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COMMUNITY ASSEMBLY ON ISOLATED ISLANDS: MACROECOLOGY MEETS EVOLUTION

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Running title: Community assembly on isolated islands

Number of words in the abstract: 299

Number of words in main body of the paper: 4973

Number of references: 50

32 **Aim**

33   Understanding how ecological and evolutionary processes synergistically determine

34 biodiversity patterns remains a central goal in biology. Using ecological theory as a

35 conceptual guide and data from multiple arthropod lineages, we use the isolated

36 archipelago of Hawaii to explore how complex communities emerge from the interplay of

37 ecological (population dynamics, dispersal, trophic interactions) and evolutionary (genetic

38 structuring, adaptation, speciation, extinction) processes.

39 **Location**

40   The Hawaiian Islands (19.5°N, 155.5°W).

41 **Methods**

42   To infer processes involved in early diversification we synthesize data on genetic

43 structure of select arthropod species across the Hawaiian Archipelago. Over the range of

44 geological ages of the current high islands (< 1 my to 5 my) we also develop and analyze a

45 plant-herbivore bipartite network. We compare the structure of these networks, measured

46 by nestedness, modularity and the degree distribution, with theoretical predictions derived

47 from the principle of maximum information entropy.

48 **Results**

49   Based on the time perspective provided by the island chronosequence and genetic

50 information, we demonstrate that species in lower trophic levels develop local divergence

51 more quickly than species of higher trophic levels. Higher trophic levels also show

52 endemism, though it evolves more slowly and over larger areas. Moreover, in analyzing

53 plant-herbivore networks across an increasing substrate age gradient we find trends of

54 higher specialization and increasing deviation from the statistical steady state expected

55 from theoretical predictions of food web structure.

56 **Main conclusions**

57   We show how ecological theory can leverage natural experiments on oceanic islands

58 of known chronologies to understand the interplay between evolutionary and ecological

59 processes in shaping present-day biodiversity. We advocate for combining perspectives

60 gained from coupled molecular and community-level data analyzed in the context of

61 ecological theory. We further show the utility of applying theory in a chronosequence

62 context to better illuminate the interplay of ecological mechanisms, speciation, extinction

63 and adaptation in driving contemporary biodiversity patterns.

64

65   **INTRODUCTION**

66   Contemporary biodiversity is an unresolved product of speciation, extinction and

67   dispersal all conditioned by ecological interactions with the biotic and abiotic environment.

68   Because these processes occur on different temporal and spatial scales and may be non-

69   linear and non-equilibrium, disentangling the relative influence of local ecological

70   mechanisms from evolutionary and historical processes is challenging (Ricklefs, 2004). The

71   integration of ecological and evolutionary theory has the potential to reveal dynamics that

72   generate biodiversity.

73   The evolutionary processes of speciation and extinction tend to be viewed as

74   regulating regional species pools, occurring in a manner largely removed from local

75   ecology (Hubbell, 2001; Cavender-Bares *et al.*, 2009; Wiens, 2011). Ecological mechanisms

76   tend to be viewed as packing standing diversity into local communities through

77   competition, facilitation, and neutral ecological drift (Hubbell, 2001; Tilman, 2004;

78   Bascompte & Jordano, 2007; Borer *et al.*, 2014). Recent theoretical advances have further

79   refined the causes and consequences of ecological drift (Hubbell, 2001; Rosindell &

80   Phillimore, 2011), re-vitalized classical niche-based mechanisms such as niche partitioning

81   (Tilman, 2004), competition and predation (Borer *et al.*, 2014), and put species interactions

82   in a network theoretic context (Williams & Martinez, 2000; Brose *et al.*, 2006).

83   New insights into evolutionary mechanisms have also emerged based on inference

84   from contemporary patterns of species, genetic, or phylogenetic diversity (e.g., Jetz *et al.*,

85   2012; Wiens, 2011). Here, we propose an integrative framework that harness both sources

86   of advancement to study evolutionary community assembly. We provide an initial test

87   using arthropod lineages in the Hawaiian Islands using mostly published data. We estimate

88   metrics of evolutionary and ecological dynamics across communities that range in age from

89   500 yr to 5 myr. We estimate taxon-specific timelines for the development of genetic

90   discontinuity. This is contextualized with macroecological metrics of community structure,

91   using predictions from statistical equilibrium and ecological network theory to examine

92   changes over the island chronosequence.

93   **Hotspot oceanic archipelagos as model systems**

94   Hotspot oceanic islands are opportune model systems for studying the interplay of

95   local ecological mechanisms and large–scale, historical, and evolutionary drivers of

96   biodiversity patterns. Such island systems are discrete in space and in time due to their

97   sequential formation as the tectonic plate moves over a volcanic hotspot. We hypothesize

98   that the contributions of evolutionary and ecological assembly will vary according to

99   geological age of the environment, taken as an indicator of the total time communities have

100 had to assemble and over which *in situ* diversification could occur. Age–structured, hot–

101 spot island archipelagoes thus have the potential to stratify the eco–evolutionary process

102 of community assembly.

103   Younger communities originate mostly from initial immigration and thus should be

104 dominated by ecological mechanisms operating on a source pool whose evolution is

105 removed from the local setting. Conversely, older islands could allow for the combined

106 interaction and feedback of diversification and local ecological dynamics. Moreover,

107 because dispersal, and hence connectivity between sites, differs between taxa, the relative

108 role of evolutionary and ecological assembly will differ between taxa. While many

109 archipelagos around the world share these biotic and geologic properties, the Hawaiian

110   archipelago provides a particularly useful system for study because its geological

111   chronology (Price & Clague, 2002) and patterns of biodiversity are well characterized

112   (Wagner & Funk, 1995).

Development of genetic discontinuity

114   Movement of individuals among localities connects their population dynamics. Even

115   moderate levels of genetic connectivity among geographically separated populations limits

116   the potential for local divergence (Slatkin, 1987). Thus, in the face of connectivity among

117   populations, one predicts that the structure of ecological communities will remain similar

118   across space. By contrast, when connectivity is low, not only are the ecologies of

119   populations in different localities free to vary, but genetic divergence is also more likely.

120   For these reasons, the magnitude of connectivity among population provides a measure of

121   the relative importance of ecological processes and evolutionary processes in determining

122   differences among ecological communities. Here, by using the chronosequence, we can

123   apply this approach to sets of communities from young to old and to taxa representing

124   different trophic levels.

Macroecological metrics

126   While we expect the mechanisms underlying the generation and maintenance of

127   biodiversity to change across chronological sequences, studies to date have rarely moved

128   beyond reporting basic patterns (Gillespie & Baldwin, 2010). Theory provides a necessarily

129   simplified view of biodiversity and deviations from theory can reveal which more

130   biologically realistic mechanisms likely underlie observed patterns. The Maximum Entropy

131   Theory of Ecology (METE; Harte, 2011) provides a prediction for idealized ecological

132   communities in statistical steady state, the situation in which a system's behavior is

133   governed by a simple set of state variables and no further mechanisms are required. Real

134   world deviations from METE can provide insights into the processes driving ecology away

135   from this statistical steady state and toward alternate system states (Harte, 2011). We

136   expect that different aged communities along the Hawaiian chronosequence will deviate

137   differently from METE, because we hypothesize the processes of speciation, extinction,

138   adaptation and colonization may themselves drive Hawaiian communities out of statistical

139   steady state.

140   METE can successfully predict various metrics of an ecological community (Harte,

141   2011), including network metrics that describe trophic interactions between species

142   (Williams, 2010; Harte, 2011). Ecological network theory derives from evolutionary

143   concepts such as coevolution (Thompson et al. 2013; Bascompte & Jordano, 2007; Donatti

144   *et al.*, 2011; Nuismer *et al.*, 2013) and so presents an opportune starting place to study

145   ecological and evolutionary feedbacks. The distribution of linkages in ecological networks

146   has been used to determine whether plant-animal interaction networks assemble neutrally

147   or through deterministic processes (Vázquez *et al.*, 2005). Analysis of other network

148   metrics such as modularity (the degree to which species interact in semi-autonomous

149   modules) and nestedness (the degree of asymmetry in interaction between specialists and

150   generalists) can further illuminate underlying eco-evolutionary processes driving patterns

151   of species interactions (Bascompte & Jordano, 2007; Donatti *et al.*, 2011; Nuismer *et al.*,

152   2013).In this paper we integrate methods from population genetics to theoretical ecology

153   using the chronosequence of the Hawaiian Archipelago to understand the nexus between

154   ecological and evolutionary forces community assembly. Moving from young to old across

155   the chronosequence we evaluate (1) the rate and pattern of genetic connectivity among

156   populations of taxa from different trophic levels as they diversify from populations to form

157   new species; (2) the processes underlying the structure of species interaction networks

158   given the backdrop of population divergence; and (3) the processes involved in

159   diversification as species form and accumulate and how this dynamic drives deviations

160   from statistical steady state. We use data (mostly published) on population genetic

161   structure and species interactions as a proof of concept. With this framework, our goal is to

162   show how communities develop over ecological-evolutionary time, and the dynamic

163   feedbacks involved assembly.

164   **METHODS**

165   **Hawaii as an eco-evolutionary study system**

166   The geological landscape of the Hawaiian Islands offers a matrix of volcanic

167   substrates mapped in fine detail by chronological age and geochemical composition

168   (Sherrod *et al.*, 2007). On Hawaii Island in particular, independent gradients in elevation

169   and precipitation interact within a matrix of substrate ages ranging from contemporary

170   (active) to 500,000 years. Ongoing volcanic activity has created a dynamic mosaic of

171   habitats with transitory to long-lasting fragmentation within landscapes. Isolation on scales

172   of hundreds to thousands of meters and hundreds to thousands of years can be sufficient

173   for genetic differentiation among some arthropod populations among habitats (Goodman

174   *et al.*, 2012; Eldon *et al.*, 2013; Bennett & O'Grady, 2013), while insufficient to isolate others

175   (Vandergast *et al.*, 2004). On larger spatial and temporal scales, distinct volcanoes and

176   islands, with their semi-independent histories of evolutionary community assembly from

177   recent to ancient, comprise a space-for-time geological chronosequence spanning from

178   present day up to 5 million years across Hawaii Island to Kauai.

179   To investigate how ecological patterns change in response to varied evolutionary contexts

180   we selected four focal sites across the chronosequence of substrate and island ages (two on

181   Hawaii Island, one on Maui and one on Kauai; Fig. 1). Focal sites were selected to have similar

182   forest composition (dominated by *Metrosideros polymorpha*: Myrtaceae), elevation (1100-

183   1400m), and climate (mean annual precipitation 2000-3000 mm).

184

185   **Compilation and analysis of genetic data**

186   To evaluate the balance between regional immigration and potential for local

187   ecological differentiation, we measured how molecular variation is partitioned within

188   species within locations of known substrate age on Hawaii Island and Maui. We compiled

189   published and new data sets for a diversity of native Hawaiian arthropod groups that

190   represent a spectrum of trophic levels:

191   1. Herbivorous *Nesosydne* planthoppers (COI and microsatellites; Goodman *et al.*,

192   2012 GenBank accession numbers XXX-XXX); *Trioza* psyllids (COI, cytB; GenBank

193   accession numbers XXX-XXX); and fungivorous *Drosophila sproati*: (COII; Eldon *et*

194   *al.*, 2013) that maintains tight host plant associations.

195   2. Detritivorous *Laupala* crickets (AFLPs; Mendelson *et al.*, 2004); and

196   3. several predatory spiders species (COI and allozymes; Roderick *et al.*, 2012)

197   In the case of previously unpublished molecular data, sequences for *Nesosydne*

198   planthoppers were generated following protocols described in (Goodman *et al.*, 2012) and

199   sequences for *Trioza* psyllids were generated following protocols described in Percy

200   (2003). Existing genetic data from across Hawaii Island and Maui (including, but not

201   limited to the focal sites), provide an estimate of how arthropod populations have

202   accumulated genetic diversity and divergence within the dynamic landscape of the focal

203   sites.

204   We used analysis of molecular variance (AMOVA) to examine how genetic variation

205   is partitioned at two scales of population structure: among sites within volcanoes and

206   among volcanoes on both Hawaii Island and Maui Nui. All analyses of allozyme and DNA

207   sequence data were performed in Arlequin v. 3.5 (Excoffier & Lischer, 2010) using the

208   AMOVA procedure to compute F_{ST}, a measure of genetic variance, or, where possible Φ_{ST},

209   an F_{ST} analog that incorporates genetic sequence information. The *Laupala* AFLP data were

210   analyzed using TFPGA v. 1.3 (Miller, 1997), using the same hierarchical approach as

211   described above. To provide a temporal framework for the population differentiation

212   analysis we assembled divergence dating information from the literature for as many of the

213   taxa as possible and additionally implemented a new divergence dating analysis for

214   *Tetragnatha* spiders (see supplementary information).

