Community assembly on isolated islands: Macroecology meets evolution

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#### Aim

Understanding how ecological and evolutionary processes together determine biodiversity patterns remains a central goal in biology. Guided by ecological theory, we use data from multiple arthropod lineages endemic to the Hawaiian archipelago to explore the interplay between ecological (population dynamics, dispersal, trophic interactions) and evolutionary (genetic structuring, adaptation, speciation, extinction) processes. Within this framework, our goal is to show how communities develop over ecological-evolutionary time and the dynamic feedbacks involved in their assembly.

#### Location

The main Hawaiian Islands (19°-22°N, 155°-160°W).

#### Methods

To infer processes involved in early diversification we synthesize genetic data of select arthropod species across the Hawaiian Archipelago to determine the relative role of dispersal-driven processes and *in situ* differentiation across the island chronosequence. From four regions spread across the range of geological ages of the current high islands ( My to 5 My), we also generate ecological metrics on plant-herbivore bipartite networks drawn from the literature. We compare the structure of these networks, measured by nestedness, modularity and the degree distribution, to theoretical predictions derived from the principle of maximum information entropy.

#### Results

Based on the perspective provided by the island chronosequence and population genetic information, we provide evidence that species at lower trophic levels develop population genetic structure at shorter temporal and smaller spatial scales than species of higher trophic levels. Network nestedness decreased while modularity increased with habitat age. Single island endemics exhibited more specialization compared to broadly distributed species but both sets of species showed the least specialization in communities on middle-aged substrates. Plant-herbivore networks also deviated least from theoretical predictions of food web structure at middle-aged communities.

#### Main conclusions

Here we develop a generalizable framework to study the feedbacks between ecological and evolutionary processes in community assembly. Using population genetic data and insect herbivore-plant networks drawn from the literature for the Hawaiian Islands, we generate testable hypotheses for broad patterns in evolutionary community assembly over geological time. Our analyses suggest that populations of species at lower trophic levels develop genetic differentiation earlier in the successional time series than higher trophic levels. For bipartite insect herbivore-plant networks, patterns of decreasing nestedness and increasing modularity suggest a shift from early assembly driven by immigration, to *in situ* co-diversification with host plants as communities age (>1 My). Single island endemics (likely the product of *in situ* diversification) were more specialized on host plants at older sites relative to broadly distributed species (those taxa more likely to be initial colonists). Finally, the observation that the younger and oldest aged sites, but not intermediate aged sites, deviate from the predictions of METE suggests that herbivore-plant communities only transiently achieve statistical steady state during the assembly process, presumably due to incomplete assembly from dispersal during early stages of assembly, and the increasing influence of island ontogeny on plant and herbivore populations on mature or senescent islands. Future work will focus on testing the conclusions presented here with intensive sampling and fine-grained site replication in concert with further theoretical development.

# Introduction

Contemporary biodiversity is a product of speciation, extinction and dispersal, contingent on the ecological interactions of organisms with the biotic and abiotic environment. The evolutionary history leading to the assembly of any given ecological community must in some way shape contemporary ecological assemblages. However, because the processes of evolution and ecology occur on different temporal and spatial scales, disentangling the relative influence of local ecological mechanisms from historical evolutionary processes on patterns of community structure patterns remains a central challenge (Ricklefs, 2004).

Evolutionary processes of speciation and extinction are classically viewed as constraints on regional species pools, occurring in a manner largely removed from local ecology (Hubbell, 2001; Cavender-Bares *et al.*, 2009; Wiens, 2011). Conversely, ecological mechanisms tend to be viewed as packing standing diversity into local communities through consumption, competition, facilitation, and – more recently – neutral ecological drift (Hubbell, 2001; Tilman, 2004; Bascompte & Jordano, 2007; Borer *et al.*, 2014). While recent theoretical advances have provided greater insight on ecological drift (Hubbell, 2001; Rosindell & Phillimore, 2011), niche partitioning (Tilman, 2004), competition, predation (Borer *et al.*, 2014), and species interaction networks (Williams & Martinez, 2000; Brose *et al.*, 2006), these insights typically do not contain realistic evolutionary assumptions (Ricklefs, 2006) or ignore them entirely.

