**ABSTRACT**

**INTRODUCTION**

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

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). 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; Rosindell *et al.*, 2012), re-vitalized classical niche-based mechanisms such as niche partitioning (Tilman, 2004; Chesson, 2000), competition and predation (Borer *et al.*, 2014), and put species interactions in a network theoretic context (Williams & Martinez, 2000; Brose *et al.*, 2006; Berlow *et al.*, 2009). The combined advances of ecological theory, with its broad predictive power, and insights into evolutionary mechanisms based on inference from contemporary patterns of species, genetic, or phylogenetic diversity (e.g., Kreft & Jetz 2007; Jetz & Fine 2012; Wiens & Donoghue 2004; Wiens et al 2011) have set the stage to address longstanding questions of how evolutionary history can drive common patterns in contemporary ecology (Ricklefs, 1987). Here, we propose an integrative framework to study evolutionary community assembly and provide an initial test using arthropod lineages in the model archipelago of the Hawaiian Islands. Using published data, we estimate (1) the development of genetic discontinuity and the extent to which taxa across communities differ in the rates that populations change from panmixia to fully differentiated species. This is contextualized with (2) macroecological metrics of community structure, using predictions from statistical steady state and ecological network theory to examine changes over the chronosequence.

*Hotspot oceanic archipelagos as model systems*

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

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

*Development of genetic discontinuity*.

As species fracture into new populations that may eventually diversify to form new species, they form genetic discontinuities while experiencing periods of isolation and reconnectance through migration. Understanding how different types of taxa, such as taxa in different trophic positions, differ in the rate and pattern of departure from genetic panmixia is fundamental to understanding the dynamics of species formation. Ecological approaches tend to treat species as static units, while evolutionary approaches tend to treat them as highly dynamic. In order to make progress towards an approach that integrates ecology and evolution in the assembly of communities, it is necessary to incorporate the dynamic nature of species into an ecological framework.

*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 2009). Theory provides a necessarily simplified view of biodiversity and deviations from theory can reveal which more biologically realistic mechanisms underlie observed patterns. The Maximum Entropy Theory of Ecology (METE; Harte 2011) provides a prediction for idealized ecological communities in statistical steady state. Statistical steady state describes the situation in which a system’s behavior is governed by a simple set of state variables and no further system-specific mechanisms are required (Harte 2011; Harte and Newman 2014). Thus METE’s predictions are similar to neutral theory (Hubbell 2001) but make fewer assumptions, allowing for the possibility that myriad ecological mechanisms to influence communities. However, METE assumes that these mechanisms have no statistical affect on the macroscopic biodiversity patterns of the system. Real world deviations from METE can provide insights into the processes driving ecology away from this statistical steady state and toward alternate system states (Harte 2011). We expect that different aged communities along the Hawaiian chronosequence will deviate differently from METE, because we hypothesize the processes of speciation, extinction, adaptation and colonization may themselves drive Hawaiian communities out of statistical steady state.

METE has been shown to successfully predict various metrics of an ecological community (Harte 2011), including network metrics that describe trophic interactions between species (Williams; Harte 2011). Ecological network theory incorporates evolutionary concepts such as coevolution (Bascompte & Jordano, 2007; Donatti *et al.*, 2011; Nuismer *et al.*, 2013) and has clear ties with macroecological questions of the distribution of abundance and body size across species (Berlow *et al.*, 2009; Williams, 2010; Harte, 2011). The distribution of linkages in ecological networks has been used to evaluate the signature of neutrality in the assembly of plant-animal interactions (Oikos frugivory paper).. 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 (cite).

In this paper we use a novel integration of methods from population genetics to theoretical ecology using the chronosequence of the Hawaiian Archipelago to understand the nexus between ecological and evolutionary community assembly. We evaluate (1) the rate and pattern of genetic connectivity among populations of taxa from different trophic levels as they diversify from populations to form new species; (2) the processes underlying the structure of species interaction networks given the backdrop of population divergence; and (3) the processes involved in diversification as species form and accumulate. We use previously published data on population genetic structure and species interactions as a proof of concept, with the goal of further developing this framework through ongoing work.

