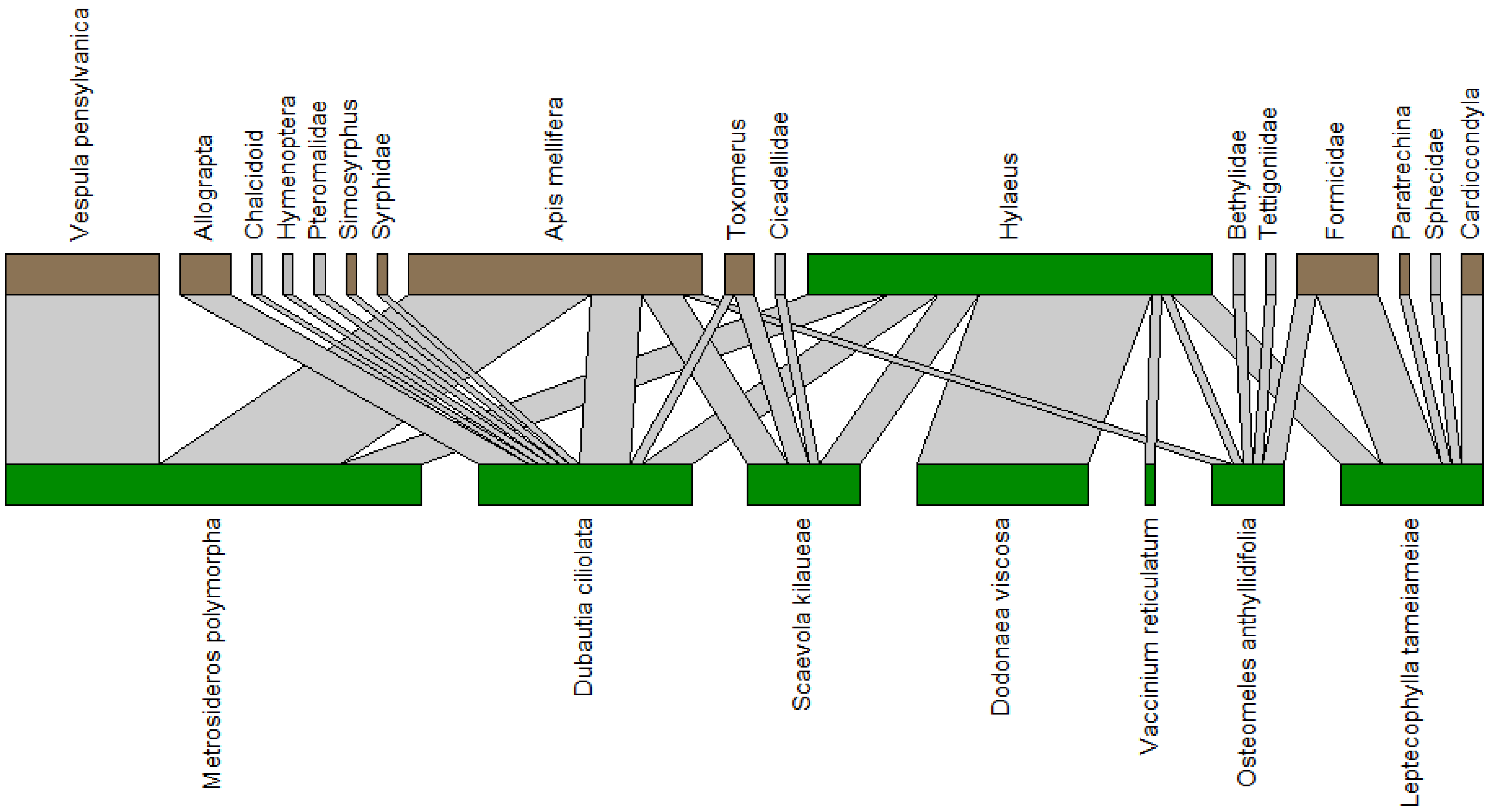
