Peer Community In Ecology

Toward an empirical synthesis on the niche versus stochastic debate

Eric Harvey *based on peer reviews by* ***Kevin Cazelles*** *and* ***Romain Bertrand***

Tadeu Siqueira, Victor S. Saito, Luis M. Bini, Adriano S. Melo, Danielle K. Petsch, Victor L. Landeiro, Kimmo T. Tolonen, Jenny Jyrkänkallio-Mikkola, Janne Soininen, Jani Heino (2019) Community size affects the signals of ecological drift and selection on biodiversity. Missing preprint_server, ver. Missing article_version, peer-reviewed and recommended by Peer Community in Ecology. https://doi.org/10.1101/515098

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As far back as Clements [1] and Gleason [2], the historical schism between deterministic and stochastic perspectives has divided ecologists. Deterministic theories tend to emphasize niche-based processes such as environmental filtering and species interactions as the main drivers of species distribution in nature, while stochastic theories mainly focus on chance colonization, random extinctions and ecological drift [3]. Although the old days when ecologists were fighting fiercely over null models and their adequacy to capture niche-based processes is over [4], the ghost of that debate between deterministic and stochastic perspectives came back to haunt ecologists in the form of the 'environment versus space' debate with the development of metacommunity theory [5]. While interest in that question led to meaningful syntheses of metacommunity dynamics in natural systems [6], it also illustrated how context-dependant the answer was [7]. One of the next frontiers in metacommunity ecology is to identify the underlying drivers of this observed context-dependency in the relative importance of ecological processus [7, 8]. Reflecting on seminal work by Robert MacArthur emphasizing different processes at different spatial scales [9, 10] (the so-called 'MacArthur paradox'), Chase and Myers proposed in 2011 that a key in solving the deterministic versus stochastic debate was probably to turn our attention to how the relative importance of local processes changes across spatial scales [3]. Scale-dependance is a well-acknowledged challenge in ecology, hampering empirical syntheses and comparisons between studies [11-14]. Embracing the scale-dependance of ecological processes would not only lead to stronger syntheses and consolidation of current knowledge, it could also help resolve many current debates or apparent contradictions [11, 15, 16]. The timely study by Siqueira et al. [17] fits well within this historical context by exploring the relative importance of ecological drift and selection across a gradient of community size (number of individuals in a given community). More specifically, they tested the hypothesis that small communities are

more dissimilar among each other because of ecological drift compared to large communities, which are mainly structured by niche selection [17]. That smaller populations or communities should be more affected by drift is a mathematical given [18], but the main questions are i) for a given community size how important is ecological drift relative to other processes, and ii) how small does a community have to be before random assembly dominates? The authors answer these questions using an extensive stream dataset with a community size gradient sampled from 200 streams in two climatic regions (Brazil and Finland). Combining linear models with recent null model approaches to measure deviations from random expectations [19], they show that, as expected based on theory and recent experimental work, smaller communities tend to have higher β-diversity, and that those β-diversity patterns could not be distinguished from random assembly processes [17]. Spatial turnover among larger communities is mainly driven by niche-based processes related to species sorting or dispersal dynamics [17]. Given the current environmental context, with many anthropogenic perturbations leading to reduced community size, it is legitimate to wonder, as the authors do, whether we are moving toward a more stochastic and thus less predictable world with obvious implications for the conservation of biodiversity [17]. The real strength of the study by Siqueira et al. [17], in my opinion, is in the inclusion of stream data from boreal and tropical regions. Interestingly and most importantly, the largest communities in the tropical streams are as large as the smallest communities in the boreal streams. This is where the study should really have us reflect on the notions of context-dependency in observed patterns because the negative relationship between community size and β-diversity was only observed in the tropical streams, but not in the boreal streams [17]. This interesting nonlinearity in the response means that a study that would have investigated the drift versus niche-based question only in Finland would have found very different results from the same study in Brazil. Only by integrating such a large scale gradient of community sizes together could the authors show the actual shape of the relationship, which is the first step toward building a comprehensive synthesis on a debate that has challenged ecologists for almost a century.

