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). There is a clear need to integrate ecological theories and studies with evolutionary dynamics of colonization, microevolution, speciation, and extinction. The confluence of ecological and evolutionary theory has the potential to greatly illuminate biodiversity dynamics through space and time. Here, we will show how ecological theory can be used to leverage natural experiments on oceanic islands of known chronologies to test how the interplay between evolutionary and ecological processes has shaped present-day biodiversity. We advocate for combining perspectives gained from coupled molecular and community-level data across broad taxonomic scales and demonstrate its potential with previously published data.

Traditionally, the evolutionary processes of speciation and extinction are viewed as regulating regional species pools, and as occurring largely removed from local ecology (Hubbell, 2001; Cavender-Bares *et al.*, 2009). Ecological processes in turn are viewed as acting 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 the ecology of 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) has set the stage to address longstanding questions of how evolutionary history can drive common patterns in contemporary ecology (Ricklefs, 1987).

Hotspot oceanic island systems, such as the Hawaiian archipelago are opportune model systems to disentangle the interplay of local ecological mechanisms and large-scale historical evolutionary drivers of biodiversity patterns. Such island systems contain simplified biotas due to their isolation and are also conveniently discrete in space and in time due to their sequential formation as the tectonic plate moves over a volcanic hotspot.

In this age structured and simplified model system the contribution of evolutionary assembly and ecological assembly will vary according to geological age of the environment, taken as an indicator of the total age over which in situ divarication could occur. The age gradient of such island systems thus has 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, 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. Moreover, because dispersal, and hence connectance 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 so well characterized (Wagner & Funk, 1995).

While we expect the mechanisms underlying the generation and maintenance of biodiversity to change across chronological sequences, identifying such change has been fraught (citation). 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) is one such theory 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). We expect that different aged communities along the Hawaiian chronosequence will deviate differently from METE. If the evolutionary context of these communities can explain these deviations then the processes of speciation, extinction, adaptation and colonization may themselves be the forces driving Hawaiian communities out of statistical steady state.

Ecological networks are a prime area for theoretical testing and advancement. Ecological network theory builds off 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 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-discrete modules (citations). 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). METE predicts a specific form of the link distribution, and deviations from METE could indicate systems under rapid or driven change due to the evolutionary process coupling plants and animals.

Other network metrics can be used to evaluate such processes. Modularity and nestedness have been hypothesized to relate directly to the evolutionary scenario underlying network formation (citations). Modularity is thought to arise through 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 forces acting to stabilize network dynamics (citation).

In this paper we propose a framework to synthesize insights from population genetic, ecological and theoretical analyses 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 connectivity of different taxa as they diversify from populations to form new species and does this differ between trophic levels; (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. While integration across all three of these elements is beyond the scope of the current paper, we use previously published data on population genetic structure and species interactions as a proof of concept.

**METHODS**

## Hawaii as an eco-evolutionary study system

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 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.

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 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 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 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 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**

**Population genetic inference of connectivity 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 the 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 having developed subsequently (Table [tab:fst]).

**Evolving network structure**

Across our chronosequence of sites 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]).

The Hemiptera species degree distribution varied across sites 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 community 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 Kohalas 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 is driven by increased intra-genus plant diversity on that island.

**DISCUSSION**

The results showed that taxa in the lower trophic levels (herbivorous sap-feeders: Hemiptera Nesosydne and Trioza) had as much or more molecular variation partitioned among sites within volcanoes than among volcanoes, in contrast to predatory spiders, for which molecular variation was largely partitioned among volcanoes (Table [tab:fst]). Sap-feeding herbivores also illustrated high population structuring among sites on the younger volcanoes, while spiders only developed population structure on the older volcanoes (Fig. [fig:volcanoFst]). At the same time, considering plant-feeding Hemiptera only, network nestedness decreased with age while modularity increased across our island chronosequence (Fig. [fig:netMet]). The distributions of the number of links assigned to each Hemiptera species showed the greatest deviation from maximum entropy predictions on the youngest and oldest sites. In the middle-aged sites in Kohala and on Maui, deviations are not different than expected by chance. Moreover, endemics show more specialization compared to more generalist species (Fig. [fig:degree]). Together, these analyses begin to reveal the dynamics of ecological and evolutionary assembly over time.