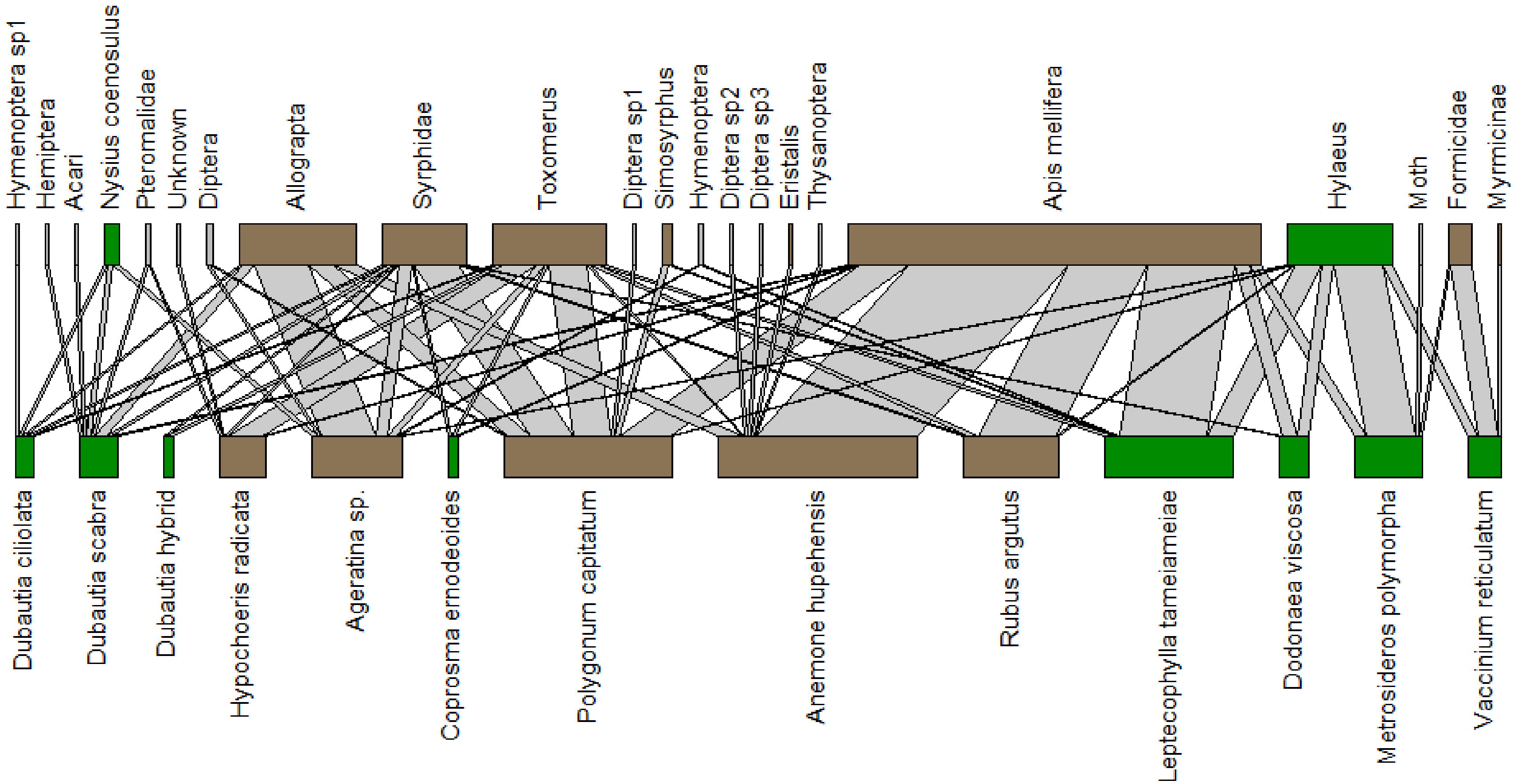