References:

[1] Clements, F. E. (1936). Nature and structure of the climax. Journal of ecology, 24(1), 252-284. doi: [10.2307/2256278](https://dx.doi.org/10.2307/2256278)

[2] Gleason, H. A. (1917). The structure and development of the plant association. Bulletin of the Torrey Botanical Club, 44(10), 463-481. doi: [10.2307/2479596](https://dx.doi.org/10.2307/2479596)

[3] Chase, J. M., and Myers, J. A. (2011). Disentangling the importance of ecological niches from stochastic processes across scales. Philosophical transactions of the Royal Society B: Biological sciences, 366(1576), 2351-2363. doi: [10.1098/rstb.2011.0063](https://dx.doi.org/10.1098/rstb.2011.0063)

[4] Diamond, J. M., and Gilpin, M. E. (1982). Examination of the "null" model of Connor and Simberloff for species co-occurrences on islands. Oecologia, 52(1), 64-74. doi: [10.1007/BF00349013](https://dx.doi.org/10.1007/BF00349013)

[5] Leibold M. A., et al. (2004). The metacommunity concept: a framework for multi-scale community ecology. Ecology letters, 7(7), 601-613. doi: [10.1111/j.1461-0248.2004.00608.x](https://dx.doi.org/10.1111/j.1461-0248.2004.00608.x)

[6] Cottenie, K. (2005). Integrating environmental and spatial processes in ecological community dynamics. Ecology letters, 8(11), 1175-1182. doi: [10.1111/j.1461-0248.2005.00820.x](https://dx.doi.org/10.1111/j.1461-0248.2005.00820.x)

[7] Leibold, M. A. and Chase, J. M. (2018). Metacommunity Ecology. Monographs in Population Biology, vol. 59. Princeton University Press.

[8] Vellend, M. (2010). Conceptual synthesis in community ecology. The Quarterly review of biology, 85(2), 183-206. doi: [10.1086/652373](https://dx.doi.org/10.1086/652373)

[9] MacArthur, R. H., and Wilson, E. O. (1963). An equilibrium theory of insular zoogeography. Evolution, 17(4), 373-387. doi: [10.1111/j.1558-5646.1963.tb03295.x](https://dx.doi.org/10.1111/j.1558-5646.1963.tb03295.x)

[10] MacArthur, R. H., and Levins, R. (1967). The limiting similarity, convergence, and divergence of coexisting species. The American Naturalist, 101(921), 377-385. doi: [10.1086/282505](https://dx.doi.org/10.1086/282505)

[11] Viana, D. S., and Chase, J. M. (2019). Spatial scale modulates the inference of metacommunity assembly processes. Ecology, 100(2), e02576. doi: [10.1002/ecy.2576](https://dx.doi.org/10.1002/ecy.2576)

[12] Chave, J. (2013). The problem of pattern and scale in ecology: what have we learned in 20 years?. Ecology letters, 16, 4-16. doi: [10.1111/ele.12048](https://dx.doi.org/10.1111/ele.12048)

[13] Patrick, C. J., and Yuan, L. L. (2019). The challenges that spatial context present for synthesizing community ecology across scales. Oikos, 128(3), 297-308. doi: [10.1111/oik.05802](https://dx.doi.org/10.1111/oik.05802)

[14] Chase, J. M., and Knight, T. M. (2013). Scale-dependent effect sizes of ecological drivers on biodiversity: why standardised sampling is not enough. Ecology letters, 16, 17-26. doi: [10.1111/ele.12112](https://dx.doi.org/10.1111/ele.12112)

[15] Horváth, Z., Ptacnik, R., Vad, C. F., and Chase, J. M. (2019). Habitat loss over six decades accelerates regional and local biodiversity loss via changing landscape connectance. Ecology letters, 22(6), 1019-1027. doi: [10.1111/ele.13260](https://dx.doi.org/10.1111/ele.13260)

[16] Chase, J. M, Gooriah, L., May, F., Ryberg, W. A, Schuler, M. S, Craven, D., and Knight, T. M. (2019). A framework for disentangling ecological mechanisms underlying the island species–area relationship. Frontiers of Biogeography, 11(1). doi: [10.21425/F5FBG40844.](https://dx.doi.org/10.21425/F5FBG40844.)