**Population structure at different trophic levels**

The analysis of available genetic data presented here indicates that divergence is occurring within the islands at small spatial scales and over short time periods (Table [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 various 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 certainly involved at some point in the process of diversification in this group (Roderick & Percy, 2008). While this stage has not yet been identified with phylogentic methods in Nesosydne it has been in the parallel leafhopper radiation, Nesophrosyne (Bennett & O’Grady, 2013). This work found that 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.

The Trioza group of psyllids (Hemiptera: Triozidae) and other herbivorous, fungivorous and detritivorous insect groups 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).

Our analysis suggests that the mechanisms implicated in the diversification of predators, notably spiders, are different. In particular, while geographic isolation is clearly implicated in the speciation process (Gillespie, 2005), ecological divergence through natural selection is assumed to play a key role in the differentiation of sister taxa on older islands (Gillespie, 2004; Blackledge & Gillespie, 2004). In taxa that do not show major ecological differentiation, such as Orsonwelles spiders, differentiation appears to have been driven almost entirely by geographic isolation (Hormiga et al., 2003), and on a much larger spatial and temporal scale than those found for herbivores, fungivores, and detritivores.

Differences in the patterns of population structure observed between trophic levels, as highlighted here, suggests that differentiation of predators requires a larger area and/or a longer time period to occur, which 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).

**Network structure**

Given the timescale provided by the genetic analysis, ecological assembly should dominate ecological communities at the youngest site, Kilauea. The results of network analysis are consistent with 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. 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. In the Kohalas, which show 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 benefit from the diversification of plant species within genera on Maui.

**Future Research**

These analyses indicate strong patterns of a dynamic assembly process despite being limited to available data. In ongoing work we are obtaining more detailed ecological and evolutionary data sets, which will allow us to understand the biodiversity dynamics in greater depth.

*Assembly of species into communities*

In terms of the distribution of abundance and body size of arthropod species, Gruner (2007) provided some key insights into changes in arboreal arthropods from Metrosideros polymorpha, showing that abundances and sample-based species richness were highest at more productive, intermediate-aged sites (Maui Nui). This study also showed that proportions of individuals and biomass varied widely across sites, and according to trophic group and taxonomic order. However, communities tended to converge in trophic structure and composition. Recent analysis of these data in the context of the maximum entropy theory of ecology (Harte, 2011) has shown that different trophic groups conform or deviate from maximum entropy predictions across the age gradient depending on their unique eco-evolutionary histories (Rominger et al., in preparation). For example, predators, whose assemblages are likely more dominated by immigration and ecological assebly (Fig. [fig:volcanoFst]) never show strong deviations from maximum entropy predictions whereas herbivores show increasing deviation with age, in agreement with the network results of this paper (Fig. [fig:degree]) (Rominger et al., in preparation).

What is clear from this work is 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, it is important that we conduct broad sampling of all macroscopic arthropod taxa at a site, thus allowing assessment of changes in overall species composition and diversity across all players in the time-calibrated landscape.

*Diversification within species*

Much work remains to determine the detailed patterns of diversification in different lineages, the extent to which patterns are associated specifically with trophic level, and the interplay between gene flow, population size and fluctuations in size in the context of speciation. Particularly important in terms of the dynamics of diversification, will be to assess the extent and location in the genome of gene flow during the course of speciation (Nosil & Crespi, 2006).

What is clear from the current study, besides showing that taxa differ in the scale at which differentiation occurs, is 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).

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 how 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), highlighting the potential role of admixture among successively introduced populations in providing the genetic variation to allow adaptive evolution.

Clearly, more work is needed in order to understand the role of genetic mixing and hybridization among recently diverged populations and the potential role of such effects in fostering adaptive radiation (Nosil & Crespi, 2006; Seehausen et al., 2014). Particularly intriguing will be to determine the extent to which novel genetic combinations might facilitate differentiation associated with ecological shifts, and the timeframe over which this tends to occur in different lineages.