Insights into the genetic, biogeographic and selective mechanisms leading to diversification have also emerged based on inference from contemporary patterns of species, genetic, or phylogenetic diversity (e.g., Wiens, 2011; Jetz *et al.*, 2012). However, it is not possible to use static contemporary patterns to infer the temporal dynamics of either the evolutionary mechanisms or their ecological consequences nor can we understand what constitutes meaningful change in a system without a baseline for comparison. Here we show how testing idealized ecological theories (such as the unified neutral theory [Hubbell, 2001] or the maximum entropy theory of ecology [Harte, 2011]) on archipelagos composed of islands formed in discrete geological sequences can help identify the shifting balance and feedback between fast-acting, local “ecological” mechanisms, and long-term, large-scale evolutionary processes in determining ecological community structure. Islands of vastly different ages of formation, along with discrete volcanoes within islands, provide approximate snapshots of eco-evolutionary processes operating at different stages of community assembly and development. Ecological theory provides an idealized “null” baseline against which to compare observed patterns.

## Hotspot oceanic archipelagos as model systems

Hotspot oceanic islands are opportune model systems for studying the interplay of local ecological mechanisms and evolutionary drivers of biodiversity patterns. Due to their sequential formation as the tectonic plate moves over a volcanic hotspot, such island systems offer a range of spatial and temporal scales over which to analyze the outcomes of ecological and evolutionary processes (Warren et al. 2015). While many archipelagos around the world share these biotic and geologic properties, the Hawaiian archipelago provides a particularly useful system for study because its linear geological chronology (Price & Clague, 2002), ecosystem developmental trajectories (Vitousek 2004), and phylogeographic patterns of biodiversity are each well characterized (Wagner & Funk, 1995). Moreover, studies of species diversity across the islands have revealed patterns that are non-uniform across the island chronosequence with marked differences between lineages (e.g., Gruner 2007; Gillespie & Baldwin, 2009) that can be used to test for biologically meaningful differences between lineages that might drive their disparate diversification patterns.

## Development of genetic structure

High levels of dispersal and associated gene flow among localities limit the extent to which populations can diverge genetically (Slatkin, 1987). However, when gene flow is low, distinct populations in different localities are free to diverge through local selective pressures and drift, which can lead to diversification (Slatkin, 1987) Thus, the magnitude of genetic connectivity among populations provides a measure of the relative importance of dispersal-driven assembly (dictated by processes removed from the local setting) in contrast to assembly by local (*in situ*) diversification in determining community composition. Using the chronosequence of the Hawaiian Archipelago, we can analyze populations from multiple sets of taxa across trophic guilds occurring in geological contexts from young to old. We predict that dispersal-driven (ecological) processes will dominate in community assembly in young habitats with the importance of *in situ* (evolutionary) processes increasing with habitat age. If evolutionary processes are not important, we predict that communities should reach a statistical steady state through ecological processes alone (Harte, 2011). If, as we expect, evolutionary processes become increasingly important in community assembly over time, we expect to find associated deviations from an ecological null model of community assembly, provided by idealized ecological theory. Differences in population structure between taxa or trophic groups could indicate whether sufficient time has passed along the chronosequence for the group of interest to experience significant evolutionary pressures.

## Macroecological metrics and idealized ecological theory

Unified theories of biodiversity (e.g. Hubbell, 2001; Harte, 2011) by their nature provide a simplified view of ecology, but deviations from theory can provide insights as to which particular ecological patterns require additional biological mechanisms for their explanation (Harte, 2011). The maximum entropy theory of ecology (METE; Harte, 2011) in particular provides predictions of species abundance distributions, species area relationships, and metabolic rate and network linkage distributions, for idealized ecological communities in which a system’s behavior is governed by a simple set of state variables. The principle of maximum information entropy (MaxEnt), from which METE is derived, is an established inference procedure that has yielded accurate predictions of diverse patterns in fields as varied as thermodynamics (Jaynes, 1957), economics (Golan *et al.*, 1996), forensics (Roussev, 2010), imaging technologies (Gull and Newton, 1986), and ecology more recently (e.g. Phillips et al., 2006; Dewar and Porté, 2008; Harte, 2011). MaxEnt works by seeking the least-biased prediction of a distribution of interest (e.g. the distribution molecular velocities in the case of thermodynamics or of species abundances in the case of ecology) while constraining that prediction to be consistent with state variables describing the macroscopic attributes of the system (e.g. temperature or the total numbers of species and individuals). These are the most ignorant possible predictions about the system. Thus, studying the unique ecological conditions and evolutionary histories of real world systems that deviate from the conditions predicted from maximizing information entropy can provide insights into the processes driving ecological systems away from the statistical steady state (Harte, 2011).

