Community ecology on isolated islands: Macroecology meets evolution

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Abstract

Aim.   Islands are bedrock model systems in the development of ecological and evolutionary theory. The Hawaiian Islands in particular have expanded our understanding of island biogeography, with phylogeographic studies of rapid diversification and the dynamics of adaptive radiation overlaid upon a detailed understanding of ecosystem development and senescence. These studies demonstrate the overriding importance of in situ speciation in biodiversity patterns of highly isolated archipelagoes, beyond the reach of equilibrium colonization dynamics. Here, we ask, how do biodiversity and complex ecosystems emerge from ecological (dispersal, trophic interactions and population dynamics) and evolutionary (speciation, extinction, adaptation and genetic structuring) processes? We synthesize these approaches to understand the processes driving emergent patterns of island biodiversity. We use the natural experiment provided by the island chronosequence to develop a novel analytical pipeline that combines both macroecological (interaction networks and maximum entropy inference) and evolutionary (population genetics and phylogenetics) approaches.

Location.   The Hawaiian Islands.

Methods.   We examine how populations of arthropods are structured across the youngest landscapes in order to ascertain processes involved in early diversification, focusing in particular on potential differences between trophic levels. We then construct food webs based on arthropod taxa found at a given site with substrates ranging 50 years to 5m years. These networks' nodes are then compared to those predicted by a theory of maximum entropy and a model of food-web dynamics. These theories lack mechanisms for diversification. Deviations of data from theory may thus illuminate mechanisms of differentiation, such as population structure, incipient speciation, ecological function, and site age in the evolutionary assembly trophic interaction networks.

Results. We show that, based on genetic information, lineages at lower trophic levels show higher endemism early on in the island chronosequence. Higher trophic levels also show local endemism, though it arises more slowly and over larger areas. Moreover, considering plant-feeding insects only, we found that younger sites were more nested and less modular than older sites.

Main conclusions. The results, although preliminary, highlight the potential of our approach in terms of understanding the interplay between ecological and evolutionary processes in the assembly of complex communities.

Introduction

Islands have played an important role in understanding many of the fundamental principles driving patters of biodiversity, from theories of evolution(Darwin, Wallace) to the ecology of species richness and abundance in and out of equilibrium (MacArthur & Wilson, 1967; Brown, 1995; Rosindell & Phillimore, 2011). The discrete and replicated nature of island systems has presented scientists with a natural experiment shedding light on general processes responsible for the generation and maintenance of biodiversity.

Understanding evolutionary change over time has generally been studied in the context of single lineages, prime examples being the adaptive radiation of Galapagos finches (citation XXX), Anolis lizards in the Caribbean (citation XXX), and cichlid fish in the great lakes of Africa (citation XXX). Studies that have examined early stages of nascent adaptive radiation in single lineages have provided some of the most important insights into adaptive diversification, although the conditions involved in the initiation of the diversification remain unclear. In particular, while competition (Rundle et al. 2003; Schluter 2003) and predation (Nosil & Crespi 2006) are implicated in species formation, diversification is also attributed to a release from such antagonistic interactions (Gillespie 2009; Yoder et al. 2010). Moreover, while some studies indicate that diversification is associated with specialization, others have

found that species diversification is linked to expansion or modification of the resource base (Schluter 2000; Wellenreuther et al. 2008; Glor 2010).

Likewise, given finite ecological opportunity, one argument suggests that the rate of diversification should decline as species numbers increase during an adaptive radiation (Harmon et al. 2008; Rabosky & Lovette 2008; Bokma 2009); other arguments highlight the importance of species themselves as a resource base for others, with diversification increasing with species number (Ehrlich and Raven 1964, niche construction book, erwin). Clearly, the community context is of critical importance in the process of diversification.