215   To explicitly evaluate the role of landscape age in allowing *in situ* genetic diversity

216   and potential for divergence we analyzed how within site F_{ST} varies with the geologic age

217   of volcanoes on Hawaii Island and Maui Nui. For each volcano we calculated F_{ST} or Φ_{ST}

218   (Excoffier & Lischer, 2010) for each taxon between sites within volcanoes.

219   **Construction of plant-herbivore networks**

220   Bipartite networks describe the topology of ecological interactions between two

221   guilds of organisms (e.g. herbivores and their plant hosts). Quantitative information on the

222   relative importance of interaction links can be incorporated into network analyses

223   (Vázquez *et al.*, 2009); however, currently available data are restricted to binary networks,

224   those that describe only the potential for interaction between any two species, but not the

225   relative frequency of that interaction to each species.

226   We compiled species lists of all endemic hemipteran herbivores for each focal site

227   from published species accounts (see supplement for full list). Species accounts and other

228   published sources were used to determine the presence, probable presence, or probable

229   absence of each Hemiptera species at each of our four focal sites. A documented presence

230   was defined as a known specimen collected at the focal site; a probable presence was

231   defined as a species whose abiotic tolerances and known geographic range (see

232   supplement) overlap with a focal site but no known specimen exists confirming its

233   presence. Probable absence was assumed when neither criteria for presence or probable

234   presence are met. Two sets of species lists for each focal site were compiled: a conservative

235   data set composed of only documented presence occurrences and a less conservative data

236   set that also included probable presences.

237   Host plants for each hemipteran species were determined from published species

238   accounts. Data on host plant use at each specific site were not available so we assumed that

239   if a known host plant was present at a site it would eventually be used. Host plant

240   occurrence in the focal sites was determined using distribution models for 1158 species of

241   Hawaiian plants (Price, 2012). Each focal site was spatially joined in a geographic

242   information system with all coincident plant distribution models that fell within its

243   boundaries. Two sets of resulting focal site-specific networks were constructed: one using

244   the conservative data set of hemipteran species presences and the other using the less

245   conservative data set.

Analysis of plant-herbivore networks

247   We hypothesize that communities differentially depart from statistical steady state

248   along the continuum form those dominated by ecological processes to those with potential

249   complex evolutionary feedbacks We used METE (Williams, 2010; Harte, 2011) to compute

250   the statistical steady state for the hemipteran degree distribution (distribution of the

251   number of plant hosts to each hemipteran species). To evaluate how well METE predicts

252   the data we simulated METE-conforming communities of the same number of species and

253   links as observed. We then calculated the log-likelihood of each simulated data set and

254   compared the resultant distribution of log-likelihoods under the hypothesis that METE is

255   true, to the observed log-likelihood. This comparison is identical in approach to a z-score

256   test using a Monte Carlo simulation to estimate the sampling distribution of log-likelihoods.

257   R scripts used for METE estimation and Monte Carlo methods are available in the

258   supplement.

259   To further investigate how *in situ* diversification leaves a potentially unique

260   signature on network structure we analyzed the number of links assigned to each

261   hemipteran species (the degree distribution) separately for island endemics (those species

262   found on only one island and thus likely derived from in situ diversification) versus island

263   cosmopolitans (those species found on multiple islands). To compare species' degree

264 distributions between endemics and cosmopolitans across sites of different ages we

265 conducted a generalized linear model with binomial error, treating site identity as a

266 categorical predictor. Binomial errors effectively account for network size due to the

267 bounded support of the binomial distribution.

268 To understand how other network properties change with ecosystem substrate age,

269 we calculated two widely used descriptive network metrics across sites—nestedness,

270 which describes the degree of asymmetry of species interactions connecting specialists and

271 generalists (Bascompte & Jordano, 2007; Ulrich *et al.*, 2009), and modularity which

272 describes the degree to which interactions are concentrated within subsets of species but

273 not between subsets (Newman & Girvan, 2004; Olesen *et al.*, 2007).

274 We calculated nestedness using the NODF metric (Almeida-Neto *et al.*, 2008) as

275 implemented in the R package vegan (Oksanen *et al.*, 2013) and modularity using a variety

276 of algorithms implemented in the R package igraph (Csardi & Nepusz, 2006). These metrics

277 are not directly comparable across networks of different size and connectance (Ulrich *et al.*,

278 2009), so for each metric in each network we calculate z-scores using a null model that

279 randomizes network structure while maintaining certain aggregate network properties

280 (Ulrich *et al.*, 2009). These z-scores are calculated as the difference between the observed

281 network metric minus the mean of the null model divided by the null model standard

282 deviation, or $(x_{obs} - \overline{x}_{sim})/sd_{sim})$. Because z-scores can be highly sensitive to the choice of

283 null model (Ulrich *et al.*, 2009) we implemented both a probabilistic null model

284 (Bascompte & Jordano, 2007) and a null model that strictly constrains the degree

285 distributions of plants and herbivores (Ulrich *et al.*, 2009). The probabilistic null using the

286 frequency of interactions as the probability that a randomized link gets assigned to that cell

287   in the interaction matrix (Bascompte & Jordano, 2007); thus the probabilistic null

288   constrains row and column sums in probability but not absolutely.

289   **RESULTS**

290   **Population genetic inference of discontinuity among populations**

291   The analysis of molecular variance (AMOVA) revealed evidence of significant

292   population genetic structure from the smallest to the largest spatial scales examined, all

293   within a very recent timeframe. For mitochondrial loci, the amount of statistically

294   significant molecular variation partitioned to among sites within volcanoes ranged from

295   0.037–0.92 and to the among volcanoes from 0–0.30. Corresponding variation at multilocus

296   nuclear loci between-sites within volcanoes ranged from 0.21–0.58 and among volcanoes,

297   0.04–0.34 (larger observed variance within volcanoes may represent the effects of

298   repeated colonization events or sampling error). Taxa in the lower trophic levels

299   (herbivorous sap-feeding Hemiptera: planthoppers and psyllids) had as much or more

300   molecular variation partitioned at the among-site, within volcano level than the among

301   volcano level, while the predatory spiders were less structured at localities within

302   volcanoes compared to between (Table 1). The analysis of genetic population structure

303   across the chronosequence of localities revealed a similar pattern. The herbivores show

304   high genetic population structure among localities on young volcanoes relative to between

305   localities on older volcanoes (Fig. 2). By contrast, predatory spiders exhibited higher

306   genetic population structure only on older volcanoes (e.g. Maui).

307   The observed levels of genetic divergence have evolved rapidly. For example, within

308   species genetic divergence in planthoppers has evolved in as little as 2,600 years

309   (Goodman *et al.*, 2012). For species from Hawaii Island for which phylogenetic data provide

310   divergence times, estimates of dates of species divergence range from 0.34–1.15 million

311   years, with additional within-species genetic divergence developed subsequently (Table 1).

312   That the estimates are older than the known age of the Big Island, suggest that divergence

313   in DNA now reflected in different lineages pre-dated their colonization of the Big Island, or

314   alternatively may be due to sampling error.

315   **Evolving network structure**

316   The Hemiptera species degree distribution varied across the chronosequence with

317   both the youngest and oldest sites deviating most from the statistical steady state

318   maximum entropy predictions (Fig. 3). In the middle aged site of Kohala, minor deviations

319   from maximum entropy are no different than expected by chance indicating the Kohala

320   Hemiptera assemblage matches the predictions of maximum entropy.

321   The generalized linear model revealed that there are also significant differences

322   between the degree distributions of island endemics (those species found on only one

323   island) versus island cosmopolitans (those species found on multiple islands; Fig. 3).

324   Endemics show significantly lower degree distributions overall (i.e., more specialization)

325   compared to more generalist cosmopolitan species. Endemics become significantly more

326   generalist on the middle aged Maui site; however this pattern disappears when analyzing

327   links to plant genera instead of species. The slightly younger Kohala shows increased

328   generalization overall. When considering the degree distribution defined by trophic links to

329   plant genera instead of plant species, the pattern of increased generalization holds for the

330   Kohala but endemics on Maui no long show a difference in their degree distributions from

331   other island endemics. This change in pattern suggests that increased generality of Maui

332   endemics may be driven by increased intra-genus plant diversity on that island.

333   Network nestedness decreased with age while modularity increased (Fig. 4). This

334   trend is found in networks constructed from both more and less stringent geographic

335   criteria (supplemental Fig. S3). Choice of null model changed the magnitude of modularity

336   and the sign of nestedness z-scores; however, the relative pattern of decreasing nestedness

337   and increasing modularity remained across the different null models used to standardize

338   network metrics (supplemental Fig. S2). The patterns are also robust to sampling intensity,

339   as demonstrated by a rarefaction analysis (supplemental Fig. S4).

340   **DISCUSSION**

341   By combining disparate data with a novel combination of analytical approaches that

342   incorporate population genetics, bipartite networks and maximum entropy theory, our

343   results present evidence for the timeline over which evolution begins to keep pace with

344   ecology in determining the local diversity of communities. Taxa in the lower trophic levels,

345   as compared to higher trophic guilds, developed genetic discontinuities more quickly along

346   the chronosequence and at much smaller spatial scales (Table 1, Fig. 2), allowing them the

347   opportunity to diverge ecologically. Network nestedness decreased while modularity

348   increased with age (Fig. 4), indicating a possible shift from assembly driven by *ex situ*

349   immigration early on, to one based on *in situ* co-diversification with host plants

350   (Bascompte & Jordano, 2007; Donatti *et al.*, 2011). This possibility is further strengthened

351   by the observation that single island endemics show more specialization compared to more

352   broadly distributed species (Fig. 3). At intermediate modularity and nestedness, the

353   distributions of the number of links assigned to each hemipteran species showed the least

354   deviation from the METE prediction (Fig. 3), suggesting that at the transition from primary

355   succession to evolutionary assembly, these plant-herbivore communities reach statistical

356   steady state.

357   **Development of genetic discontinuity at different trophic levels**

358   The analysis of available genetic data presented here indicates that divergence is

359   occurring within the islands at small spatial scales and over short time periods (Table 1,

360   Fig. 2). Furthermore, the scale of population structure varies with trophic position, with the

361   sap-feeding herbivores in this study showing structure at smaller scales compared to

362   detritivorous crickets and predatory spiders (Table 1, Fig. 2). Population structure within

363   species allows for populations to take independent evolutionary trajectories, especially

364   when aided by other evolutionary processes that may be acting differentially across each

365   species' range. A variety of factors have been implicated in the genetic divergence of

366   populations and species in lineages described here, including combinations of genetic drift

367   associated with geographic isolation (Percy, 2003; Mendelson & Shaw, 2005; O'Grady *et al.*,

368   2011; Goodman *et al.*, 2012), adaptation associated with ecological interactions of

369   competition, predation, and mutualism (Gillespie, 2004; Roderick & Percy, 2008), and

370   sexual signaling (Mendelson & Shaw, 2005; Percy & Kennedy, 2006; Magnacca *et al.*, 2008;

371   Goodman *et al.*, in review).

372   The sap-feeding Hemiptera group *Nesosydne* (Goodman *et al.*, 2012) provide

373   evidence that some period of geographic isolation preceded divergence of sexual signals

374   (Goodman *et al.*, in review). Shifts in plant host use are also involved in the process of

375   diversification in this group (Roderick & Percy, 2008). In a similar radiation of leafhoppers,

376   *Nesophrosyne* (Bennett & O'Grady, 2013), host plant specialization was implicated in

377   driving species radiations up until approximately 1 million years ago, when plant niches

378   were mostly exhausted on Maui; following this period, speciation, largely on the Hawaii

379   Island, shifted to geographic mechanisms of diversification. Our network analysis indicates

380   that specialization and modularity begin to show pronounced signals in network data on

381   Maui (Figs. 4, 3), in agreement with the *Nesophrosyne* results and indicating that an

382   approximate age of 1 million years may be necessary for host plant specialization to

383   become the dominant process in the sequence of diversification. Other taxa at lower

384   trophic levels, such as the herbivorous *Trioza* psyllids, detritivorous *Laupala* crickets and

385   fungivorous *Drosophila*, show similar signals of geographic isolation combined with

386   ecological and sexual processes driving genetic divergence and diversification across sites

387   as young as those on the Hawaii Island (Percy, 2003; Percy & Kennedy, 2006; Mendelson &

388   Shaw, 2005; Magnacca *et al.*, 2008; O'Grady *et al.*, 2011). As a contrast, spiders, which are

389   predatory, only develop genetic discontinuities at larger spatial and temporal scales. Most

390   important in the context of community assembly is that endemic sap-feeding herbivores

391   developed structure quickly - on the order of less than 0.1 million years (assuming timing

392   of speciation is reflected by divergence in mtDNA; Table 1), with predatory spiders

393   showing local endemicity more slowly (Table 1).