Ecological networks are complex systems forming hierarchical structures to which the principle of MaxEnt has recently been applied (Williams, 2010; Harte, 2011) and are a prime study focus because networks of interacting species embody both the ecology of trophic links and evolutionary processes such as coevolution (Bascompte & Jordano, 2007; Donatti *et al.*, 2011; Nuismer *et al.*, 2013; Thompson et al. 2013). Thus they present an opportune starting place to study ecological and evolutionary feedbacks. The distribution of linkages in ecological networks can test whether plant-animal interaction networks assemble neutrally or through deterministic processes such as coevolution of traits involved in foraging (Vázquez *et al.*, 2005). Analysis of other network metrics such as modularity (the degree to which species interact in semi-autonomous modules) and nestedness (the degree of asymmetry in interaction between specialists and generalists) can further illuminate underlying eco-evolutionary processes driving patterns of species interactions (Bascompte & Jordano, 2007; Donatti *et al.*, 2011; Nuismer *et al.*, 2013). In these networks, species with fewer interactions (i.e. more specialized species) will interact with a subset of the species with which generalists interact.

To gain insights into community assembly as it happens, we propose an integrative framework that harnesses advances in both evolutionary and ecological theory, placed in the context of age-structured archipelagos. Mechanistically simplified ecological theories such as METE (Harte, 2011) can be used as powerful null models; deviations from expectations of the theories can flag biological phenomena warranting further study. Here we demonstrate how community-level data from age-structured island systems, combined with population genetic and phylogenetic data, can test the extent to which the evolutionary histories behind such communities drive their deviation from theoretical expectations. We provide an initial test of this concept using a synthesis of published data on arthropod lineages in the Hawaiian Islands. We provide metrics of ecological and evolutionary dynamics across communities from settings that range in geological age from 500 yr to 5 Myr. We estimate taxon-specific timelines for the development of population genetic structure for both herbivores and predators and couple these results with macroecological measures of community structure, using predictions from statistical steady state and ecological network theory to provide insights into changes in community structure over the extended timeframe provided by the island chronosequence.

# Methods

## Dispersal-driven processes to *in situ* differentiation across the island chronosequence

To evaluate the balance between regional immigration and potential for local differentiation, we measured how molecular variation is partitioned among populations within species across locations of known substrate age on Hawaii Island and Maui (Fig. 1). We compiled published (DNA sequences, AFLPs, and allozymes) and new data sets for a diversity of native Hawaiian arthropod groups that represent a spectrum of trophic levels (Table 1). New sequences were included for sap-feeding Hemiptera group *Nesosydne* planthoppers (COI: data generated following the protocols in Goodman *et al.*, 2012 GenBank accession numbers XXX-XXX) and *Trioza* psyllids (COI, cytB: data generated following protocols in Percy 2003; GenBank accession numbers XXX-XXX). Samples were from the focal sites described below for the ecological analysis as well as from locations across Hawaii Island and Maui. These data were used to provide an estimate of how arthropod populations have accumulated genetic population structure within the focal sites of different geological age.

We used analysis of molecular variance (AMOVA) to examine how genetic variation is partitioned at two scales of population structure: among sites within volcanoes and among volcanoes on both Hawaii Island and the islands of the Maui Nui complex (Maui, Molokai, Lanai). All analyses of allozyme and DNA sequence data were performed in Arlequin v. 3.5 (Excoffier & Lischer, 2010) using the AMOVA procedure to compute , a measure of genetic variance, or, where possible,, an analog that incorporates genetic sequence information. The *Laupala* AFLP data were analyzed using TFPGA v. 1.3 (Miller, 1997), using the same hierarchical approach of comparing within and between volcanoes as described above. To provide a temporal framework for the population differentiation analysis we assembled divergence dating information from the literature for as many of the taxa as possible and additionally implemented a new divergence.

To explicitly test the association between landscape age and potential for *in situ* genetic divergence we analyzed how within site varies with the geologic age of volcanoes on Hawaii Island and Maui Nui. For each volcano we calculated or (Excoffier & Lischer, 2010) for each taxon among sites within volcanoes.