Considering ecological patterns during a given snapshot in time, islands systems have been critical in developing our understanding of the role of stochastic immigration and extinction in structuring local biodiversity and linking local scale patterns to regional dynamics (e.g. Hubbell's local and meta communities (Hubbell, 2001)). Stemming from the success and failure of Hubbell's stochastically-focused theory, other researchers have advanced our understanding of the maintenance of biodiversity both through re-invigorating classical ecological mechanisms, such as niche partitioning and preemption (**??**), and also continuing to explore the statistical properties of large ecological assemblages (**???**Harte, 2011). Concurrently, researchers have combined statistical and deterministic perspectives to gain insight into the structure and stability of ecological networks (Williams & Martinez, 2000; Brose *et al.*, 2006; Berlow *et al.*, 2009; Romanuk *et al.*, 2009; Harte, 2011).

These synthetic theories of biodiversity, at the level of community composition and interaction networks, promise the distillation of universal ecological mechanisms from disparate and noisy data. However, incorporating an evolutionary perspective remains a challenge and limitation to the scope of insights from these theories (Ricklefs, 1987; Qian *et al.*, 2005). There is a clear need to advance these and similar ecological theories from the static to the dynamic, so as to understand how biodiversity changes during evolutionary community assembly, via the processes of invasion, extinction, and in situ diversification. Ecological networks provide a prime starting place due to the existing body of theories on both the eco-

logical outcome of complex interactions (Williams & Martinez, 2000; Brose *et al.*, 2006) but also the evolution of mutualism (**??**), plant-animal and plant-pathogen interactions (**????**) and predation (**?**).

Biodiversity research has progressed tremendously over recent years (**?**) following these largely separate trajectories of lineage-specific evolutionary studies and macroscopic (i.e. multi-taxon and large spatial/temporal scale) ecological studies. Merging these two areas of research is key for understanding the dynamics of biodiversity through space and time, and in light of environmental change. However, merging theories that gain their predictive power from large-scale patterns across multiple species (Brown, 1995; Harte, 2011) with those that yield information on the dynamic nature of single lineages is not straightforward. Here, we outline a set of eco-evolutionary hypotheses to confront this challenge by predicting the structure of biological assemblages along a continuum of evolutionary assembly to ecological assembly. We show how the age-structure landscape of the Hawaiian archipelago, and similar oceanic island systems, provides an ideal natural experiment for testing these hypotheses. We compile published data to present a preliminary exploration of our hypotheses in Hawaii.

Eco-evolutionary hypotheses and age-structured landscapes

Evolution has largely been viewed as the process responsible for generating diversity while ecology is said to maintain it (**?**). However, it has long been recognized, and recent research has crystalized the fact, that ecology and evolution feedback on each other in a dynamic process. Ecology drives evolution by both providing opportunities for selective differentiation and potentially imposing limits to invasion of new diversity—either diversity derived from immigration or *in situ* differentiation/divergence. This can happen through ecological interactions between species and their biotic and abiotic environments producing selective pressures, facilitation and/or competition. Demographic processes (e.g. dispersal, population fluctuation) can also lead to diversification through fragmentation of the gene pool.

Age structured landscapes offer multiple snapshots in time after differing durations of

community assembly and evolution. These "freeze frames" provide the opportunity to assess if different ecological pressures become more or less relevant during a lineage's diversification. For example, demographic stochasticity could be critical in generating initial barriers to gene flow between young incipient species that are then further driven apart by differential selection. Continued selection could then drive species further up fitness peaks, increasing isolation and governing community dynamics through the mechanisms of niche differentiation and fitness differences. Conversely if niches (i.e. position in the adaptive landscape) differ between species but fitnesses are roughly equal then diversity will be determined by neutral drift during periods of abiotic environmental stability and Gleasonian assembly during environmental change. Detailed data on population structure and selection will be needed to test such hypotheses, data that does not currently exist but which we intend to collect.

The evolutionary context of community assembly is also critical for understanding spatial patterns in diversity during a snapshot in time (Ricklefs, 1987; Losos *et al.*, 2003; Gillespie, 2004; **?**). As evidenced above, the evolutionary history of a lineage in a given region determines its exploration of its adaptive landscape, in turn potentially driving the long-term stability and diversity of the communities it invades (**??**). Evolution can also lead to unique ecological outcomes if diversification happens coincidentally with ecological assembly in space and time. Under such a scenario ecology and evolution could feedback on each other to produce a constantly shifting biodiversity baseline.

