Community assembly on isolated islands: Macroecology meets evolution

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1 Abstract

2 **Aim** Understanding how ecological and evolutionary processes synergistically determine
3 biodiversity patterns remains a central goal in biology. In highly isolated archipelagoes such
4 as the Hawaiian Islands, beyond the reach of frequent colonization, rapid *in situ* diversifi-
5 cation has the potential to keep pace with ecological dynamics such as biotic filtering and
6 demography in structuring local biodiversity. Using ecological theory as a conceptual guide
7 and data from multiple arthropod lineages across the Hawaiian model system, we explore
8 how complex communities emerge from the interplay of ecological (population dynamics, dis-
9 persal, trophic interactions) and evolutionary (genetic structuring, adaptation, speciation,
10 extinction) processes.

11 **Location** The Hawaiian Islands (19.5N, 155.5W).

12 **Methods** To infer processes involved in early diversification we synthesize data on genetic
13 structure of select arthropod species across Hawaiian landscapes of known age. Across the
14 range of geological ages of the current high islands ($<$ 1 my to 5 my) we also develop and
15 analyze a plant-herbivore bipartite network. We compare the structure of these networks,
16 measured by nestedness, modularity and the degree distributions, with theoretical predic-
17 tions derived from the principle of maximum information entropy.

18 **Results** Based on the time perspective provided by the island chronosequence and genetic
19 information, we demonstrate that species in lower trophic levels develop local divergence
20 more quickly than species of higher trophic levels. Higher trophic levels also show endemism,
21 though it evolves more slowly and over larger areas. Moreover, in analyzing plant-herbivore
22 networks across an increasing substrate age gradient we find trends of higher specialization
23 and increasing deviation from the statistical steady state expected from theoretical predic-
24 tions of food web structure.

Main conclusions   We show how ecological theory can leverage natural experiments on oceanic islands of known chronologies to understand how the interplay between evolutionary and ecological processes has shaped present-day biodiversity. We advocate for combining perspectives gained from coupled molecular and community-level data analyzed in the context of ecological theory. Theory provides a lens through which to identify interesting biological outliers. We further show the utility of applying theory in a chronosequence context to better illuminate the interplay of ecological mechanisms, speciation, extinction and adaptation in driving contemporary biodiversity patterns.

Introduction

Contemporary biodiversity is an unresolved product of speciation, extinction and dispersal all conditioned by ecological interactions with the biotic and abiotic environment. Because these processes occur on different temporal and spatial scales and may be interactive with nonlinear feedbacks and lags among them, disentangling the relative influence of local ecological mechanisms from evolutionary and historical processes is challenging (Ricklefs, 2004). The integration of ecological and evolutionary theory has the potential to reveal dynamics that generate biodiversity.

The evolutionary processes of speciation and extinction tend to be viewed as regulating regional species pools, occurring in a manner largely removed from local ecology (Hubbell, 2001; Cavender-Bares *et al.*, 2009; Wiens, 2011). Ecological mechanisms tend to be viewed as packing standing diversity into local communities through competition, facilitation, and neutral ecological drift (Hubbell, 2001; Tilman, 2004; Bascompte & Jordano, 2007; Chase & Myers, 2011; Borer *et al.*, 2014). Recent theoretical advances have further refined the causes and consequences of ecological drift (Hubbell, 2001; Rosindell & Phillimore, 2011; Rosindell *et al.*, 2012), re-vitalized classical niche-based mechanisms such as niche partitioning (Tilman, 2004; Chesson, 2000), competition and predation (Borer *et al.*, 2014), and put species interactions in a network theoretic context (Williams & Martinez, 2000; Brose

et al., 2006; Berlow *et al.*, 2009). The combined advances of ecological theory, with its broad predictive power, and insights into evolutionary mechanisms based on inference from contemporary patterns of species, genetic, or phylogenetic diversity (e.g., Kreft & Jetz, 2007; Jetz *et al.*, 2012; Wiens & Donoghue, 2004; Wiens, 2011) have set the stage to address longstanding questions of how evolutionary history can drive common patterns in contemporary ecology (Ricklefs, 1987). Here, we propose an integrative framework to study evolutionary community assembly. We then provide an initial test using arthropod lineages in the model archipelago of the Hawaiian Islands using mostly published data. We estimate metrics of evolutionary and ecological dynamics across communities that range in age from 500 yr to 5 myr: (1) The timeline for the development of genetic discontinuity and the extent to which taxa across communities differ in the rates that populations change from panmixia to fully differentiated species. This is contextualized with (2) macroecological metrics of community structure, using predictions from statistical steady state and ecological network theory to examine changes over the island chronosequence.

Hotspot oceanic archipelagos as model systems

Hotspot oceanic island systems are opportune model systems for studying the interplay of local ecological mechanisms and large–scale, historical, and evolutionary drivers of biodiversity patterns. Such island systems are discrete in space and in time due to their sequential formation as the tectonic plate moves over a volcanic hotspot. We hypothesize that the contributions of evolutionary and ecological assembly will vary according to geological age of the environment, taken as an indicator of the total time communities have had to assemble and over which *in situ* diversification could occur. Age–structured, hot–spot island archipelagoes thus have the potential to stratify the eco–evolutionary process of community assembly.

