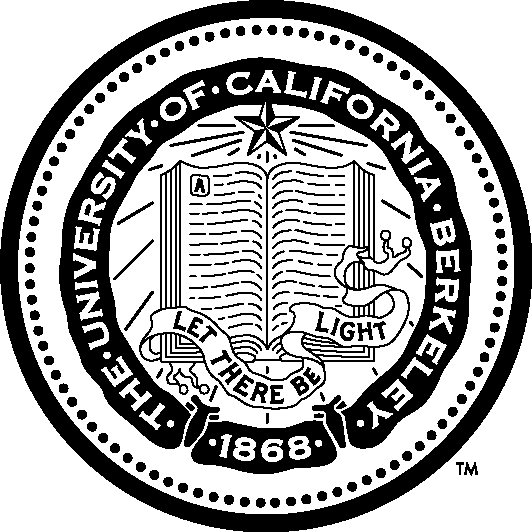
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April 7th 2015

Dear Editors and Reviewers,

Thank you for taking the time to review and comment on this manuscript, we appreciate your thorough efforts. We believe this review process has greatly enhanced and clarified our contribution and will increase its impact in *Global Ecology and Biogeography*. Below we have listed your comments followed by our response, indicated by a bullet. We hope you find our edits have improved the manuscript to your satisfaction and look forward to your comments.

Best wishes,

Rosemary Gillespie

EDITOR-IN-CHIEF'S COMMENTS TO AUTHORS  
  
l. 49 -- What does "develop local divergence" mean?

* This has been changed to “population genetic structure”

Abstract, Main Conclusions -- These are not conclusions; they are distressingly vague feel-good statements.  What does "leverage" mean in operational terms?   How do you know that you understand?  Why tell the reader what you can conclude, and let him/her decide whether this "illuminates" something.   Was it uncertain before this study that "the interplay of ecological mechanisms, speciation, extinction and adaptation in driv[es] contemporary biodiversity patterns"?  The Main conclusions should be citable; these are not.

* We completely rewrote this section to be more “citable” (L66-84).

The legend on the table seems to have gone missing.

* The table legend is included.

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EDITOR'S COMMENTS TO AUTHORS  
Editor: Ricklefs, Robert  
Comments to the Author:  
Editor comments on revised manuscript (R.E. Ricklefs)  
  
Line 9, presumably the asterisk refers to equal contributions.

* That is correct, the asterisk was cut off accidentally in the last submission and has been corrected.

Line 69, what is the meaning of ‘unresolved’ in this context?

* We removed this word from the sentence, it was unnecessary to our argument.

Line 71, you might leave out “and may be non-linear and non-equilibrium”.

* We removed this phrase.

Lines 76-85, this paragraph expresses some truths, but it is unclear how these are related to the phenomena addressed in this manuscript. It might be more useful to start right out by saying that archipelagoes with islands of different size and age enable us to sort out the effects on diversity of processes operating on different temporal and spatial scales.

* We have re-written this to read: “Islands of different ages of formation, along with discrete volcanoes within islands, provide the opportunity to study diversification of species and the assembly of communities in different stages.“ (L113-115).

Line 88, “harnesses”

* Corrected.

Line 99, is it that archipelagoes are discrete, or that they offer a range of temporal and spatial scales over which to observe outcomes of ecological and evolutionary processes?

* Your point is accurate and well taken. We changed the phrasing (L121-123).

Line 107, differential dispersal abilities of organisms to a newly formed island might also reflect properties of organisms that are inherent to larger taxa in a larger geographic context, i.e., flying organisms disperse more readily between islands than nonvolant organisms. Likely, the biota that initially colonizes an island might reflect that of the source area, but evolution within the source area likely does not include adaptation for dispersal, and the initial colonists will reflect dispersal abilities as much as competitive outcomes in the source pool.

* We agree that the unique conditions of islands make them conducive to novel selective pressures. Some of the Hawaiian biota initially colonized and diversified on ancient islands now part of the “Northwest Hawaiian” chain.

Line 123, “populations”

* Corrected.

Lines 123-125, I’m not sure what you are saying here, that communities with gene flow cut off are not influenced by ecological processes, but only evolutionary processes?

* We re-wrote this section to better articulate our motivation for using population genetic data. Our goal is to evaluate the role of dispersal and immigration (with a population genetic signature of little to no structure) in driving community composition versus the role of local adaptation and potential for *in situ* diversification (with population genetic signature of high structure). (L 135-154)

Line 126, you haven’t outlined an ‘approach’ yet.