Macroecological metrics: Network structure and steady state

394

395   On the geologically youngest volcano, Kilauea, ecological assembly should be the

396   dominant process there. The results of network analysis support this hypothesis with

397   Kilauea showing substantial nestedness and limited modularity (Fig. 4). Nestedness is

398   likely to result if new species arriving by immigration have a high probability to eat or be

399   eaten by the generalist species already present at the site (Bascompte & Jordano, 2007). In

400   this way we might expect Kilauea to also conform to the statistical steady state predication

401   of maximum entropy. However, the observed deviations from maximum entropy at Kilauea

402   are largely driven by a surplus of singleton links (Fig. 3). These in turn likely result from

403   incomplete assembly, and thus lower species richness, of the plant and herbivore biotas.

404   Future research should focus on the observation from genetic analysis that indicates

405   discontinuities can arise within species on short timescales that, in some taxa, include the

406   greater landscape of Kilauea (Table 1). Conversely, Kohala shows a statistically significant

407   agreement with maximum entropy perhaps because the Kohala site, at intermediate age

408   (150 ky), has experienced complete ecological succession but is still too young to be driven

409   away from statistical steady state by specialization and rapid in situ diversification driven

410   by host plant preference

411   The older Maui and Kauai sites show strong deviations from expectations of

412   maximum entropy theory (Fig. 4), which is consistent with our hypothesis that the

413   influence of evolutionary assembly on these biotas drives them away from statistical steady

414   state. The application of maximum entropy to ecology does not currently take into account

415   evolution (Harte, 2011). Indeed the use of maximum entropy in ecology is inspired by its

416   application to physical systems whose change through time is simple and lacks the

417   evolutionary memory of biological systems, potentially a far cry from the complex change

418   through time produced by speciation, extinction and adaption to novel ecosystems. Maui

419   and Kauai show strong evidence of evolutionary assembly driven by specialization and

420   diversification on host plants, particularly demonstrated by decreased nestedness and

421   increased modularity (Fig. 4). Modularity is known to result from coevolution selectively

422   driving the traits of interacting species towards convergence (Donatti *et al.*, 2011; Nuismer

423   *et al.*, 2013).

424   The analysis of island endemic and cosmopolitan (archipelago-wide) Hemiptera

425   species sheds further light on the evolution of the networks they form. Endemics are

426   always more specialized than cosmopolitans, further supporting the hypothesis that in situ

427   diversification and evolutionary assembly favor coevolution. At the Kohala site , which

428   showed the best fit to maximum entropy theory, endemic and cosmopolitan species alike

429   show increased generalization (i.e. higher degree; Fig 3), while at the youngest site Kilauea,

430   specialist endemics are limited by low plant diversity and thus show more apparent

431   specialization (Fig 3). Conversely at the oldest site on Kauai, where plant diversity is not

432   limiting (Kitayama & Mueller-Dombois, 1995), endemics again show decreased degree and

433   thus genuine specialization (Fig. 3). On Maui, endemics show statistically significant

434   increases in apparent generalization but this pattern disappears when analyzing the data at

435   the resolution of plant genera, thus suggesting that Hemiptera species endemic to Maui are

436   no more generalized on plant genera but instead may benefit from the diversification of

437   plant species within genera on Maui.

Future Research

438

439   The analyses presented here indicate strong patterns of a dynamic assembly

440 process leading to contrasting hypotheses concerning the relative importance of ecological

441 and evolutionary depending on the evolutionary age of the community under observation.

442 In future work we will tackle these hypotheses using detailed quantitative ecological and

443 genomic data collected from across the Hawaiian archipelago.

444   1.   In younger communities we hypothesize that

445   a.   during periods of ecological assembly, communities strongly influenced

446   by immigration will resemble random samples from regional source

447   pools and thus metrics describing these communities will largely match

448   expectations of statistical steady state after primary succession has

449   completed;

450   b.   the exception will be communities still undergoing primary succession,

451   which will change rapidly through time and represent non–random

452   samples of source pools;

453   c.   we also predict that these communities will exhibit a nested network

454   structure, assuming new species will eat or be eaten by the generalist

455   species (Bascompte & Jordano, 2007) already present in the community.

456   2.   Following the same logic, in older communities we hypothesize that

457   a.   during periods of evolutionary assembly, if processes such as niche

458   exploration, adaptation and speciation happen fast enough to keep pace

459   with immigration, the resultant communities could be driven into

460   alternate evolutionary states that fail to meet the predictions of purely

461   statistical theories that do not account for evolutionary dynamics (Harte,

462   2011);

463   b.   networks in such communities should exhibit higher levels of

464   specialization and modularity (Bascompte & Jordano, 2007; Donatti *et al.*,

465   2011; Nuismer *et al.*, 2013).

466   3.   Systems undergoing rapid ecological and evolutionary change are generally

467   expected to deviate most from statistical steady state; thus we expected

468   populations in such communities to show genetic signatures of rapid change,

469   from bottlenecks or population expansion to selection.

Evolutionary data: Diversification within species

471   The current study demonstrates that taxa of different trophic guilds differ in the

472   scale at which differentiation occurs, and highlights the importance of fragmentation of the

473   landscape in facilitating differentiation. Future work is aimed at gathering genomic SNP

474   data for focal taxa within this system that represent different trophic levels. We will use it

475   to understand taxonomic differences in the rate of differentiation, to assess the roles of

476   genetic fusion and fission (Gillespie and Roderick 2014), and to detail the relative rates of

477   speciation and extinction across the island chronosequence. When coupled with ecological

478   data on abundances and interactions, the population genetic data will allow us to explore

479   explicit aspects of the Geographic Mosaic Theory of evolution, such as trait remixing and

480   selection mosaics. (Thompson et al. 2013).

481 *Ecological data: Assembly of species into communities*

482 Our results show that the island chronosequence can reveal that ecological

483 processes dominate in younger environments, with evolutionary processes becoming more

484 important later. However, in order to build a more rigorous understand of the assembly

485 process future work is focusing on conducting broad sampling of all macroscopic

486 arthropod taxa at a large number of sites across the age gradient, thus allowing assessment

487 of changes in overall species composition and diversity across all players in the time-

488 calibrated landscape (*sensu* Gruner, 2007).

489 Such data will allow us to test how entire arthropod communities of different aged

490 substrates deviate from statistical steady state as predicted by METE (Harte, 2011). For

491 example, predators, whose assemblages are likely more dominated by immigration and

492 ecological assembly (Fig. 2) may never show strong deviations from METE predictions

493 whereas herbivores could show increasing deviation with age in agreement with the

494 network results of this paper (Fig. 3).

495

496 The current study provides a framework for the use of chronologically arranged

497 oceanic island systems to examine the interplay between evolutionary and ecological

498 processes in shaping biodiversity and demonstrates how this approach can provide

499 insights into the development of communities over ecological–evolutionary time, and the

500 dynamic feedbacks involved in assembly.

ACKNOWLEDGEMENT

BIOSKETCH

The authors are part of a large team involved in understanding how biodiversity and complex ecosystems emerge from ecological and evolutionary processes. The project, funded by the National Science Foundation's "Dimensions in Biodiversity", focuses on the geological chronosequence provided by the Hawaiian Islands.

516   **FIGURE CAPTIONS**

517   **Figure 1.** Substrate age map of the islands of Kauai, Maui and Hawaii Island. Colors

518   correspond to substrate age from young (yellow) to old (blue). Focal sites are shown as

519   black circles while sampling sites for genetic data are represented by gray circles.

520

521   **Figure 2.** Genetic population structure (F_{ST}) among sites within volcanoes with volcano

522   age for insects and spiders. The plant-feeding groups, specifically the sap-feeding

523   Hemiptera, show high genetic structure among sites on young volcanoes relative to older

524   volcanoes whereas detritivores (crickets), fungivores (*Drosophila*), and in particular

525   predators (spiders), show little structure on young volcanoes. For spiders, substantial

526   structure develops only later in the chronosequence, e.g., on Maui at approximately 1

527   million years. Numbers refer to different species: 1. *Nesosydne chambersi*, 2. *Nesosydne*

528   *raillardiae*, 3. *Nesosydne bridwelli*, 4. *Trioza HB*, 5. *Trioza HC*, 6. *Drosophila sproati*, 7.

529   *Laupala cerasina*, 8. *Tetragnatha anuenue*, 9. *Tetragnatha brevignatha*, 10. *Tetragnatha*

530   *quasimodo*, 11. *Theridion grallator*.

531

532   **Figure 3.** Patterns in degree distributions (distribution of number of links assigned to each

533   herbivore) across sites and different biogeographic classifications of taxa. Top panels show

534   that networks deviate most from MaxEnt on youngest and oldest sites. Inset figures show

535   the distribution of simulated mean squared errors; if the red line falls within the gray

536   region (95% confidence interval) the data conform to maximum entropy; thus the

537   observed minor deviation on Kohala is not different than expected by chance. Kohala

538   shows minimal modularity, and maximal connectance. The bottom panel shows the

539   number of links for island endemics versus island cosmopolitans. Endemics show lower

540   linkage overall, but significantly increase on the middle aged site Maui (highlighted with

541   dotted box). Kohala shows increased linkage overall (highlighted with solid box). When

542   looking at links to plant genera this pattern holds except that endemics on Maui no long

543   show a difference in generality, indicating that the pattern is driven in part by plant

544   diversity.

545

546   **Figure 4.** Trends in network metric nestedness and modularity through time. Nestedness

547   decreases while modularity increases. Error bars represent 95% confidence intervals from

548   a null model simulation. While the sign of the z-score depends on null model and method of

549   calculating modules (see supplemental figure) the overall trend is robust. Some level of

550   nestedness is likely a statistical property of these networks, however it could also be driven

551   by stabilizing ecological mechanisms. Modularity is thought to be a sign of coevolution

552   driving convergence in traits of plants and herbivores. Note the very interesting peaks on

553   Maui where adaptive diversification may be at its maximum.

554

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682   Additional references to the data sources may be found in Appendix S1 at [URL].
683

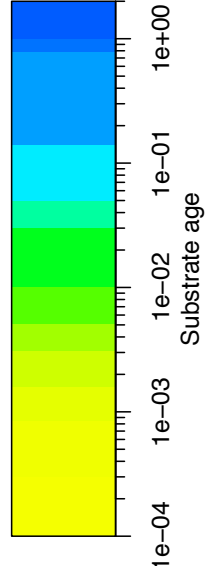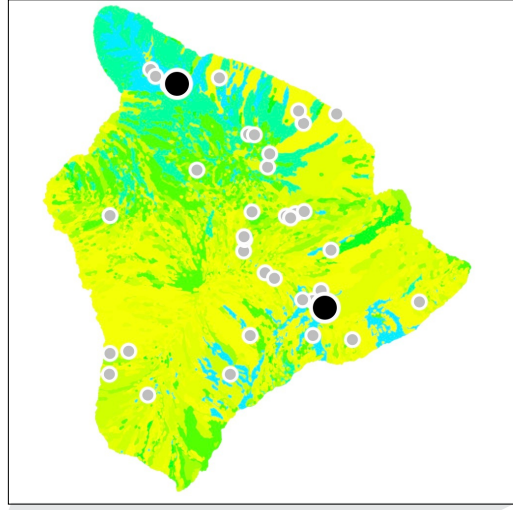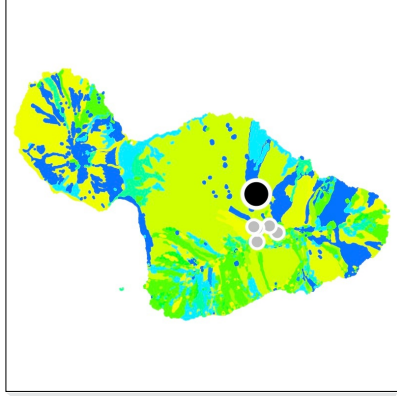| Group	Species	Island(s)	Data (# individuals: length/ # markers)	Between Volcanoes % variation (p-value)	Within volcanoes % variation (p-value)	Data source	Timeframe citation
Planthoppers	*Nesosydne chambersi*	Hawaii	mtDNA COI (187:653) msat (292:13)	0.05*** -- 0.04***	0.77*** -- 0.21***	Goodman et al. 2012	WSD[1]: Saddle Road pops=2.6 (95% HPD: 1.2-35.1) x 10^3 yrs WSD[1]: Mauna Kea/Mauna Loa pops: 20.1 (95%HPD: 7.4-135.0) x 10^3 yrs Goodman et al. 2012
	Nesosydne raillardiae	Hawaii	mtDNA COI (33:581)	0.26***	0.49***	this paper	na
	Nesosydne bridwelli	Maui	mtDNA COI (34:677)	na	0.18**	this paper	na
Psyllids	*Trioza HB[4]*	Hawaii	mtDNA COI & cytB (29:857)	-0.14***	0.92***	this paper	na
	Trioza HC[4]	Hawaii	mtDNA COI & cytB (17:857)	0.17**	0.53**	this paper	na
Fly	*Drosophila sproati*	Hawaii	mtDNA COII (232:570)	0.11***	0.81***	Eldon et al. 2013	Max age[2]=1.15 (95%HPD: 0.75-1.5) my. Magnacca and Price, in review
Cricket	*Laupala cerasina*	Hawaii	AFLP (631)	0.30***	0.58***	Mendelson and Shaw 2005	na
Spiders	*Tetragnatha anuenue*	Hawaii	mtDNA COI (162: 607) allozymes (12:9)	0.23*** na	0.041*** na	Roderick et al. 2012	na
	Tetragnatha brevignatha	Hawaii	mtDNA COI (54:605)	0.16*	0.00	Roderick et al. 2012	*T. macracantha* Max age[2]=0.34 (95%HPD: 0.14-0.58) my. *Supplementary info, this paper*
	Tetragnatha quasimodo	Hawaii	mtDNA COI (149:439) allozymes (46:9)	0.09*** 0.34***	0.037*** na	Roderick et al. 2012	Node age[2]=0.80 (95%HPD: 0.50-1.16) my. *Supplementary info, this paper*
	Theridion grallator	Hawaii	mtDNA COI (209:1270) allozymes (224:8)	0.30*** 0.19***	0.05*** na	Roderick et al. 2012	Node age[3]=0.56 (95%HPD: 0.37-0.75) my. Croucher et al. 2012
	Ariamnes spp.	Hawaii	mtDNA COI (8:420)	0.05	na	Roderick et al. 2012	na