For the history influence we hypothesize...

We hypothesize that the contribution of evolutionary assembly and ecological assembly will vary between taxa and between ages of lineages in communities. Specifically we hypothesize that during periods of ecological assembly, strongly influenced by immigration communities will statistical assemblages matching expectations of statistical steady state (Harte, 2011) after primary succession has completed. Before primary succession has completed such communities will likely be in transitory states as they progress toward statistical steady state. We hypothesize that if a lineage experiences *in situ* diversification rapidly

enough to keep pace with ecological processes that the ecological communities they form could be driven into alternate evolutionary states that fail to meet the predictions of purely statistical theories that do not account for evolutionary dynamics.

[how to test these hypotheses in the context of Hawaii...we want to actually leave quite a few hypotheses untestable given current data so we motivate future work]

Two key interlinked types of studies needed for a broad understanding of biodiversity dynamics are: (i) examination of diversification across multiple lineages that co-occur across the same dynamic landscape in order to evaluate systematic differences between lineages in rates and patterns of diversification; and (ii) measurement of macroecological metrics within these communities as they have changed over time in order to assess the nature of ecological change, trophic levels, or other functional roles.

[how we do a proof of concept in this paper]

Here we use data gathered from the primary literature to present a proof-of-concept of our eco-evolutionary hypotheses and explore future directions to more rigorously test and extend our framework.

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 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 over several hundred years can be sufficient for genetic differentiation of arthropod populations among habitats Goodman, Vandergast). On larger spatial scales, distinct volcanoes and islands, with their semi-independent histories of evolutionary community as-

sembly 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 (2) the age-structured landscape is constrained to sites with similar forest composition (dominated by Metrosideros polymorpha [Myrtaceae]), elevation (1100-1400m), and climate (mean annual precipitation 2000-3000 mm), which allows for comparison of replicate communities differing markedly in their age of assembly.

Construction of plant-herbivore networks

To test our hypothesis that network structure should change with island age due to changes in the relative contributions of ecological and evolutionary assembly we compiled bipartite (plant-herbivore) networks at the four focal sites for a set of particularly well studied arthropods. These arthropods correspond to herbivorous members of the order Hemiptera. We compiled published species accounts of native Hawaiian Hemiptera (see supplemental Table 1) and extracted information on their geographic ranges and known host plants. Host plant identity was then matched to a list of probable plant occurrences for each site extracted from the native Hawaiian plant database (**?**). 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

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)—to understand how overall network structure changes with age. We calculate

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 `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 for each network we calculate the z-score using a null model that randomizes network structure while maintaining certain aggregate network properties. 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 $(x_{obs} - \bar{x}_{sim})/sd_{sim})$. Because z-scores can be highly sensitive to null model (Ulrich *et al.*, 2009) we implement both the probabilistic null model of Bascompte et al. (Bascompte *et al.*, 2003) and a null model that strictly constrains the degree distributions of plants and herbivores (Ulrich *et al.*, 2009).

To test the hypothesis that communities should differentially depart from statistical steady state during their succession and evolution we compared the species-level degree distributions of Hemiptera species to that predicted by maximizing information entropy relative to the constraint of average degree (**?**). The entropy-maximized (EntMax) prediction represents the hypothesis of statistical steady state (Harte, 2011).

To test the hypothesis that *in situ* and *ex situ* diversification scenarios should differ in they type of interactions they favor we analyzed the degree distribution separately for island endemic and island cosmopolitan species. 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 categorical predictor. Binomial errors effectively account for network size due to the bounded support of the binomial distribution.

Compilation and analysis of genetic data

In this paper we use existing pop gen data to understand timeline of differentiation and compile checklist if interacting plants and bugs to understand how ecology of interactions changes across chronosequence in context of differentiation timeline.

As a first pass in our assessment of how lineages diversify across the landscape of the islands, we determine the key factors that explain genetic structure across different scales of age and isolation. Across a diversity of taxonomic lineages, we first asked how within-species genetic variation is partitioned among and within volcanoes of Maui Nui and the Big Island.