For example, younger communities by necessity originate mostly from initial immigration (from neighboring older volcanoes and islands or from the mainland, depending on the level of isolation), and thus should be dominated by ecological mechanisms operating on a source

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pool whose evolution is removed from the local setting. Conversely, older islands could allow observation of the combined interaction and feedback of the diversification of the source pool and local ecological dynamics. The temporal stratification within such archipelagoes hence provides an opportunity to disentangle these interacting processes. Moreover, because dispersal, and hence connectivity between sites, differs between taxa, the relative role of evolutionary and ecological assembly will differ between taxa. While many archipelagos around the world share these biotic and geologic properties, the Hawaiian archipelago provides a particularly useful system for study because its geological chronology (Price & Clague, 2002) and patterns of biodiversity are well characterized (Wagner & Funk, 1995).

Development of genetic discontinuity

Movement of individuals among localities connects the population dynamics of those localities. Even moderate levels of genetic connectivity among geographically separated populations limits the potential for local divergence (Wright, 1978; Slatkin, 1987). Thus, in the face of connectivity among populations, one predicts that the structure of ecological communities will remain similar across space. By contrast, when connectivity is low, not only are the ecologies of populations in different localities free to vary, but genetic divergence is also more likely. For these reasons, the magnitude of connectivity among population provides a measure of the relative importance of ecological processes and evolutionary processes in determining differences among ecological communities. Here, by using the chronosequence, we can apply this approach to sets of communities from young to old and to taxa representing different trophic levels.

Macroecological metrics

While we expect the mechanisms underlying the generation and maintenance of biodiversity to change across chronological sequences, studies to date have rarely moved beyond reporting basic patterns (Gillespie & Baldwin, 2010). Theory provides a necessarily simplified view of biodiversity and deviations from theory can reveal which more biologically realistic

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mechanisms likely underlie observed patterns. The Maximum Entropy Theory of Ecology (METE; Harte, 2011) provides a prediction for idealized ecological communities in statistical steady state. Statistical steady state describes the situation in which a system's behavior is governed by a simple set of state variables and no further system-specific mechanisms are required (Harte, 2011; Harte & Newman, 2014). Thus METE, while in a sense neutral, makes fewer assumptions than neutral theory (Hubbell, 2001), allowing for the possibility that myriad ecological mechanisms influence communities. However, METE assumes that these mechanisms have no statistical effect on the macroscopic biodiversity patterns of the system. Real world deviations from METE can provide insights into the processes driving ecology away from this statistical steady state and toward alternate system states (Harte, 2011). We expect that different aged communities along the Hawaiian chronosequence will deviate differently from METE, because we hypothesize the processes of speciation, extinction, adaptation and colonization may themselves drive Hawaiian communities out of statistical steady state.

METE can successfully predict various metrics of an ecological community (Harte, 2011), including network metrics that describe trophic interactions between species (Williams, 2010; Harte, 2011). Ecological network theory incorporates evolutionary concepts such as coevolution (Bascompte & Jordano, 2007; Donatti *et al.*, 2011; Nuismer *et al.*, 2013) and has clear ties with macroecological questions of the distribution of abundance and body size across species (Berlow *et al.*, 2009; Williams, 2010; Harte, 2011). The distribution of linkages in ecological networks has been used to determine whether plant-animal interaction networks assemble neutrally or through deterministic processes (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 this paper we integrate methods from population genetics to theoretical ecology using

the chronosequence of the Hawaiian Archipelago to understand the nexus between ecological and evolutionary forces community assembly. Moving rom young to old across the chronosequence we evaluate (1) the rate and pattern of genetic connectivity among populations of taxa from different trophic levels as they diversify from populations to form new species; (2) the processes underlying the structure of species interaction networks given the backdrop of population divergence; and (3) the processes involved in diversification as species form and accumulate and how this dynamic drives deviations from statistical steady state. We use data (mostly published) on population genetic structure and species interactions as a proof of concept. With this framework, our goal is to show how communities develop over ecological-evolutionary time, and the dynamic feedbacks involved assembly.

Methods

Hawaii as an eco-evolutionary study system

The geological landscape of the Hawaiian Islands offers a matrix of volcanic substrates mapped in fine detail by chronological age and geochemical composition (Sherrod *et al.*, 2007). On Hawaii Island in particular, independent gradients in elevation and precipitation interact within a matrix of substrate ages ranging from contemporary (active) to 500,000 years. Ongoing volcanic activity has created a dynamic mosaic of habitats with transitory to long-lasting fragmentation within landscapes. Isolation on scales of hundreds to thousands of meters and hundreds to thousands of years can be sufficient for genetic differentiation among some arthropod populations among habitats (Goodman *et al.*, 2012; Eldon *et al.*, 2013; Bennett & O'Grady, 2013), while insufficient to isolate others (Vandergast *et al.*, 2004). On larger spatial and temporal scales, distinct volcanoes and islands, with their semi-independent histories of evolutionary community assembly from recent to ancient, comprise a space-for-time geological chronosequence spanning from present day up to 5 million years across Hawaii Island to Kauai.

