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Community assembly on isolated islands: macroecology meets evolution

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ABSTRACT

Aim Understanding how ecological and evolutionary processes together determine patterns of biodiversity remains a central aim in biology. Guided by ecological theory, we use data from multiple arthropod lineages across the Hawaiian archipelago to explore the interplay between ecological (population dynamics, dispersal, trophic interactions) and evolutionary (genetic structuring, adaptation, speciation, extinction) processes. Our goal is to show how communities develop from the dynamic feedbacks that operate at different temporal and spatial scales.

Location The Hawaiian islands (19–22° N, 155–160° W).

Methods We synthesize genetic data from selected arthropods across the Hawaiian archipelago to determine the relative role of dispersal and *in situ* differentiation across the island chronosequence. From four sites on three high islands with geological ages ranging from < 1 Ma to 5 Ma, we also generate ecological metrics on plant–herbivore bipartite networks drawn from the literature. We compare the structure of these networks with predictions derived from the principle of maximum information entropy.

Results From the perspective of the island chronosequence we show that species at lower trophic levels develop population genetic structure at smaller temporal and spatial scales than species at higher trophic levels. Network nestedness decreases while modularity increases with habitat age. Single-island endemics exhibit more specialization than broadly distributed species, but both show the least specialization in communities on middle-aged substrates. Plant–herbivore networks also show the least deviation from theoretical predictions in middle-aged communities.

Main conclusions The application of ecological theory to island chronosequences can illuminate feedbacks between ecological and evolutionary processes in community assembly. We show how patterns of population genetic structure, decreasing network nestedness, increasing network modularity and increased specialization shift from early assembly driven by immigration, to *in situ* diversification after > 1 Myr. Herbivore–plant communities only transiently achieve statistical steady state during assembly, presumably due to incomplete assembly from dispersal in the early stages, and the increasing influence of island ontogeny on older islands.

Keywords

Arthropods, chronosequence, Hawaii, maximum entropy, networks, population genetics.

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INTRODUCTION

Current biodiversity is a product of speciation, extinction and dispersal, contingent on the ecological interactions of organisms with their biotic and abiotic environment. The evolutionary history leading to the assembly of any given ecological community must in some way shape current 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 remains a central challenge (Ricklefs, 2004).

The 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 into 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 current patterns of species, genetic or phylogenetic diversity (e.g. Wiens, 2011; Jetz *et al.*, 2012). However, it is not possible to use current static 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 a discrete geological sequence 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 having different ages of formation, along with discrete volcanoes within islands, provide the opportunity to study diversification of species and the assembly of communities in different stages. 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 the 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 analyse the outcomes of ecological and evolutionary processes (Warren *et al.*, 2015). While many archipelagos around the world share these biotic and geological 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 among lineages (e.g. Gruner, 2007; Gillespie & Baldwin, 2009) that can be used to test for biologically meaningful differences among 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. 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 analyse 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 would expect to find associated deviations from an ecological null model of community assembly, provided by idealized ecological theory. Differences in population structure among 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

By their nature, unified theories of biodiversity (e.g. Hubbell, 2001; Harte, 2011) provide a simplified view of ecology, but deviations from theory can provide insights into 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 the

behaviour of a system is governed by a simple set of state variables. The principle of maximum information entropy (MaxEnt), from which the 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 & Newton, 1986) and, more recently, ecology (e.g. Phillips *et al.*, 2006; Dewar & 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 number 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 co-evolution (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 co-evolution 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 the underlying eco-evolutionary processes driving patterns of species interactions (Bascompte & Jordano, 2007; Donatti *et al.*, 2011; Nuismer *et al.*, 2013). In nested networks, species with fewer interactions (i.e. more specialized species) will interact with a subset of the species with which generalists interact. In this way interaction nestedness is mathematically equivalent to island nestedness (in which islands that are less species rich are subsets of islands that are more species rich). However, we only consider network nestedness here.