Structure of genetic differentiation among populations To assess the spatial scale at which differentiation occurs within the islands, we analyzed how molecular variation is partitioned within species on the Big Island and Maui. We used existing and new data sets for a diversity of Hawaiian endemic arthropod groups representing several species of spiders and 3 orders of insects (spiders (COI, allozymes), Roderick et al 2012; Drosophila sproati (COII), Eldon et al. 2013; Laupala crickets (AFLPs), Mendelson et al 2004; Nesosydne planthoppers (COI, microsatellites), Goodman et al. 2012 and GenBank accession numbers XXX-XXX (generated following protocols described in Goodman et al. 2012); Trioza psyllids (COI, cytB), GenBank accession numbers XXX-XXX (generated following protocols described in Percy 2003; primers given in Simon et al. 1994 and Timmermans et al. 2010).

We used a Standardized AMOVA to examine how genetic variation is partitioned among 2 scales of population structure: within sites within volcanoes and among volcanoes on both the Big Island and Maui Nui. All analyses except for of the Laupala AFLP data were performed in Arlequin (Schneider et al. 2000) using the AMOVA procedure to compute FST, a measure of genetic variance among populations. The Laupala data were analyzed using XXX (George, citation), using the same hierarchical approach as described above. To provide a temporal framework for the divergence analysis we assembled divergence dating information from the literature for as many of the taxa as possible. In addition, we provide a novel divergence dating analysis for Tetragnatha spiders (see supplementary information for methods).

To test the hypothesis that taxa accumulate *in situ* genetic diversity at different rates we analyzed between population, within volcano F_{st}.

Results

Evolving network structure

Across our chronosequence of sites network nestedness decreased with age while modularity increased (Fig. 2). This trend is found in networks constructed from both more and less stringent geographic criteria used in constructing networks (supplemental Figure XX). 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 Figure XX). The patterns are also robust to sampling intensity, as demonstrated by a rarifaction analysis (supplemental Figure XX).

The distributions of the number of links assigned to each Hemiptera species (i.e. the degree distribution) varied across sites with both the youngest and oldest sites deviating most from the statistical steady state EntMax predictions (Fig. 3). Networks deviate most from EntMax on the youngest and oldest sites. In the middle aged Kohalas site deviations are not different than expected by chance.

There are also significant differences between the degree distributions of island endemics versus island cosmopolitans Hemipter (Fig. 3. Endemics show lower degree overall (i.e. more specialization) compared to more generalist cosmopolitan species. Edemics become significantly more generalist on the middle aged Haleakala site. The slightly younger Kohalas show increased generalization overall. When looking at the degree distribution define by trophic links to plant genera, instead of plant species, the pattern of increased gereralization holds for the Kohalas but endemics on Haleakala no long show a difference in their degree distributions from other island edemics. This change in pattern indicates that increased generality of Maui endemics is driven by increased intra-genus plant diversity on that island.

Population genetic inference of connectivity among populations

The analysis of molecular variance revealed evidence of genetic divergence from the smallest to the largest spatial scales examined, all within a very recent timeframe. At the mitochondrial loci, the amount of significant molecular variation partitioned to the between-sites, within volcano level of analysis ranged from 0.037 0.92 and at the between volcanoes level of analysis it ranged from 0-0.30. At the multilocus nuclear loci, the amount of significant molecular variation partitioned to the between-sites, within volcano level of analysis ranged from 0.21 0.58; at the between volcanoes level of analysis it ranged from 0.04-0.34. Planthoppers, psyllids, the cricket and the fly tended to have more molecular variation partitioned at the between-site, within volcano level than the between volcano level while the spiders had the opposite pattern (Table 1). This observed level of genetic divergence has 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 Big Island where we have ages estimated from phylogenetic-based divergence dating studies, estimates of species origination range from 0.34-1.15 million years, with all the within-species genetic divergence having developed subsequent to that (Table 1).