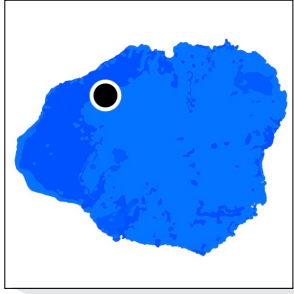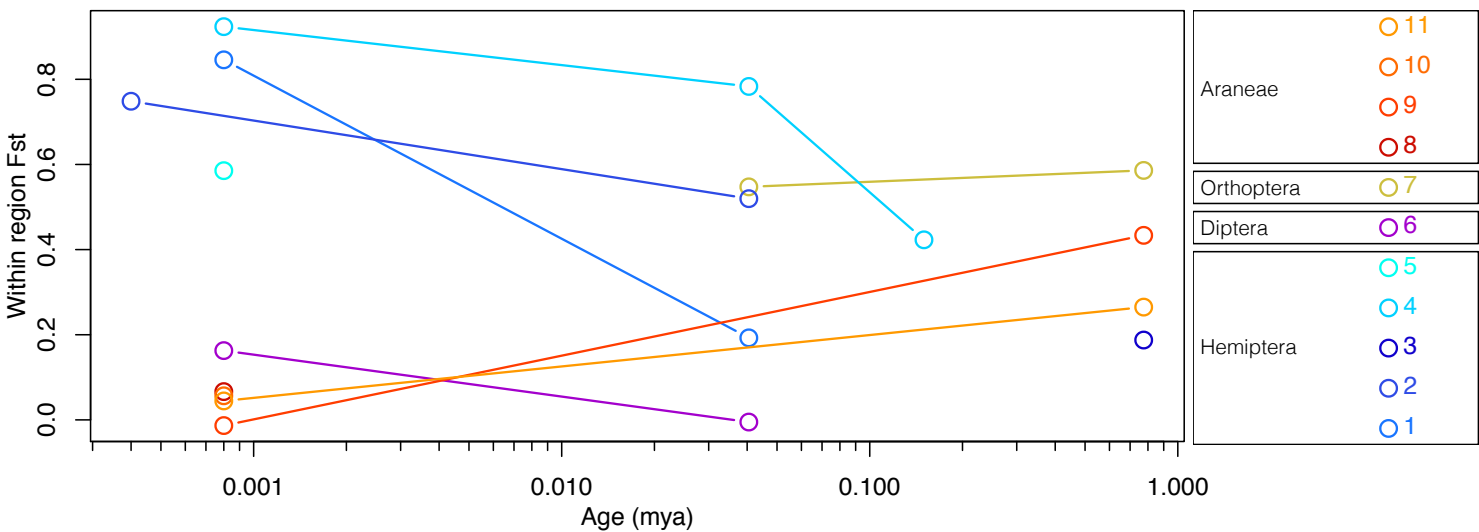*** < 0.001, ** < 0.05, *<0.10; na = no information available

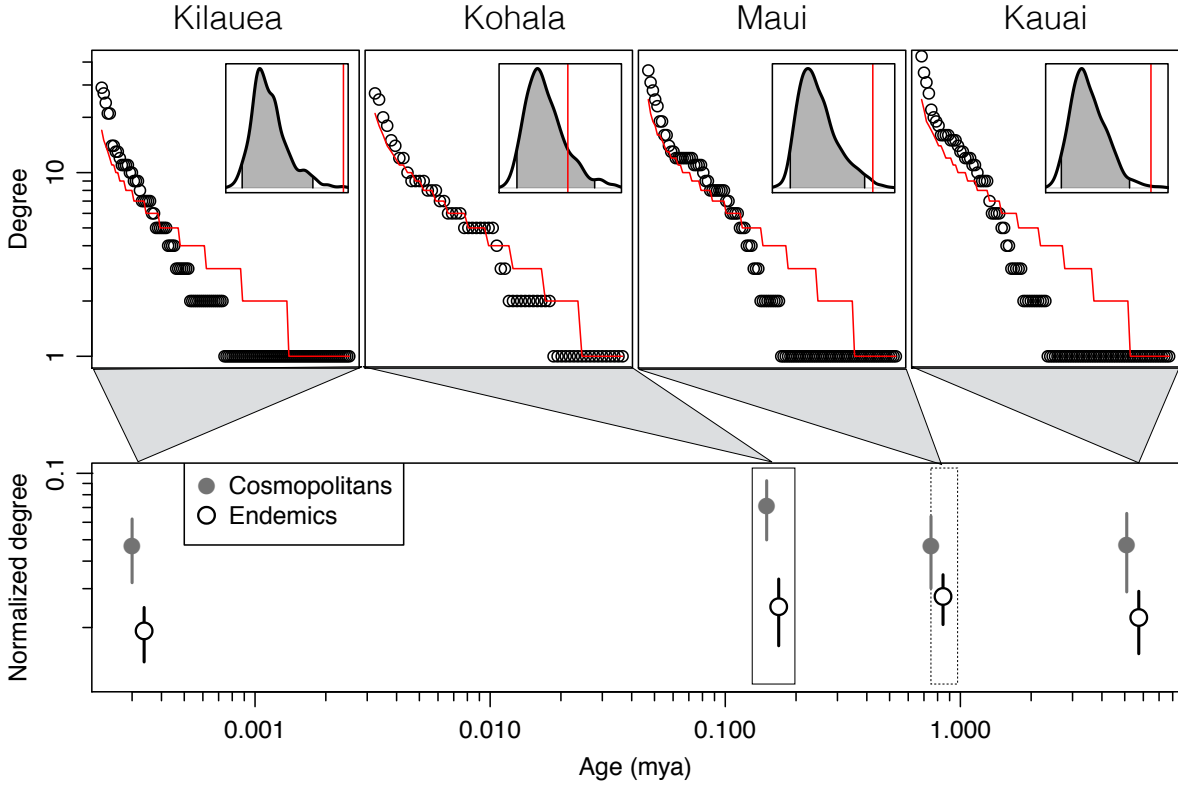[1]WSD = Within-species divergence, estimated using IM.

[2]Max age = the node age of the phylogenetic split between this species and its sister species, calculated using divergence dating analyses performed in BEAST. In most cases, this will be an overestimate of the node age of the species itself, but is the best information we have at present.
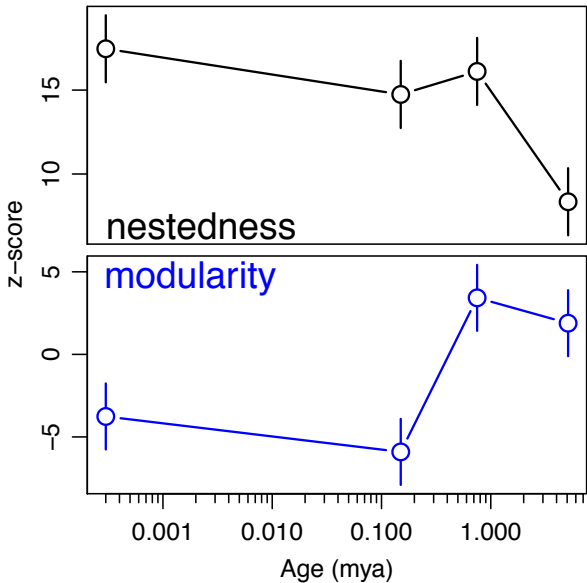
[3]Node age = Age of the most recent common ancestor of the monophyletic group on Hawaii Island, estimated using BEAST.

[4] These *Trioza* species are in the process of being described; HB and HC are their provisional identifiers (Percy in prep).

COMMUNITY ASSEMBLY ON ISOLATED ISLANDS: MACROECOLOGY MEETS EVOLUTION

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Keywords: networks, modularity maximum entropy, arthropods, population genetics, chronosequence, Hawaii

Running title: Community assembly on isolated islands

Number of words in the abstract: 297 325 299

Number of words in main body of the paper: 5117 4973

Number of references: 81 50

ABSTRACT

Aim

Understanding how ecological and evolutionary processes synergistically determine biodiversity patterns remains a central goal in biology. ~~In highly isolated archipelagoes such as the Hawaiian Islands, beyond the reach of equilibrium~~frequent colonization dynamics, rapid *in situ* diversification and speciation ~~have~~has the potential to keep pace ~~with ecological dynamics. such as biotic filtering and demography.~~Using ecological theory as a conceptual guide and data from multiple arthropod lineages ~~across the Hawaiian model system~~, we use the isolated archipelago of Hawaii to explore how complex communities emerge from the interplay of ecological (population dynamics, dispersal, trophic interactions) and evolutionary (genetic structuring, adaptation, speciation, extinction) processes.

Location

The Hawaiian Islands (19.5°N, 155.5°W).

Methods

~~We~~To infer processes involved in early diversification we synthesize data on genetic structure of select arthropod species across the Hawaiian ~~landscapes of known age, which is used to infer processes involved in early diversification. We also develop a plant-herbivore bipartite network across~~Archipelago. ~~Across~~Over the range of geological ages of the current high islands (< 1 my to 5 my~~), analyzing measures of~~) we also develop and analyze a plant-herbivore bipartite network. We compare the structure of these networks,

56 measured by nestedness, modularity and the degree distributions. These are then

57 compareddistribution, with theoretical predictions derived from the principle of maximum

58 information entropy.

Results

60   Based on the time perspective provided by the island chronosequence and genetic

61 information, we demonstrate that species in lower trophic levels develop local divergence

62 more quickly than species of higher trophic levels. Higher trophic levels also show

63 endemism, though it evolves more slowly and over larger areas. Moreover, in analyzing the

64 plant-herbivore networks across an increasing substrate age gradient we find trends of

65 higher specialization and increasing deviation from the statistical steady state expected

66 from theoretical predictions of food web structure.

Main conclusions

68 A holistic approach informed by a combination of population genetic and community-level

69 data within a clear temporal framework suggests that assembly by immigration and short

70 time scale ecological processes gives way to evolutionary processes in the assembly of

71 these complex Hawaiian communities. These findings also provide motivation to expand

72 ecological theory to better incorporate dynamic evolutionary processes.

73   We show how ecological theory can leverage natural experiments on oceanic islands

74 of known chronologies to understand the interplay between evolutionary and ecological

75 processes in shaping present-day biodiversity. We advocate for combining perspectives

76 gained from coupled molecular and community-level data analyzed in the context of

77   ecological theory. We further show the utility of applying theory in a chronosequence

78   context to better illuminate the interplay of ecological mechanisms, speciation, extinction

79   and adaptation in driving contemporary biodiversity patterns.

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INTRODUCTION

A central challenge in biology is understanding how the spectacularly diverse ecosystems that sustain life on Earth emerge from ecological and evolutionary processes. Thought to occur on largely different spatiotemporal scales, ecology and evolution developed into largely separate disciplines. However, new findings along with genomic and computational techniques have re-opened scientists' eyes to the rich and dynamic interplay between these processes. These advances allow renewed focus on a synthetic understanding of how evolutionary and ecological processes and their interactions generate and maintain the biodiversity and function of communities and ecosystems. Much of such research seeks the integrated knowledge of the genetic, phylogenetic, and functional dimensions of biodiversity including interactions among these dimensions and their synergistic roles in critical ecological and evolutionary processes. Islands have been key to developing the basic yet largely separate knowledge of these processes.

Indeed, islands are bedrock model systems in the development of fundamental principles driving patterns of biodiversity, from theories of evolution (Darwin, 1959; Wallace, 1862) to the ecology of species richness and abundance in and out of equilibrium (MacArthur & Wilson, 1967; Brown, 1995; Rosindell & Phillimore, 2011). Due to their isolation and discretization islands are naturally simplified systems compared to mainlands and this simplification has been central to the success of using islands to identify general mechanisms underlying biodiversity. Similarly, island systems could provide critical opportunities for tackling the difficult task of better integrating insights from short time scale ecological theories with long-term evolutionary dynamics.