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 the METE (Harte, 2011) can be used as powerful null models; deviations from theoretical expectations can flag biological phenomena that warrant 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 years to 5 Ma. 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 the potential for local differentiation, we measured how molecular variation is partitioned among populations within species across locations of known substrate age on the islands of Hawaii and Maui (Fig. 1). We compiled published [DNA sequences, amplified fragment length polymorphism (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: KT023113–KT023179] and *Trioxa* psyllids [COI, cytB; data generated following protocols in Percy (2003); GenBank accession numbers: KR108061–KR108144]. Samples were from the focal sites described below for the ecological analysis, as well as from other locations across Hawaii 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 the island of Hawaii 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 F_{ST} , a measure of genetic variance, or, where possible, Φ_{ST} , an F_{ST} analogue that incorporates genetic sequence information. The *Laupala* AFLP data were analysed using TFPGA v.1.3 (Miller, 1997), using the same hierarchical approach of comparing within and among 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.

To explicitly test the association between landscape age and the potential for *in situ* genetic divergence we analysed how within-site F_{ST} varies with the geological age of volcanoes on the

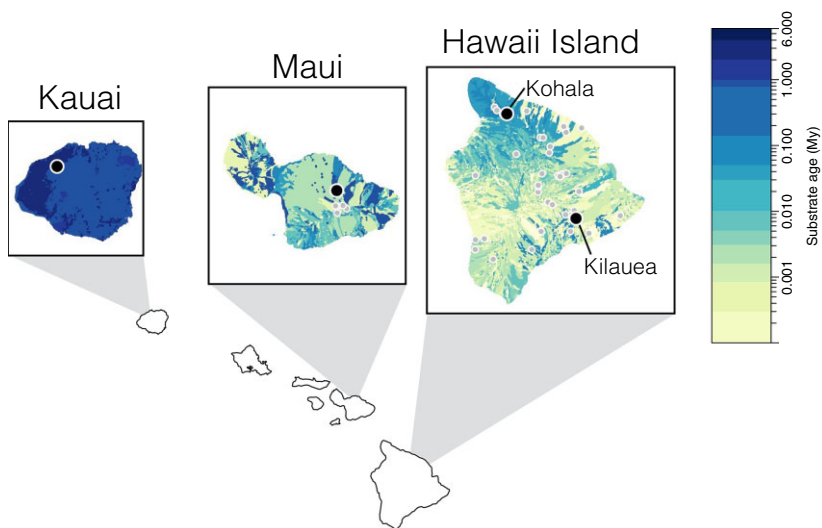


Figure 1 Map of substrate age (millions of years, My) of the islands of Kauai, Maui and Hawaii. Colours correspond to substrate age from young (light) to old (dark). Focal sites are shown as black circles (on Hawaii, Kohala is in the north, Kilauea in the south) while sampling sites for genetic data are represented by grey circles.

islands of Hawaii and Maui Nui. For each volcano we calculated F_{ST} or Φ_{ST} (Excoffier & Lischer, 2010) for each taxon among sites within volcanoes. This analysis assumes that volcano age parallels habitat age, allowing more or less time for the presence of the populations.

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 the island of Hawaii, one on Maui and one on Kauai; Fig. 1) of approximately 12 km² (each was defined as a point with a 2-km radius buffer). Focal sites were selected to have similar forest composition (dominated by *Metrosideros polymorpha*; Myrtaceae), elevation (1100–1400 m) 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 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 Table S1 in the Supporting Information for a 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 overlap with a focal site but no known specimen exists confirming its presence. Probable absence was assumed when the criteria for presence or for probable presence

are not 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 the 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 the METE predicts the data we simulated METE-conforming communities having 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 the METE is true with 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 (v.3.1.1; R Core Team, 2014) used for METE estimation and Monte Carlo methods are available in Appendix 1.

To investigate how speciation may in part drive network patterns and deviations from those predicted by idealized ecological theory, we analysed the number of links assigned to each Hemiptera species (the degree distribution) separately for

Table 1 Results of the analyses of molecular variance (AMOVA) that partitions molecular genetic variation among volcanoes and among sites within volcanoes for arthropod lineages found within the study sites on the island of Hawaii. 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.