Discussion

General outline:

1. Draw links between results

    (a) coevolution and niche exploration on Maui and genetic structure

    (b) generalization of endemics on Maui

    (c) genetic structure

    (d) statistical assembly (and steady state) versus alternate evolutionary state

2. Future research

(a) more detailed genetics to tease apart demography

(b) further assessment of statistical assembly

(c) ability to re-construct evol rates

(d) theory to link evol and ecol

Here's what we have so far:

Netrwork sturcture

Some notes to expand on: Nestedness is likely to be, at least in part, a statistical property of these networks, however it could also be driven by stabilizing ecological mechanisms. Modularity is thought to be a sign of coevolution driving convergence in traits of plants and herbivores. This very interesting peaks on Maui where adaptive diversification may be at its peak.

EntMax—the quantitative hypothesis expressing a purely statistical process—fits best in Kohalas where we see minimal modularity, and maximal connectance

Genetic structure

The analysis of molecular variance presented here first shows evidence that genetic divergence is occurring within the islands at small spatial and temporal scales, allowing for the potential for independent processes to be acting across each species' range. In terms of differences between different trophic groups, we find that...

A variety of factors have been implicated in the divergence of lineages described here, with various combinations of ecological processes, processes involved in sexual selection, and drift associated with geographic isolation. Among the herbivores, fungivores, and detritivores that we examined, geographic isolation coupled with differentiation in sexual signals appear to have played the dominant role in fostering diversification, with ecological factors playing a secondary role. Thus, in Nesosydne planthoppers it appears that some period of geographic isolation (Goodman et al. 2012), precedes divergence of sexual signals (Goodman et al.,

in review). Shifts in hosts are certainly involved at some point in the process in this group (citation), but the stage has not yet been identified. Similarly, diversification in the Hawaiian Drosophila is influenced by multiple processes, including geographic isolation, divergence in micro and macro habitat specialization, and with sexual selection playing a key role in species recognition(Carson 1997; Magnacca et al 2008; O'Grady et al 2011). In the same way, diversification in Laupala crickets is known to be associated with geographic isolation together with divergence in acoustic sexual behavior, with taxa maintaining overall ecological similarity (Mendelson and Shaw 2005). Finally, diversification in Trioza psyllids appears to be a product of geographic isolation and is most likely also promoted by divergence in vibratory sexual signals as well (e.g., Percy 2003; Percy et al. 2006).

The mechanisms implicated in the diversification of predators, notably spiders, is somewhat different. In particular, while geographic isolation is clearly implicated in the speciation process (Gillespie 2005) ecological divergence often plays a key role in the differentiation of sister taxa (Gillespie 2004, Blackledge & Gillespie 2005). 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 scale than is found for herbivores, fungivores, and detritivores.

The difference in the patterns of genetic differentiation between trophic levels, as highlighted here, suggests that differentiation of predators requires a larger area and/or a longer time period, for differentiation, which might be expected given the larger area requirement of predators compared to herbivores. Most important in the context of the entire community is that early evolving communities will quickly develop endemic herbivores, although ecological differences appear somewhat later. Spiders develop local endemicity more slowly. However, among those that show adaptive diversification, ecological differences appear early. Thus we might expect maximal ecological exploration in the community to occur at a roughly similar time, at approximately the age of the oldest volcano of Hawaii or the youngest of Maui.

This could lead into the part on coevolution and niche exploration on Maui and genetic

structure???

Future Research

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 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 of gene flow, and across what parts of the genome, during the course of speciation (Nosil). 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 relative to the organism in question, plays a key role in dictating the effects of fragmentation. For some taxa it clearly allows genetic separation. For others, in particular those that are more connected, the fragmentation can provide a way of enhancing adaptive differentiation. Indeed, 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 2004, Rius & Darling 2014)). There have been a number of studies demonstrating how the negative effects of genetic founder effects may be offset if different colonization events result in multiple genotypes within the introduced population (Kolbe et al. 2004), 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, Nadeau et al 2013, Seehausen et al. 2014 Nature Reviews Genetics). 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.

References

Almeida-Neto, M., Gumarães, P., Gumarães, P., Loyola, R. & Ulrich, W. (2008) A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. *Oikos*, **117**, 1227–1239.