**METHODS**

## Hawaii as an eco-evolutionary study system

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

To investigate how ecological patterns change in response to varied evolutionary contexts we selected four focal sites across the chronosequence of substrate and island ages (two on Hawaii Island, one on Maui and one on Kauai) from which to compile interaction network data. Focal sites were selected to have similar forest composition (dominated by *Metrosideros polymorpha*: Myrtaceae), elevation (1100-1400m), and climate (mean annual precipitation 2000-3000 mm), while deliberately varying substrate age. These forested montane sites are well-studied and primarily composed of native plant and arthropod species . The four sites span the chronosequence from 0.0002–5 million years (Kilauea and Kohala (Hawaii Island); Waikamoi (Maui), Kokee (Kauai); see Fig. [fig:map]). 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.

## Compilation and analysis of genetic data

We first asked 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 from several spiders species (COI and allozymes; Roderick *et al.*, 2012; Croucher *et al.*, 2012) to three orders of insects: detritivorous *Laupala* crickets (AFLPs; Mendelson *et al.*, 2004); herbivorous *Nesosydne* planthoppers (COI and microsatellites; Goodman *et al.*, 2012; GenBank accession numbers XXX-XXX); herbivorous *Trioza* psyllids (COI, cytB; GenBank accession numbers XXX-XXX); and fungivorous *Drosophila sproati*: (COII; Eldon *et al.*, 2013). In the case of previously unpublished molecular data, sequences for *Nesosydne* planthoppers were generated following protocols described in (Goodman *et al.*, 2012) and sequences for *Trioza* psyllids were generated following protocols described in Percy (2003) with primers given in Simon *et al.* (1994) and Timmermans *et al.* (2010).

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 , a measure of genetic variance, or, where possible , an analog that incorporates genetic sequence information. The *Laupala* AFLP data were analyzed using TFPGA v. 1.3 (Miller, 1997), using the same hierarchical approach 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 Fst varies with the geologic age of volcanoes on Hawaii Island and Maui Nui. For each volcano we calculated or (Excoffier and Schneider 2005) for each taxon between sites within volcanoes.

## Construction of plant-herbivore networks

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 (cite); however, currently available data restrict our analysis to binary networks, those that describe only the potential for interaction between any two species, but not the relative frequency of that interaction to each species.

We compiled species lists of all endemic hemipteran herbivores (sap feeders) for each focal site from published species accounts (e.g. the Hawaiian Arthropod Checklist, Nishida (2002); see supplement for full list). Species accounts and other published sources were used to determine the presence, probable presence or probable absence of each Hemiptera species at each of our four focal sites. A documented presence was defined as a known specimen collected at the focal site; a probable presence was defined as a species whose abiotic tolerances and known geographic range (see supplement) overlap with a focal site but no known specimen exists confirming its presence. Probable absence was assumed when neither criteria for presence or probable presence are met. Two sets of species lists for each focal site were compiled: a conservative data set composed of only documented presence occurrences and a less conservative data set that also included probable presences.

Host plants for each hemipteran species were determined from published species accounts. Host plant occurrence in the focal sites was determined using distribution models for 1158 species of Hawaiian plants (Price, 2012). Each focal site was spatially joined in a geographic information system (GIS) 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

To test the hypothesis that communities differentially depart from statistical steady state during ecological succession versus potential eco-evolutionary feedback, 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). We compared observed degree distributions to METE predictions by comparing the likelihood that the observed data came from the METE distribution to the sampling distribution of likelihood scores assuming METE is true. This comparison is identical in approach to a z-score test using a Monte Carlo simulation to estimate the sampling distribution of likelihoods. R scripts used for METE estimation and Monte Carlo methods will be made 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 *et al.*, 2003; 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 R package vegan (Oksanen *et al.*, 2013) and modularity using a variety of algorithms implemented in the R package igraph (Csardi & Nepusz, 2006). These metrics are not directly comparable across networks of different size and connectance (Ulrich *et al.*, 2009), so for each metric in each network we calculate z-scores using a null model that randomizes network structure while maintaining certain aggregate network properties (Ulrich *et al.*, 2009). These z-scores are calculated as the difference between the observed network metric minus the mean of the null model divided by the null model standard deviation, or (. Because z-scores can be highly sensitive to the choice of null model (Ulrich *et al.*, 2009) we implemented both a probabilistic null model (Bascompte *et al.*, 2003) and a null model that strictly constrains the degree distributions of plants and herbivores (Ulrich *et al.*, 2009).

