Understanding how the 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 local ecological processes from evolutionary and historical processes, which operate at large spatial and temporal scales, remains challenging (Ricklefs 2004). Traditionally evolution is viewed as regulating regional species pools, a process happening largely removed from local ecology (Hubbell, 2001; Cavender-Bares *et al.*, 2009). While we can observe and test local ecological phenomena, testing evolutionary mechanisms is often based on inference from contemporary patterns of species, 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; Wiens & Donoghue 2004; Wiens et al 2011).

Ecology in turn is viewed as the processes that act to pack standing diversity 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 network theoretic context (Williams & Martinez, 2000; Brose *et al.*, 2006; Berlow *et al.*, 2009).

Ecological theories have 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.

Islands, due to their relative ecological simplicity and discrete nature, are opportune systems to disentangle the interplay of local ecological mechanisms and large scale historical evolutionary drivers of biodiversity patterns. In addition to definite boundaries in space, hotspot oceanic island systems, such as the Hawaiian archipelago, are also discrete in time due to their sequential formation as the tectonic plate moves over a volcanic hotspot. The age gradient of such island systems thus has the potential to stratify the eco-evolutionary process of community assembly. For example, younger communities may have originated 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, on older islands the longer time scale could allow observation of the combined interaction and feedback of the diversification of the source pool and local ecological dynamics. The temporal stratification provides an opportunity to disentangle these interacting forces.

The Hawaiian archipelago provides a useful system for study because its geological chronology (Price & Clague, 2002) and biota are well-characterized (Wagner & Funk, 1995). In this age structured and simplified model system we hypothesize that the contribution of evolutionary assembly and ecological assembly will vary among taxa and ages of lineages in communities. 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 from present day up to 5 million years across Hawaii Island to Kauai.

Ecological network theory is an opportune starting place to integrate the mechanisms of ecology and evolution because this body of theory already builds off evolutionary hypotheses 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 structure of ecological networks is often characterized by the distribution of links among species and the degree to which those links asymmetrically connect specialists and generalists (a pattern known as nestedness) and connect species into semi-descrete modules (citations). Modularity and nestedness have been hypothesized to relate directly to the evolutionary scenario underlying network formation (citations). Modularity is though to arise due to diffuse coevolution between animals (be they in the role of herbivore, frugivore or pollinator) and plants, with the traits of both groups evolving to either optimize mutualism or avoid antagonism (citations). Nestedness has been proposed to arise through multiple dynamics including stochastic sampling of source pools (citation), preferential interaction with generalists (citation) and forcing acting to stabilize network dynamics (citation).

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) and lends itself to analysis using tools built to understand other pervasive patterns in ecology such as the species abundance distribution. The Maximum Entropy Theory of Ecology (METE; Harte 2011) is one such tool that can predict the statistical steady state of a community, and thus real world deviations from METE can provide insights into the processes driving ecology toward alternate system states (Harte 2011; Harte and Newman 2014; Newman in press). In the context of ecological networks, deviations from METE predictions could indicate systems under rapid or driven change due to the evolutionary process coupling plants and animals.

In this paper, we use the age-structured template of the Hawaiian Archipelago as a basis from which to study evolutionary community assembly, combining analytical approaches from network analysis, the METE (Harte 2011), and population genetics. We analyze existing population genetic data to evaluate the connectivity of populations across the landscape and evaluate whether this differs across trophic levels. Within this evolutionary context calibrated by population genetic structure we 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 through time.

**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.

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. 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 evolutionary calibration of how arthropod populations have accumulated genetic diversity and divergence within the dynamic landscape of the focal sites.

## 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 landscape 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 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 was determined from the 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 species presences and the other using the less conservative data set.

## 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 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 test the hypothesis that communities should differentially depart from statistical steady state during ecological succession versus potential eco-evolutionary feedback, 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).

**RESULTS**