To investigate how ecological patterns change in response to varied evolutionary contexts

we selected four focal sites across the chronosequence of substrate and island ages (two on Hawaii Island, one on Maui and one on Kauai). Focal sites were selected to have similar forest composition (dominated by *Metrosideros polymorpha*: Myrtaceae), elevation (1100-1400m), and climate (mean annual precipitation 2000-3000 mm), while deliberately varying substrate age. These forested montane sites are well-studied and primarily composed of native plant and arthropod species . The four sites span the chronosequence from 0.00025 million years (Kilauea and Kohala (Hawaii Island); Waikamoi (Maui), Kokee (Kauai); see Fig. 1).

Compilation and analysis of genetic data

To evaluate the balance between region immigration and potential for local ecological differentiation, we measured how molecular variation is partitioned within species within locations of known substrate age on Hawaii Island and Maui. We compiled published and new data sets for a diversity of native Hawaiian arthropod groups that represent a spectrum of trophic levels:

1. Herbivorous *Nesosydne* planthoppers (COI and microsatellites; Goodman *et al.*, 2012, GenBank accession numbers XXX-XXX); *Trioza* psyllids (COI, cytB; GenBank accession numbers XXX-XXX); and fungivorous *Drosophila sproati*: (COII; Eldon *et al.*, 2013) that maintain tight host plant associations.

2. Detritivorous *Laupala* crickets (AFLPs; Mendelson *et al.*, 2004); and

3. several predatory spiders species (COI and allozymes; Roderick *et al.*, 2012; Croucher *et al.*, 2012)

In the case of previously unpublished molecular data, sequences for *Nesosydne* planthoppers were generated following protocols described in (Goodman *et al.*, 2012) and sequences for *Trioza* psyllids were generated following protocols described in Percy (2003) with primers given in Simon *et al.* (1994) and Timmermans *et al.* (2010). Existing genetic data from across Hawaii Island and Maui (including, but not limited to the focal sites), provide an estimate of how arthropod populations have accumulated genetic diversity and divergence within the

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182 dynamic landscape of the focal sites.

183 We used analysis of molecular variance (AMOVA) to examine how genetic variation is
184 partitioned at two scales of population structure: among sites within volcanoes and among
185 volcanoes on both Hawaii Island and Maui Nui. All analyses of allozyme and DNA sequence
186 data were performed in Arlequin v. 3.5 (Excoffier & Lischer, 2010) using the AMOVA pro-
187 cedure to compute F_{ST}, a measure of genetic variance, or, where possible Phi_{ST}, an F_{ST}
188 analog that incorporates genetic sequence information. The *Laupala* AFLP data were ana-
189 lyzed using TFPGA v. 1.3 (Miller, 1997), using the same hierarchical approach as described
190 above. To provide a temporal framework for the population differentiation analysis we as-
191 sembled divergence dating information from the literature for as many of the taxa as possible
192 and additionally implemented a new divergence dating analysis for *Tetragnatha* spiders (see
193 supplementary information).

194 To explicitly evaluate the role of landscape age in allowing *in situ* genetic diversity and
195 potential for divergence we analyzed how within site F_{ST} varies with the geologic age of
196 volcanoes on Hawaii Island and Maui Nui. For each volcano we calculated F_{ST} or Φ_{ST}
197 (Excoffier & Lischer, 2010) for each taxon between sites within volcanoes.

198 Construction of plant-herbivore networks

199 Bipartite networks describe the topology of ecological interactions between two guilds of
200 organisms (e.g. herbivores and their plant hosts). Quantitative information on the relative
201 importance of interaction links can be incorporated into network analyses (Vázquez *et al.*,
202 2009); however, currently available data are restricted to binary networks, those that describe
203 only the potential for interaction between any two species, but not the relative frequency of
204 that interaction to each species.

205 We compiled species lists of all endemic hemipteran herbivores for each focal site from
206 published species accounts (see supplement for full list). Species accounts and other pub-
207 lished sources were used to determine the presence, probable presence, or probable absence

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of each Hemiptera 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 hemipteran species 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 was 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, 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 hemipteran species presences and the other using the less conservative data set.

Analysis of plant-herbivore networks

We hypothesize that communities differentially depart from statistical steady state along the continuum form those dominated by ecological processes to those with potential complex evolutionary feedbacks We used METE (Williams, 2010; Harte, 2011) to compute the statistical steady state for the hemipteran degree distribution (distribution of the number of plant hosts to each hemipteran species). 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

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₂₃₄ used for METE estimation and Monte Carlo methods are available in the supplement.

₂₃₅ To further investigate how *in situ* diversification leaves a potentially unique signature on
₂₃₆ network structure we analyzed the number of links assigned to each hemipteran species (the
₂₃₇ degree distribution) separately for island endemics (those species found on only one island
₂₃₈ and thus likely derived from in situ diversification) versus island cosmopolitans (those species
₂₃₉ found on multiple islands). To compare species' degree distributions between endemics and
₂₄₀ cosmopolitans across sites of different ages we conducted a generalized linear model with
₂₄₁ binomial error, treating site identity as a categorical predictor. Binomial errors effectively
₂₄₂ account for network size due to the bounded support of the binomial distribution.

₂₄₃ To understand how other network properties change with ecosystem substrate age, we
₂₄₄ calculated two widely used descriptive network metrics across sites—nestedness, which de-
₂₄₅ scribes the degree of asymmetry of species interactions connecting specialists and generalists
₂₄₆ (Bascompte *et al.*, 2003; Ulrich *et al.*, 2009), and modularity which describes the degree
₂₄₇ to which interactions are concentrated within subsets of species but not between subsets
₂₄₈ (Newman & Girvan, 2004; Olesen *et al.*, 2007).