* Reworded to better articulate our project framework (L189-191).

Line 131, theory itself is not a single thing; also, deviations from theory permit rejection of mechanisms, but do not reveal alternatives.

* We changed the wording to acknowledge that there are multiple theories making macroecological predictions, and that deviations from theoretical expectations whilst unable to reveal mechanism per se, can still indicate whether more biologically realistic processes are necessary to describe the observed patterns. (L154-173)

Lines 129 ff., I find this description of METE very unsatisfying, as there isn’t a clear indication of the character of the ‘idealized’ ecological community, or the particular deviations one will obtain from particular ecological or evolutionary mechanisms. Readers not familiar with METE will not develop an intuitive feeling for its relevance to the issues addressed in this paper.

* Thank you for this comment. We significantly restructured the discussion of METE to better motivated its use and explain its interpretation. (L153-172)

Lines 203-206, of what relevance are the data from outside the focal sites to genetic properties within focal sites? This sentence is confusing.

* We regret the confusion but appreciate the opportunity to clarify. The taxa we studied are known from the focal sites, but because we are using previously collected data, the samples used in this analysis were not necessarily collected within the focal sites. The results are still relevant because in this analysis we are concerned with the relative scale of genetic differentiation. We have removed the phrase “including, but not limited to the focal sites” to reduce confusion.

Lines 207-209, are these sites restricted to focal sites, or are sites outside the focal sites included?

* The samples used for the population genetic analysis are not necessarily restricted to focal sites – we have clarified this in the text:

“Samples were from the focal sites described below for the ecological analysis as well as from other locations across Hawaii Island and Maui. These data were used to provide an estimate of how arthropod populations have accumulated genetic population structure within the focal sites of different geological age.” (L214-217)

Lines 218-221, does this assume that population age parallels volcano age? What about relating Fst to the age of the populations themselves?

* Yes, we assume this by proxy - it assumes that volcano age parallels habitat age, allowing more or less time for the presence of the populations. We would prefer to relate Fst to the age of the populations but we don't have those data for most of the populations in hand. (L231-232)

Line 243, any idea about how good the distribution models are for predicting presence or absence of a plant species at a particular site?

* The distribution models were prepared with (presence only) museum records and the best available environmental variables. They are meant for generating expected plant lists and facilitating field surveys, but their predictive power has not been tested systematically.

Line 252, what are the underlying assumptions of the predictions from METE? That is, what is the null hypothesis, and what would deviations from the null distributions actually mean?

* Our discussion of METE has been greatly changed to clarify this. (L153-172, 389-411)

Lines 262-266, in situ diversification implies (to me) more than one species within one area; also, how are cosmopolitans different on individual islands from island endemics?

* We have clarified this language to now refer to single island endemics and multi-island endemics.

Line 301, replace ‘repeated colonization events’ with ‘colonization from multiple, isolated areas’.

* Thank you, we replaced the original text with your suggestion.

Line 307, make ‘among’ and ‘between’ parallel, i.e., use one or the other, preferably among if more than two sites.

* We replaced ‘between’ with ‘among’ for consistency.

Line 324 ff., this paragraph describes relationships that do not appear to test particular predictions from theoretical considerations, and which seem to show contrasting patterns. Suggesting explanations, as in lines 334-5, doesn’t help to sort out the processes that are producing these patterns, but come across as a post hoc attempt to make sense out of complicated results.

* Thank you for this insight. Our revision includes better articulated motivation for why we consider single island endemics and multi island endemics separately. The goal was to generate multiple possible angles from which to examine what evolutionary or ecological mechanisms drive observed network patterns and deviations from maximum entropy predictions. (L274-280)

Line 336, The relationships shown in Figure 4 also are not particularly convincing, except that there are differences between islands. It is also not clear why the age axis is log transformed. What is the interpretation of the logarithm of time (this would apply to other figures, as well)?

* We greatly restructured the discussion to focus less on interpreting our results as definitive answers about network evolution on islands and more as the exploration of existing data to demonstrate how or why island chronosequences can be useful for addressing questions in evolutionary ecology. The age axis is log-transformed simply to visualize a long age gradient spanning 4 orders of magnitude on a single axis, with more sampling toward the younger limits. This is now explained in the figure legend.

Line 346, what is meant by ‘evolution begins to keep pace with ecology’?

* In our revision, we removed this section entirely.

Line 348, Figure 2 doesn’t seem to show any particular change in Fst with increasing age for a particular type of arthropod, nor is any information cited on ecological divergence.