103   ~~Traditionally we view evolution as responsible for~~ Contemporary biodiversity is an

104   unresolved product of speciation, extinction and dispersal all conditioned by ecological

105   interactions with the biotic and abiotic environment. Because these processes occur on

106   different temporal and spatial scales and may be non-linear and non-equilibrium,

107   disentangling the relative influence of local ecological mechanisms from evolutionary and

108   historical processes is challenging (Ricklefs, 2004). The integration of ecological and

109   evolutionary theory has the potential to reveal dynamics that generate biodiversity.

110   The evolutionary processes of speciation and extinction tend to be viewed as

111   regulating regional species pools, ~~a process happening~~occurring in a manner largely

112   removed from local ecology (Hubbell, 2001; Cavender-Bares *et al.*, 2009~~). Evolutionary~~

113   ~~change over time in island systems has generally been studied in the context of single~~

114   ~~lineages, e.g. the adaptive radiation of Galapagos finches (Grant & Grant, 2007), Anolis~~

115   ~~lizards in the Caribbean (Losos, 2009), and cichlid fish in the great lakes of Africa~~

116   ~~(Seehausen, 2006). Such studies have reached varied conclusions about the drivers of~~

117   ~~diversification including competition (Rundle, 2003; Schluter, 2003), predation (Nosil &~~

118   ~~Crespi, 2006), ecological release (Gillespie, 2009; Yoder *et al.*, 2010) and specialization or~~

119   ~~generalization (Schluter, 2000; Wellenreuther *et al.*, 2008; Glor, 2010). Likewise, given~~

120   ~~finite ecological opportunity, it has been suggested that the rate of diversification should~~

121   ~~decline~~; Wiens, 2011). Ecological mechanisms tend to be viewed as ~~species numbers~~

122   ~~increase during an adaptive radiation (Harmon *et al.*, 2008; Rabosky & Lovette, 2008;~~

123   ~~Bokma, 2009) while other arguments highlight the importance of species themselves as a~~

124   ~~resource base for others, with diversification increasing with species number (Odling-Smee~~

125   ~~*et al.*, 2003; Erwin, 2008).~~

126   ~~Ecology in turn is traditionally viewed as the process acting on~~packing standing

127   diversity ~~to pack it~~ into local communities through competition, facilitation, and neutral

128   ecological drift (Hubbell, 2001; Tilman, 2004; Bascompte & Jordano, 2007; Borer *et al.*,

129   2014). ~~Island systems have been instrumental in developing our understanding of all these~~

130   ~~processes, especially through the conceptual lens provided by the equilibrium theory of~~

131   ~~MacArthur and Wilson (1967).~~ Recent theoretical advances have further refined the causes

132   and consequences of ecological drift (Hubbell, 2001; Rosindell & Phillimore, 2011), re-

133   vitalized classical niche-based mechanisms such as niche partitioning (Tilman, 2004),

134   competition and predation (Borer *et al.*, 2014), and put ~~ecology~~species interactions in a

135   network theoretic context (Williams & Martinez, 2000; Brose *et al.*, 2006).

136   New insights into evolutionary mechanisms have also emerged based on inference

137   from contemporary patterns of species, genetic, or phylogenetic diversity (e.g., Jetz *et al.*,

138   2012; Wiens, 2011). Here, we propose an integrative framework that harness both sources

139   of advancement to study evolutionary community assembly. We provide an initial test

140   using arthropod lineages in the Hawaiian Islands using mostly published data. We estimate

141   metrics of evolutionary and ecological dynamics across communities that range in age from

142   500 yr to 5 myr. We estimate taxon-specific timelines for the development of genetic

143   discontinuity. This is contextualized with macroecological metrics of community structure,

144   using predictions from statistical equilibrium and ecological network theory to examine

145   changes over the island chronosequence.

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146 ~~Ecological networks are a prime starting place~~ Hotspot oceanic archipelagos as model

147 systems

148 Hotspot oceanic islands are opportune model systems for ~~integrating~~studying the

149 interplay of local ecological mechanisms ~~of ecology~~ and ~~evolution because ecological~~

150 ~~network analysis already builds off~~ large-scale, historical, and evolutionary

151 ~~hypotheses~~drivers of biodiversity patterns. Such island systems are discrete in space and in

152 time due to their sequential formation as the tectonic plate moves over a volcanic hotspot.

153 We hypothesize that the contributions of evolutionary and ecological assembly will vary

154 according to geological age of the environment, taken as an indicator of the total time

155 communities have had to assemble and over which *in situ* diversification could occur. Age-

156 structured, hot-spot island archipelagoes thus have the potential to stratify the eco-

157 evolutionary process of community assembly.

158 Younger communities originate mostly from initial immigration and thus should be

159 dominated by ecological mechanisms operating on a source pool whose evolution is

160 removed from the local setting. Conversely, older islands could allow for the combined

161 interaction and feedback of diversification and local ecological dynamics. Moreover,

162 because dispersal, and hence connectivity between sites, differs between taxa, the relative

163 role of evolutionary and ecological assembly will differ between taxa. While many

164 archipelagos around the world share these biotic and geologic properties, the Hawaiian

165 archipelago provides a particularly useful system for study because its geological

166 chronology (Price & Clague, 2002) and patterns of biodiversity are well characterized

167 (Wagner & Funk, 1995).

Development of genetic discontinuity

Movement of individuals among localities connects their population dynamics. Even moderate levels of genetic connectivity among geographically separated populations limits the potential for local divergence (Slatkin, 1987). Thus, in the face of connectivity among populations, one predicts that the structure of ecological communities will remain similar across space. By contrast, when connectivity is low, not only are the ecologies of populations in different localities free to vary, but genetic divergence is also more likely. For these reasons, the magnitude of connectivity among population provides a measure of the relative importance of ecological processes and evolutionary processes in determining differences among ecological communities. Here, by using the chronosequence, we can apply this approach to sets of communities from young to old and to taxa representing different trophic levels.

Macroecological metrics

While we expect the mechanisms underlying the generation and maintenance of biodiversity to change across chronological sequences, studies to date have rarely moved beyond reporting basic patterns (Gillespie & Baldwin, 2010). Theory provides a necessarily simplified view of biodiversity and deviations from theory can reveal which more biologically realistic mechanisms likely underlie observed patterns. The Maximum Entropy Theory of Ecology (METE; Harte, 2011) provides a prediction for idealized ecological communities in statistical steady state, the situation in which a system's behavior is governed by a simple set of state variables and no further mechanisms are required. Real world deviations from METE can provide insights into the processes driving ecology away

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190   from this statistical steady state and toward alternate system states (Harte, 2011). We

191   expect that different aged communities along the Hawaiian chronosequence will deviate

192   differently from METE, because we hypothesize the processes of speciation, extinction,

193   adaptation and colonization may themselves drive Hawaiian communities out of statistical

194   steady state.

195   METE can successfully predict various metrics of an ecological community (Harte,

196   2011), including network metrics that describe trophic interactions between species

197   (Williams, 2010; Harte, 2011). Ecological network theory derives from evolutionary

198   concepts such as coevolution (Thompson, et al. 200513; Bascompte & Jordano, 2007;

199   Donatti *et al.*, 2011; Nuismer *et al.*, 2013) and so presents an opportune starting place to

200   study ecological and evolutionary feedbacks. and has clear ties with macroecology (Berlow

201   *et al.*, 2009; Williams, 2010; Harte, 2011). The distribution of linkages in ecological

202   networks has been used to determine whether plant-animal interaction networks assemble

203   neutrally or through deterministic processes (Vázquez *et al.*, 2005). Analysis of other

204   network metrics such as modularity (the degree to which species interact in semi-

205   autonomous modules) and nestedness (the degree of asymmetry in interaction between

206   specialists and generalists) can further illuminate underlying eco-evolutionary processes

207   driving patterns of species interactions (Bascompte & Jordano, 2007; Donatti *et al.*, 2011;

208   Nuismer *et al.*, 2013To further aid in integrating ecology and evolution we also make use of

209   the maximum entropy theory of ecology which uses principles from thermodynamics to

210   predict the statistical steady state of ecological communities (Harte, 2011). Statistical

211   steady state refers to the condition under which the aggregate properties of a community,

212   such as the distribution of trophic links, are not influenced by any unique biological

213 mechanism but instead conform to predictions of an idealized statistical system. Deviations

214 from maximum entropy theory have been identified as indications of ecological systems in

215 rapid transition and out of steady state (Harte, 2011; Harte & Newman,

216 2014).Nevertheless, this and other ecological research historically has been poorly

217 integrated with evolutionary perspectives (Cavender-Bares *et al.*, 2009), missing the

218 opportunity to understand how evolutionary history can drive common patterns in

219 contemporary ecology (Ricklefs, 1987; Qian *et al.*, 2005). There is a clear need to steer

220 ecological theories and studies toward incorporating biodiversity dynamics during

221 evolutionary community assembly, via the processes of invasion, microevolution,

222 speciation, and extinction.

223   The confluence of ecological and evolutionary theory has the potential to greatly

224 illuminate biodiversity dynamics through space and time. In practice, merging theories that

225 gain their predictive power from large-scale patterns across multiple species (Brown,

226 1995; Hubbell, 2001; Harte, 2011) with those that yield information on the dynamic nature

227 of single lineages is challenging. We confront the challenge of analyzing the interface of

228 ecological and evolutionary processes by outlining a set of hypotheses that predict the

229 structure of biological assemblages along a continuum from ecological to evolutionary

230 assembly.

231   We define ecological assembly as the process that results form ecological

232 mechanisms (e.g. neutral drift (Hubbell, 2001) or niche-based coexistence (Tilman, 2004;

233 Chesson, 2000)) packing standing diversity into communities. In contrast, we define

234 evolutionary assembly as the process that results from ecology and evolution having the

235 ability to feed back on each other because they happen coincidentally in space and time

236 (Schluter, 2000; Gillespie, 2004; Gillespie & Baldwin, 2010). These two modes of

237 community assembly fall on a continuum and are not unique to islands. However, islands

238 are opportune systems to study the consequences of these contrasting assembly modes

239 due to their relative simplicity and discrete nature. In addition to definite boundaries in

240 space oceanic island systems are also discrete in time due to their sequential formation

241 over volcanic hotspots. The age gradient of such island systems thus has the potential to

242 stratify ecological assembly and evolutionary assembly processes. For example, younger

243 communities may be dominated by ecological assembly from initial immigration from the

244 mainland, whereas on older islands, we might observe evolution keeping pace with

245 ecology. This stratification provides an opportunity to disentangle these interacting forces.

246   The Hawaiian archipelago is a prime example because its geological chronology

247 (Price & Clague, 2002) and biota are well-known (Wagner & Funk, 1995).In this age

248 structured and simplified model system we hypothesize that the contribution of

249 evolutionary assembly and ecological assembly will vary between taxa and between ages of

250 lineages in communities. Specifically, we hypothesize that:

251   During periods of ecological assembly, communities strongly influenced by

252 immigration will resemble random samples from regional source pools and thus metrics

253 describing these communities will largely match expectations of statistical steady state

254 after primary succession has completed (Harte, 2011). The exception will be communities

255 still undergoing primary succession (Harte, 2011) which will change rapidly through time

256 and represent non-random samples of source pools. We also predict that these

257   communities will exhibit a nested network structure, assuming new species will eat or be

258   eaten by the generalist species (Bascompte *et al.,* 2003) already present in the community.

259   Alternatively, if evolutionary processes of niche exploration, adaptation and

260   speciation happen fast enough to keep pace with immigration, ecological communities

261   formed by such assembly could be driven into alternate evolutionary states that fail to

262   meet the predictions of purely statistical theories that do not account for evolutionary

263   dynamics (Harte, 2011). We expect networks in such communities to exhibit higher levels

264   of specialization and modularity (Bascompte & Jordano, 2007; Donatti *et al.,* In this paper

265   we integrate methods from population genetics to theoretical ecology using the

266   chronosequence of the Hawaiian Archipelago to understand the nexus between ecological

267   and evolutionary forces community assembly. Moving from young to old across the

268   chronosequence we evaluate (1) the rate and pattern of genetic connectivity among

269   populations of taxa from different trophic levels as they diversify from populations to form

270   new species; (2) the processes underlying the structure of species interaction networks

271   given the backdrop of population divergence; and (3) the processes involved in

272   diversification as species form and accumulate and how this dynamic drives deviations

273   from statistical steady state. We use data (mostly published) on population genetic

274   structure and species interactions as a proof of concept. With this framework, our goal is to

275   show how communities develop over ecological-evolutionary time, and the dynamic

276   feedbacks involved assembly.

277   1.   2011; Nuismer *et al.,* 2013).

