



## Community assembly on isolated islands: Macroecology meets evolution

Journal:	<i>Global Ecology and Biogeography</i>
Manuscript ID:	GEB-2014-0207.R1
Manuscript Type:	Special Issue Article
Date Submitted by the Author:	16-Nov-2014
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Keywords:	networks, arthropods, population genetics, chronosequence, Hawaii, modularity

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For Peer Review

# COMMUNITY ASSEMBLY ON ISOLATED ISLANDS: MACROECOLOGY MEETS EVOLUTION

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Running title: Community assembly on isolated islands

Number of words in the abstract: 299

Number of words in main body of the paper: 4973

Number of references: 50

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**Aim**

Understanding how ecological and evolutionary processes synergistically determine biodiversity patterns remains a central goal in biology. Using ecological theory as a conceptual guide and data from multiple arthropod lineages, we use the isolated archipelago of Hawaii to explore how complex communities emerge from the interplay of ecological (population dynamics, dispersal, trophic interactions) and evolutionary (genetic structuring, adaptation, speciation, extinction) processes.

**Location**

The Hawaiian Islands (19.5°N, 155.5°W).

**Methods**

To infer processes involved in early diversification we synthesize data on genetic structure of select arthropod species across the Hawaiian Archipelago. Over the range of geological ages of the current high islands (< 1 my to 5 my) we also develop and analyze a plant-herbivore bipartite network. We compare the structure of these networks, measured by nestedness, modularity and the degree distribution, with theoretical predictions derived from the principle of maximum information entropy.

**Results**

Based on the time perspective provided by the island chronosequence and genetic information, we demonstrate that species in lower trophic levels develop local divergence more quickly than species of higher trophic levels. Higher trophic levels also show endemism, though it evolves more slowly and over larger areas. Moreover, in analyzing

plant-herbivore networks across an increasing substrate age gradient we find trends of higher specialization and increasing deviation from the statistical steady state expected from theoretical predictions of food web structure.

## **Main conclusions**

We show how ecological theory can leverage natural experiments on oceanic islands of known chronologies to understand the interplay between evolutionary and ecological processes in shaping present-day biodiversity. We advocate for combining perspectives gained from coupled molecular and community-level data analyzed in the context of ecological theory. 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.

**Keywords:** networks, maximum entropy, arthropods, population genetics, chronosequence, Hawaii

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**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 non-linear and non-equilibrium, 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; Borer *et al.*, 2014). Recent theoretical advances have further refined the causes and consequences of ecological drift (Hubbell, 2001; Rosindell & Phillimore, 2011), re-vitalized classical niche-based mechanisms such as niche partitioning (Tilman, 2004), competition and predation (Borer *et al.*, 2014), and put species interactions in a network theoretic context (Williams & Martinez, 2000; Brose *et al.*, 2006).

New insights into evolutionary mechanisms have also emerged based on inference from contemporary patterns of species, genetic, or phylogenetic diversity (e.g., Jetz *et al.*, 2012; **Wiens, 2011**). Here, we propose an integrative framework that harness both sources of advancement to study evolutionary community assembly. We provide an initial test using arthropod lineages in 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. We estimate taxon-specific timelines for the development of genetic discontinuity. This is contextualized with macroecological metrics of community structure, using predictions from statistical equilibrium and ecological network theory to examine changes over the island chronosequence.

## Hotspot oceanic archipelagos as model systems

Hotspot oceanic islands 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, hotspot island archipelagos thus have the potential to stratify the eco-evolutionary process of community assembly.

Younger communities originate mostly from initial immigration and thus should be dominated by ecological mechanisms operating on a source pool whose evolution is removed from the local setting. Conversely, older islands could allow for the combined interaction and feedback of diversification and local ecological dynamics. 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

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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 their population dynamics. Even  
moderate levels of genetic connectivity among geographically separated populations limits  
the potential for local divergence (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 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, the situation in which a system's behavior is governed by a simple set of state variables and no further mechanisms are required. 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 derives from evolutionary concepts such as coevolution (Thompson et al. 2013; Bascompte & Jordano, 2007; Donatti et al., 2011; Nuismer et al., 2013) and so presents an opportune starting place to study ecological and evolutionary feedbacks. 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 from young to old across