Bascompte, J., Jordano, P., Melian, C.J. & Olesen, J.M. (2003) The nested assembly of plant-animal mutualistic networks. *Proc. Natl Acad. Sci. USA*, **100**, 9383–9387.

Berlow, E.L., Dunne, J.A., Martinez, N.D., Stark, P.B., Williams, R.J. & Brose, U. (2009) Simple prediction of interaction strengths in complex food webs. *Proceedings of the National Academy of Sciences*, **106**, 187–191.

Brose, U., Williams, R.J. & Martinez, N.D. (2006) Allometric scaling enhances stability in complex food webs. *Ecology Letters*, **9**, 1228–1236.

Brown, J.H. (1995) *Macroecology*. University of Chicago Press.

Csardi, G. & Nepusz, T. (2006) The igraph software package for complex network research. *InterJournal*, **Complex Systems**, 1695.

Gillespie, R. (2004) Community assembly through adaptive radiation in hawaiian spiders. *Science*, **303**, 356–359.

Harte, J. (2011) *The Maximum Entropy Theory of Ecology*. Oxford University Press.

Hubbell, S.P. (2001) *The unified neutral theory of biodiversity and biogeography (MPB-32)*, vol. 32. Princeton University Press.

Losos, J.B., Leal, M., Glor, R.E., de Queiroz, K., Hertz, P.E., Schettino, L.R., Lara, A.C., Jackman, T.R. & Larson, A. (2003) Niche lability in the evolution of a caribbean lizard community. *Nature*, **424**, 542–545.

MacArthur, R.H. & Wilson, E.O. (1967) *The theory of island biogeography.* Princeton University Press.

Newman, M. & Girvan, M. (2004) Finding and evaluating community structure in networks. *Physical Review E*, **69**, 026113.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H. & Wagner, H. (2013) *vegan: Community Ecology Package.*

Olesen, J., Bascompte, J., Dupont, Y. & Jordano, P. (2007) The modularity of pollination networks. *Proc. Natl Acad. Sci. USA*, **104**, 19891–19896.

Qian, H., Ricklefs, R.E. & White, P.S. (2005) Beta diversity of angiosperms in temperate floras of eastern asia and eastern north america. *Ecology Letters*, **8**, 15–22.

Ricklefs, R.E. (1987) Community diversity: relative roles of local and regional processes. *Science*, **235**, 167–171.

Romanuk, T.N., Zhou, Y., Brose, U., Berlow, E.L., Williams, R.J. & Martinez, N.D. (2009) Predicting invasion success in complex ecological networks. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **364**, 1743–1754.

Rosindell, J. & Phillimore, A.B. (2011) A unified model of island biogeography sheds light on the zone of radiation. *Ecology Letters*, **14**, 552–560.

Ulrich, W., Almeida-Neto, M. & Gotelli, N.J. (2009) A consumer's guide to nestedness analysis. *Oikos*, **118**, 3–17.

Williams, R.J. & Martinez, N.D. (2000) Simple rules yield complex food webs. *Nature*, **404**, 180–183.
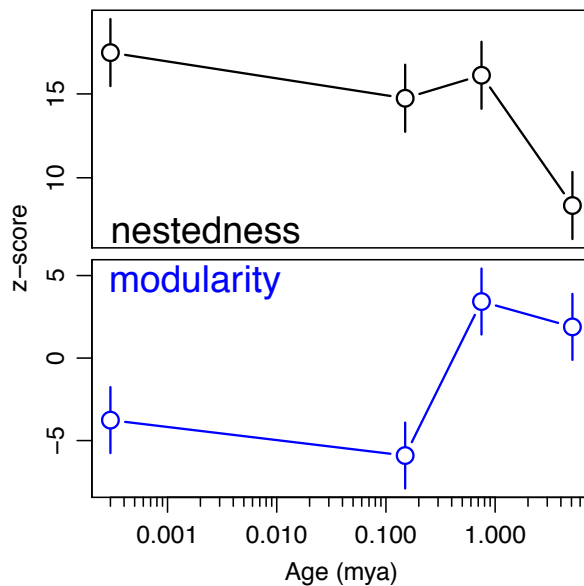
Figures