[17] Siqueira T., Saito V. S., Bini L. M., Melo A. S., Petsch D. K. , Landeiro V. L., Tolonen K. T., Jyrkänkallio-Mikkola J., Soininen J. and Heino J. (2019). Community size affects the signals of ecological drift and niche selection on biodiversity. bioRxiv 515098, ver. 4 peer-reviewed and recommended by PCI Ecology. doi: [10.1101/515098](https://dx.doi.org/10.1101/515098)

[18] Hastings A., Gross L. J. eds. (2012). Encyclopedia of theoretical ecology (University of California Press, Berkeley).

[19] Chase, J. M., Kraft, N. J., Smith, K. G., Vellend, M., and Inouye, B. D. (2011). Using null models to disentangle variation in community dissimilarity from variation in α-diversity. Ecosphere, 2(2), 1-11. doi: [10.1890/ES10-00117.1](https://dx.doi.org/10.1890/ES10-00117.1)

Reviews

Evaluation round #2

DOI or URL of the preprint: **10.1101/515098**
Version of the preprint: 2

Authors' reply, 22 May 2019

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Decision by **Eric Harvey**, posted 14 May 2019

Decision on prepint 515098 for PCI Ecology recommendation

Dear Dr. Siqueira,

I am happy to announce that your article entitled "*Community size affects the signals of ecological drift and selection on biodiversity*" is accepted for recommendation at PCI Ecology pending minor revisions. We therefore invite you to revise and resubmit your final manuscript version. The manuscript will not be sent for further peer review.

Both reviewers and myself were satisfied with the way each earlier concern was addressed. There are still some minor concerns from one reviewer and myself about clarity, especially related to the justification behind using both incidence-based and abundance-based metrics, expectations and interpretation of the results. There is also a point raised by myself and one of the reviewer about the habitat heterogeneity co-variant and the way it is interpreted (or should be) in the light of the negative relationship between beta-deviation and community size that needs further clarifications. I would invite you to consider especially those points, but also others raised by the two reviewers and myself, which I think could improve the manuscript.

The two reviewers comments are attached to this email and my own comments are copied below,

Best wishes, Eric Harvey, Recommender at PCI Ecology,

_____Minor comments on "*Community size affects the signals of ecological drift and selection on biodiversity*" Introduction

[from line : to line]

[92:96] This would effectively mean that small communities could maintain high diversity via neutral co-existence (on the long term leading to one dominant species, of course). Diversity in smaller communities could even be higher than in larger communities where convergence to dominance by a few strong competitors might occur faster without disturbance. (just a general point to consider - no need to modify anything here)

[180:241] This new addition is great! I think the writing is a bit unclear and should be clarified. For instance for E1 and E2 it would be clearer, I think, to refer to predictions for 'beta-diversity' and 'beta-deviation' rather than 'beta-diversity' and 'null expectations' - to be coherent with the text above in terms of wording.

[184:189] Would not it be as likely that largest communities would have lower beta-deviation than expected by chance? The authors reject that possibility right away, but in both case (lower or higher than expected by chance) niche selection and dispersal rates could be the main processes. There are two things to consider I think: **(i)** the scale of habitat heterogeneity (HET): if within sampling site HET is very high vs. among sites (in one watershed) - then niche based processes should lead to lower dissimilarity than expected by chance, while if HET is low within site, but high among sites - then niche based processes should lead to more dissimilarity than expected by chance. **(ii)** dispersal: sufficient dispersal will work along with the species sorting scenarios mentioned at point (i) but very high will lead to mass effect (and thus lower dissimilarity than expected by chance) while limiting dispersal will lead to higher dissimilarity than expected by chance. Because you are testing for HET with the PERMDISP, then it can give an idea whether results are influenced by HET or dispersal. For instance, negative beta-deviation with community size, with no HET effect could only be explained by high dispersal limitation, right?

[240:241] "are also expected to increase b-diversity" - remove "be"

Figure 1 nice figure! I guess the red and blue points represent subtropical vs. boreal locations but this should be stated in the legend. Also for E1 to E3 on the second panel of figure 1 - should it be 'beta-deviation' instead of 'beta-diversity'? Methods

I am very satisfied with the changes. The two beta-deviation procedures are very well explained and Figure S1 help to clarify.