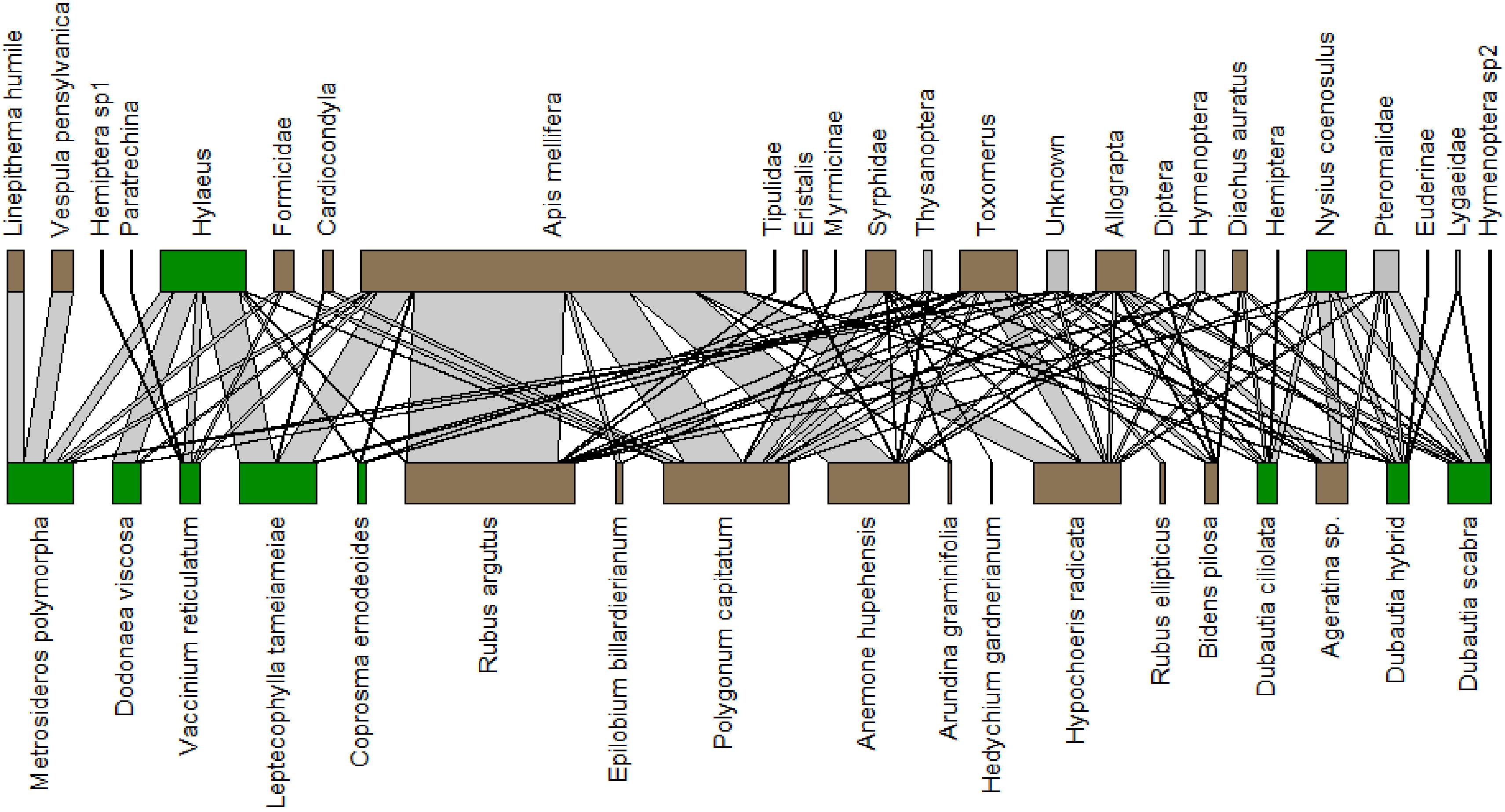