Figure 1: sampling site map with ages

Figure 2: Trends in network metric nestedness and modularity through time. Nestedness decreases while modularity increases. Error bars come from null model simulation. While sign of z-score depends on null model and method of calculating modules (see supplemental figure) overall trend is robust. Some level of nestedness is likely a statistical property of these networks, however it could also be driven by stabilizing ecological mechanisms. Modularity is thought to be a sign of coevolution driving convergence in traits of plants and herbivores. This very interesting peaks on Maui where adaptive diversification may be at its peak.
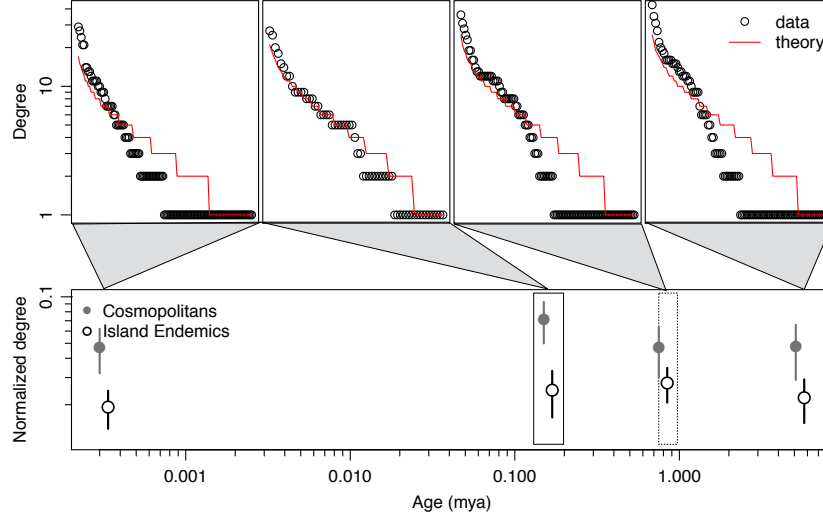
Figure 3: Patterns in degree distributions across sites and different biogeographic classifications of taxa. Top panels show that networks deviate most from MaxEnt on youngest and oldest sites. Deviation on Koh is not different than expected by chance. Koh shows minimal modularity, and maximal connectance. Bottom panel shows number of links for island endemics versus island cosmopolitans. Endemics show lower linkage overall, but significantly increase on the middle aged site Hal. Koh shows increased linkage overall. When looking at links to plant genera this pattern holds except that endemics on Hal no long show a difference in generality, indicating that the pattern is driven in part by plant diversity.
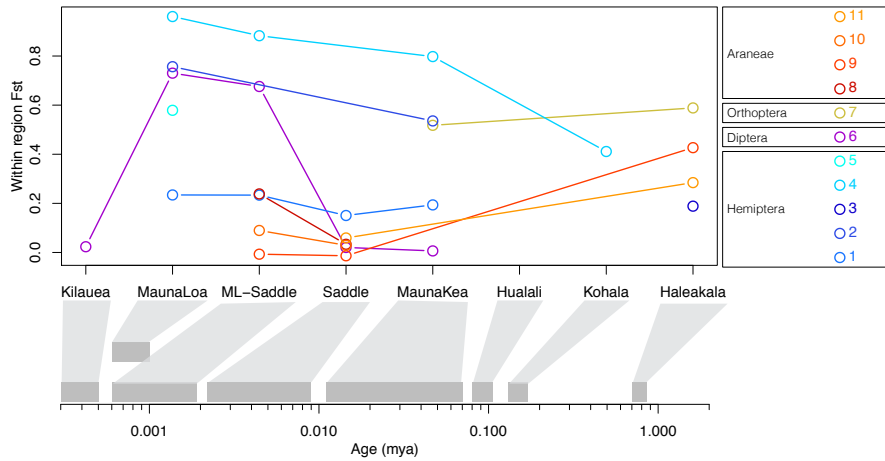

Figure 4: Within volcano F_{st} showing how volcano age influences this measure of structure and diversity.

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Tables

Table 1: Table of between volcano F_{st}, best viewed in dropbox right now.