* In this figure, we attempt to show 1) that the herbivores show higher genetic structure among sites on young volcanoes, relative to older volcanoes, whereas 2) predatory spiders show higher genetic structure on older volcanoes relative to younger volcanoes. This figure is not meant to depict ecological divergence.

Line 348, Figure 2: In addition, the statement that nestedness and modularity change with age is based on 4 points, which is not sufficient to describe a trend. About all that can be said is that Kaui has different nestedness than the other islands, and that the Maui and Kauai samples are different in modularity than the samples from Hawaii. It is hard to see how a temporal story can be constructed from this, particularly without including more information on the particular environments on each of the islands.

* Our analysis is preliminary and intended to provide an initial test and proof of concept for a synthesis of evolutionary and ecological mechanisms in long-term community assembly. Following the advice of our editors and reviewers, we greatly re-shaped the structure of our manuscript (particularly the discussion) to focus more on how our preliminary analysis helps to guide hypothesis generation, validate the utility of combining ecological theory with evolutionary biology on remote islands, and identify necessary data to successfully test hypotheses.

Line 354, to what extent is the relationship between degree and endemism due to broader within-island distribution of cosmopolitan species?

* Good point. We argue in part that because cosmopolitans are more generalist that single-island endemics (due to in situ diversification) may indicate coevolution with host plants. (L426-441)

Line 368, implication is not the same as demonstration; to what degree have any of these mechanisms actually been demonstrated? Also, is there any evidence (line 366) that different subpopulations are differentiating ecologically?

* Another good point; we changed ‘implicated’ to ‘associated with’ (L362). There is evidence that signaling has differentiated among populations (see the citations listed). Also, in the planthopper species under study for the larger project, we see evidence for differentiation in host use between the Kohalas and the rest of the Big Island.

Lines 428-430, is it also possible that generalization leads to cosmopolitan distributions through increasing population sizes and density-driven dispersal?

* While it is possible that generalists have a far wider range of possible hosts and hence are less constrained by the geographic distribution of a small number of compatible host species, large dietary breadth may also result from local adaptation for the exploitation of locally abundant hosts within a wide-ranging species. We have included a statement that our study does not disentangle the direction of causality. (L426-428)

Line 448, are you implying that probability of dispersal and colonization is a random draw from a source pool? This seems very unlikely.

* Here we propose that immigration of generalists early on, followed by *in situ* diversification of specialists, would be consistent with the observed pattern. Generalists, due to their high abundance alone, seem likely to be initial colonists (L451-453).

Line 456, is prediction (c) borne out by the data assembled in this study?

* We clarified that this prediction comes both from the primary literature (citations are more prominent in the text) and it is motivated by our finding that more widespread (and thus likely dispersal-prone) species are also generalists (L451-453).

Line 460 ff, this seems like a very weak prediction because it depends on an unknown pattern of processes playing out in a particular way. How would the prediction be rejected without knowing about the rate of ‘exploration, adaptation, and speciation’?

* This prediction indeed hinged on the ability to estimate macroevolutionary rates. If such rates could be modeled and measured (work which is underway) then testing this hypothesis could prove exceptionally interesting. To provide more realistic discussion we have re-focused our prediction to not depend on currently unquantifiable rates (L454-458).

Prof. Robert Ricklefs, Editor  
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REVIEWER COMMENTS TO AUTHORS  
  
Referee: 1  
  
Comments to the Author  
Papers that study and use, multiple scales, multiple types of data and multiple analytical approaches are certainly a significant step forward to improving our understanding of biodiversity patterns and the underlying mechanisms. The present work has all the above and it has the potential to be a significant contribution to the field. My understanding is that the authors have significantly improved the ms, addressing many of the issues raised in the first round of review.

However, I personally believe that it is far from publication standards, mainly because there is a lack of clarity in terms of the actual aims of this work-it appears to be a discontinuity between the results of the different analyses and their complementarity; thus a clear take home message is lacking. Having highlighted the importance of the work carried out, I personally believe that it could be presented as an Research Review paper, putting forward the hypotheses presented in 'future research' upfront and then looking for supporting evidence from the Hawaiian data in hand but from other oceanic archipelagos too, if available.

* We appreciate the positive comments and constructive criticisms from the referee. We acknowledge these problems in our prior manuscript, and we believe the current submission is far more effective in using our synthesis of genetic and ecological network data from the Hawaiian Islands to guide hypothesis generation, validate the utility of combining ecological theory with evolutionary biology on remote islands, and identify necessary data to successfully test hypotheses we propose. The suggestion to synthesize data of similar structure from other oceanic archipelagoes in a review is a compelling idea for future work. However, that objective this lies well beyond the scope of the current paper, which relies heavily on our intimate knowledge of the Hawaiian system as a prototypical case study.