## Ecological metrics across the island chronosequence

## To investigate how ecological patterns change as communities age, we selected four focal sites across the chronosequence and island ages (two on Hawaii Island, one on Maui and one on Kauai; Fig. 1). Focal sites were selected to have similar forest composition (dominated by *Metrosideros polymorpha*: Myrtaceae), elevation (1100-1400m), and rainfall (mean annual precipitation 2000-3000 mm). We then constructed bipartite interaction networks between native herbivorous Hemiptera species and native plants at each of the study sites. Bipartite networks describe the topology of ecological interactions between two guilds of organisms (e.g. herbivores and their plant hosts). Quantitative information on the relative importance of interaction links can be incorporated into network analyses (Vázquez *et al.*, 2009); however, currently available data are restricted to binary networks: those that describe only the potential for interaction between any two species, but not the relative frequency of that interaction to each species.

We compiled species lists of all native herbivorous Hemiptera for each focal site from published species accounts (see supplement for full list). Species accounts and other published sources were used to determine the presence, probable presence, or probable absence of each species at each of our four focal sites. A documented presence was defined as a known specimen collected at the focal site; a probable presence was defined as a species whose abiotic tolerances and known geographic range (see supplement) overlap with a focal site but no known specimen exists confirming its presence. Probable absence was assumed when neither criteria for presence or probable presence are met. Two sets of species lists for each focal site were compiled: a conservative data set composed of only documented presence occurrences and a less conservative data set that also included probable presences.

Host plants for each species of Hemiptera were determined from published species accounts. Data on host plant use at each specific site were not available so we assumed that if a known host plant were present at a site it would eventually be used. Host plant occurrence in the focal sites was determined using distribution models for 1158 species of Hawaiian plants (Price et al., 2012). Each focal site was spatially joined in a geographic information system with all coincident plant distribution models that fell within its boundaries. Two sets of resulting focal site-specific networks were constructed: one using the conservative data set of Hemiptera species presences and the other using the less conservative data set.

We hypothesized that potentially complex evolutionary feedbacks contributing to community assembly should result in departures from the predicted ecological statistical steady state. We used METE (Williams, 2010; Harte, 2011) to compute the statistical steady state for the distribution of the number of host plants used by each Hemiptera species (hereafter referred to as degree distribution). To evaluate how well METE predicts the data we simulated METE-conforming communities of the same number of species and links as observed. We then calculated the log-likelihood of each simulated data set and compared the resultant distribution of log-likelihoods under the hypothesis that METE is true, to the observed log-likelihood. This comparison is identical in approach to a z-score test using a Monte Carlo simulation to estimate the sampling distribution of log-likelihoods. R scripts (v3.1.1; R Core Team, 2014) used for METE estimation and Monte Carlo methods are available in the supplement.

To investigate how speciation may in part drive network patterns and deviations from those predicted by idealized ecological theory, we analyzed the number of links assigned to each Hemiptera species (the degree distribution) separately for single island endemics (those species found on only one island and thus likely derived from *in situ* diversification) versus multi-island endemics (those species found on multiple islands). Although multiple processes can lead to a species being a single-island endemic (Whittaker et al., 2008), such taxa provide a proxy for how much speciation occurs within islands. To compare species’ degree distributions between single-island endemics and multi-island endemics across sites of different ages we conducted a generalized linear model with binomial error, treating site identity as a categorical predictor. Binomial errors effectively account for network size due to the bounded support of the binomial distribution.

To understand how other network properties change with ecosystem substrate age, we calculated two widely used descriptive network metrics across sites – nestedness and modularity. Nestedness describes the degree of asymmetry of species interactions connecting specialists and generalists (Bascompte & Jordano, 2007; Ulrich *et al.*, 2009). We calculated nestedness using the NODF metric (Almeida-Neto *et al.*, 2008) as implemented in the R package *vegan* (Oksanen *et al.*, 2013) and modularity using a variety of algorithms implemented in the R package *igraph* (Csardi & Nepusz, 2006). These metrics are not directly comparable across networks of different size and connectance (Ulrich *et al.*, 2009), so for each metric in each network we calculate z-scores using a null model that randomizes network structure while maintaining certain aggregate network properties (Ulrich *et al.*, 2009). These z-scores are calculated as the difference between the observed network metric minus the mean of the null model divided by the null model standard deviation, or (. Because z-scores can be highly sensitive to the choice of null model (Ulrich *et al.*, 2009) we implemented both a probabilistic null model (Bascompte & Jordano, 2007) and a null model that strictly constrains the degree distributions of plants and herbivores (Ulrich *et al.*, 2009). The probabilistic null using the frequency of interactions as the probability that a randomized link gets assigned to that cell in the interaction matrix (Bascompte & Jordano, 2007); thus the probabilistic null constrains row and column sums in probability but not absolutely.