Figure 6: Comparing networks across three summers at the Byron Ledge mixed plant site

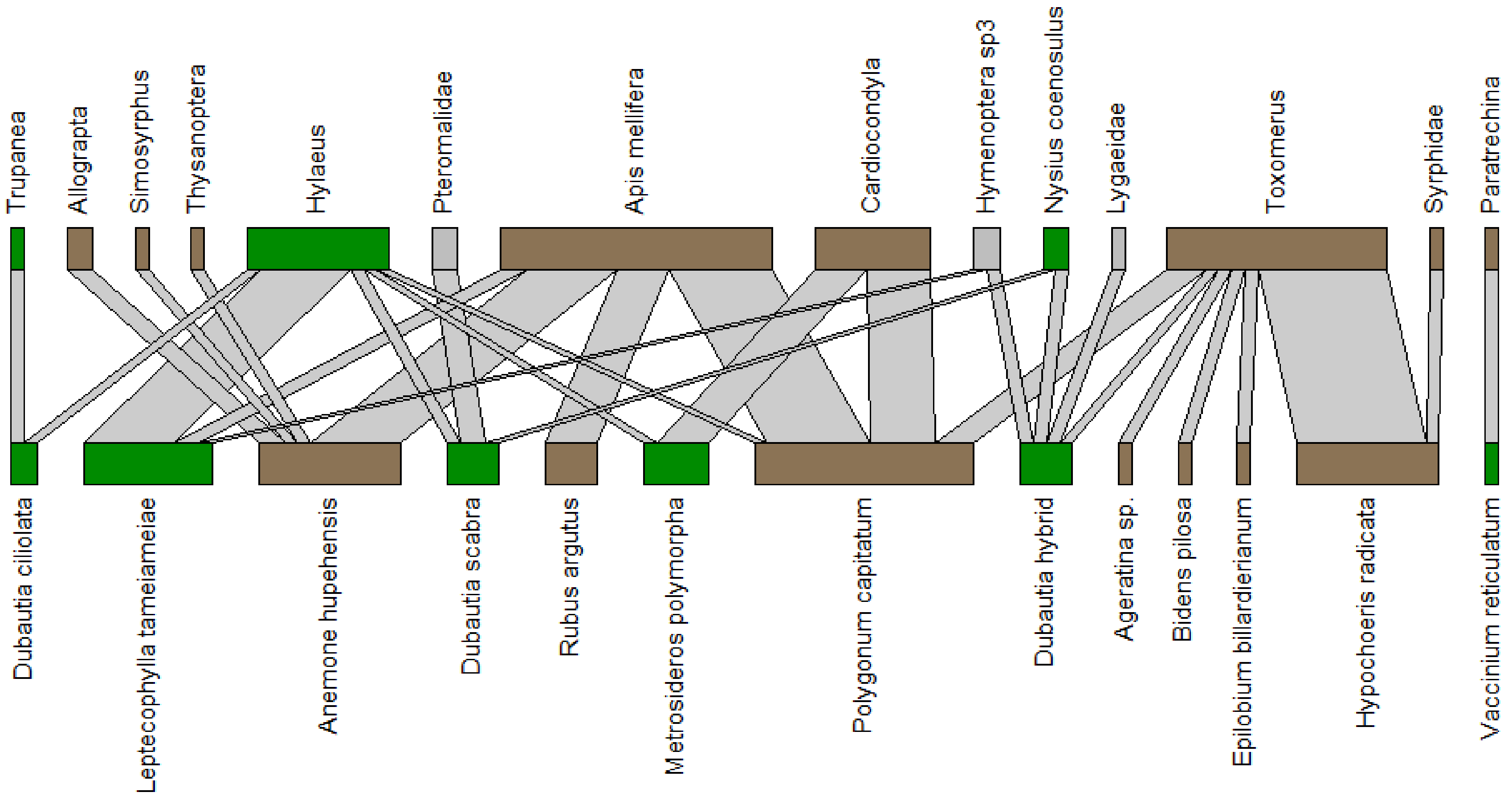
A. Summer 2008:



B. Summer 2009:



C. Summer 2010



Appendix 2: Summit eruption of Kilauea volcano

Figure 1: Eruptive plume from Kilauea summit eruption, taken on the morning of March 19, 2008

Figure 2: Ash-laden volcanic plume on March 25, 2008 as seen from viewpoints near the (A) Byron Ledge mixed site and (B) Hilina Pali native site

A.

B.