₂₄₉ We calculated nestedness using the NODF metric (Almeida-Neto *et al.*, 2008) as imple-
₂₅₀ mented in the R package `vegan` (Oksanen *et al.*, 2013) and modularity using a variety of
₂₅₁ algorithms implemented in the R package `igraph` (Csardi & Nepusz, 2006). These metrics
₂₅₂ are not directly comparable across networks of different size and connectance (Ulrich *et al.*,
₂₅₃ 2009), so for each metric in each network we calculate z-scores using a null model that ran-
₂₅₄ domizes network structure while maintaining certain aggregate network properties (Ulrich
₂₅₅ *et al.*, 2009). These z-scores are calculated as the difference between the observed network
₂₅₆ metric minus the mean of the null model divided by the null model standard deviation, or
₂₅₇ $(x_{obs} - \bar{x}_{sim})/sd_{sim})$. Because z-scores can be highly sensitive to the choice of null model
₂₅₈ (Ulrich *et al.*, 2009) we implemented both a probabilistic null model (Bascompte *et al.*, 2003)
₂₅₉ and a null model that strictly constrains the degree distributions of plants and herbivores
₂₆₀ (Ulrich *et al.*, 2009). The probabilistic null using the frequency of interactions as the proba-

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bility that a randomized link gets assigned to that cell in the interaction matrix (Bascompte *et al.*, 2003); thus the probabilistic null constrains row and column sums in probability but not absolutely.

Results

Population genetic inference of discontinuity among populations

The analysis of molecular variance (AMOVA) revealed evidence of significant population genetic structure from the smallest to the largest spatial scales examined, all within a very recent timeframe. For mitochondrial loci, the amount of statistically significant molecular variation partitioned to among sites within volcanoes ranged from 0.037-0.92 and to the among volcanoes from 0-0.30. Corresponding variation at multilocus nuclear loci between-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 between (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 on young volcanoes relative to between localities on older volcanoes (Fig. 2). By contrast, predatory spiders exhibited higher genetic population structure only on older volcanoes (e.g. Maui).

The observed levels of genetic divergence have evolved rapidly. For example, within species genetic divergence in planthoppers has evolved in as little as 2,600 years (Goodman *et al.*, 2012). For species from Hawaii Island for which phylogenetic data provide divergence times, estimates of dates of species divergence range from 0.341.15 million years, with additional within-species genetic divergence developed subsequently (Table 1).

Evolving network structure

The Hemiptera species degree distribution 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 middle aged site of Kohala, minor deviations from maximum entropy are no different than expected by chance indicating the Kohala Hemiptera assemblage matches the predictions of maximum entropy.

The generalized linear model revealed that there are also significant differences between the degree distributions of island endemics (those species found on only one island) versus island cosmopolitans (those species found on multiple islands; Fig. 3). Endemics show significantly lower degree distributions overall (i.e., more specialization) compared to more generalist cosmopolitan species. Endemics become significantly more generalist on the middle aged Maui site; however this pattern disappears when analyzing links to plant genera instead of species. The slightly younger Kohala shows increased generalization overall. When considering the degree distribution defined by trophic links to plant genera instead of plant species, the pattern of increased generalization holds for the Kohala but endemics on Maui no long 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 intra-genus plant diversity on that island.

Network nestedness decreased with age while modularity increased (Fig. 4). This trend is found in networks constructed from both more and less stringent geographic criteria (supplemental Fig. 3). 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. 2). The patterns are also robust to sampling intensity, as demonstrated by a rarefaction analysis (supplemental Fig. 4).

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Discussion

By combining disparate data with a novel combination of analytical approaches that incorporate population genetics, bipartite networks and maximum entropy theory, our results present evidence for the timeline over which evolution begins to keep pace with ecology in determining the local diversity of communities. Taxa in the lower trophic levels, as compared to higher trophic guilds, developed genetic discontinuities more quickly along the chronosequence and at much smaller spatial scales (Table 1, Fig. 2), allowing them the opportunity to diverge ecologically. Network nestedness decreased while modularity increased with age (Fig. 4), indicating a possible shift from assembly driven by *ex situ* immigration early on, to one based on *in situ* co-diversification with host plants (Bascompte & Jordano, 2007; Donatti *et al.*, 2011). This possibility is further strengthened by the observation that single island endemics show more specialization compared to more broadly distributed species (Fig. 3). At intermediate modularity and nestedness, the distributions of the number of links assigned to each hemipteran species showed the least deviation from the METE prediction (Fig. 3), suggesting that at the transition from primary succession to evolutionary assembly, these plant-herbivore communities reach statistical steady state.

Development of genetic discontinuity at different trophic levels

The analysis of available genetic data presented here indicates 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 the sap-feeding herbivores in this study showing structure at smaller scales compared to detritivorous crickets and predatory spiders (Table 1, Fig. 2). Population structure within species allows for populations to take independent evolutionary trajectories, especially when aided by other evolutionary processes that may be acting differentially across each species' range. A variety of factors have been implicated in the genetic divergence of populations and species in lineages described here, including combinations of genetic drift associated with geographic isolation

(Percy, 2003; Gillespie, 2005; Mendelson & Shaw, 2005; O'Grady *et al.*, 2011; Goodman *et al.*, 2012), adaptation associated with ecological interactions of competition, predation, and mutualism (Gillespie, 2004; Blackledge & Gillespie, 2004; Roderick & Percy, 2008), and sexual signaling (Mendelson & Shaw, 2005; Percy & Kennedy, 2006; Magnacca *et al.*, 2008; Goodman *et al.*, in review).