278   Combining novel data with that gathered from the primary literature, we present

279   evidence for the timeline over which evolution begins to keep pace with ecology using a

280 ~~combination of analytical approaches that incorporate population genetics, bipartite~~

281 ~~networks and maximum entropy theory. Given the paucity of available data and abundant~~

282 ~~potential directions for theoretical exploration, we also present future directions to extend~~

283 ~~and more rigorously test our framework.~~

METHODS

Hawaii as an eco-evolutionary study system

286   The geological landscape of the Hawaiian Islands offers a matrix of volcanic

287 substrates mapped in fine detail by chronological age and geochemical composition

288 (Sherrod *et al.*, 2007). On Hawaii Island in particular, independent gradients in elevation

289 and precipitation interact within a matrix of substrate ages ranging from contemporary

290 (active) to 500,000 years. Ongoing volcanic activity has created a dynamic mosaic of

291 habitats with transitory to long-lasting fragmentation within landscapes. Isolation on scales

292 of hundreds to thousands of meters and hundreds to thousands of years can be sufficient

293 for genetic differentiation ~~of~~among some arthropod populations among habitats

294 (~~Vandergast *et al.*, 2004;~~ Goodman *et al.*, 2012; Eldon *et al.*, 2013; Bennett & O'Grady,

295 2013~~)~~.), while insufficient to isolate others (Vandergast *et al.*, 2004). On larger spatial and

296 temporal scales, distinct volcanoes and islands, with their semi-independent histories of

297 evolutionary community assembly from recent to ancient, comprise a space-for-time

298 geological chronosequence spanning from present day up to 5 million years ~~from~~across

299 Hawaii Island to Kauai.

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300 ~~We use this age-structured template as a basis from which to assess~~

301 ~~evolutionary community assembly. At least two aspects of the system make this~~

302 ~~approach feasible:~~

303 ~~1.   the limited diversity of lineages allows precise identification of~~ To

304 investigate how ecological ~~affinities of taxa, and hence the role of ecological~~

305 ~~opportunity~~patterns change in ~~adaptive radiation, and~~

306 ~~2.   the age-structured landscape offers~~response to varied evolutionary

307 contexts we selected four focal sites across the chronosequence ~~that~~of substrate

308 and island ages (two on Hawaii Island, one on Maui and one on Kauai; Fig. 1).

309 Focal sites were selected to have similar forest composition (dominated by

310 *Metrosideros polymorpha*: Myrtaceae), elevation (1100-1400m), and climate

311 (mean annual precipitation 2000-3000 mm). ~~which allows for comparison of~~

312 ~~replicate communities differing markedly in their age of assembly.~~

313 ~~Compilation and analysis of genetic data~~To provide an evolutionary context for our

314 ~~network analysis we assessed the spat~~

315

316 **Compilation and analysis of genetic data**

317 ~~temporal scales at which genetic~~To evaluate the balance between regional

318 immigration and potential for local ecological differentiation ~~occurs across the landscape of~~

319 ~~the islands. We first asked~~, we measured how molecular variation is partitioned within

320 species within locations of known substrate age on ~~the~~ Hawaii Island and Maui. We

321 compiled ~~existing~~published and new data sets for a diversity of native Hawaiian arthropod

322 groups that represent a spectrum of trophic levels. The arthropods represent several

323 species of spiders and three orders of insects (spiders: COI, allozymes, (Roderick *et al.,*:

324   1. Herbivorous 2012; Croucher *et al.,* 2012); *Laupala* crickets AFLPs, (Mendelson *et*

325   *al.,* 2004); *Nesosydne* planthoppers: (COI, and microsatellites, (: Goodman *et al.,*

326   2012), GenBank accession numbers XXX-XXX generated following protocols

327   described in (Goodman *et al.,* 2012); *Trioza* psyllids: (COI, cytB,; GenBank

328   accession numbers XXX-XXX, generated following protocols described in (Percy,

329   2003); primers given in (Simon *et al.,* 1994; Timmermans *et al.,* 2010);); and

330   fungivorous *Drosophila sproati*: (COII, (; Eldon *et al.,* 2013).) that maintains tight

331   host plant associations.

332   2. Detritivorous *Laupala* crickets (AFLPs; Mendelson *et al.,* 2004); and

333   3. several predatory spiders species (COI and allozymes; Roderick *et al.,* 2012)

334   In the case of previously unpublished molecular data, sequences for *Nesosydne*

335 planthoppers were generated following protocols described in (Goodman *et al.,* 2012) and

336 sequences for *Trioza* psyllids were generated following protocols described in Percy

337 (2003). Existing genetic data from across Hawaii Island and Maui (including, but not

338 limited to the focal sites), provide an estimate of how arthropod populations have

339 accumulated genetic diversity and divergence within the dynamic landscape of the focal

340 sites.

341   We used analysis of molecular variance (AMOVA) to examine how genetic variation

342 is partitioned at two scales of population structure: among sites within volcanoes and

343 among volcanoes on both the Hawaii Island and Maui Nui. All analyses of allozyme and

344 DNA sequence data were performed in Arlequin v. 3.5 (Excoffier & Lischer, 2010) using the

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345 AMOVA procedure to compute F_{ST}, a measure of genetic variance, or, where possible

346 ~~Φ_{ST}~~, Φ_{ST}, an F_{ST} analog that incorporates genetic sequence information. The *Laupala*

347 AFLP data were analyzed using TFPGA v. 1.3 (Miller, 1997), using the same hierarchical

348 approach as described above. To provide a temporal framework for the population

349 differentiation analysis we assembled divergence dating information from the literature for

350 as many of the taxa as possible and additionally implemented a new divergence dating

351 analysis for *Tetragnatha* spiders (see supplementary information).

352 To explicitly evaluate the role of <u>landscape</u> age in allowing *in situ* genetic diversity

353 and potential for divergence we analyzed how ~~population structure~~ <u>within site F_{ST}</u> varies

354 with the ~~chronosequence~~<u>geologic age</u> of volcanoes on Hawaii Island and Maui Nui. For each

355 volcano we calculated F_{ST} or ~~Φ_{ST}~~ Φ_{ST} (Excoffier ~~and Schneider 2005~~<u>& Lischer, 2010</u>) for

356 each taxon between sites within ~~each volcanos~~<u>volcanoes</u>.

Construction of plant-herbivore networks

358 ~~To test our hypothesis that network structure should change with island age due to~~

359 ~~changes in the relative contributions~~<u>Bipartite networks describe the topology</u> of ecological

360 ~~and evolutionary assembly we selected four sites according to the criteria above that span~~

361 ~~the chronosequence from 0.0002–5 million years (Kilauea and Kohala (Hawaii Island);~~

362 ~~Waikamoi (Maui), Kokee (Kauai); see Fig. 1). We constructed bipartite networks of plant-~~

363 ~~herbivore~~ interactions between ~~all native Hemiptera~~ <u>two guilds of organisms (e.g.</u>

364 herbivores <u>(sap feeders)</u> and their ~~host plant species in the Hawaiian Islands within the~~

365 ~~study sites. Each site's set~~ <u>plant hosts). Quantitative information on the relative importance</u>

366 of ~~herbivores was determined from the literature including the Hawaiian Arthropod~~

367 ~~Checklist (Nishida 2002) and~~ interaction links can be incorporated into network analyses

368 (Vázquez *et al.*, 2009); however, currently available data ~~indicating whether a species has~~

369 ~~been detected or is likely~~are restricted to ~~occur within~~binary networks, those that describe

370 only the ~~sites~~potential for interaction between any two species, but not the relative

371 frequency of that interaction to each species.

372 　　We compiled species lists of all endemic hemipteran herbivores for each focal site

373 from published species accounts (see supplement~~). The~~ for full list~~of~~). Species accounts

374 and other published sources were used to determine the presence, probable presence, or

375 probable absence of each Hemiptera species at each of our four focal sites. A documented

376 presence was defined as a known specimen collected at the focal site; a probable presence

377 was defined as a species whose abiotic tolerances and known geographic range (see

378 supplement) overlap with a focal site but no known specimen exists confirming its

379 presence. Probable absence was assumed when neither criteria for presence or probable

380 presence are met. Two sets of species lists for each focal site were compiled: a conservative

381 data set composed of only documented presence occurrences and a less conservative data

382 set that also included probable presences.

383 　　Host plants for each ~~site was generated~~hemipteran species were determined from

384 published species accounts. Data on host plant use at each specific site were not available

385 so we assumed that if a known host plant was present at a site it would eventually be used.

386 Host plant occurrence in the focal sites was determined using distribution models for 1158

387 species of Hawaiian plants (Price, 2012). Each ~~study~~focal site was spatially joined in a

388 geographic information system with all coincident plant distribution models that fell within

389 its boundaries. ~~Resulting~~Two sets of resulting focal site-specific networks were constructed

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390 ~~both for~~ : one using the conservative ~~estimates of the geographic ranges~~data set of

391 ~~Hemiptera (considering only sites with definite specimen localities)~~hemipteran species

392 presences and ~~more liberal estimates (extrapolating between known localities surrounding~~

393 ~~our focal sites and with habitat comparable to our focal sites).~~the other using the less

394 conservative data set.

Analysis of plant-herbivore networks

396 ~~To understand how overall network structure changes with age, we calculated two~~

397 ~~widely used descriptive network metrics across sites—nestedness (Bascompte *et al.,* 2003;~~

398 ~~Ulrich *et al.,* 2009) and modularity (Newman & Girvan, 2004; Olesen *et al.,* 2007). We~~

399 ~~calculated nestedness using the NODF metric (Almeida-Neto *et al.,* 2008) as implemented~~

400 ~~in~~ ~~R package vegan (Oksanen *et al.,* 2013) and modularity using a variety of algorithms~~

401 ~~implemented in the R package igraph (Csardi & Nepusz, 2006). These metrics are not~~

402 ~~directly comparable across networks of different size and connectance (Ulrich *et al.,* 2009)~~

403 ~~so for each metric in each network we calculate z-scores using a null model that~~

404 ~~randomizes network structure while maintaining certain aggregate network properties~~

405 ~~(Ulrich *et al.,* 2009). Z-scores are calculated as the difference between the observed~~

406 ~~network metric minus the mean of the null model divided by the null model standard~~

407 ~~deviation, or $(x_{obs} - \bar{x}_{sim})/sd_{sim}$. Because z-scores can be highly sensitive to the choice of~~

408 ~~null model (Ulrich *et al.,* 2009) we implemented both a probabilistic null model~~

409 ~~(Bascompte *et al.,* 2003) and a null model that strictly constrains the degree distributions~~

410 ~~of plants and herbivores (Ulrich *et al.,* 2009).~~

411   ~~To more explicitly test the hypothesis that communities dominated by evolutionary~~

412   ~~assembly and *in situ* diversification processes should differ from those dominated by~~

413   ~~ecological assembly and immigration,~~ We hypothesize that communities differentially

414   depart from statistical steady state along the continuum form those dominated by

415   ecological processes to those with potential complex evolutionary feedbacks We used

416   METE (Williams, 2010; Harte, 2011) to compute the statistical steady state for the

417   hemipteran degree distribution (distribution of the number of plant hosts to each

418   hemipteran species). To evaluate how well METE predicts the data we simulated METE-

419   conforming communities of the same number of species and links as observed. We then

420   calculated the log-likelihood of each simulated data set and compared the resultant

421   distribution of log-likelihoods under the hypothesis that METE is true, to the observed log-

422   likelihood. This comparison is identical in approach to a z-score test using a Monte Carlo

423   simulation to estimate the sampling distribution of log-likelihoods. R scripts used for METE

424   estimation and Monte Carlo methods are available in the supplement.

425   To further investigate how *in situ* diversification leaves a potentially unique

426   signature on network structure we analyzed the number of links assigned to each

427   ~~Hemiptera~~hemipteran species (the degree distribution) separately for island endemics

428   (those species found on only one island and thus likely derived from in situ diversification)

429   versus island cosmopolitans (those species found on multiple islands). ~~We hypothesized~~

430   ~~that evolutionary assembly should favor specialization and thus expected island endemics~~

431   ~~to be more specialized.~~ To compare species' degree distributions between endemics and

432   cosmopolitans across sites of different ages we conducted a generalized linear model with

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433 binomial error, treating site identity as a categorical predictor. Binomial errors effectively

434 account for network size due to the bounded support of the binomial distribution.

435 ~~To test the hypothesis that communities should differentially depart from statistical~~

436 ~~steady state during their ecological succession and evolution, we compared the degree~~

437 ~~distributions to that predicted by maximizing information entropy relative to the~~

438 ~~constraint of average degree (Williams, 2010). The maximum entropy prediction~~

439 ~~represents the hypothesis of statistical steady state (Harte, 2011).~~

440 To understand how other network properties change with ecosystem substrate age,

441 we calculated two widely used descriptive network metrics across sites—nestedness,

442 which describes the degree of asymmetry of species interactions connecting specialists and

443 generalists (Bascompte & Jordano, 2007; Ulrich *et al.*, 2009), and modularity which

444 describes the degree to which interactions are concentrated within subsets of species but

445 not between subsets (Newman & Girvan, 2004; Olesen *et al.*, 2007).