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3 158 the chronosequence we evaluate (1) the rate and pattern of genetic connectivity among  
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8 160 new species; (2) the processes underlying the structure of species interaction networks  
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10 161 given the backdrop of population divergence; and (3) the processes involved in  
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12 162 diversification as species form and accumulate and how this dynamic drives deviations  
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15 163 from statistical steady state. We use data (mostly published) on population genetic  
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18 164 structure and species interactions as a proof of concept. With this framework, our goal is to  
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20 165 show how communities develop over ecological-evolutionary time, and the dynamic  
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27 167 **METHODS**  
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31 168 **Hawaii as an eco-evolutionary study system**  
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34 169 The geological landscape of the Hawaiian Islands offers a matrix of volcanic  
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36 170 substrates mapped in fine detail by chronological age and geochemical composition  
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38 171 (Sherrod *et al.*, 2007). On Hawaii Island in particular, independent gradients in elevation  
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40 172 and precipitation interact within a matrix of substrate ages ranging from contemporary  
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42 173 (active) to 500,000 years. Ongoing volcanic activity has created a dynamic mosaic of  
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44 174 habitats with transitory to long-lasting fragmentation within landscapes. Isolation on scales  
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46 175 of hundreds to thousands of meters and hundreds to thousands of years can be sufficient  
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48 176 for genetic differentiation among some arthropod populations among habitats (Goodman  
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51 177 *et al.*, 2012; Eldon *et al.*, 2013; Bennett & O’Grady, 2013), while insufficient to isolate others  
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55 178 (Vandergast *et al.*, 2004). On larger spatial and temporal scales, distinct volcanoes and  
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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; Fig. 1). 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).

### Compilation and analysis of genetic data

To evaluate the balance between regional 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 maintains 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)

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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). 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 dynamic landscape of the focal sites.

We used analysis of molecular variance (AMOVA) to examine how genetic variation is partitioned at two scales of population structure: among sites within volcanoes and among volcanoes on both Hawaii Island and Maui Nui. 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  $\Phi_{ST}$ , an  $F_{ST}$  analog that incorporates genetic sequence information. The *Laupala* AFLP data were analyzed using TFPGA v. 1.3 (Miller, 1997), using the same hierarchical approach as described above. To provide a temporal framework for the population differentiation analysis we assembled divergence dating information from the literature for as many of the taxa as possible and additionally implemented a new divergence dating analysis for *Tetragnatha* spiders (see supplementary information).

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

## 222 Construction of plant-herbivore networks

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

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

240 Host plants for each hemipteran species were determined from published species  
241 accounts. Data on host plant use at each specific site were not available so we assumed that  
242 if a known host plant was present at a site it would eventually be used. Host plant  
243 occurrence in the focal sites was determined using distribution models for 1158 species of  
244 Hawaiian plants (Price, 2012). Each focal site was spatially joined in a geographic

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

To further investigate how *in situ* diversification leaves a potentially unique signature on network structure we analyzed the number of links assigned to each hemipteran species (the degree distribution) **separately for island endemics (those species found on only one island and thus likely derived from in situ diversification)** versus island **cosmopolitans** (those species found on multiple islands). To compare species' degree

distributions between endemics and cosmopolitans across sites of different ages we conducted a generalized linear model with binomial error, treating site identity as a categorical predictor. Binomial errors effectively account for network size due to the bounded support of the binomial distribution.

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

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  $(x_{obs} - \bar{x}_{sim})/sd_{sim}$ . 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 using the frequency of interactions as the probability that a randomized link gets assigned to that cell

in the interaction matrix (Bascompte & Jordano, 2007); thus the probabilistic null  
constrains row and column sums in probability but not absolutely.

**RESULTS**

**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 (larger observed variance within volcanoes may represent the effects of  
repeated colonization events or sampling error). 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 0.34–1.15 million years, with additional within-species genetic divergence developed subsequently (Table 1). That the estimates are older than the known age of the Big Island, suggest that divergence in DNA now reflected in different lineages pre-dated their colonization of the Big Island, or alternatively may be due to sampling error.

### **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

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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. S3). Choice of null model changed the magnitude of modularity and the sign of nestedness z-scores; however, the relative pattern of decreasing nestedness and increasing modularity remained across the different null models used to standardize network metrics (supplemental Fig. S2). The patterns are also robust to sampling intensity, as demonstrated by a rarefaction analysis (supplemental Fig. S4).

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

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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 (assuming timing of speciation is reflected by divergence in mtDNA; Table 1), with predatory spiders showing local endemism more slowly (Table 1).

### 397 **Macroecological metrics: Network structure and steady state**

398       On the geologically youngest volcano, Kilauea, ecological assembly should be the  
399 dominant process there. The results of network analysis support this hypothesis with  
400 Kilauea showing substantial nestedness and limited modularity (Fig. 4). Nestedness is  
401 likely to result if new species arriving by immigration have a high probability to eat or be  
402 eaten by the generalist species already present at the site (Bascompte & Jordano, 2007). In  
403 this way we might expect Kilauea to also conform to the statistical steady state predication  
404 of maximum entropy. However, the observed deviations from maximum entropy at Kilauea  
405 are largely driven by a surplus of singleton links (Fig. 3). These in turn likely result from  
406 incomplete assembly, and thus lower species richness, of the plant and herbivore biotas.  
407 Future research should focus on the observation from genetic analysis that indicates  
408 discontinuities can arise within species on short timescales that, in some taxa, include the  
409 greater landscape of Kilauea (Table 1). Conversely, Kohala shows a statistically significant  
410 agreement with maximum entropy perhaps because the Kohala site, at intermediate age  
411 (150 ky), has experienced complete ecological succession but is still too young to be driven  
412 away from statistical steady state by specialization and rapid in situ diversification driven  
413 by host plant preference