Group	Functional group	Species	Data (no. of individuals: length/no. of markers)	Between volcanoes ¹ % variation (P-value)	Within volcanoes ¹ % variation (P-value)	Timeframe
Planthoppers	Herbivore	<i>Nesosydne chambersi</i> ²	mtDNA: COI (187:653)	0.05***	0.77***	Within-species divergence ¹¹ = 2600 [95% HPD (1.2–35.1) × 10 ³], and 20,100 [95% HPD (7.4–135.0) × 10 ³] years for two population pairs ²
			nucDNA: microsatellites (292:13)	0.04***	0.21***	
Psyllids	Herbivore	<i>Nesosydne raillardi</i> ³	mtDNA: COI (33:581)	0.26***	0.49***	na
	Herbivore	<i>Nesosydne bridwelli</i> ³	mtDNA: COI (34:677)	na	0.18**	na
	Herbivore	<i>Trioxa HB</i> ^{3,4}	mtDNA: COI and cytb (29:857)	-0.14***	0.92***	na
	Herbivore	<i>Trioxa HC</i> ^{3,4}	mtDNA: COI and cytb (17:857)	0.17**	0.53**	na
	Fly	<i>Drosophila sproati</i> ⁵	mtDNA: COII (232:570)	0.11***	0.81***	Max age ¹² = 1.15 (95% HPD 0.75–1.5) Ma ⁸
Crickets	Detritivore	<i>Laupala cerasina</i> ⁶	nucDNA: AFLP (631)	0.30***	0.58***	na
Spiders	Predator	<i>Tetragnatha anuenue</i> ⁷	mtDNA: COI (162:607)	0.23***	0.041***	Max age ¹² = 3.0 (95% HPD 2.5–4.5) Ma ¹⁰
	Predator	<i>Tetragnatha brevigutha</i> (Hawaii Island) ⁷	mtDNA: COI (54:605)	0.16*	0.00	Max age ¹² = 4.0 (95% HPD 3.0–4.75) Ma ¹⁰
Predator	Predator	<i>Tetragnatha quasimodo</i> ⁷	mtDNA: COI (149:439)	0.09***	0.037***	Max age ¹² = 2.5 Ma ¹⁰
			nucDNA: allozymes (46:9)	0.34***	na	
Predator	Predator	<i>Theridion gallator</i> ⁷	mtDNA: COI (209:1270)	0.30***	0.05***	Node age ¹³ = 0.56 (95% HPD 0.37–0.75) Ma ⁹
			nucDNA: allozymes (224:8)	0.19***	na	
Predator	Predator	<i>Ariamnes</i> spp. ⁷	mtDNA: COI (8:420)	0.05	na	na

mtDNA, mitochondrial DNA; nucDNA, nuclear DNA; HPD, highest posterior density; na, no information available.

*** $P < 0.001$, ** $P < 0.05$, * $P < 0.10$.

¹mtDNA and microsatellites are calculated as Phi-st; AFLPs and allozymes are calculated as F_{ST} .

²Goodman *et al.* (2012).

³This paper.

⁴These *Trioxa* species are in the process of being described; HB and HC are their provisional identifiers (D.M.P., in prep).

⁵Eldon *et al.* (2013).

⁶Mendelson and Shaw (2005).

⁷Roderick *et al.* (2012).

⁸Magnacca and Price (in press).

⁹Croucher *et al.* (2012).

¹⁰Casquet *et al.* (2015).

¹¹Within-species divergence, estimated using Isolation with Migration (IM; see Goodman *et al.* 2012)

¹²Max 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.

¹³Node age = age of the most recent common ancestor of the monophyletic group on the island of Hawaii, estimated using BEAST.

single-island endemics (those species found on only one island and thus probably 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 age of the ecosystem substrate, 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 $(x_{\text{obs}} - \bar{x}_{\text{sim}})/SD_{\text{sim}}$. 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 uses 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 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 to 0.92 and among volcanoes from 0 to 0.30. Corresponding variation at multilocus nuclear loci among sites within volcanoes ranged from 0.21 to 0.58 and among volcanoes from 0.04 to 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 with 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; this was higher among volcanoes, with values increasing with age across the chronosequence.