**Comments from the attached pdf:**

Pg 5, line 76: considering extinction to act only at the evolutionary level, is half of the story. Extinction plays a role at the local level too.

* This is a good point and an interesting hypothesis to be tested with more detailed data. We now include discussion of how local extinction could drive our observed patterns. (L411-412)

Pg 5, line 88: Change the order of the references according to year of publication.

* The order has been changed for all citations as directed.

Pg 6, line 92-93: a short description of genetic discontinuity would be helpful for the reader.

* We changed ‘discontinuity’ to ‘structure’.

Pg 6, line 94-95: Unfortunately the aims of the paper remain unclear. An issue raised by the reviewers and handling editor in the first round of review. I am not persuaded that the issue has been addressed adequately. I dont support that certain hypotheses should be presented in the first place, but a more specific aim should be put forward.

* We regret our revisions were not satisfactory. As noted in responses to the editor and referee #1 above, we greatly restructured the abstract and introduction to be more specific and clear about our objectives, findings, and hypotheses proposed.

Pg 6, line 106-108: I suggest re-phrasing this part. You practically compare communities with islands-which is problematic. Young communities can be found on old islands too and not just on young islands, for various reasons. Thus, the direct connection of young communities with young islands only, can be misleading.

* We have removed this wording.

Pg. 7, line 120: Please clarify to what exactly 'structure' refers to. Is it at the species level, functional or phylogenetic level? The reference to the trophic level at the end of the paragraph provides a hint but it is incomplete. Please elaborate further.

* We rewrote this paragraph in an attempt to clarify this ambiguity.

Pg 8, line 146-147: arrange references chronologically.

* As above, corrected in all instances.

Pg 8, line 155-157: This paragraph seems to be misplaced. It practically repeats things already presented. At the same time the patterns and processes evaluated further below seem to be unconnected with the text above. I suggest that the authors try to re-structure the ms so as the aims are more clearly presented from the beginning.

* The MS has been restructured to make the aims more clear: “To gain insights into community assembly as it happens, we propose an integrative framework that harnesses advances in both evolutionary and ecological theory, placed in the context of age-structured archipelagos. Mechanistically simplified ecological theories such as METE (Harte, 2011) can be used as powerful null models; deviations from expectations of the theories can flag biological phenomena warranting further study. Here we demonstrate how community-level data from age-structured island systems, combined with population genetic and phylogenetic data, can test the extent to which the evolutionary histories behind such communities drive their deviation from theoretical expectations. We provide an initial test of this concept using a synthesis of published data on arthropod lineages in the Hawaiian Islands.” (L188-196)

Pg. 9, line 177: re-arrange references chronologically

* Corrected.

Pg. 10, line 183: which was the area of each of these sites ?

* The area of each site was approximately about 12 km2 (each was defined as a point with a 2km radius buffer). (L236)

Pg. 10, line 191: How many locations were considered overall? Are these locations similar in terms of vegetation structure?

* For this analysis, we were restricted to using available data, and we used all available population data we could find. Thus, not all collections were made at sites with the same vegetation structure. We believe the analysis is still informative because it establishes the relative spatial scale of observed population genetic structure within each taxon. We do not attempt to correlate that population genetic structure to forest structure.

Pg. 12, line 229: do you mean archipelagic endemic?

* Yes, that is correct. We clarified this in the text. (L245)

Pg. 13, line 252: full-stop is missing.

* Corrected.

Pg. 13, line 264-266: Although single island endemics species are often used in island studies to describe, crudely, evolutionary dynamics, there are a number of pitfalls to be considered (see Whittaker, R.J., Triantis, K.A. & Ladle, R.J. (2008) A general dynamic theory of oceanic island biogeography. Journal of Biogeography, 35, 977–994.

* Thank you for this insight. There are valid issues with crude metrics such as single island endemics. Notably, such species may be the result of range contraction of a previously widespread species, or they may be future multiple island endemics that have yet to disperse. We now make note of these caveats and argue, for the sake of exploring data to generate hypotheses, that such a rudimentary method must suffice given incomplete phylogenetic data and the fact that the most cutting edge efforts to understand range dynamics on islands using phylogenies are still under development

Pg. 13, line 266: would suggest to use the term 'multiple islands species' instead of cosmopolitan.