The sap-feeding Hemiptera group *Nesosydne* (Goodman *et al.*, 2012) provide evidence that some period of geographic isolation preceded divergence of sexual signals (Goodman *et al.*, in review). Shifts in plant host use are also involved in the process of diversification in this group (Roderick & Percy, 2008). In a similar radiation of leafhoppers, *Nesophrosyne* (Bennett & O'Grady, 2013), host plant specialization was implicated in driving species radiations up until approximately 1 million years ago, when plant niches were mostly exhausted on Maui; following this period, speciation, largely on the Hawaii Island, shifted to geographic mechanisms of diversification. Our network analysis indicates that specialization and modularity begin to show pronounced signals in network data on Maui (Figs. 4, 3), in agreement with the *Nesophrosyne* results and indicating that an approximate age of 1 million years may be necessary for host plant specialization to become the dominant process in the sequence of diversification. Other taxa at lower 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 the Hawaii Island (Percy, 2003; Percy & Kennedy, 2006; Mendelson & Shaw, 2005; Magnacca *et al.*, 2008; O'Grady *et al.*, 2011). As a contrast, spiders, which are predatory, only develop genetic discontinuities at larger spatial and temporal scales. Most important in the context of community assembly is that endemic sap-feeding herbivores developed structure quickly (on the order of less than 0.1 million years; Table 1), with predatory spiders showing local endemicity more slowly (Table 1).

Macroecological metrics: Network structure and steady state

On the geologically youngest volcano, Kilauea, ecological assembly should be the dominant process there. The results of network analysis support this hypothesis with Kilauea showing substantial nestedness and limited modularity (Fig. 4). Nestedness is likely to result if new species arriving by immigration have a high probability to eat or be eaten by the generalist species already present at the site (Bascompte *et al.*, 2003). In this way we might expect Kilauea to also conform to the statistical steady state predication of maximum entropy. However, the observed deviations from maximum entropy at Kilauea are largely driven by a surplus of singleton links (Fig. 3). These in turn likely result from incomplete assembly, and thus lower species richness, of the plant and herbivore biotas. Future research should focus on the observation from genetic analysis that indicates discontinuities can arise within species on short timescales that, in some taxa, include the greater landscape of Kilauea (Table 1). Conversely, Kohala shows a statistically significant agreement with maximum entropy perhaps because the Kohala site, at intermediate age (150 ky), has experienced complete ecological succession but is still too young to be driven away from statistical steady state by specialization and rapid in situ diversification driven by host plant preference

The older Maui and Kauai sites show strong deviations from expectations of maximum entropy theory (Fig. 4), which is consistent with our hypothesis that the influence of evolutionary assembly on these biotas drives them away from statistical steady state. The application of maximum entropy to ecology does not currently take into account evolution (Harte, 2011). Indeed the use of maximum entropy in ecology is inspired by its application to physical systems whose change through time is simple and lacks the evolutionary memory of biological systems, potentially a far cry from the complex change through time produced by speciation, extinction and adaption to novel ecosystems (Eldredge, 1989). Maui and Kauai show strong evidence of evolutionary assembly driven by specialization and diversification on host plants, particularly demonstrated by decreased nestedness and increased modularity (Fig. 4). Modularity is known to result from coevolution selectively driving the traits of

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interacting species towards convergence (Donatti *et al.*, 2011; Nuismer *et al.*, 2013).

The analysis of island endemic and cosmopolitan (archipelago-wide) Hemiptera species sheds further light on the evolution of the networks they form. Endemics are always more specialized than cosmopolitans, further supporting the hypothesis that in situ diversification and evolutionary assembly favor coevolution. At the Kohala site , which showed the best fit to maximum entropy theory, endemic and cosmopolitan species alike show increased generalization (i.e. higher degree; Fig 3), while at the youngest site Kilauea, specialist endemics are limited by low plant diversity and thus show more apparent specialization (Fig 3). Conversely at the oldest site on Kauai, where plant diversity is not limiting (Kitayama & Mueller-Dombois, 1995), endemics again show decreased degree and thus genuine specialization (Fig. 3). On Maui, endemics show statistically significant increases in apparent generalization but this pattern disappears when analyzing the data at the resolution of plant genera, thus suggesting that Hemiptera species endemic to Maui are no more generalized on plant genera but instead may benefit from the diversification of plant species within genera on Maui.

Future Research

The analyses presented here indicate strong patterns of a dynamic assembly process leading to contrasting hypotheses concerning the relative importance of ecological and evolutionary depending on the evolutionary age of the community under observation. In future work we will tackle these hypotheses using detailed quantitative ecological and genomic data collected from across the Hawaiian archipelago.

1. In younger communities we hypothesize that

    (a) during periods of ecological assembly, communities strongly influenced by immigration will resemble random samples from regional source pools and thus metrics describing these communities will largely match expectations of statistical steady state after primary succession has completed;

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(b) the exception will be communities still undergoing primary succession, which will change rapidly through time and represent non–random samples of source pools;

(c) we also predict that these communities will exhibit a nested network structure, assuming new species will eat or be eaten by the generalist species (Bascompte *et al.*, 2003) already present in the community.

