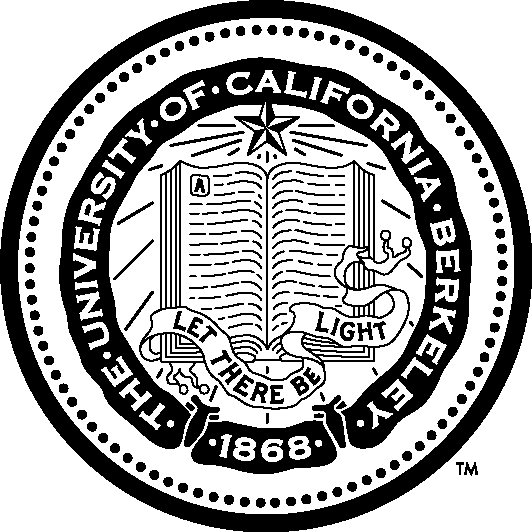
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April 7th 2015

Dear Editors and Reviewers,

Thank you for taking the time to review and comment on this manuscript, we really appreciate your thorough efforts. 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 have completely rewritten this section to more citable.

The legend on the table seems to have gone missing.

* The table legend has been 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 accidentally cut off in the last submission and has been corrected.

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

* We have removed this word from the sentence. We meant how these factors interact is an unresolved problem, but its use was unnecessary.

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

* We have 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.

* Well said. This phrasing has been incorporated into the third paragraph.

Line 88, “harnesses”

* This has been 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?

* That is more accurate and we have changed the phrasing.

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 produce novel selective pressures. Some of the Hawaiian biota initially colonized and diversified on ancient islands now part of the “Northwest Hawaiian” chain. We have highlighted this in our section on **Hawaii as an eco-evolutionary study system** in the methods section.

Line 123, “populations”

* This has been 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?

* This section has been re-written 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).

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

* This has been reworded.

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

* The wording has been changed to acknowledge that there are multiple theories for biodiversity, 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.

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.

* We have greatly restructured the discussion of METE to better motivated its use and explain its interpretation.

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

* The taxa that are studied are found within the focal sites, but because we are using existing 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?

* They are not necessarily– we have clarified this in the text:

“Because these are existing data, the samples used in this analysis were not necessarily collected within the focal sites described above for the ecological analysis. They were collected from across Hawaii Island and Maui and are used here to provide an estimate of how arthropod populations have accumulated genetic diversity and divergence within the dynamic landscape of the focal sites.”

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

* Yes, by proxy - it assumes that volcano age parallels habitat age, allowing more or less time for the presence of the populations. We would love to relate Fst to the age of the populations but don't have that information for most of the populations in hand.

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 we do not believe their predictive power has been tested.

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.

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’.

* The original text has been replaced by your suggestion.

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

* We have 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.

* We have included better motivation of why we consider single island endemics and multi island endemics separately. The goal is to generate multiple possible angles from which to examine what evolutionary or ecological mechanisms drive observed network patterns and deviations from maximum entropy predictions.

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 have 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 that can be used to demonstrate why island chronosequences can be useful for addressing questions in evolutionary ecology. The age axis is log transformed simply for the sake of visualizing a long age gradient (with more sampling toward the young end) on a single axis. This has been explained in the figure legend.

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

* In our revision this section has been removed 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.

* What we are trying to show in this figure is that the herbivores, show higher genetic structure among sites on young volcanoes relative to older volcanoes whereas predators 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 very preliminary and following the sound advice of our editors and reviewers we have greatly re-shaped the structure of our manuscript (particularly the discussion) to focus more on how our preliminary analysis helps guide hypothesis generation, helps validates the utility of combining ecological theory with evolutionary biology on remote islands, and helps 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) represent coevolution

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?

* ‘Implicated’ has been changed to ‘associated with’. There is evidence that signaling has differentiated among populations (see the citations listed). Also, in the species of planthopper being studied for the larger project, we do see 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 be due to 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.

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 are proposing 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.

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

* We have clarified that this prediction comes both from the primary literature (citation has been made more prominent in text) and is motivated by our finding that more widespread and thus likely dispersal prone species are also generalists.

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 hinges on being able to estimate macroevolutionary rates. If such rates could be modeled and measured (work which is underway) then testing this hypothesis could prove exceptionally interesting. We have acknowledged the methodological needs of testing this hypothesis.

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.

**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. We now include discussion of how local extinction could drive our observed patterns, an interesting hypothesis to be tested with more nuanced data.

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

* The order has been changed.

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

* We have 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 have greatly restructured the abstract and introduction to be more specific and clear.

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 attempt to clarify these issues with the following revised text (L# XXX): “The youngest communities in primary succession must first colonize via immigration, and we expect their assembly over time will depend on progressive development of ecosystem productivity and vegetative community composition in a young landscape (Gruner 2007). Therefore we expect classical species interactions and assembly mechanisms should operate from a source pool whose evolution is of secondary importance to the local context. Conversely, older landscapes and islands bear the signature of many such iterations, with higher diversity of plants and associated insects that may facilitate feedbacks of diversification and local ecological dynamics.”

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.

* This paragraph has been rewritten in an attempt to clarify this.

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

* These have been rearranged.

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 restructures.

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

* These have been rearranged.

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

* An area of about 12 km (each was a point with a 2km radius buffer around it)

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. It is still informative because all it seeks to do is establish the relative spatial scale that we observe genetic structure within each taxa. We are not trying to correlate that structure to the forest structure.

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

* Yes, that is correct. We have made it clearer in the text

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

* It has been inserted.

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.

* There are of course valid issues with such a crude metric as single island endemics, notably the fact that 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 this and argue that for the sake of exploring data to generate hypotheses such a rudimentary method will have to suffice given incomplete phylogenetic data and the fact that the most cutting edge efforts to understand range dynamics on island using phylogenies are still under development (e.g. the work of Luise Valente and Rampal Ettiene).

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

* We agree that our original terminology may be confusing and have changed out phrasing in the text and labels in our 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.

* This section has been clarified to reflect the distinction.

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.

* This has been addressed (see above).

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

* Thanks for pointing this out, it has been 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.

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.

* This is a neat idea and would be super interesting, we agree. However, there are no other archipelagos with the same type of data available. Hawaii is exceptionally well-studied due to efforts of early biologists and the Hawaiian Biological Survey.

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. However, because herbivores are quite localized and their dietary preferences are never 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.