414       The older Maui and Kauai sites show strong deviations from expectations of  
415 maximum entropy theory (Fig. 4), which is consistent with our hypothesis that the  
416 influence of evolutionary assembly on these biotas drives them away from statistical steady  
417 state. The application of maximum entropy to ecology does not currently take into account  
418 evolution (Harte, 2011). Indeed the use of maximum entropy in ecology is inspired by its  
419 application to physical systems whose change through time is simple and lacks the

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evolutionary memory of biological systems, potentially a far cry from the complex change through time produced by speciation, extinction and adaption to novel ecosystems. 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 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.

## 441 Future Research

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

- 447 1. In younger communities we hypothesize that
  - 448 a. during periods of ecological assembly, communities strongly influenced  
449 by immigration will resemble random samples from regional source  
450 pools and thus metrics describing these communities will largely match  
451 expectations of statistical steady state after primary succession has  
452 completed;
  - 453 b. the exception will be communities still undergoing primary succession,  
454 which will change rapidly through time and represent non-random  
455 samples of source pools;
  - 456 c. we also predict that these communities will exhibit a nested network  
457 structure, assuming new species will eat or be eaten by the generalist  
458 species (Bascompte & Jordano, 2007) already present in the community.
- 459 2. Following the same logic, in older communities we hypothesize that
  - 460 a. during periods of evolutionary assembly, if processes such as niche  
461 exploration, adaptation and speciation happen fast enough to keep pace  
462 with immigration, the resultant communities could be driven into  
463 alternate evolutionary states that fail to meet the predictions of purely

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3 464 statistical theories that do not account for evolutionary dynamics (Harte,  
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8 466 b. networks in such communities should exhibit higher levels of  
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12 468 2011; Nuismer *et al.*, 2013).  
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15 469 3. Systems undergoing rapid ecological and evolutionary change are generally  
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18 470 expected to deviate most from statistical steady state; thus we expected  
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20 471 populations in such communities to show genetic signatures of rapid change,  
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22 472 from bottlenecks or population expansion to selection.  
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26 473 ***Evolutionary data: Diversification within species***  
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29 474 The current study demonstrates that taxa of different trophic guilds differ in the  
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31 475 scale at which differentiation occurs, and highlights the importance of fragmentation of the  
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33 476 landscape in facilitating differentiation. Future work is aimed at gathering genomic SNP  
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35 477 data for focal taxa within this system that represent different trophic levels. We will use it  
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37 478 to understand taxonomic differences in the rate of differentiation, to assess the roles of  
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39 479 genetic fusion and fission (Gillespie and Roderick 2014), and to detail the relative rates of  
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41 480 speciation and extinction across the island chronosequence. When coupled with ecological  
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43 481 data on abundances and interactions, the population genetic data will allow us to explore  
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45 482 explicit aspects of the Geographic Mosaic Theory of evolution, such as trait remixing and  
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47 483 selection mosaics. (Thompson *et al.* 2013).  
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484 *Ecological data: Assembly of species into communities*

485 Our results show that the island chronosequence can reveal that ecological  
486 processes dominate in younger environments, with evolutionary processes becoming more  
487 important later. However, in order to build a more rigorous understand of the assembly  
488 process future work is focusing on conducting broad sampling of all macroscopic  
489 arthropod taxa at a large number of sites across the age gradient, thus allowing assessment  
490 of changes in overall species composition and diversity across all players in the time-  
491 calibrated landscape (*sensu* Gruner, 2007).

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

499 The current study provides a framework for the use of chronologically arranged  
500 oceanic island systems to examine the interplay between evolutionary and ecological  
501 processes in shaping biodiversity and demonstrates how this approach can provide  
502 insights into the development of communities over ecological–evolutionary time, and the  
503 dynamic feedbacks involved in assembly.

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**ACKNOWLEDGEMENT**

We are indebted to many scientists and land managers in Hawaii that have provided access to the lands: Pat Bily (The Nature Conservancy of Hawaii), Melissa Dean, Christian Giardina, and Tabetha Block (Hawaii Experimental Tropical Forests), Betsy Gagne (Natural Area Reserve System), Lisa Hadway and Joey Mello (Department of Forestry and Wildlife Hilo), Cynthia King and Charmian Dang (Department of Land and Natural Resources), and Rhonda Loh (Hawaii Volcanoes National Park). We thank Robert Ricklefs, Lauren Ponisio and Anna Hiller for thoughtful commentary. We are very grateful to Guida Santos, Richard Field and Robert Ricklefs for inviting us to contribute to this special issue. The research was supported by the National Science Foundation DEB 1241253.