2. Following the same logic, in older communities we hypothesize that

(a) during periods of evolutionary assembly, if processes such as niche exploration, adaptation and speciation happen fast enough to keep pace with immigration, the resultant communities could be driven into alternate evolutionary states that fail to meet the predictions of purely statistical theories that do not account for evolutionary dynamics (Harte, 2011);

(b) networks in such communities should exhibit higher levels of specialization and modularity (Bascompte & Jordano, 2007; Donatti *et al.*, 2011; Nuismer *et al.*, 2013).

3. Systems undergoing rapid ecological and evolutionary change are generally expected to deviate most from statistical steady state; thus we expected populations in such communities to show genetic signatures of rapid change, from bottlenecks or population expansion to selection.

Evolutionary data: Diversification within species

The current study demonstrates that taxa of different trophic guilds differ in the scale at which differentiation occurs, and highlights the importance of fragmentation of the landscape in facilitating differentiation. For some taxa fragmentation clearly allows genetic separation. For others, in particular those that are more connected, the fragmentation can provide a way of enhancing adaptive differentiation (Gillespie & Roderick, 2014). Future work is aimed at gathering genomic SNP data for focal taxa within this system that represent different trophic levels. We will use it to understand taxonomic differences in the rate of differentiation, to assess the roles of genetic fusion and fission, and to detail the relative rates of speciation and

extinction across the island chronosequence.

For lineages characterized by extensive ecological diversification, recent work has highlighted the potential role of multiple colonizations and admixture in enhancing variability: while a break in gene flow is necessary for adaptive differentiation, hybridization and genetic admixture are key in the generation of adaptive variation and functional novelty (Seehausen & Schluter, 2004; Rius & Darling, 2014). Numerous studies demonstrate that the negative effects of genetic founder effects may be offset if different colonization events result in multiple genotypes within the introduced population (see Rius & Darling, 2014, and citations therein). This highlights the potential role of admixture among successively introduced populations in providing the genetic variation to allow adaptive evolution over surprisingly short time scales.

Ecological data: Assembly of species into communities

Our results show that the island chronosequence can reveal important insights into the process of community assembly, namely that ecological processes dominate in younger environments, with evolutionary processes becoming more important later. However, in order to understand the nature of the assembly process and the dynamic nature of the feedbacks involved, future work is focusing on conducting broad sampling of all macroscopic arthropod taxa at a number of sites across the age gradient, thus allowing assessment of changes in overall species composition and diversity across all players in the time-calibrated landscape (*sensu Gruner, 2007*).

Such data will also allow us to test how entire arthropod communities of different aged substrates deviate from statistical steady state as predicted by METE (Harte, 2011). For example, predators, whose assemblages are likely more dominated by immigration and ecological assembly (Fig. 2) are hypothesized to never show strong deviations from METE predictions whereas herbivores are hypothesized to show increasing deviation with age and potentially at the youngest sites as well in agreement with the network results of this paper (Fig. 3).

The current study provides a framework for the use of chronologically arranged oceanic island systems to examine the interplay between evolutionary and ecological processes in shaping biodiversity. We analyze preliminary molecular and community–level data together in the context of ecological theory to demonstrate how this approach can provide insights into how communities develop over ecological–evolutionary time, and the dynamic feedbacks involved in assembly.

Acknowledgement

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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. Each of the co-authors are involved in the effort, although Rominger, working closely with Goodman, Lim, and Valdavinos, played the key role in tying the elements together for the current manuscript. Macroecological tools that have been employed for the study include those developed by Harte and Martinez. From the more empirical side, Gruner has long standing projects in the Hawaiian Islands on the ecological underpinnings of community diversity. Rominger, Lim and Fernandez bring a macroecological perspective to the project. From the evolutionary perspective, Shaw's research focuses on *Laupala* crickets; Ewing on nitidulid beetles, Goodman Bennet and Roderick on Hawaiian planthoppers; Percy on endemic psyllids; O'Grady and Price on Hawaiian *Drosophila*; and Cotoras with Gillespie on spiders.