# Results

## Dispersal-driven processes to *in situ* differentiation across the island chronosequence

The analysis of molecular variance (AMOVA) revealed significant genetic population structure from the smallest to the largest spatial scales examined, all within a very recent timeframe. For mitochondrial loci, statistically significant molecular variation partitioned among sites within volcanoes ranged from 0.037–0.92 and among volcanoes from 0–0.30. Corresponding variation at multilocus nuclear loci among-sites within volcanoes ranged from 0.21–0.58 and among volcanoes, 0.04–0.34. Taxa in the lower trophic levels (herbivorous sap-feeding Hemiptera: planthoppers and psyllids) had as much or more molecular variation partitioned at the among-site, within volcano level than the among volcano level, while the predatory spiders were less structured at localities within volcanoes compared to among them (Table 1). The analysis of genetic population structure across the chronosequence of localities revealed a similar pattern. The herbivores show high genetic population structure among localities even on young volcanoes (Fig. 2). By contrast, predatory spiders exhibited little genetic population structure within sites on the same volcano, higher between volcanoes, with values increasing with age across the chronosequence.

The observed levels of genetic divergence have evolved rapidly. For example, for species from Hawaii Island for which phylogenetic data provide divergence times, estimates of dates of species divergence range from 0.5–4 million years, with additional within-species genetic divergence having developed subsequently (Casquet et al., 2014). That some of these estimates are older than the known age of the Big Island suggests that genetic divergence pre-dates their colonization to Hawaii Island, or alternatively that estimates include sampling error. For the one species where population genetic data was used to estimate divergence times between populations, herbivorous *Nesosydne* planthoppers, it was determined that populations diverged as little as 2,600 years ago (Goodman *et al.*, 2012) (Table 1).

## Ecological metrics across the island chronosequence

The degree distribution of Hemiptera species varied across the chronosequence with both the youngest and oldest sites deviating most from the statistical steady state maximum entropy predictions (Fig. 3). In the intermediate-aged site of Kohala, deviations from maximum entropy are not significantly different from predictions of maximum entropy.

The generalized linear model revealed significant differences between the degree distributions of single-island endemics (species whose distributions are restricted to only one island) versus archipelagic endemics that are found across multiple islands (Fig. 3). Single-island endemics show significantly lower degree distributions overall (i.e., more specialization) compared to more generalist species found across multiple islands. Furthermore, single-island endemics use more host plant species on the intermediate-aged Maui site. The slightly younger Kohala shows increased generalization for both single island endemics and archipelago endemics. However, when considering the degree distribution defined by trophic links to plant genera instead of plant species, the pattern of increased generalization holds for Kohala but endemics on Maui no longer show a difference in their degree distributions from other island endemics. This change in pattern suggests that increased generality of Maui endemics may be driven by increased plant species diversity within genera on that island.

Network nestedness decreased with habitat age while modularity increased (Fig. 4). This trend was recovered in networks constructed from both more and less stringent geographic criteria (supplemental Fig. S3). Choice of null model changed the magnitude of modularity and the sign of nestedness z-scores; however, the relative pattern of decreasing nestedness and increasing modularity remained across the different null models used to standardize network metrics (supplemental Fig. S2). The patterns were also robust to sampling intensity, as demonstrated by a rarefaction analysis (supplemental Fig. S4).

# Discussion

## Development of genetic population structure at different trophic levels

The analysis of available genetic data presented here indicate that divergence is occurring within the islands at small spatial scales and over short time periods (Table 1, Fig. 2). Furthermore, the scale of population structure varies with trophic position, with structure developing in sap-feeding herbivore lineages at smaller scales (and hence shorter time frames in the context of the chronosequence) compared to detritivorous crickets and predatory spiders (Table 1, Fig. 2). Structure within species may allow populations to take independent evolutionary trajectories, especially when aided by other evolutionary processes acting differentially across species geographic ranges. A variety of factors have been associated with the genetic divergence of populations and species in lineages described here, including combinations of genetic drift associated with geographic isolation (Percy, 2003; Mendelson & Shaw, 2005; O’Grady *et al.*, 2011; Goodman *et al.*, 2012), adaptation associated with competition, predation, and mutualism (Gillespie, 2004; Roderick & Percy, 2008; Brewer *et al.* 2015), and sexual signaling (Mendelson & Shaw, 2005; Percy *et al*. 2006; Magnacca *et al.*, 2008; Goodman *et al.*, 2015).