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

For Peer Review

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**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. Numbers refer to different species: 1. *Nesosydne chambersi*, 2. *Nesosydne raillardiae*, 3. *Nesosydne bridwelli*, 4. *Trioza HB*, 5. *Trioza HC*, 6. *Drosophila sproati*, 7. *Laupala cerasina*, 8. *Tetragnatha anuenue*, 9. *Tetragnatha brevignatha*, 10. *Tetragnatha quasimodo*, 11. *Theridion grallator*.

**Figure 3.** Patterns in degree distributions (distribution of number of links assigned to each herbivore) 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 longer show a difference in generality, indicating that the pattern is driven in part by plant diversity.

**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. 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.

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

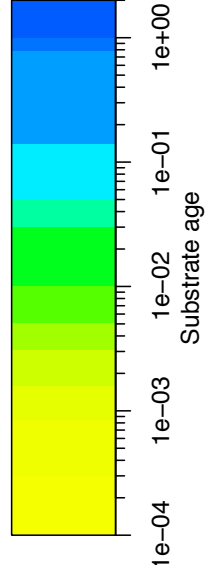
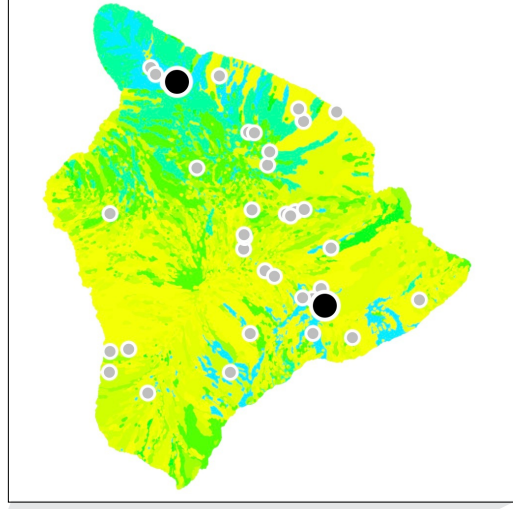
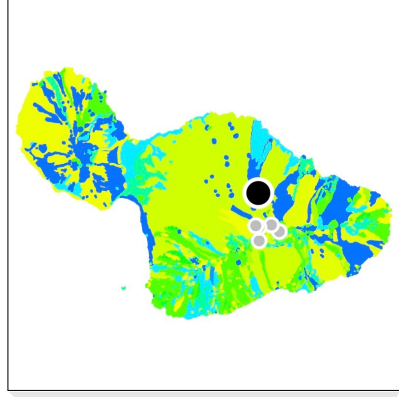
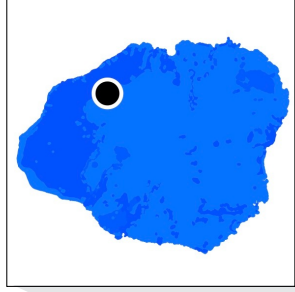
\*\*\* < 0.001, \*\* < 0.05, \* < 0.10; na = no information available

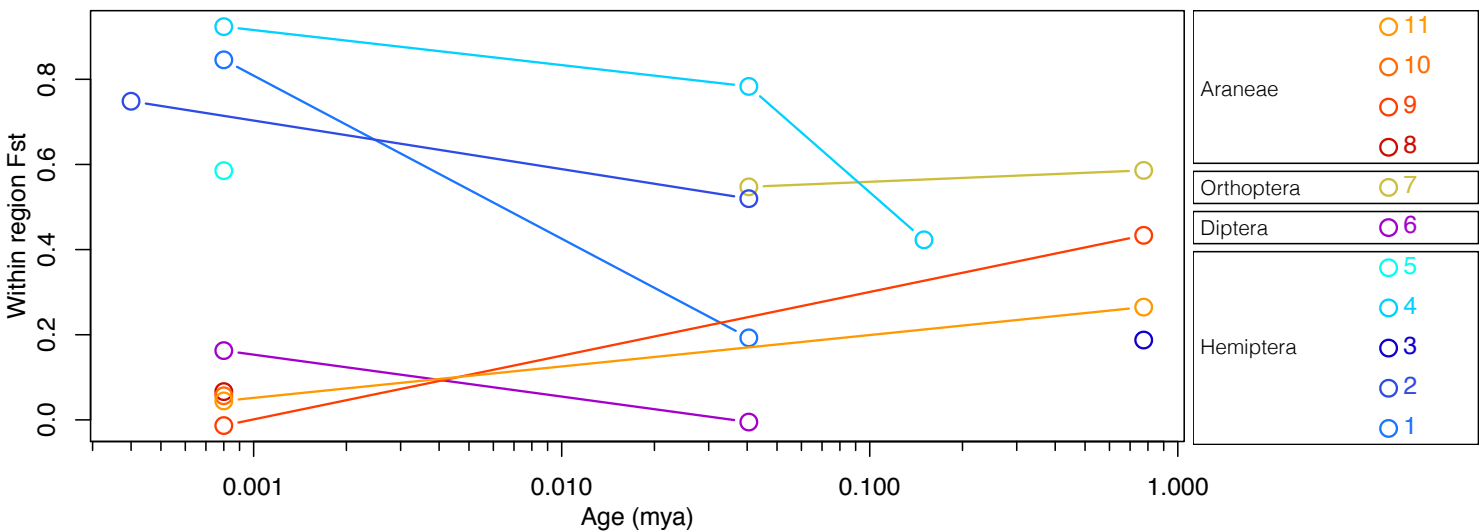
<sup>1</sup>WSD = Within-species divergence, estimated using IM.