Tables

Group	Species	Island(s)	Data (# individuals: length/ # markers)	Between Volcanoes % variation (p-value)	Within volcanoes % variation (p-value)	Data source	Timeframe citation
Planthoppers	*Nesosydne chambersi*	Hawaii	mtDNA COI (187:653) msat (292:13)	0.05*** -- 0.04***	0.77*** -- 0.21***	Goodman et al. 2012	WSD[1]: Saddle Road pops=2.6 (95% HPD: 1.2-35.1) x 10^3yrs / WSD[1]: Mauna Kea/Mauna Loa pops: 20.1 (95%HPD: 7.4-135.0) x 10^3yrs / Goodman et al. 2012
	Nesosydne raillardiae	Hawaii	mtDNA COI (33:581)	0.26***	0.49***	this paper	na
	Nesosydne bridwelli	Maui	mtDNA COI (34:677)	na	0.18**	this paper	na
Psyllids	*Trioza HB[4]*	Hawaii	mtDNA COI & cytB (29:857)	-0.14***	0.92***	this paper	na
	Trioza HC[4]	Hawaii	mtDNA COI & cytB (17:857)	0.17**	0.53**	this paper	na
Fly	*Drosophila sproati*	Hawaii	mtDNA COII (232:570)	0.11***	0.81***	Eldon et al. 2013	Max age[2]=1.15 (95%HPD: 0.75-1.5) my. Magnacca and Price, in review
Cricket	*Laupala cerasina*	Hawaii	AFLP (631)	0.30***	0.58***	Mendelson and Shaw 2005	na
Spiders	*Tetragnatha anuenue*	Hawaii	mtDNA COI (162: 607) allozymes (12:9)	0.23*** na	0.041*** na	Roderick et al. 2012	na
	Tetragnatha brevignatha	Hawaii	mtDNA COI (54:605)	0.16*	0.00	Roderick et al. 2012	*T. macracantha* Max age[2]=0.34 (95%HPD: 0.14-0.58) my. *Supplementary info, this paper*
	Tetragnatha quasimodo	Hawaii	mtDNA COI (149:439) allozymes (46:9)	0.09*** 0.34***	0.037*** na	Roderick et al. 2012	Node age[2]=0.80 (95%HPD: 0.50-1.16) my. *Supplementary info, this paper*
	Theridion grallator	Hawaii	mtDNA COI (209:1270) allozymes (224:8)	0.30*** 0.19***	0.05*** na	Roderick et al. 2012	Node age[3]=0.56 (95%HPD: 0.37-0.75) my. Croucher et al. 2012
	Ariamnes spp.	Hawaii	mtDNA COI (8:420)	0.05	na	Roderick et al. 2012	na

*** < 0.001, ** < 0.05, *<0.10; na = no information available
[1]WSD = Within-species divergence, estimated using IM.
[2]Max age = the node age of the phylogenetic split between this species and its sister species, calculated using divergence dating analyses performed in BEAST. In most cases, this will be an overestimate of the node age of the species itself, but is the best information we have at present.
[3]Node age = Age of the most recent common ancestor of the monophyletic group on Hawaii Island, estimated using BEAST.
[4] These *Trioza* species are in the process of being described; HB and HC are their provisional identifiers (Percy in prep).

Table 1: Proportion of genetic variation distributed at between volcanoes and among sites within volcanoes.

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 while sampling sites for genetic data are represented by gray circles.

Figure 2. Genetic population structure (F_{ST}) among sites within volcanoes with volcano age for insects and spiders. The plant-feeding groups, specifically the sap-feeding Hemiptera, show high 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. Number 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 and different biogeographic classifications of taxa. Top panels show that networks deviate most from MaxEnt 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 conform to maximum entropy; thus the observed minor deviation on Kohala is not different than expected by chance. Kohala shows minimal modularity, and maximal connectance. The bottom panel shows the number of links for island endemics versus island cosmopolitans. Endemics show lower linkage overall, but significantly increase on the middle aged site Maui (highlighted with dotted box). Kohala shows increased linkage overall (highlighted with solid box). When looking at links to plant genera this pattern holds except that endemics on Maui no long show a difference in generality, indicating that the pattern is driven in part by plant diversity.