The *Nesosydne* planthoppers (Goodman *et al.*, 2012) provide evidence that some period of geographic isolation preceded divergence of sexual signals (Goodman *et al.*, 2015). Shifts in plant host use are also associated with diversification in this group (Roderick & Percy, 2008). In a phylogenetic study of a radiation of sap-feeding *Nesophrosyne* (Cicadellidae) leafhoppers, host plant specialization was implicated in driving species radiations up until approximately 1 million years ago (Bennett & O’Grady, 2013). Our network analysis indicates that specialization and modularity are more pronounced on Maui than on Hawaii Island (Figs. 3, 4), consistent with the phylogenetic results from *Nesophrosyne*. Available dating analyses of other arthropod taxa indicate that population genetic structure can develop in much less than 1 million years (Table 1), and suggests that landscape fragmentation processes (e.g. lava flows) may dominate the earliest stages of diversification across taxa in the Hawaiian Islands. Other taxa at low trophic levels, such as the herbivorous *Trioza* psyllids, detritivorous *Laupala* crickets and fungivorous *Drosophila*, show similar signals of geographic isolation combined with ecological and sexual processes driving genetic divergence and diversification across sites as young as those on Hawaii Island (Percy, 2003; Percy *et al*. 2006; Mendelson & Shaw, 2005; Magnacca *et al.*, 2008; O’Grady *et al.*, 2011). By contrast, spiders, which are predatory, develop genetic discontinuities at larger spatial and temporal scales with a strong signature of increasing structure with age of the chronosequence (Roderick et al., 2012;Table 1). Further work is needed to assess the generality of this pattern of slower genetic differentiation in predators compared to herbivores.

## Macroecological metrics: Network structure and steady state

Across the Hawaiian archipelago, nestedness appears to decrease generally with site age, and is highest on the geologically youngest volcano, Kilauea. High nestedness on Kilauea may arise with high immigration of new species with high probabilities to eat or be eaten by the generalist species already present at the site (Bascompte & Jordano, 2007). However, despite high nestedness on Kilauea, and thus potential for neutral colonization driven assembly, this site did not conform to the statistical steady state predication of METE. The observed deviations from METE at Kilauea appear to be largely driven by a surplus of singleton links (Fig. 3), which may reflect a state of “incomplete” assembly, possibly by lower species richness of the plant and herbivore biotas. Conversely, at Kohala, at intermediate age (150 ky), observations were not significantly different from predictions from METE. We posit that the reason theoretical predictions fit Kohala so well is that the site has had sufficient time to undergo ecological succession, and thus arrive at a statistical steady state, but is still too young to be affected by ecological specialization and rapid *in situ* diversification associated with host plants on older islands.

Interestingly, the communities on older Maui and Kauai sites show strong deviations from expectations of METE (Fig. 4). METE is agnostic about what mechanisms are determining the values of the state variables that lead to its macroecological predictions (Harte, 2011). It does not account for the evolutionary history of biological systems. Thus, one possible explanation for the strong deviations from expectations of METE, compared with observations at our intermediate-aged site (Kohala), is that while the ages of Maui and Kauai are sufficient for evolutionary assembly driven by specialization and diversification on host plants, the older island age of these islands may have led to range contractions and possibly extinction of plant species on the oldest island of Kauai (Whittaker et al 2008).

Our results show decreased nestedness and increased modularity on Maui and Kauai. Coevolution between interacting species should lead to greater modularity (Donatti *et al.*, 2011; Nuismer *et al.*, 2013). However, the influence of certain network properties such as nestedness on stability is still unknown, and so theoretical predictions of how network properties should change over evolutionary time, generally, are lacking. Theoretical and empirical studies have suggested that nestedness may or may not promote stability (Allesina & Tang 2012; Suweis *et al*. 2014). Furthermore, almost all studies of food webs have focused primarily on single, or short ecological timespans of network development that do not span as large an amount of evolutionary time as included here (e.g., Albrecht et al 2010). Food webs are dynamic emergent entities, with broad topological characteristics that may change dramatically over time (e.g., Yeakel et al 2013). To our knowledge, our study represents the first to evaluate network topology over larger temporal scales, and we argue that age-structured landscapes such as the Hawaiian archipelago are promising for resolving longstanding debates on the causes and consequences of network properties such as nestedness.