* We agree that our original terminology was confusing. We changed the phrasing as suggested in the text and figures.

Pg. 14, line 272: This definition of nestedness is not in concordance with the usage of the term is island theory, as the authors are aware of. It would be useful to just refer to the different context of the term.

* We clarified this section to reflect the distinction as suggested (L177-179).

Pg. 16, line 324-328: I guess you mean single island endemics here. Based on the description of the data above, all the species considered are endemic to the archipelago and the major distinction is between SIE and multi-island endemics.

* As indicated above, we addressed this with changes in the text and figures.

Pg. 17, line 333: longer? (typo of long):

* Corrected.

Pg. 17, line 334-335: The discussion of the plant-herbivore networks doesn't take into account the possible effects of (local) species extinctions, especially in the older islands. For older islands a higher rate of extinction can be inferred for various reasons and this could affect the structure of the networks.

* This is a very good point. We now include in our discussion the hypothesis that the higher rate of extinction on older islands may be causing the observed deviations from our theoretical macroecological predictions of network structure. (L410-411)

Pg. 17: Discussion: Reading through the text, I feel that the ms would be ideal to be presented as a review and synthesis article but with the addition of similar data and analyses from other oceanic archipelagos. I understand that this would require additional effort but at the same time in its current form there is some discontinuity between the different parts of the ms and a clear take home message. Putting forward the hypotheses presented in 'future research' upfront and then looking for supporting evidence from the Hawaiian data in hand but from other archipelagos too, seems to me the best way to structure the paper.

* We agree this is an excellent idea for future work. However, we are unaware of other age-structured island archipelagos with the same resolution of data available at all levels of analysis. Hawaii is exceptionally well-studied due to efforts of early biologists and the Hawaiian Biological Survey. Yet this may be a viable research path in collaboration with biologists working with other island groups in the future.

Referee: 2  
  
Comments to the Author  
I carefully studied the new version of this manuscript. I recognize the effort the authors made to improve the manuscript. Having said that, I still thinking there are deep problems with the main elements of the manuscript.   
  
First, I still missed a clear link with the literature of ecology and evolution of species interactions. For example, the relationship between generalization and larger geographic distributions is a pattern previously described in plant-herbivore systems (see the work by Lewinsohn, Novotny and others). Accordingly, as I mentioned before, the study by Suweiss showed that optimization at population level (a way of modeling density-dependet natural selection) lead to nestedness. Thus, nestedness is also an potential evolutionary outcome

* We have incorporated a more detailed discussion of the proposed causes and consequences of the topological properties of trophic network, as well as a discussion of the literature on dietary breadth and geographic range.

Second, although the authors improved the motivation for using METE, the manuscript still hermetic. There is no clear explanation for the predictions derived from METE. The underlying reasoning, the assumptions, the logical steps for generate the predictions are missed. To state that prediction is derived from the notion of a statistical steady state is not enough.

* This is a point well taken, please see our response to similar concerns raised by Prof. Ricklefs.

Third, and more importantly, I have strong reservations to the network analysis. My main concern about the previous draft was that “it is impossible to verify in the current draft the quality of the data used to build up the ecological networks”.  In this new draft the authors clarify how they build up the networks. Unfortunately, my concerns were corroborated. The authors discuss and deal with the networks as if they are empirical networks, however these are theoretical networks. Networks derived from the combination of models of spatial distribution of host plants, potential (or empirical) distributions of herbivores and previous, non-local feeding information of herbivores. Thus, this is an exercise of potential networks and how they change due to the potential assembly of plants and herbivores and not a study of how empirical networks evolve across time. Therefore, I am afraid that the reasoning behind the claim this paper provides empirical evidence for how networks evolve cannot be supported.

* Thanks to the feedback of our editors and reviewers, we have shifted the message of our manuscript away from a formal and final test of predictions about eco-evolutionary patterns across the age gradient to instead explore possible patterns and hypothesized mechanisms. We thus use our analysis to help focus this exploration but make no pretense that the analysis is final, nor complete, nor based on an ideal dataset. Indeed we propose what more ideal data would look like. The current analysis is based on modeled plant distributions and literature review for arthropod localities and host use. However, because herbivores are quite localized and, in the case of Hawaiian hemipterans, their dietary preferences are not known to be no more specific than at the level of plant genus, our links are likely robust. We included analyses based on strict empirical insect distributions (presented in the main text) and also based on interpolated insect distributions (presented in the supplement). Our results hold for both analysis and we will make data available through Dryad (<http://datadryad.org/>) or other similar archive with the final manuscript.