446 We calculated nestedness using the NODF metric (Almeida-Neto *et al.*, 2008) as

447 implemented in the R package vegan (Oksanen *et al.*, 2013) and modularity using a variety

448 of algorithms implemented in the R package igraph (Csardi & Nepusz, 2006). These metrics

449 are not directly comparable across networks of different size and connectance (Ulrich *et al.*,

450 2009), so for each metric in each network we calculate z-scores using a null model that

451 randomizes network structure while maintaining certain aggregate network properties

452 (Ulrich *et al.*, 2009). These z-scores are calculated as the difference between the observed

453 network metric minus the mean of the null model divided by the null model standard

454 deviation, or $(x_{obs} - \bar{x}_{sim})/sd_{sim}$. Because z-scores can be highly sensitive to the choice of

455 null model (Ulrich *et al.*, 2009) we implemented both a probabilistic null model

(Bascompte & Jordano, 2007) and a null model that strictly constrains the degree
distributions of plants and herbivores (Ulrich *et al.*, 2009). The probabilistic null using the
frequency of interactions as the probability that a randomized link gets assigned to that cell
in the interaction matrix (Bascompte & Jordano, 2007): thus the probabilistic null
constrains row and column sums in probability but not absolutely.

RESULTS

Population genetic inference of connectivitydiscontinuity among populations

The analysis of molecular variance (AMOVA) revealed evidence of significant
population genetic structure from the smallest to the largest spatial scales examined, all
within a very recent timeframe. For mitochondrial loci, the amount of statistically
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 (larger observed variance within volcanoes may represent the effects of
repeated colonization events or sampling error). 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 compared to between (Table 1). 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 comparedrelative to

477　between localities on older volcanoes (Fig. 2). By contrast, predatory spiders exhibited

478　higher genetic population structure only on older volcanoes (e.g. Maui).

479　　　　The observed levels of genetic divergence have evolved rapidly. ~~Within~~For example,

480　within species genetic divergence in planthoppers has evolved in as little as 2,600 years

481　(Goodman *et al.*, 2012). For species from ~~the~~ Hawaii Island for which phylogenetic data

482　provide divergence times, estimates of dates of species ~~origination~~ divergence range from

483　0.34–1.15 million years, with ~~all~~ additional within-species genetic divergence ~~having~~

484　developed subsequently (Table 1). That the estimates are older than the known age of the

485　Big Island, suggest that divergence in DNA now reflected in different lineages pre-dated

486　their colonization of the Big Island, or alternatively may be due to sampling error.

487　**Evolving network structure**

488　~~Across our chronosequence of sites network nestedness decreased with age while~~

489　~~modularity increased (Fig. 3). This trend is found in networks constructed from both more~~

490　~~and less stringent geographic criteria (supplemental Fig 3). Choice of null model changed~~

491　~~the magnitude of modularity and the sign of nestedness z-scores; however, the relative~~

492　~~pattern of decreasing nestedness and increasing modularity remained across the different~~

493　~~null models used to standardize network metrics (supplemental Fig. 2). The patterns are~~

494　~~also robust to sampling intensity, as demonstrated by a rarefaction analysis (supplemental~~

495　~~Fig. 4).~~

496　　　　The Hemiptera species degree distribution varied across ~~sites~~the chronosequence

497　with both the youngest and oldest sites deviating most from the statistical steady state

498　maximum entropy predictions (Fig. ~~4~~3). In the middle aged site of Kohala, minor deviations

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499   from maximum entropy are no different than expected by chance indicating the Kohala

500   Hemiptera communityassemblage matches the predictions of maximum entropy.

501   The generalized linear model revealed that there are also significant differences

502   between the degree distributions of island endemics (those species found on only one

503   island) versus island cosmopolitans (those species found on multiple islands) (; Fig. 43).

504   Endemics show significantly lower degree distributions overall (i.e.;, more specialization)

505   compared to more generalist cosmopolitan species. Endemics become significantly more

506   generalist on the middle aged Maui site; however this pattern disappears when analyzing

507   links to plant genera instead of species. The slightly younger Kohala shows increased

508   generalization overall. When looking atconsidering the degree distribution defined by

509   trophic links to plant genera instead of plant species, the pattern of increased

510   generalization holds for the KohalasKohala but endemics on Maui no long show a

511   difference in their degree distributions from other island endemics. This change in pattern

512   indicatessuggests that increased generality of Maui endemics ismay be driven by increased

513   intra-genus plant diversity on that island.

514   Network nestedness decreased with age while modularity increased (Fig. 4). This

515   trend is found in networks constructed from both more and less stringent geographic

516   criteria (supplemental Fig. S3). Choice of null model changed the magnitude of modularity

517   and the sign of nestedness z-scores; however, the relative pattern of decreasing nestedness

518   and increasing modularity remained across the different null models used to standardize

519   network metrics (supplemental Fig. S2). The patterns are also robust to sampling intensity,

520   as demonstrated by a rarefaction analysis (supplemental Fig. S4).

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DISCUSSION

~~The~~ By combining disparate data with a novel combination of analytical approaches that incorporate population genetics, bipartite networks and maximum entropy theory, our results ~~showed that taxa~~present evidence for the timeline over which evolution begins to keep pace with ecology in determining the local diversity of communities. Taxa in the lower trophic levels ~~(herbivorous sap-feeders: Hemiptera *Nesosydne* and *Trioza* had~~, as ~~much or~~compared to higher trophic guilds, developed genetic discontinuities 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~~quickly along the chronosequence and at much smaller spatial scales (Table 1~~.~~ ~~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. 2~~). At the same time, considering plant-feeding Hemiptera only, network~~), allowing them the opportunity to diverge ecologically. Network nestedness decreased ~~with age~~while modularity increased ~~across our~~with age (Fig. 4), indicating a possible shift from assembly driven by *ex situ* immigration early on, to one based on *in situ* co-diversification with host plants (Bascompte & Jordano, 2007; Donatti *et al.*, 2011). This possibility is further strengthened by the observation that single island ~~chronosequence (Fig.~~endemics show more specialization compared to more broadly distributed species (Fig. 3). ~~The~~At intermediate modularity and nestedness, the distributions of the number of links assigned to each ~~Hemiptera~~hemipteran species showed the ~~greatest~~least 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~~

544   ~~show more specialization compared to more generalist species (Fig. 4). Together, these~~

545   ~~analyses begin to reveal the dynamics of ecological and~~the METE prediction (Fig. 3),

546   suggesting that at the transition from primary succession to evolutionary assembly ~~over~~

547   ~~time~~, these plant-herbivore communities reach statistical steady state.

548   **~~Population structure~~Development of genetic discontinuity at different trophic levels**

549   The analysis of available genetic data presented here indicates that divergence is

550   occurring within the islands at small spatial scales and over short time periods (Table 1,

551   Fig. 2). Furthermore, the scale of population structure varies with trophic position, with the

552   sap-feeding herbivores in this study showing structure at smaller scales compared to

553   ~~cricket detritivores~~detritivorous crickets and predatory spiders (Table 1, Fig. 2).

554   Population structure within species allows for populations to take independent

555   evolutionary trajectories, especially when aided by other evolutionary processes that may

556   be acting differentially across each species' range. A variety of factors have been implicated

557   in the genetic divergence of populations and species in lineages described here, including

558   ~~various~~ combinations of genetic drift associated with geographic isolation (Percy, 2003;

559   Mendelson & Shaw, 2005; O'Grady *et al.*, 2011; Goodman *et al.*, 2012), adaptation

560   associated with ecological interactions of competition, predation, and mutualism (Gillespie,

561   2004; Roderick & Percy, 2008), and sexual signaling (Mendelson & Shaw, 2005; Percy &

562   Kennedy, 2006; Magnacca *et al.*, 2008; Goodman *et al.*, in review).

563   The sap-feeding Hemiptera group *Nesosydne* (Goodman *et al.*, 2012) provide

564   evidence that some period of geographic isolation preceded divergence of sexual signals

565   (Goodman *et al.*, in review). Shifts in plant host use are ~~certainly~~also involved ~~at some point~~

566 in the process of diversification in this group (Roderick & Percy, 2008). ~~While this stage has~~

567 ~~not yet been identified with phylogentic methods in~~ *Nesosydne* ~~it has been in the parallel~~

568 ~~leafhopper~~In a similar radiation of leafhoppers, *Nesophrosyne* (Bennett & O'Grady, 2013~~).~~

569 ~~This work found that~~). host plant specialization ~~drove~~was implicated in driving species

570 radiations up until approximately 1 million years ago, when plant niches were mostly

571 exhausted on Maui~~. Following:~~ following this period, speciation, largely on the Hawaii

572 Island, shifted to geographic mechanisms of diversification. Our network analysis indicates

573 that specialization and modularity begin to show pronounced signals in network data on

574 Maui (Figs. 4, 3~~, 4~~), in agreement with the *Nesophrosyne* results and indicating that an

575 approximate age of 1 million years may be necessary for host plant specialization to

576 become the dominant process in the sequence of diversification.

577 ~~The~~ Other taxa at lower trophic levels, such as the herbivorous *Trioza* ~~group of~~

578 psyllids ~~(Hemiptera: Triozidae),~~ detritivorous *Laupala* crickets and ~~other herbivorous,~~

579 fungivorous ~~and detritivorous insect groups~~*Drosophila*, show similar signals of geographic

580 isolation combined with ecological and sexual processes driving genetic divergence and

581 diversification across sites as young as those on the Hawaii Island (Percy, 2003; Percy &

582 Kennedy, 2006; Mendelson & Shaw, 2005; Magnacca *et al.*, 2008; O'Grady *et al.*, 2011).

583 ~~Our analysis suggests that the mechanisms implicated in the diversification of~~

584 ~~predators, notably~~ As a contrast, spiders, which are ~~different. In particular, while~~

585 ~~geographic isolation is clearly implicated in the speciation process (Gillespie, 2005),~~

586 ~~ecological divergence through natural selection is assumed to play a key role in the~~

587 ~~differentiation of sister taxa on older islands (Gillespie, 2004; Blackledge & Gillespie, 2004).~~

588 ~~In taxa that do not show major ecological differentiation, such as *Orsonwelles* spiders,~~

589 ~~differentiation appears to have been driven almost entirely by geographic isolation~~

590 ~~(Hormiga *et al.*, 2003), and on a much~~predatory, only develop genetic discontinuities at

591 larger spatial and temporal ~~scale than those found for herbivores, fungivores, and~~

592 ~~detritivores.~~

593 ~~Differences in the patterns of population structure observed between trophic levels,~~

594 ~~as highlighted here, suggests that differentiation of predators requires a larger area and/or~~

595 ~~a longer time period to occur, which might be expected given the larger area requirement~~

596 ~~of predators compared to herbivores.~~scales. Most important in the context of community

597 assembly is that endemic sap-feeding herbivores developed structure quickly ~~(~~ - on the

598 order of less than 0.1 million years (assuming timing of speciation is reflected by

599 divergence in mtDNA; Table 1), with predatory spiders showing local endemicity more

600 slowly (Table 1). ~~Furthermore, among those lineages that show adaptive diversification,~~

601 ~~ecological differences appear early in the process of differentiation (Percy, 2003; Gillespie,~~

602 ~~2004; Blackledge & Gillespie, 2004; Percy & Kennedy, 2006; Magnacca *et al.*, 2008; O'Grady~~

603 ~~*et al.*, 2011; Goodman *et al.*, 2012).~~

604 **Macroecological metrics: Network structure and steady state**

605 ~~Given~~On the ~~timescale provided by the genetic analysis~~geologically youngest

606 volcano, Kilauea, ecological assembly should ~~dominate ecological communities at the~~

607 ~~youngest site, Kilauea.~~be the dominant process there. The results of network analysis ~~are~~

608 ~~consistent with~~support this hypothesis with Kilauea showing substantial nestedness and

609 limited modularity (Fig. ~~3~~4). Nestedness is likely to result if new species arriving by

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610 immigration have a high probability to eat or be eaten by the generalist species already

611 present at the site (Bascompte & Jordano, 2007). In this way we might expect Kilauea to

612 also conform to the statistical steady state predication of maximum entropy. However, the

613 observed deviations from maximum entropy at Kilauea are largely driven by a surplus of

614 singleton links (Fig 4. 3). These in turn likely result from incomplete assembly, and thus

615 lower species richness, of the plant and herbivore biotas. Future research should focus on

616 the observation from genetic analysis that indicates discontinuities can arise within species

617 on short timescales that, in some taxa, include the greater landscape of Kilauea (Table 1).

618 Conversely, Kohala shows a statistically significant agreement with maximum entropy

619 perhaps because the KohalasKohala site, at intermediate age (150 ky), havehas

620 experienced complete ecological succession but areis still too young to be driven away

621 from statistical steady state by specialization and rapid in situ diversification driven by

622 host plant preference.