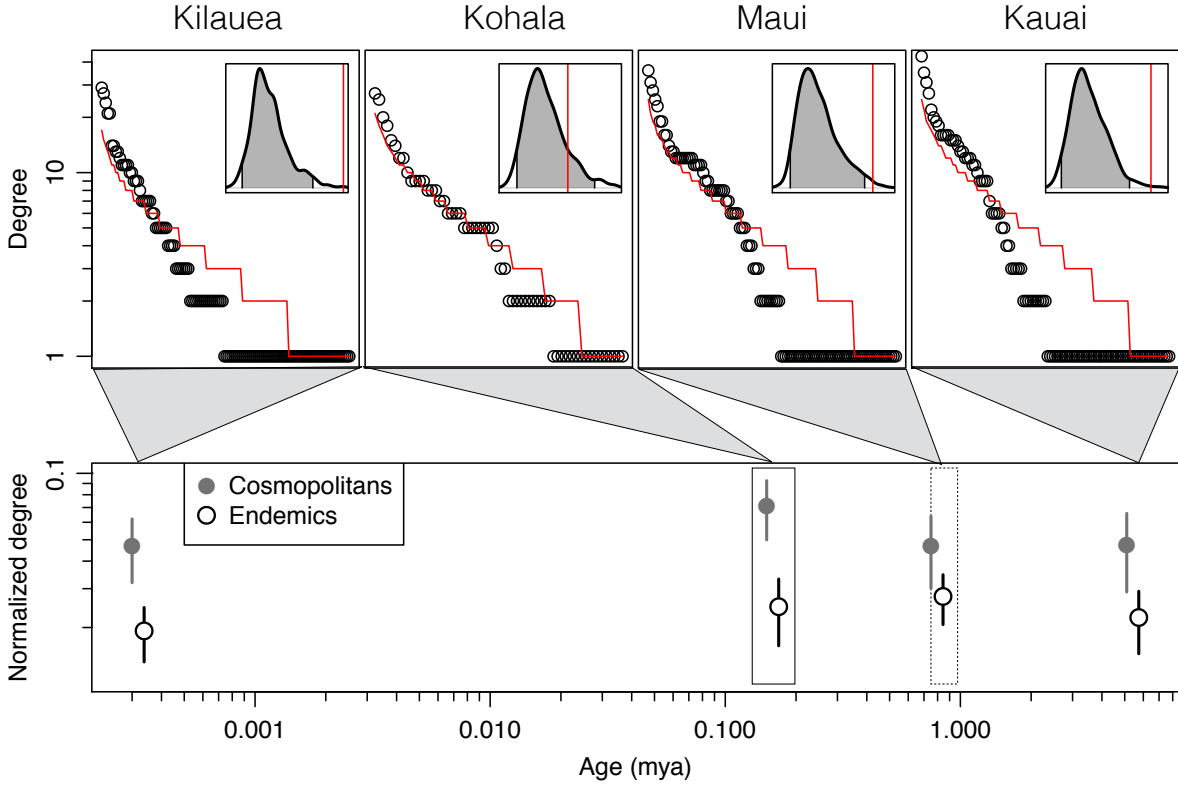
<sup>2</sup>Max age = the node age of the phylogenetic split between this species and its sister species, calculated using divergence dating analyses performed in BEAST. In most cases, this will be an overestimate of the node age of the species itself, but is the best information we have at present.

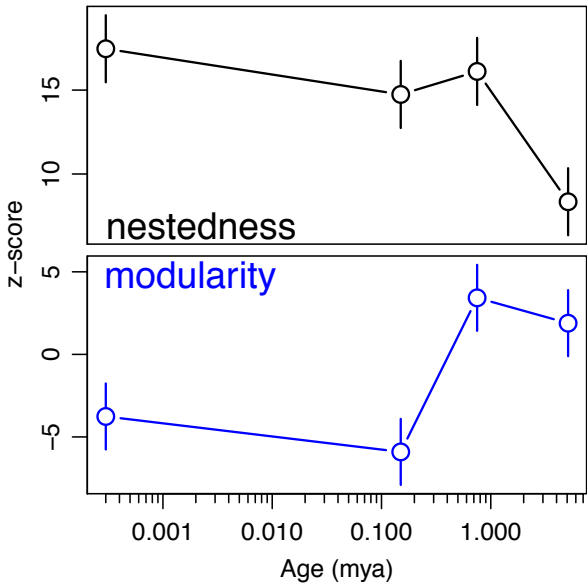
<sup>3</sup>Node age = Age of the most recent common ancestor of the monophyletic group on Hawaii Island, estimated using BEAST.