The observed levels of genetic divergence have evolved rapidly in many cases. For example, for species from the island of Hawaii for which phylogenetic data provide divergence times, estimates of dates of species divergence range from 0.5–4 Ma, with additional within-species genetic divergence having developed subsequently (Table 1). 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, or alternatively that estimates include sampling error. For the one species where popula-

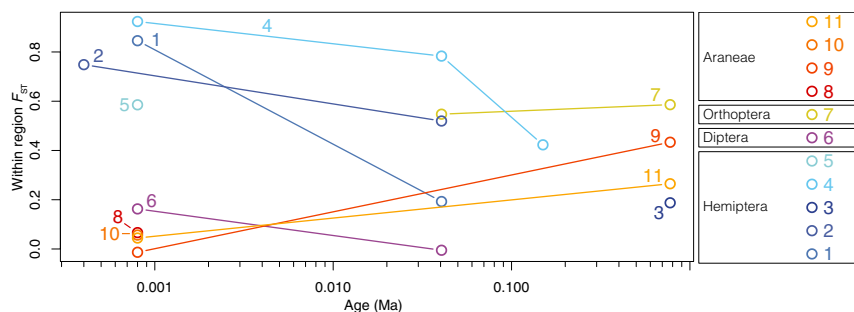


Figure 2 Genetic population structure (Φ_{ST} for all taxa except *Laupala* for which we used F_{ST}) among sites within volcanoes with volcano age for insects and spiders. Calculations were based on mitochondrial DNA only (see Table 1 for details). The plant-feeding groups, specifically the sap-feeding 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, for example on Maui at approximately 1 Ma. Numbers refer to different species: 1, *Nesosydne chambersi*; 2, *Nesosydne raillardiae*; 3, *Nesosydne bridwelli*; 4, *Triozia* HB; 5, *Triozia* HC; 6, *Drosophila sproati*; 7, *Laupala cerasina*; 8, *Tetragnatha anuenue*; 9, *Tetragnatha brevisnatha*; 10, *Tetragnatha quasimodo*; 11, *Theridion grillator*.

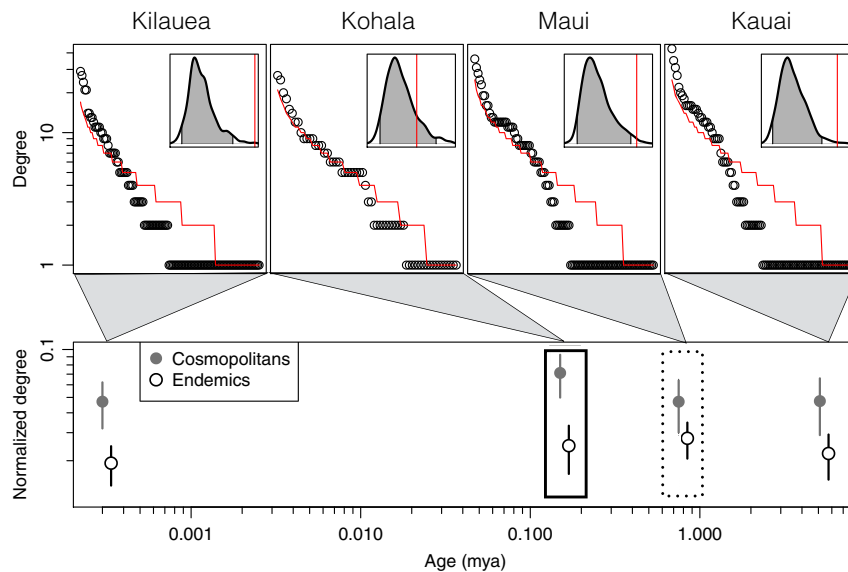


Figure 3 Patterns in degree distributions across sites, comparing archipelago-wide endemics (cosmopolitans) with single-island endemic (Endemics) taxa. The top panels show that networks deviate most from the predictions of the maximum entropy theory of ecology on the youngest and oldest sites. Inset figures show the distribution of simulated mean squared errors; if the vertical/red line falls within the grey region (95% confidence interval) the data are not significantly different from the predictions of maximum entropy theory. All sites except Kohala deviate from the predictions. 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 a solid box).

tion genetic data were used to estimate divergence times between populations, herbivorous *Nesosydne* planthoppers, it was determined that populations diverged as little as 2600 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 are not significantly different from the 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 with 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 (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 (Fig. S2). The patterns were also robust to sampling intensity, as demonstrated by a rarefaction analysis (Fig. S4).

