**Why studying ecol evol feedback matters**

Understanding how the spectacularly diverse ecosystems that sustain life on Earth emerge from ecological and evolutionary processes remains a central goal in biology. However, disentangling the relative influence of evolutionary and historical processes, which operate at larger spatial and temporal scales, from local ecological processes remains challenging (Ricklefs 2004). Traditionally evolution is view as regulating regional species pools, a process that is largely removed from local ecology (Hubbell, 2001; Cavender-Bares *et al.*, 2009). Studies have reached various conclusions about the drivers of diversification including competition (Rundle, 2003; Schluter, 2003), predation (Nosil & Crespi, 2006), ecological release (Gillespie, 2009; Yoder *et al.*, 2010) and specialization or generalization (Schluter, 2000; Wellenreuther *et al.*, 2008; Glor, 2010). Likewise, given finite ecological opportunity, it has been suggested that the rate of diversification should decline as species numbers increase during an adaptive radiation (Harmon *et al.*, 2008; Rabosky & Lovette, 2008; Bokma, 2009) while other arguments highlight the importance of species themselves as a resource base for others, with diversification increasing with species number (Odling-Smee *et al.*, 2003; Erwin, 2008).

Ecology in turn is viewed as the process acting on standing diversity to pack it into local communities through competition, facilitation, and neutral ecological drift (Hubbell, 2001; Tilman, 2004; Bascompte & Jordano, 2007; Borer *et al.*, 2014). Recent 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 ecology in a theoretical network context (Williams & Martinez, 2000; Brose *et al.*, 2006; Berlow *et al.*, 2009). Together, these advances offer even more predictions to be tested about the processes that structure and stabilize trophic interactions.

While we can observe and test local ecological phenomena, testing evolutionary mechanisms is often based on inference from contemporary patterns of species, as well as genetic or phylogenetic diversity. At the largest spatial scales, studies have typically focused on identifying the abiotic and historical determinants of patterns of species diversity (e.g., Kreft & Jetz 2007; Jetz & Fine 2012). At the same time, the increasing accessibility of phylogenetic information for a wide range of groups have helped elucidate the importance of historical processes on contemporary biogeographic patterns of richness (Wiens & Donoghue 2004; Wiens et al 2011).

**What’s missing**

Nevertheless, this and other ecological research historically has been poorly integrated with evolutionary perspectives (Cavender-Bares *et al.*, 2009), missing the opportunity to understand how evolutionary history can drive common patterns in contemporary ecology (Ricklefs, 1987; Qian *et al.*, 2005). There is a clear need to steer ecological theories and studies toward incorporating biodiversity dynamics during evolutionary community assembly, via the processes of invasion, microevolution, speciation, and extinction.

The confluence of ecological and evolutionary theory has the potential to greatly illuminate biodiversity dynamics through space and time. In practice, merging theories that gain their predictive power from large-scale patterns across multiple species (Brown, 1995; Hubbell, 2001; Harte, 2011) with those that yield information on the dynamic nature of single lineages is challenging. We confront the challenge of analyzing the interface of ecological and evolutionary processes by outlining a set of hypotheses that predict the structure of biological assemblages along a continuum from ecological to evolutionary assembly.

Despite the massive data and innovative analyses, the approaches to date are limited in inferring past processes from current observations. What’s missing is observations of small scale ecological processes, including colonization, ecological fitting, etc, that together give rise to larger and longer term processes of diversification and adaptation. The importance of understanding how the gradual change from “ecological” to “evolutionary” processes plays out is the black box of biodiversity that has been found to be so critical for other processes. Because biological processes vary unpredictably over time, the details along the way are vital to understanding biodiversity.

**Why Hawaii/Islands**

islands are opportune systems to study the consequences of these contrasting assembly modes due to their relative simplicity and discrete nature. In addition to definite boundaries in space oceanic island systems are also discrete in time due to their sequential formation over volcanic hotspots. The age gradient of such island systems thus has the potential to stratify ecological assembly and evolutionary assembly processes. For example, younger communities may be dominated by ecological assembly from initial immigration from the mainland, whereas on older islands, we might observe evolution keeping pace with ecology. This stratification provides an opportunity to disentangle these interacting forces.

The Hawaiian archipelago is a prime example because its geological chronology (Price & Clague, 2002) and biota are well-known (Wagner & Funk, 1995).In this age structured and simplified model system we hypothesize that the contribution of evolutionary assembly and ecological assembly will vary between taxa and between ages of lineages in communities.

Age-structured landscapes such as the Hawaiian archipelago provide a unique lens with which to view how ecology and evolution feedback on each other to produce biodiversity over time. The well-defined geological setting and chronology (Price & Clague 2002) effectively creates snapshots over time, and can provide insights into how ecological and evolutionary processes interact, and how specific differences between taxa affect the nature of the dynamic. 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).