623   The older Maui and Kauai sites show strong deviations from expectations of

624 maximum entropy theory (Fig. 34), which is consistent with our hypothesis that the

625 influence of evolutionary assembly on these biotas drives them away from statistical steady

626 state. The application of maximum entropy to ecology does not currently take into account

627 evolution (Harte, 2011). Indeed the use of maximum entropy in ecology is inspired by its

628 application into physical systems whose change through time is simple and purely

629 Markovianlacks the evolutionary memory of biological systems, potentially a far cry from

630 the complex change through time undergoneproduced by biological systems as they

631 changespeciation, extinction and adaptadaption to theirnovel ecosystems. Maui and Kauai

632 show strong evidence of evolutionary assembly driven by specialization and diversification

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633 on host plants, particularly demonstrated by decreased nestedness and increased

634 modularity (Fig. ~~3~~4). Modularity is known to result from coevolution selectively driving the

635 traits of interacting species towards convergence (Donatti *et al.*, 2011; Nuismer *et al.*,

636 2013).

637   The analysis of island endemic and cosmopolitan (archipelago-wide) Hemiptera

638 species sheds further light on the evolution of the networks they form. Endemics are

639 always more specialized than cosmopolitans, further supporting the hypothesis that in situ

640 diversification and evolutionary assembly favor coevolution. ~~In~~At the ~~Kohalas~~Kohala site ,

641 which ~~show~~showed the best fit to maximum entropy theory, endemic and cosmopolitan

642 species alike show increased generalization (i.e. higher degree; Fig ~~4~~3), while at the

643 youngest site Kilauea, specialist endemics are limited by low plant diversity and thus show

644 more apparent specialization (Fig ~~4~~3). Conversely at the oldest site on Kauai, where plant

645 diversity is not limiting (Kitayama & Mueller-Dombois, 1995), endemics again show

646 decreased degree and thus genuine specialization (Fig. ~~4~~3). On Maui, endemics show

647 statistically significant increases in apparent generalization but this pattern disappears

648 when analyzing the data at the resolution of plant genera, thus ~~indicating~~suggesting that

649 ~~Maui endemic~~ Hemiptera species endemic to Maui are no more generalized on plant genera

650 but instead may benefit from the diversification of plant species within genera on Maui.

651

652 **Future Research**

653   ~~These~~The analyses presented here indicate strong patterns of a dynamic assembly

654 process ~~despite being limited~~leading to ~~available data. In ongoing work we are obtaining~~

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655 ~~more detailed~~ contrasting hypotheses concerning the relative importance of ecological and

656 evolutionary ~~data sets, which will allow us to understand the biodiversity dynamics in~~

657 ~~greater depth.~~

658 *~~Assembly of species into communities~~*

659 ~~In terms of the distribution of abundance and body size of arthropod species,~~

660 ~~Gruner (2007) provided some key insights into changes in arboreal arthropods from~~

661 *~~Metrosideros polymorpha~~*~~, showing that abundances and sample-based species richness~~

662 ~~were highest at more productive, intermediate-aged sites (Maui Nui). This study also~~

663 ~~showed that proportions of individuals and biomass varied widely across sites, and~~

664 ~~according to trophic group and taxonomic order. However, communities tended to~~

665 ~~converge in trophic structure and composition. Recent analysis of these data in the context~~

666 ~~of the maximum entropy theory of ecology (Harte, 2011) has shown that different trophic~~

667 ~~groups conform or deviate from maximum entropy predictions across the age gradient~~

668 depending on ~~their unique eco~~ the evolutionary ~~histories (Rominger *et al.*, in preparation).~~

669 ~~For example, predators, whose assemblages are likely more dominated by immigration~~

670 ~~and~~age of the community under observation. In future work we will tackle these

671 hypotheses using detailed quantitative ecological ~~assebly (Fig. 2) never show strong~~

672 ~~deviations from maximum entropy predictions whereas herbivores show increasing~~

673 ~~deviation with age, in agreement with the network results of this paper (Fig. 4) (Rominger~~

674 *~~et al.~~*~~, in preparation).~~and genomic data collected from across the Hawaiian archipelago.

675 1. In younger communities we hypothesize that

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676 a. during periods of ecological assembly, communities strongly influenced

677 by immigration will resemble random samples from regional source

678 pools and thus metrics describing these communities will largely match

679 expectations of statistical steady state after primary succession has

680 completed;

681 b. the exception will be communities still undergoing primary succession,

682 which will change rapidly through time and represent non–random

683 samples of source pools;

684 2.c. we also predict that these communities will exhibit a nested network

685 structure, assuming new species will eat or be eaten by the generalist

686 species (Bascompte & Jordano, 2007) already present in the community.

687 What is clear from this work is that the island chronosequence can reveal

688 fascinating and important insights into the process of community assembly. However, in

689 order to understand the nature of the assembly process and the dynamic nature of the

690 feedbacks involved, it is important that we conduct broad sampling of all macroscopic

691 arthropod taxa at a site, thus allowing assessment of changes in overall species

692 composition and diversity across all players in the time-calibrated landscape.

693 2. Following the same logic, in older communities we hypothesize that

694 a. during periods of evolutionary assembly, if processes such as niche

695 exploration, adaptation and speciation happen fast enough to keep pace

696 with immigration, the resultant communities could be driven into

697 alternate evolutionary states that fail to meet the predictions of purely

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698   statistical theories that do not account for evolutionary dynamics (Harte,

699   2011);

700   b.   networks in such communities should exhibit higher levels of

701   specialization and modularity (Bascompte & Jordano, 2007; Donatti *et al.*,

702   2011; Nuismer *et al.*, 2013).

703   3.   Systems undergoing rapid ecological and evolutionary change are generally

704   expected to deviate most from statistical steady state; thus we expected

705   populations in such communities to show genetic signatures of rapid change,

706   from bottlenecks or population expansion to selection.

707 ***Evolutionary data:*** ***Diversification within species***

708   ~~Much work remains to determine the detailed patterns of diversification in different~~

709 ~~lineages, the extent to which patterns are associated specifically with trophic level, and the~~

710 ~~interplay between gene flow, population size and fluctuations in size in the context of~~

711 ~~speciation. Particularly important in terms of the dynamics of diversification, will be to~~

712 ~~assess the extent and location in the genome of gene flow during the course of speciation~~

713 ~~(Nosil & Crespi, 2006).~~

714   ~~What is clear from the~~The current study~~, besides showing~~ demonstrates that taxa of

715 different trophic guilds differ in the scale at which differentiation occurs, ~~is~~and highlights

716 the importance of fragmentation of the landscape in facilitating differentiation. ~~The scale at~~

717 ~~which this fragmentation occurs is relative to the organism in question and plays a key role~~

718 ~~in dictating the effects of fragmentation. For some taxa fragmentation clearly allows genetic~~

719 ~~separation. For others, in particular those that are more connected, the fragmentation can~~

720　~~provide a way of enhancing adaptive differentiation (Gillespie & Roderick, 2014).~~Future

721　work is aimed at gathering genomic SNP data for focal taxa within this system that

722　represent different trophic levels. We will use it to understand taxonomic differences in the

723　rate of differentiation, to assess the roles of genetic fusion and fission (Gillespie and

724　Roderick 2014), and to detail the relative rates of speciation and extinction across the

725　island chronosequence. When coupled with ecological data on abundances and

726　interactions, the population genetic data will allow us to explore explicit aspects of the

727　Geographic Mosaic Theory of evolution, such as trait remixing and selection mosaics.

728　(Thompson et al. 2013).

729　~~Clearly, more work is needed in order to understand the role of genetic mixing and~~

730　~~hybridization among recently diverged populations and the potential role of such effects in~~

731　~~fostering adaptive radiation (Nosil & Crespi, 2006; Seehausen *et al.*, 2014). Particularly~~

732　~~intriguing will be to determine the extent to which novel genetic combinations might~~

733　~~facilitate differentiation associated with ecological shifts, and the timeframe over which~~

734　~~this tends to occur in different lineages.~~

735　***Ecological data: Assembly of species into communities***

736　Our results show that the island chronosequence can reveal that ecological

737　processes dominate in younger environments, with evolutionary processes becoming more

738　important later. However, in order to build a more rigorous understand of the assembly

739　process future work is focusing on conducting broad sampling of all macroscopic

740　arthropod taxa at a large number of sites across the age gradient, thus allowing assessment

of changes in overall species composition and diversity across all players in the time-calibrated landscape (*sensu* Gruner, 2007).

Such data will allow us to test how entire arthropod communities of different aged substrates deviate from statistical steady state as predicted by METE (Harte, 2011). For example, predators, whose assemblages are likely more dominated by immigration and ecological assembly (Fig. 2) may never show strong deviations from METE predictions whereas herbivores could show increasing deviation with age in agreement with the network results of this paper (Fig. 3).

The current study provides a framework for the use of chronologically arranged oceanic island systems to examine the interplay between evolutionary and ecological processes in shaping biodiversity. and We analyze preliminary molecular and community-level data together in the context of ecological theory to demonstrates how this approach can provide insights into howthe development of communities develop over ecological-evolutionary time, and the dynamic feedbacks involved in assembly.

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782

783 **BIOSKETCH**

784   The authors are part of a large team involved in understanding how biodiversity

785 and complex ecosystems emerge from ecological and evolutionary processes. The project,

786 funded by the National Science Foundation's "Dimensions in Biodiversity", focuses on the

787 geological chronosequence provided by the Hawaiian Islands. ~~Each of the co-authors are~~

788 ~~involved in the effort, although Rominger, working closely with Goodman, Lim, and~~

789 ~~Valdavinos, played the key role in tying the elements together for the current manuscript.~~

790 ~~Macroecological tools that have been employed for the study include those developed by~~

791 ~~Harte and Martinez. From the more empirical side, Gruner has long standing projects in the~~

792 ~~Hawaiian Islands on the ecological underpinnings of community diversity. Rominger, Lim~~

793 ~~and Fernandez bring a macroecological perspective to the project. From the evolutionary~~

794 ~~perspective, Shaw's research focuses on *Laupala* crickets; Ewing on nitidulid beetles,~~

795 ~~Goodman and Roderick on Hawaiian planthoppers; Percy on endemic psyllids; O'Grady and~~

796 ~~Price on Hawaiian *Drosophila*; and Cotoras with Gillespie on spiders.~~

FIGURE CAPTIONS

Figure 1. Substrate age map of the islands of Kauai, Maui and Hawaii Island. Colors correspond to substrate age from young (yellow) to old (blue). Focal sites are shown as black circles while sampling sites for genetic data are represented by gray circles.

Figure 2. Genetic population structure (F_{ST}) among sites within volcanoes with volcano age for insects and spiders. The plant-feeding groups, specifically the sap-feeding Hemiptera, show high genetic structure among sites on young volcanoes relative to older volcanoes whereas detritivores (crickets), fungivores (*Drosophila*), and in particular predators (spiders), show little structure on young volcanoes. For spiders, substantial structure develops only later in the chronosequence, e.g., on Maui at approximately 1 million years. Numbers refer to different species: 1. *Nesosydne chambersi*, 2. *Nesosydne raillardiae*, 3. *Nesosydne bridwelli*, 4. *Trioza HB*, 5. *Trioza HC*, 6. *Drosophila sproati*, 7. *Laupala cerasina*, 8. *Tetragnatha anuenue*, 9. *Tetragnatha brevignatha*, 10. *Tetragnatha quasimodo*, 11. *Theridion grallator*.

Figure 3.

Figure 3. Trends in network metric nestedness and modularity through time. Nestedness decreases while modularity increases. Error bars come from a null model simulation. While the sign of the z-score depends on null model and method of calculating modules (see supplemental figure) the 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

819 ~~convergence in traits of plants and herbivores. Note the very interesting peaks on Maui~~

820 ~~where adaptive diversification may be at its maximum.~~

821 ~~Figure 4.~~ Patterns in degree distributions (distribution of number of links assigned to each

822 herbivore) across sites and different biogeographic classifications of taxa. Top panels show

823 that networks deviate most from MaxEnt on youngest and oldest sites. Inset figures show

824 the distribution of simulated mean squared errors; if the red line falls within the gray

825 region (95% confidence interval) the data conform to maximum entropy; thus the

826 observed minor deviation on Kohala is not different than expected by chance. Kohala

827 shows minimal modularity, and maximal connectance. The bottom panel shows the

828 number of links for island endemics versus island cosmopolitans. Endemics show lower

829 linkage overall, but significantly increase on the middle aged site Maui (highlighted with

830 dotted box). Kohala shows increased linkage overall (highlighted with solid box). When

831 looking at links to plant genera this pattern holds except that endemics on Maui no long

832 show a difference in generality, indicating that the pattern is driven in part by plant

833 diversity.

834

835 **Figure 4.** Trends in network metric nestedness and modularity through time. Nestedness

836 decreases while modularity increases. Error bars represent 95% confidence intervals~~come~~

837 ~~from a null model simulation.~~ While the sign of the z-score depends on null model and

838 method of calculating modules (see supplemental figure) the overall trend is robust. Some

839 level of nestedness is likely a statistical property of these networks, however it could also

840 be driven by stabilizing ecological mechanisms. Modularity is thought to be a sign of

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841   coevolution driving convergence in traits of plants and herbivores. Note the very

842   interesting peaks on Maui where adaptive diversification may be at its maximum.

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969   Additional references to the data sources may be found in Appendix S1 at [URL].

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