DISCUSSION

Development of genetic population structure 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 structure developing in sap-feeding herbivore lineages at smaller scales (and hence shorter timeframes in the context of the chronosequence) compared with detritivorous crickets and predatory spiders (Table 1, Fig. 2). Structure within species may allow populations to take independent evolutionary trajectories,

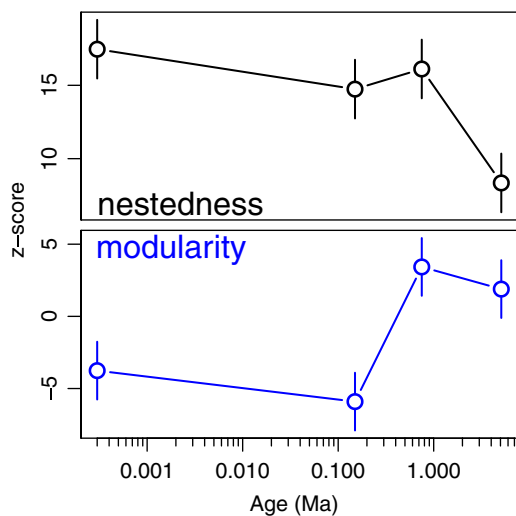


Figure 4 Trends in network metric nestedness and modularity through time. Nestedness decreases while modularity increases. Error bars represent 95% confidence intervals from a null model simulation.

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 the 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 signalling (Mendelson & Shaw, 2005; Percy *et al.*, 2006; Magnacca *et al.*, 2008; Goodman *et al.*, 2015).

The *Nesosydne* planthoppers provide evidence that some period of geographic isolation preceded the divergence of sexual signals (Goodman *et al.*, 2012, 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, species divergence was associated with host plant specialization between 1 and 5 Ma, but only with geography on the younger island (Bennett & O'Grady, 2013). Our network analysis shows that specialization and modularity are more pronounced on Maui than on Hawaii (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 Myr (Table 1), and suggest 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 (Percy, 2003; Mendelson & Shaw, 2005; Percy *et al.*, 2006; Magnacca *et al.*, 2008; O'Grady *et al.*, 2011). By con-

trast, 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 with 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 the potential for neutral colonization-driven assembly, this site did not conform to the statistical steady-state prediction of the METE. The observed deviations from the 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 ka), observations were not significantly different from the METE predictions. We posit that the reason why 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 the older Maui and Kauai sites show strong deviations from the METE expectations (Fig. 4). The METE is agnostic about which mechanisms determine 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 the METE expectations, 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 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. Co-evolution 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 time spans of network development that do not span as much evolutionary time as is 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 long-standing 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. Although dietary breadth has been positively associated with geographic range size (Lewinsohn *et al.*, 2005), the direction of causality is unclear (Slatyer *et al.*, 2013): while dietary breadth may allow some species to colonize other islands, it may also 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 co-evolution 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. a 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 are again 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 analysing 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 an ecological statistical steady state. An exception will be communities that are still undergoing the 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 chronosequence.

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 (Gruner, 2007). Such data will allow us to test entire arthropod communities for deviations from METE predictions of statistical steady state (Harte, 2011) across substrates of different ages. For example, predators, whose assemblages are likely to be 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 & 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 about how entire communities develop over an 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 archipelagos.

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 with 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 (probably the product of *in situ* diversification) show more specialization at older sites than 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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Additional references to the data sources may be found in Appendix S1.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1 Compilation of networks and metric validation.

Figure S1 Comparison of different null models ('Prob' and 'Quasiswap') used to standardize network metrics and comparison of different algorithms for assessing modularity ('edge between' and 'walk drap'). Choice of null model has a strong influence on the sign and magnitude of metrics but not on their relative trends. The different modularity algorithms lead to largely similar qualitative patterns.

Figure S2 Metrics NODF and modularity calculated for networks based on more biogeographically conservative assignment of Hemiptera to localities.

Figure S3 Result from rarefaction analysis showing sensitivity of network metrics to the number of Hemiptera sampled.

Table S1 Published sources of trophic information used to construct networks.

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 of Biodiversity', focuses on the geological chronosequence provided by the Hawaiian islands.

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