**RESULTS**

**Population genetic inference of discontinuity among populations**

The analysis of molecular variance (AMOVA) revealed evidence of significant genetic structure from the smallest to the largest spatial scales examined, all within a very recent timeframe. For mitochondrial loci, the amount of significant molecular variation partitioned to among-sites, within volcanoes ranged from 0.037–0.92 and to the among volcanoes from 0–0.30. Corresponding variation at multilocus nuclear loci between-sites, within volcanoes ranged from 0.21–0.58 and among volcanoes, 0.04–0.34. Taxa in the lower trophic levels (herbivorous sap-feeding Hemiptera: planthoppers and psyllids) had as much or more molecular variation partitioned at the among-site, within volcano level than the among volcano level while the predatory spiders were less structured at localities within volcanoes (Table [tab:fst]). 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 compared to localities on older volcanoes (Fig. [fig:volcanoFst]). 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. 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 origination range from 0.34–1.15 million years, with all additional within-species genetic divergence developed subsequently (Table [tab:fst]).

**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. [fig:degree]). 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. [fig:degree]). 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 looking at the degree distribution defined by trophic links to plant genera instead of plant species, the pattern of increased generalization holds for the Kohala but endemics on Maui no long show a difference in their degree distributions from other island endemics. This change in pattern indicates 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. [fig:netMet]). This trend is found in networks constructed from both more and less stringent geographic criteria (supplemental Fig [figSupp:netCons]). 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. [figSupp:netMetComp]). The patterns are also robust to sampling intensity, as demonstrated by a rarefaction analysis (supplemental Fig. [figSupp:rfy]).

**DISCUSSION**

By combining novel data with that gathered from the primary literature and using a 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. The results showed that taxa in the lower trophic levels developed genetic discontinuities at much smaller spatial and temporal scales than those at higher trophic levels. At the same time, network nestedness decreased with age while modularity increased across our island chronosequence (Fig. [fig:netMet]), indicating that (x and y). Furthermore, the distributions of the number of links assigned to each insect species in the network showed the greatest deviation from maximum entropy predictions on the youngest and oldest sites, suggesting that (x and y). Moreover, endemics show more specialization compared to more generalist species, which indicates (x and y). Together, these analyses reveal patterns that allow us to generate hypotheses about the dynamics of ecological and evolutionary assembly over time. In this age structured and simplified model system we hypothesize that the contribution of evolutionary assembly and ecological assembly vary between taxa and between ages of lineages in communities.

**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 [tab:fst], Fig. [fig:volcanoFst]). 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 cricket detritivores and predatory spiders (Table [tab:fst], Fig [fig:volcanoFst]). Population structure within species allows for populations to take independent evolutionary trajectories, especially when aided by other evolutionary processes that may be acting differentially across each species’ range. A variety of factors have been implicated in the genetic divergence of populations and species in lineages described here, including combinations of genetic drift associated with geographic isolation (Percy, 2003; Gillespie, 2005; Mendelson & Shaw, 2005; O’Grady et al., 2011; Goodman et al., 2012), adaptation associated with ecological interactions of competition, predation, and mutualism (Gillespie, 2004; Blackledge & Gillespie, 2004; Roderick & Percy, 2008), and sexual signaling (Mendelson & Shaw, 2005; Percy & Kennedy, 2006; Magnacca et al., 2008; Goodman et al., in review).