<sup>4</sup> These *Trioza* species are in the process of being described; HB and HC are their provisional identifiers (Percy in prep).











# Supplement to “Community assembly on isolated islands: Macroecology meets evolution”

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# 1 Time Estimation Methods

Sequence data for two mitochondrial gene regions, Cytochrome Oxidase 1 (COI) and the large ribosomal subunit (16S), from Hawaiian *Tetragnatha* spiders were obtained from existing databases and new sequences (GenBank numbers XXX-XXX). Sequences were generated following protocols described in Gillespie (2004). Divergence time estimations and topology inferences were performed using a Bayesian relaxed-clock method implemented in the BEAST v1.7.5 (Drummond & Rambaut, 2007). The times to most recent common ancestors (TMCA) were estimated for all terminals using a fixed Hawaiian *Tetragnatha* COI specific rate of molecular evolution: 3.55% per million years. This was calculated by averaging COI rates from *Tetragnatha quasimodo* and *Tetragnatha restricta*, each of which are situated with reciprocally monophyletic populations on Maui and Hawaii. To generate the most conservative rate possible, the date of the earliest emergence of the island of Hawaii was used, 0.9 million years (see discussion in Supplementary Information from (Goodman *et al.*, 2012). The rate obtained is very similar to the revised general insect COI rate of 3.54% per million years (Papadopoulou *et al.*, 2010). The separate codon positions of COI were combined under a single clock rate but were given separate models of molecular evolution. The 16S rate was estimated based on the COI rate. Appropriate models of molecular evolution were chosen using PARTITIONFINDER (Lanfear *et al.*, 2012) and are as follows: 16S (254 bp) TrN+I+G; COI (484 bp) pos1 TrN+I+G, pos2 TrN, pos3 HKY+G. The ingroup was constrained as monophyletic, and analyses were run for 50 x 10<sup>6</sup> generations with a random starting tree under a “Speciation: Birth-Death” tree prior. Trees and parameters were sampled every 1,000 generations. TRACER version 1.7.5 was used to assure the estimated sample sizes were large enough, and the resulting posterior distribution of trees were combined using TREEANNOTATOR version 1.7.5 after discarding the first ten percent of trees as burn-in. The final consensus tree is shown in Figure 1.

## 2 Compilation of networks and metric validation

We compiled plant-herbivore networks from published sources as described in the main text.

Table 1 lists publications used in compiling these networks.

Researchers have put forward to set of “network metrics,” including nestedness (Bascompte *et al.*, 2003; Ulrich *et al.*, 2009) and modularity (Newman & Girvan, 2004; Olesen *et al.*, 2007), to understand the complex structure of ecological networks. Null models are used to evaluate the statistical significance of these metrics and to compare between networks of different size Ulrich *et al.* (2009). We compare the results derived from two common null models: the “probabilistic null” of Bascompte *et al.* (2003) using the relative degree distributions of plants and herbivores as weights while randomizing links and suffers from high Type II error (Ulrich *et al.*, 2009); the “fixed-fixed null” (Ulrich *et al.*, 2009) maintains the exact number of links assigned to each species while randomizing which interactors fill the requisite set of links and suffers from high Type I error (Ulrich *et al.*, 2009). We find that using these different null models does not change any trends in our network statistics across the Hawaiian chronosequence but different null models do influence the sign and significance of the network metrics (Fig. 2). We therefore do not interpret the sing or significance of the metrics but only their relative trends across site age.

Because these networks are based on opportunistic data associated with species descriptions, and not based on standardized ecological surveys, we cannot interpret patterns in network metrics without evaluating possible sampling biases (Nielsen & Bascompte, 2007; Gibson *et al.*, 2011; Rivera-Hutinel *et al.*, 2012). To do so we rarefy networks by the number of Hemiptera species included and, for each subsampled network, re-calculate nestedness and modularity z-scores. This rarefaction procedure shows that nestedness is very sensitive to network size (Fig. 4), a known property of nestedness (Nielsen & Bascompte, 2007; Gibson *et al.*, 2011; Rivera-Hutinel *et al.*, 2012). However the relative nestedness z-scores across networks remain qualitatively similar to those observed for the complete networks (Fig. 4). Modularity depends on network size in a more variable way (Fig. 4). Modularity

is expected to decrease with network size (Rivera-Hutinel *et al.*, 2012) and so the marked increase in modularity with network size on Haleakala is unexpected. However in light of the large number of highly specialized taxa this pattern is more reasonable—if most species only have within module links then removing these species through subsampling will only reduce overall modularity. Thus this pattern speaks to the high level of specialization on Haleakala, and to a lesser extent at Kokee which also shows a slight increase in modularity with network size (Fig. 4).