We found that single-island endemics were always more specialized than multiple-island endemics. While dietary breadth has been positively associated with geographic range size, the direction of causality is unclear (Slatyer et al., 2013): while dietary breadth may allow some species to colonize other islands, it also may be driven by adaptation to exploit locally abundant hosts across a large range. Nevertheless, both scenarios are consistent with the hypothesis that *in situ* formation of single-island endemics may be the product of coevolution and specialization. At the Kohala site, which showed the best fit to maximum entropy theory, single-island endemic and multiple-island endemic species alike showed increased generalization (i.e. higher degree, or more links; Fig 3), while at the youngest site of Kilauea, specialist single-island endemics may be limited by low plant diversity and thus appear more specialized (Fig 3). Conversely at the oldest site on Kauai, where plant diversity is high (Kitayama & Mueller-Dombois, 1995), single-island endemics again are associated with decreased degree and thus genuine specialization (Fig. 3). On Maui, single-island endemics show statistically significant increases in generalization but this pattern disappears when analyzing the data at the resolution of plant genera, thus suggesting that Hemiptera species endemic to Maui may benefit from the diversification of plant species within genera.

## Future Research

The data and analyses presented here describing insect and plant communities across a chronosequence of habitats in Hawaii generate testable hypotheses concerning the relative importance of ecological and evolutionary processes in community assembly. Our work to date suggests the overarching hypothesis that ecological processes dominate community assembly in younger environments, with evolutionary processes becoming increasingly important as communities age. We can also make predictions about the sequence of community assembly based on proposed mechanisms.

In younger communities we predict characteristics of ecological assembly, with species resembling random samples through immigration from regional source pools. Thus, metrics describing these communities will approach expectations of ecological statistical steady. An exception will be communities still undergoing initial stages of primary succession, which will change rapidly through time and represent non–random samples of source pools. We also predict that these communities will exhibit a nested network structure, assuming new species will eat or be eaten by the generalist species already present in the community, as suggested by previous work on nestedness (Bascompte & Jordano, 2007) and by our finding that widespread species tend to be generalists (Fig. 4).

Following the same logic, in older communities we expect to see characteristics of evolutionary assembly, dominated by processes such as adaptive exploration of niche space, giving way to speciation. Thus, we predict increasing specialization and modularity with time (Bascompte & Jordano, 2007; Donatti *et al.*, 2011; Nuismer *et al.*, 2013) as reflected by age across the chronoseqeunce.

### Ecological data: Assembly of species into communities

In order to build a more rigorous understanding of the assembly process in both younger and older communities, fine-grained sampling of all macroscopic arthropod taxa is needed from a large number of sites across the island chronosequence. This will allow an assessment of changes in overall species composition and diversity across all players in the time-calibrated landscape (*sensu* Gruner, 2007). Such data will allow us to test entire arthropod communities for deviations from METE predictions of statistical steady state (Harte, 2011) across different aged substrates. For example, predators, whose assemblages are likely more dominated by immigration and ecological assembly (Fig. 2) may never show strong deviations from METE predictions whereas herbivores could show increasing deviation with age in agreement with the network results of this paper (Fig. 3).

### Evolutionary data: Diversification within species

The current study demonstrates that taxa from different trophic guilds differ in the scale at which differentiation occurs and highlights the importance of fragmentation of the landscape in facilitating differentiation. Future work will be aimed at gathering data for additional focal taxa within this system spanning different trophic levels. We will use these data to understand taxonomic and functional differences in the rate of differentiation, to assess the roles of genetic fusion and fission and the spatial scale over which they are important in fostering diversification (Gillespie and Roderick 2014), and to detail the relative rates of speciation and extinction across the island chronosequence.

