# Introduction

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). While we can observe and test local ecological phenomena, testing evolutionary mechanisms is less straightforward, and are often based upon 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). 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), advanced our understanding of local community assembly within regional contexts (Cavender-Bares et al 2009; Lessard et al 2012; Carstensen et al 2013), and led to greater understanding of ecological limits to diversification (Rabosky & Lovette 2008, Phillimore & Price 2008).

Nevertheless, while such approaches have greatly advanced our understanding of diversity patterns in space and time, there has been far less work aimed at understanding how smaller-scale ecological processes contribute to speciation. Both environmental and spatial barriers to gene flow can contribute to genetic isolation (Wright 1943; Wang & Summers 2010), and recent studies have focused on parsing out the relative contribution of distance and ecology on genetic divergence (Wang et al 2013, Sexton et al 2014). Such studies, however, are based upon contemporary patterns of genetic diversity that have arisen over long periods of history.

Age-structured landscapes such as the Hawaiian archipelago, on the other hand, provide a unique lens with which to view how genetic and ecological divergence develop 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). 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.

[Jun: Warning. Everything after this point is VERY experimental]

Arthropod lineages on Hawai’i often show different distinct phylogeographic patterns. Whereas certain lineages have undergone repeated and sequentially colonization of islands and subsequent in-situ diversification within the individual islands they colonize, other lineages are more characterized by ‘cosmopolitan’ distributions owing to their high dispersal ability (Gillespie & Roderick 1998).

Here, we choose to focus on arthropods and their associated interactions with plants, by constructing bipartite networks of plants and herbivores across islands of different age.

Merits of ecological networks. Bridge between an ecological process (biotic interaction) at the species level, and evolutionary processes at the population level (i.e., cosmopolitan species versus endemics)

At the same time, to evaluate the connectivity of populations across the landscape, we compiled published? population genetic data from multiple taxa across different trophic levels.

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.

**>> Move this to Ongoing and Future Research in the Discussion**

Our objectives are to understand:

1. The extent to which taxa in communities are connected ecologically in space and time. Here, we use genetic tools to infer gene flow and connectivity between communities.
   1. What is the rate and pattern of connectivity of different taxa as they diversify from populations to form new species? And, are differences among taxa predictable, especially taxa in different trophic levels?
   2. Do communities and their resulting networks become more independent with time with relatively more species added to the community through evolutionary processes as community assembly becomes more complex?
2. The processes underlying macroecological metrics of community structure..
   1. Using predictions from Network Theory, ask how do network structures and component interactions change over ecological and evolutionary time?
   2. Using predictions from the Maximum Entropy Theory of Ecology, ask why do species abundance distributions differ between taxonomic groups and over ecological and evolutionary time?
3. The processes involved in diversification as taxa species form and accumulate
   1. Role of genetic fusion and fission and how this differs across taxonomic groups, potentially leading to genetic enrichment and/or divergence, and at different rates.
   2. Role of adaptation and divergent selection versus drift during the process of population divergence.
   3. Relative rates of speciation and extinction, and how these change over time to give rise to temporal diversity characteristics of a lineage.

IV. *What we will do in this paper*–The current paper provides preliminary data to show how we will address (1) and (2). We are currently generating detailed molecular data using Next Generation sequencing technologies in order to test (3)

# 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. 2) 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. 4) (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.

**Orphaned text and stuff from v7 that could be incorporated somehow:**

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. To this end, we focus on the youngest island of the Hawaiian chain.

**Old text:**

Traditionally we view evolution as responsible for regulating regional species pools, through processes largely removed from local ecology (Hubbell, 2001; Cavender-Bares *et al.*, 2009). Evolutionary change over time in island systems has generally been studied in the context of single lineages, e.g. the adaptive radiation of Galapagos finches (Grant & Grant, 2007), Anolis lizards in the Caribbean (Losos, 2009), and cichlid fish in the great lakes of Africa (Seehausen, 2006). Such studies have reached varied 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). Add Wiens

Ecology in turn is traditionally 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). Island systems have been instrumental in developing our understanding of all these processes, especially through the conceptual lens provided by the equilibrium theory of MacArthur and Wilson (1967). 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). Together, these advances offer even more predictions to be tested about the processes that structure and stabilize trophic interactions. (Rahbek, Jetz)

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). To further aid in integrating ecology and evolution we also make use of the maximum entropy theory of ecology which uses principles from thermodynamics to predict the statistical steady state of ecological communities (Harte, 2011). Statistical steady state refers to the condition under which the aggregate properties of a community, such as the distribution of trophic links, are not influenced by any unique biological mechanism but instead conform to predictions of an idealized statistical system. Deviations from maximum entropy theory have been identified as indications of ecological systems in rapid transition and out of steady state (Harte, 2011; Harte & Newman, 2014).

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.

**Old hypotheses:**

Specifically, we hypothesize that:

1. During periods of ecological assembly, 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). 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. 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. Alternatively, 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). 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).