The only thing I would add is a justification of using the two different beta-deviation methods (as mentionned by one of the reviewer that part of the study still remain unclear and poorly justified). The text describes well how they are technically different, but what were the authors trying to compare or to gain from using both methods? That would help to build up expectations for each approach in terms of processes and mechanisms and to interpret the results. Results

line 489 and 491-492 are stating the same information, I think.

[494:495] That's interesting - I would have expected environment heterogeneity to explain the beta-deviation results - otherwise what sort of niche-based processes can explain the results? (dispersal as mentionned above or is it that the heterogeneity variable used is simply missing the important piece of the environment that might drive the pattern? As mentionned by one of the reviewer - this should be clarified)

[524:525] "species abundances AND genus composition" Since Raup-crick is negative with community size I would expect that the positive relationship with Bray-Curtis beta-deviation could only be explained by the abundance turnover part of Bray-curtis, right? (i.e., Raup-crick covers the composition only turnover part and it goes in the opposite direction)

[603:605] Beta-diversity would give that information but, here, should not that be rephrased as something like: "This suggests that departure from null expectations related to compositional change is similar in..." ? Discussion

[704:741] Statements in this paragraph are correct. But since environmental heterogeneity did not correlate with bray-cutis beta-deviation, I am wondering what the authors think could be the main driver of selection in those system that could explain higher dissimilarity than expected by chance in the largest communities (if not dispersal limitation nor among-sites habitat heterogeneity)?

[763:765] That means that within watershed environmental heterogeneity does not explain the negative relationship between beta-deviation and community size.

[784:824] Very good paragraph with nice additions.

[854] stochastic processes: I would add between parenthesis that the study refers to stochastic processes related to changes in richness and abundances.

[863:864] given no effects of environmental heterogeneity in the results - I am not sure what are the evidence for local environmental filtering in the results?

Finally and this is just for the sake of the discussion, I will quote here a comment I made in the previous round of revision and the authors reply. After I will respond to that reply (nothing needs to be changed here):

< **Comments**. The results suggest that smaller communities should have higher beta-diversity but also higher < local richness compared to larger communities dominated by a few species. I apologize for the self-advertisement < (I generally avoid to do this), but in that case I feel like this recent study would be very relevant to cite: < "Harvey Eric, Gounand Isabelle, Fronhofer Emanuel A., and Altermatt Florian. 2018. Disturbance reverses classic < biodiversity predictions in river-like landscapes. Proceedings of the Royal Society B: Biological Sciences < 285:20182441." - but I will leave this at the authors discretion (this is only a suggestion). < **Response**. That was not the case. Smaller communities should have lower species richness and higher beta < diversity if there are mainly driven by drift. The point here is that each locality has a different set of < (reduced) species composition, making beta diversity higher. Also, with low richness, even one local extinction < of species affects pairwise dissimilarities strongly while does not so in high richness. In larger communities, < local species richness is higher, but a set of species with high fitness occur in most of the >localities, < making beta diversity lower.

In a sufficiently large regional pool, I could easily imagine smaller communities having higher species richness than larger communities but still having higher beta-diversity. Imagine that smaller communities experience higher drift because of constant disturbance reducing community size, leading to neutral co-existence (as mentioned in your manuscript), while larger communities experience no disturbance and higher dominance.

This could effectively lead to higher richness in smaller communities. You could still have higher beta-diversity among the smaller communities however because of random extinctions and turnover (i.e., replacement from the regional pool). The same would be true, however, just with random demographic variations without actual extinctions (if you use a beta-diversity indice influenced by relative abundances). I am happy to continue that discussion.

Reviewed by Kevin Cazelles, 28 April 2019

I have enjoyed reading the new version of this manuscript. I think that Dr. Siqueira and colleagues have carefully addressed the large set of comments we collectively (the recommender and the two reviewers) made. I am overall satisfied with the response to my own set of comments and many additions done by the authors are very helpful. The current manuscript reads well, and in my humble opinion, this version of the manuscript is very close to be a publishable manuscript (and so, close to be recommended by PCI). For this round of review, I have very few suggestions to further improve the manuscript.