## CONCLUSIONS

We have shown how a chronosequence can be used to understand biodiversity dynamics across an ecological-evolutionary continuum. Focusing on entire communities of arthropods in the Hawaiian Islands allows us to incorporate predictions from idealized ecological theories to understand eco-evolutionary feedbacks and generate predictions of how entire communities develop over extended time. Such an approach may prove fruitful for investigating the separate and interactive roles of ecological and evolutionary drivers of community assembly using age structured systems as a simplified natural experiment, as exemplified by oceanic archipelagoes

We have demonstrated how taxa in the lower trophic levels developed genetic structure even in the youngest habitats of the observed chronosequence and at smaller spatial scales (Table 1, Fig. 2). Thus, lower trophic levels are affected by *in situ* processes of diversification very early in the chronosequence, compared to higher trophic levels, though *in situ* processes become more important over time in the latter. Network nestedness decreased while modularity increased with age (Fig. 4), again indicating a possible shift from assembly driven by *ex situ* immigration early on, to one based on *in situ* diversification, such as in co-diversification of insect herbivores with host plants (Bascompte & Jordano, 2007; Donatti *et al.*, 2011). That single island endemics (likely the product of *in situ* diversification) show more specialization at older sites compared to more broadly distributed species (those taxa more likely to be initial colonists; Fig. 3) also supports this hypothesis.

This study provides a framework for using chronologically arranged oceanic island systems to examine the interplay between evolutionary and ecological processes in shaping biodiversity. Our initial results provide a clear hypothesis that ecological processes dominate community assembly in younger environments, with evolutionary processes becoming more important as communities age. We demonstrate how this approach can provide insights into the development of communities over ecological–evolutionary time, and the dynamic feedbacks involved in assembly.

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# Biosketch

The authors are part of a large team involved in understanding how biodiversity and complex ecosystems emerge from ecological and evolutionary processes. The project, funded by the National Science Foundation’s “Dimensions in Biodiversity”, focuses on the geological chronosequence provided by the Hawaiian Islands.

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# TABLES

**Table 1.** Results of the analyses of molecular variance (AMOVA) that partitions molecular genetic variation ( for all taxa except *Laupala* for which we used *FST*) between volcanoes and between sites within volcanoes for arthropod lineages found within the study sites on Hawaii Island. Where estimates of divergence through molecular dating are available for the taxa, they are presented to show the timeframe within which this genetic structure has developed.

# Figure captions

**Figure 1.** Substrate age map of the islands of Kauai, Maui and Hawaii Island. Colors correspond to substrate age from young (yellow) to old (blue). Focal sites are shown as black circles (on Hawaii Island, Kohala is in the north, Kiluea in the south) while sampling sites for genetic data are represented by gray circles.

**Figure 2.** Genetic population structure ( for all taxa except *Laupala* for which we used *FST*) among sites within volcanoes with volcano age for insects and spiders. Calculations were based on mitochondrial DNA only (see Table 1 for details). The plant-feeding groups, specifically the sap-feeding Hemiptera, show higher genetic structure among sites on young volcanoes relative to older volcanoes whereas detritivores (crickets), fungivores (*Drosophila*), and in particular predators (spiders), show little structure on young volcanoes. For spiders, substantial structure develops only later in the chronosequence, e.g., on Maui at approximately 1 million years. Numbers refer to different species: 1. *Nesosydne chambersi*, 2. *Nesosydne raillardiae*, 3. *Nesosydne bridwelli*, 4. *Trioza HB*, 5. *Trioza HC*, 6. *Drosophila sproati*, 7. *Laupala cerasina*, 8. *Tetragnatha anuenue*, 9. *Tetragnatha brevignatha*, 10. *Tetragnatha quasimodo*, 11. *Theridion grallator*.

**Figure 3.** Patterns in degree distributions across sites, comparing archipelago-wide endemics (Cosmopolitans) with single island endemic (Endemics) taxa. Top panels show that networks deviate most from METE predictions on youngest and oldest sites. Inset figures show the distribution of simulated mean squared errors; if the red line falls within the gray region (95% confidence interval) the data are not significantly different from the predictions of maximum entropy theory; all sites except Kohala deviate from the predications. The bottom panel shows the number of links for endemics versus cosmopolitans. Endemics show lower linkage overall, but significantly increase on the intermediate-aged site Maui (highlighted with dotted box). Kohala shows increased linkage overall (highlighted with solid box).

**Figure 4.** Trends in network metric nestedness and modularity through time. Nestedness decreases while modularity increases. Error bars represent 95% confidence intervals from a null model simulation.

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Additional references to the data sources may be found in Appendix S1 at [URL].