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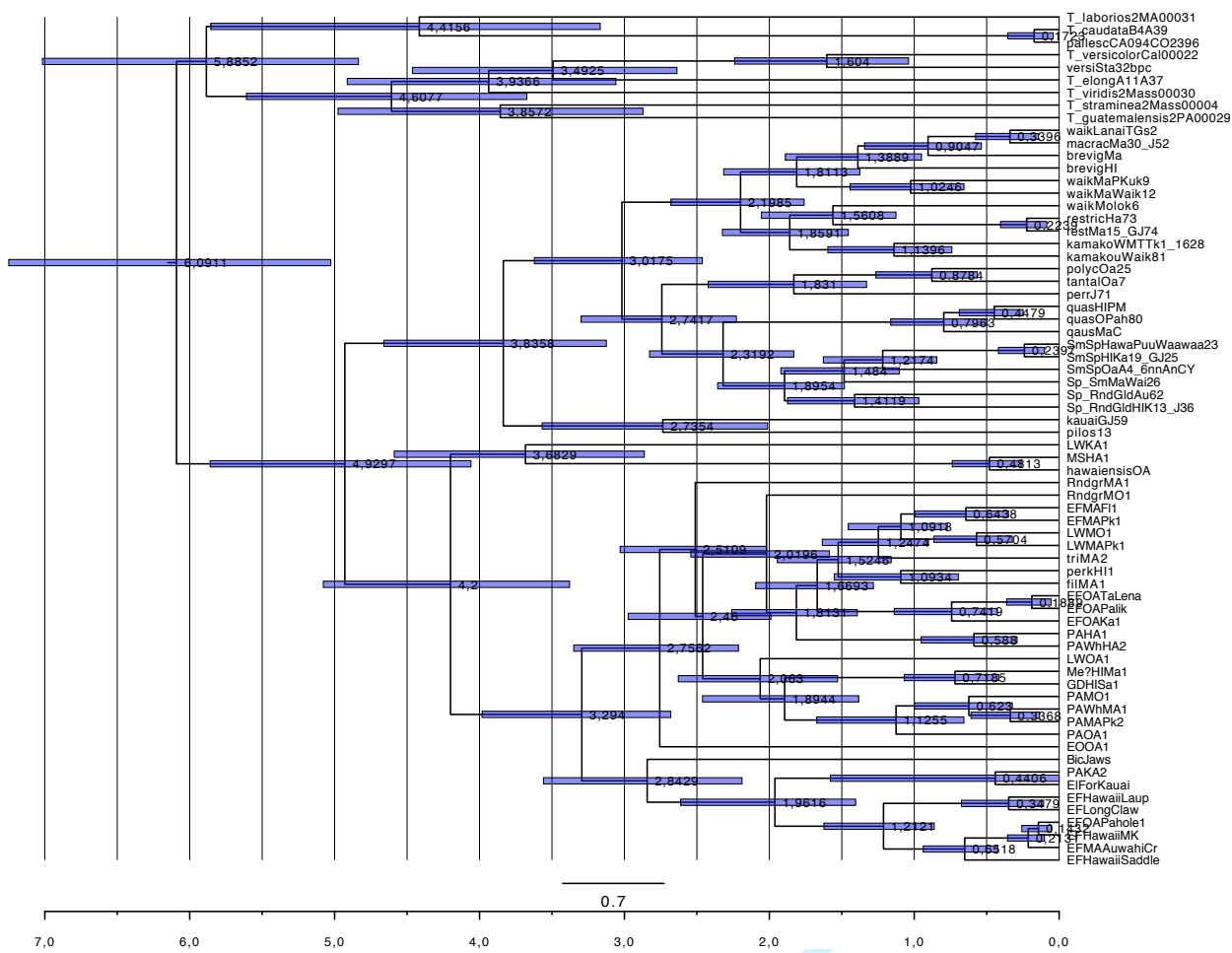
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3 Supplemental Figures