- l.114-115, I would add "two": "[...] in *two* climatically highly different regions [...]".
- l. 117-119: I suggest to slightly reword the two sentences.
  - The first sentence should mention the existence of the community size gradient and describe it. It would make a lot of sense to include the following part: *"the smallest boreal stream communities are as large as the largest tropical communities"* that is currently mentioned l. 140-141. This is important because the reader need to be aware of this early in the manuscript to understand the expectations after.
  - The second sentence should only describe the first expectation (E1).

  I would slightly reword the expectations:
- 1. E1 should state that departure from null expectation is high for large community and small for small communities (because of the choice of the null model);
  2. E2 should be about the sign of that departure for large community (positive or negative deviation);
  3. E3 will be clear enough once the part about the community size gradient between the two regions is made clear at that point of the manuscript.

To be clear about the changes for E1 and E2, below are the changes I would make to lines l.119-124:

> [...] *we expected that (E1) β-diversity would be high and close to null expectations* KC: I would remind the reader of the nature of the null model *in watersheds with the smallest communities (some watersheds in Brazil only; Fig. 1). This would indicate that ecological drift plays a major role in structuring these small subtropical communities. Second, all else being equal, we expected that (E2) β-diversity in watersheds with the largest communities in Brazil and Finland would be far from null expectations* KC: this first part of E2 should actually be part of E1 *, but lower than in the smallest watersheds (Fig. 1)*.

- l. 323-334, I would again recall what are the null expectations here (what is the null model used to generate them).
- Figure 1: I would add the meaning of the colors in the caption.
- I think the authors should combine Figure 1 and S1 (and maybe S2), this would be a great summary of the methods and expectations.

Reviewed by Romain Bertrand, 09 May 2019

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Evaluation round #1

DOI or URL of the preprint: **10.1101/515098**
Version of the preprint: 1

Authors' reply, 02 April 2019

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Decision by Eric Harvey, posted 12 February 2019

Decision on prepint 515098 for PCI Ecology recommendation

Dear Dr. Siqueira,

Thank you very much for submitting your manuscript "Community size affects the signals of selection and ecological drift on biodiversity for recommendation" at PCI Ecology. The reviewers and I appreciate the work you have accomplished. Based on the reviews, we will not be able to recommend this manuscript at this point, but will be happy to consider a revised version.

Both reviewers and I agree that this manuscript tackles a topic relevant to re- searchers interested in stream ecology as well as, more broadly, to community ecologists. In particular, I think that the contrast between boreal and tropical systems is very interesting as it provides potential explanations for the idiosyncrasies observed in the many studies addressing this issue at different specific locations.

However, both reviewers raise concerns, mainly about some of the assumptions behind the null model approach, and the interpretation of the results. Those issues should be addressed clearly in the manuscript. I also agree with one reviewer that the fact that the data is only described in Heino et al., 2018 leads to some unclarity in the Methods section that should be addressed. Both reviewers and myself found that the different approaches used to define community size need to be clarified. Another important issue is with expectations and interpretations of the slope of the relationship between beta-deviation (and beta-diversity) and community size. The authors state clearly predictions for a beta-deviation of 0 versus 1 or -1 but they do not provide clear interpretations for the slope itself (positive versus negative). One reviewers made suggestions to help with that. This would greatly improve the clarity since they found that with one metric the slope is positive and with the other one the slope is positive. Finally both reviewers suggest complementary analyses that should be considered to clarify those issues.

Should you decide to revise the manuscript for further consideration here, your revisions should address the specific points made by myself (this email and minor comments attached with this email) and each reviewer. Please include a cover letter indicating your responses to the review comments and the changes you have made in the manuscript. If you disagree with a reviewer's point, explain why. Also, please add line numbering to the manuscript so that it is easier to refer to specific lines.

Sincerely, Dr. Eric Harvey Recommender, PCI Ecology **Download recommender's annotations**

Reviewed by Romain Bertrand, 10 February 2019

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Reviewed by **Kevin Cazelles**, 01 February 2019

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