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 of arthropod populations among habitats (Vandergast *et al.*, 2004; Goodman *et al.*, 2012; Eldon *et al.*, 2013; Bennett & O’Grady, 2013). On larger spatial 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 up to 5 million years from Hawaii Island to Kauai.

We use this age-structured template as a basis from which to assess evolutionary community assembly. At least two aspects of the system make this approach feasible:

1. the limited diversity of lineages allows precise identification of ecological affinities of taxa, and hence the role of ecological opportunity in adaptive radiation, and

**Genetic data as an evolutionary guide**

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 of arthropod populations among habitats (Vandergast *et al.*, 2004; Goodman *et al.*, 2012; Eldon *et al.*, 2013; Bennett & O’Grady, 2013). On larger spatial 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 up to 5 million years from Hawaii Island to Kauai.

**Why webs**

Ecological networks are a prime starting place for integrating the mechanisms of ecology and evolution because ecological network analysis already builds off evolutionary hypotheses such as coevolution (Bascompte & Jordano, 2007; Donatti *et al.*, 2011; Nuismer *et al.*, 2013) and has clear ties with macroecology (Berlow *et al.*, 2009; Williams, 2010; Harte, 2011).

Little bit about what has been hypothesized and demonstrated about evolving networks.

**What we hope to find**

In this paper, we use this age-structured template as a basis from which to assess evolutionary community assembly, combining analytical approaches from network analysis, Maximum Entropy Theory of Ecology (METE: Harte XXXX), and population genetics. We: (1) develop bipartite interaction networks of plants and herbivores across an age gradient and use the resulting patterns to generate hypotheses about the dynamics underlying community assembly across time, (2) <**Something about METE**>, and (3) analyze existing population genetic data to evaluate the connectivity of populations across the landscape and evaluate whether this differs across trophic levels. Together, our results begin to reveal the dynamics of ecological and evolutionary assembly over time.

**METHODS**

## Hawaii as an eco-evolutionary study system

## 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 at which to compile interaction network data. Existing genetic data from across Hawaii Island and Maui provide an evolutionary calibration of how arthropod populations have accumulated genetic diversity and divergence within the dynamic landscape of the focal sites.

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 selected four sites according to the criteria above that span the chronosequence from 0.0002–5 million years (Kilauea and Kohala (Hawaii Island); Waikamoi (Maui), Kokee (Kauai); see Fig. [fig:map]). Focal sites were also selected to coincide with areas of intensive research in arthropod diversity, allowing us to leverage existing data on the presence or probably absence of many arthropod taxa based on published data alone (see Supp for list of citations).

## Compilation and analysis of genetic data

To provide an evolutionary context for our network analysis we assessed the spatial and temporal scales at which genetic differentiation occurs across the landscape of the islands. 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 age in allowing *in situ* genetic diversity and potential for divergence we analyzed how population structure 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 (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 importance of that interaction to each species.

We compiled host plant identities for all Hemiptera herbivores (sap feeders) native to Hawaii from published species accounts (see supplement for full list). Species accounts and other published sources (e.g. the Hawaiian Arthropod Checklist, Nishida (2002); see supplement for full list) 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 is defined as a known specimen collected at the focal site; a probable presence is 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 is assumed when neither criteria for presence or probable presence are met. Analyses on network metrics were completed on data sets composed of both strict presence occurrences and strict presence combined with probable presence.

Plants were determined….

and their native host plant species within the study sites. Each site’s set of herbivores was determined from the literature including the Hawaiian Arthropod Checklist (Nishida 2002) and available data indicating whether a species has been detected or is likely to occur within the sites (see supplement). The list of plants for each site was generated using distribution models for 1158 species of Hawaiian plants (Price, 2012). Each study site was spatially joined with all coincident plant distribution models that fell within its boundaries. Resulting site-specific networks were constructed both for conservative estimates of the geographic ranges of Hemiptera (considering only sites with definite specimen localities) and more liberal estimates (extrapolating between known localities surrounding our focal sites and with habitat comparable to our focal sites).

## Analysis of plant-herbivore networks

To understand how overall network structure changes with age, we calculated two widely used descriptive network metrics across sites—nestedness (Bascompte *et al.*, 2003; Ulrich *et al.*, 2009) and modularity (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). 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).

To more explicitly test the hypothesis that communities dominated by evolutionary assembly and *in situ* diversification processes should differ from those dominated by ecological assembly and immigration, we analyzed the number of links assigned to each Hemiptera species (the degree distribution) separately for island endemics (those species found on only one island) versus island cosmopolitans (those species found on multiple islands). We hypothesized that evolutionary assembly should favor specialization and thus expected island endemics to be more specialized. To compare species’ degree 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 test the hypothesis that communities should differentially depart from statistical steady state during their ecological succession and evolution, we compared the degree distributions to that predicted by maximizing information entropy relative to the constraint of average degree (Williams, 2010). The maximum entropy prediction represents the hypothesis of statistical steady state (Harte, 2011).