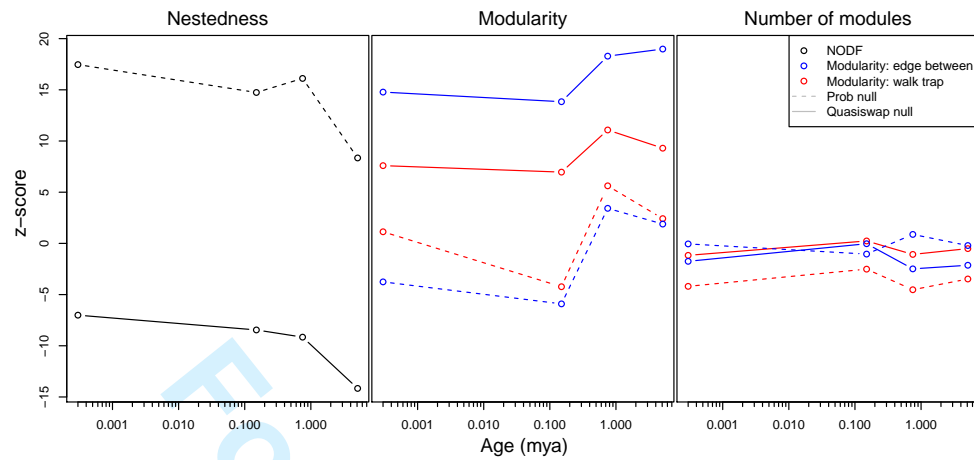


Figure 2: Comparison of different null models (“Prob” and “Quasiswap”) used to standardize network metrics and comparison of different algorithms for assessing modularity (“edge between” and “walk trap”). Choice of null model has a strong influence on the sign and magnitude of metrics but not on their relative trends. The different modularity algorithms lead to largely similar qualitative patterns.

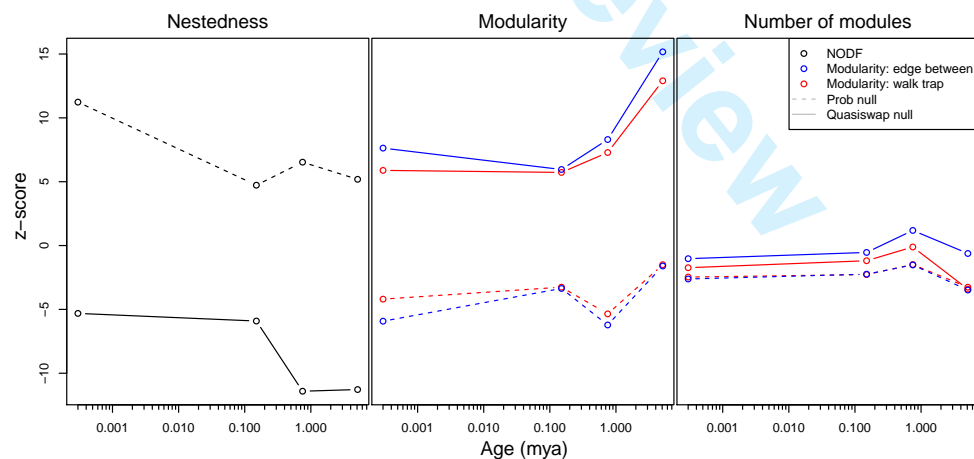


Figure 3: Metrics NODF and modularity calculated for networks based on more biogeographically conservative assignment of Hemiptera to localities. Colors and metric specifics as in Figure 2.

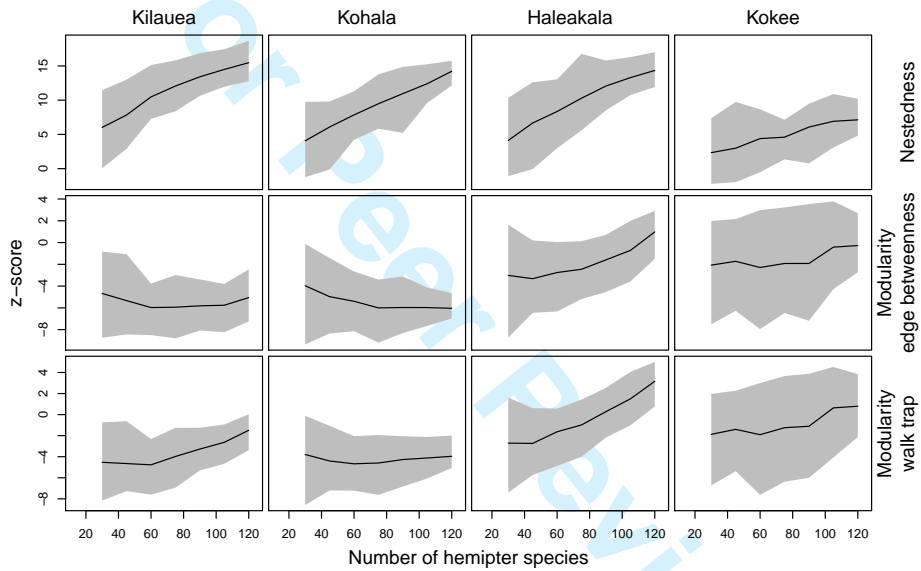


Figure 4: Result from rarification analysis showing sensitivity of network metrics to number of Hemiptera sampled.



## Supplemental Tables

As part of the final submission we will make available our compiled list of Hemiptera and their plant hosts from published sources.

Table 1: Published sources of trophic information used to construct networks.

For Peer Review