The sap-feeding Hemiptera group *Nesosydne* (Goodman et al., 2012) provide evidence that some period of geographic isolation preceded divergence of sexual signals (Goodman et al., in review). Shifts in plant host use are also involved in the process of diversification in this group (Roderick & Percy, 2008). In a similar radiation of leafhoppers, *Nesophrosyne* (Bennett & O’Grady, 2013), host plant specialization drove 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. [fig:netMet], [fig:degree]), 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, seem to require larger spatial and temporal scales to develop genetic discontinuities. This might be expected given the larger area requirement of predators compared to herbivores. Most important in the context of community assembly is that endemic sap-feeding herbivores developed structure quickly (on the order of less than 0.1 million years; Table [tab:fst]), with predatory spiders showing local endemicity more slowly (Table [tab:fst]). Furthermore, among those lineages that show adaptive diversification, ecological differences appear early in the process of differentiation (Percy, 2003; Gillespie, 2004; Blackledge & Gillespie, 2004; Percy & Kennedy, 2006; Magnacca et al., 2008; O’Grady et al., 2011; Goodman et al., 2012).

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

Because Kilauea is such a young site, ecological assembly should be the dominant process there. The results of network analysis support this hypothesis with Kilauea showing substantial nestedness and limited modularity (Fig. [fig:netMet]). Nestedness is likely to result if new species arriving by immigration have a high probability to eat or be eaten by the generalist species already present at the site (Bascompte et al., 2003). In this way we might expect Kilauea to also conform to the statistical steady state predication of maximum entropy. However, the observed deviations from maximum entropy at Kilauea are largely driven by a surplus of singleton links (Fig [fig:degree]). These in turn likely result from incomplete assembly, and thus lower species richness, of the plant and herbivore biotas. Future research needs to focus on the added observation that the genetic analysis indicates that discontinuities arise within species on very short timescales across taxa (table), timescales that in some taxa include the greater landscape of Kiluaea. Because of this, whether or not assembly is entirely driven by ecological processes should be considered. Conversely, Kohala shows a statistically significant agreement with maximum entropy perhaps because the Kohalas, at intermediate age (150 ky), have experienced complete ecological succession but are still too young to be driven away from statistical steady state by specialization and rapid in situ diversification driven by host plant preference

The older Maui and Kauai sites show strong deviations from expectations of maximum entropy theory (Fig. [fig:netMet]), which is consistent with our hypothesis that the influence of evolutionary assembly on these biotas drives them away from statistical steady state. The application of maximum entropy to ecology does not currently take into account evolution (Harte, 2011). Indeed the use of maximum entropy in ecology is inspired by its application in physical systems whose change through time is simple and purely Markovian, potentially a far cry from the complex change through time undergone by biological systems as they change and adapt to their ecosystems (Eldredge, 1989; Arnold et al., 2001). 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. [fig:netMet]). 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 [fig:degree]), while at the youngest site Kilauea, specialist endemics are limited by low plant diversity and thus show more apparent specialization (Fig [fig:degree]). 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. [fig:degree]). 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 indicating that Maui endemic Hemiptera are no more generalized on plant genera but instead may benefit from the diversification of plant species within genera on Maui.

**Future Research**

These analyses indicate strong patterns of a dynamic assembly process leading to contrasting hypotheses depending on the timescale community under observation:

1. In younger communities we hypothesize that

a) During periods of ecological assembly (younger communities), communities strongly influenced by immigration will resemble random samples from regional source pools and thus metrics describing these communities will largely match expectations of statistical steady state after primary succession has completed (Harte, 2011).

b) The exception will be communities still undergoing primary succession (Harte, 2011), which will change rapidly through time and represent non-random samples of source pools.

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

2. Alternative in older communities we hypothesize that

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

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

3. A hypothesis about how genetic metrics (discontinuities, gene flow, drift, pop size fluctuation) that provide details on how species are dynamic may influence ecological metrics such as network structure and macroecological variables, which consider species to be static units.

In ongoing work we are obtaining more detailed ecological and evolutionary data sets in order to better address these hypotheses and understand the biodiversity dynamics underlying this system.

*Ecological data: Assembly of species into communities*

Our results show that the island chronosequence can reveal fascinating and important insights into the process of community assembly. However, in order to understand the nature of the assembly process and the dynamic nature of the feedbacks involved, future work is focusing on conducting broad sampling of all macroscopic arthropod taxa at a number of sites across the age gradient, thus allowing assessment of changes in overall species composition and diversity across all players in the time-calibrated landscape.

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

*Evolutionary data: Diversification within species*

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

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