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Figure 4. Trends in network metric nestedness and modularity through time. Nestedness decreases while modularity increases. Error bars come from a null model simulation. While the sign of the z-score depends on null model and method of calculating modules (see supplemental figure) the overall trend is robust. Some level of nestedness is likely a statistical property of these networks, however it could also be driven by stabilizing ecological mechanisms. Modularity is thought to be a sign of coevolution driving convergence in traits of plants and herbivores. Note the very interesting peaks on Maui where adaptive diversification may be at its maximum.
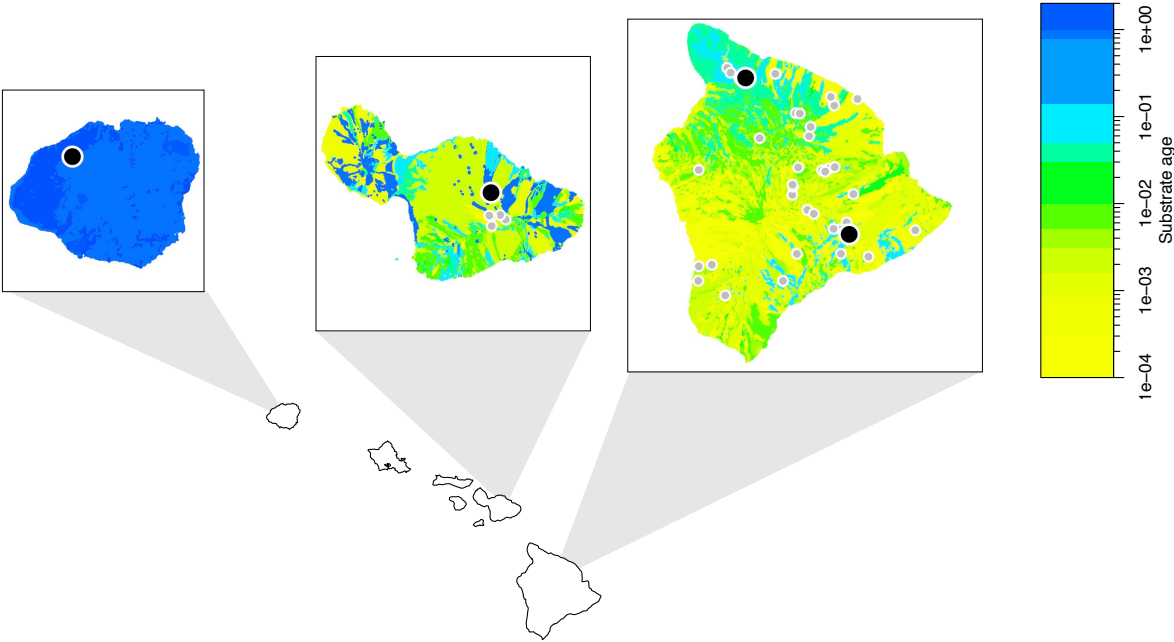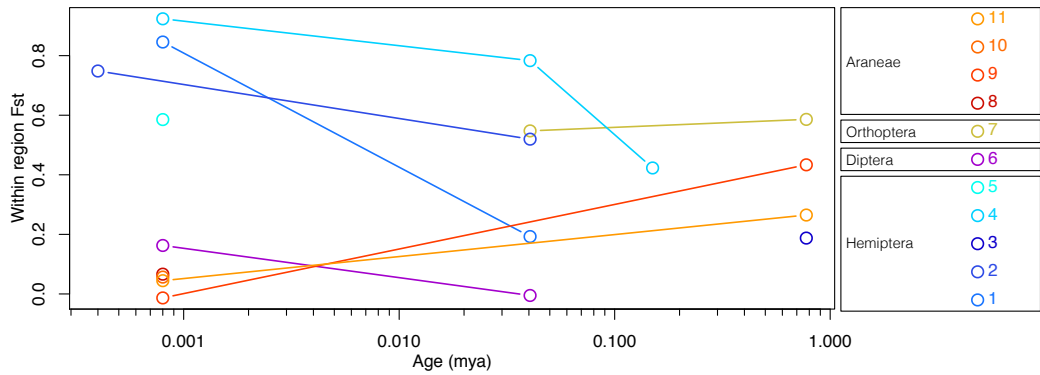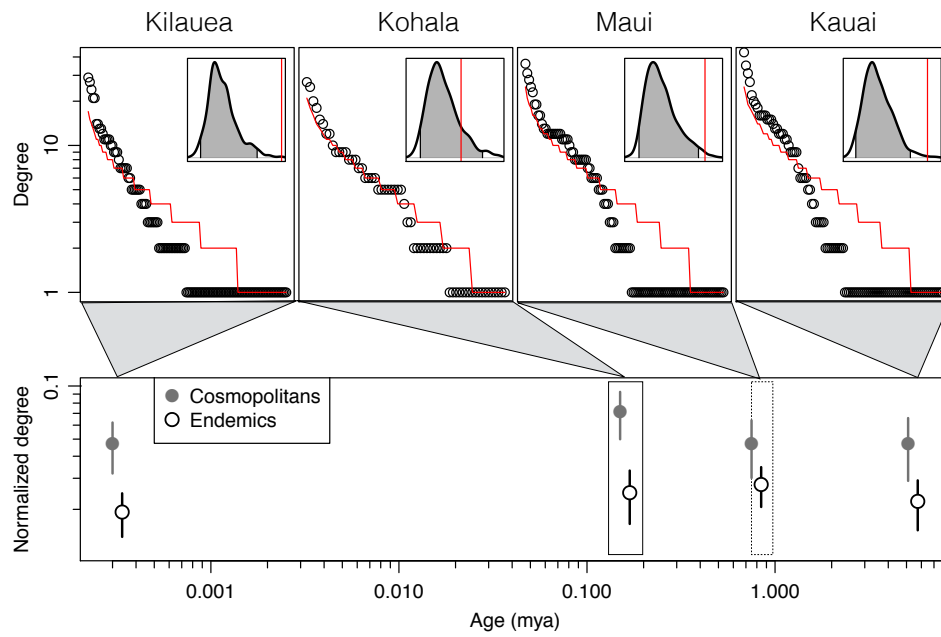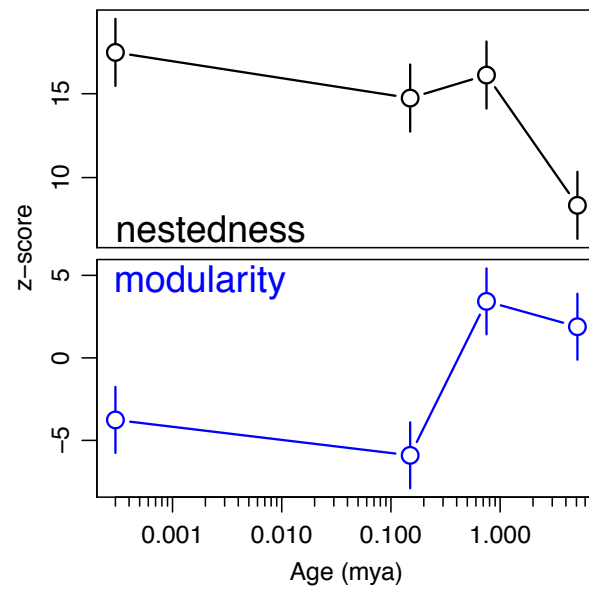
Figures

Figure 1:

Figure 2:

Figure 3:

Figure 4: