REVISION OF THE PAPER "COEXISTENCE OF MANY SPECIES UNDER A RANDOM COMPETITION-COLONIZATION TRADE-OFF" BY ZACHARY R. MILLER, MAXIME CLENET, KATJA DELLA LIBERA, FRANÇOIS MASSOL, AND STEFANO ALLESINA

Dear Editor,

Please find associated to this letter a revised version of our manuscript *"Coexistence of many species under a random competition-colonization trade-off"*. We would like to thank the reviewers for their encouraging report and thorough reading of our paper. Their comments have helped us think more deeply about the presentation of our results and improve the quality of the paper. We comment hereafter on all of the questions and suggestions raised in the report.

Reviewer #1

(1) *In their research, Miller et al. explored the coexistence of various species in a random metacommunity with a competition-colonization trade-off. Their findings revealed that, across a broad range of random setups, the number of surviving species followed a binomial distribution mean of half the original species pool size. These results are novel and add to the growing interest in understanding what occurs when a community is unstable, rather than solely determining if it is stable or not. The study is well-written, although it may not be easily accessible to empirical researchers. I checked the derivations in the main text (not the SI) and they all seem solid. I congratulate the authors for this nice work. I do not have any major concerns. However, I believe it would be beneficial if the authors could establish a stronger connection between this work and existing literature. I have included more detailed comments below.*

We thank the Reviewer for the positive assessment, as well as the thoughtful suggestions below. In response to the Reviewer comments, we have made several changes that we hope will improve the accessibility of our work for empirical researchers (such as clarifying our discussion of priority effects and using improved language for assembly scenarios). Also, while our original draft emphasized connections to the existing literature on competition-colonization trade-off models, the Reviewer's suggestions helped us expand connections to other models of community assembly and other trade-off models (discussed below).

(2) *Spacing of colonization rates (Figure 4). I was a bit surprised that the colonization rates of surviving species mimic the original distribution. This relates to the work by Scheffer et al. [1] on emergent neutrality where they found the initial niche spacing and the survived quite different. What drives the fundamental difference between these results? To be clear, I am not*

asking for a detailed comparison; some speculations are sufficient, although analytic arguments would be great.

We agree with the Reviewer that this result is somewhat surprising. We believe the simplest way to understand this result is that the competition-colonization trade-off levels the fitness of all species (in expectation), so that there are no inherently "good" or "bad" strategies. As a result, each species is equally likely to persist in the assembled community, and consequently the marginal distribution of traits in the assembled community typically mimics the distribution of the pool.

It is an interesting question to consider how and why our results differ from other theoretical predictions for community assembly. The work of Scheffer *et al.* [1] (and other studies such as Fort et al. [2], D'Andrea *et al.* [3]) suggests that community assembly should lead to both "repulsion" in niche space due to limiting similarity, as well as the emergence of clusters of similar species. In our analysis, we find clear repulsion between persisting species, in agreement with this literature (see Figure 4b, which shows that the spacing of traits is markedly different before and after assembly). In this respect, there *is* a substantial difference between niche spacing in the pool vs. the assembled community, although this difference only becomes clear when considering the joint distribution of species traits.

Unlike these earlier studies, however, we do not find clusters of similar species. This difference can be explained by two factors. First, we study only the equilibrium community, while the clusters found by Scheffer et al. and others are transient phenomena in the absence of additional stabilizing mechanisms (see, e.g., Barabas et al. [4]). It is possible that more complex transient patterns may emerge in the competition-colonization trade-off model we study; whether these transients are ecologically meaningful will depend on system-specific timescales of interest. Second, and more fundamentally, the trade-off model studied here differs from the models of Scheffer et al. and other models of emergent neutrality in that species with nearly identical traits (here, colonization rates) are *not* nearly competitively equivalent. In models based on similarity of resource use (or other trait overlap), very similar species have nearly neutral dynamics, with competitive exclusion happening on very long timescales. In our model, the better competitor always wins locally, regardless of how similar two species are in their colonization rates. This is an important assumption of the model, which we refer to as "perfectly asymmetric competition" and highlight in lines 185-186. This assumption has been critiqued (for example, by Adler and Mosquera [5]) and relaxed (for example, by Calcagno *et al.* [6]) in other studies, which we discuss and cite. While there are circumstances where this assumption may be unrealistic, it is consistent with simple models of local competition for a single limiting resource, for example.

Additionally, we now highlight in the revised manuscript the connection between our results and a recent theoretical study of some other trade-off models by Detto *et al.* [7]. We believe that the similarity between these results is due to the assumption of strongly asymmetric competition in both the competition-colonization trade-off model and the models of light competition studied by Detto *et al.*. The earlier studies of emergent

neutrality noted by the Reviewer instead focus on symmetric interactions arising from trait overlap. We thank the Reviewer for pointing out the contrasting predictions of these two classes of models. We now note the connection between the "perfectly asymmetric competition" assumption and the emergence of trait repulsion without trait clustering (lines 190-192).

(3) *Unlimited species richness (Figure 2). I am curious if the unlimited species richness is likely to be stably maintained regarding parameter perturbation. As a context, this result reminds me of another study showing unlimited richness can be supported with facilitation among competitors (Gross [8]), however, later studies have found it increasingly less robust to parameter perturbation (Barabás et al. [9]). I think this problem applies to many other models allowing infinite species richness. Of course, the model setups between that model and this paper are quite different, but I am curious if the same issue occurs here. If so, perhaps this is at least worth highlighting in the discussion.*

The Reviewer points to a very interesting paper on sensitivity analysis of coexistence (Barabás *et al.* [9]). This paper demonstrates that coexistence in any model will become less robust to parameter perturbations as species become more similar to one another. In our model, as in any non-trivial model of many-species coexistence, species in the persisting community become more similar on average as the number of persisting species grows (and niche space becomes densely packed). Thus, we agree that communities with greater numbers of species will be progressively more sensitive to parameter perturbations. However, as noted by the Reviewer, this is likely a very general feature of any model that allows large numbers of species to coexist without including a trait space that grows with species richness.

Importantly, in our model, any community of finite size is robust to parameter perturbations that are sufficiently small (here we take parameter perturbations to mean a small change in the species' colonization rates). In fact, our mathematical analysis relies on the fact that we can neglect small terms in the niche shadow calculations (of the order X_i^2/ℓ_{i-1}) without much change in the predicted final community (for a graphical example, see Figures S3-S5). Thus, we expect the coexisting communities to be robust to at least this magnitude of parameter perturbation. On the other hand, perturbations of the same magnitude as the spacing between species would effectively yield a new randomized pool (as if the S persisting species were again sampled at random). In this case, our results imply that about half of the species (so about one quarter of the original pool) would persist following the parameter perturbation. So, overall, we expect that all species would coexist following a small parameter perturbation, and half following a very large perturbation. Perturbations of an intermediate size would cause the loss of an intermediate fraction of species.

While very large assembled communities are necessarily less robust to parameter perturbations, we emphasize that the *assembly* of these communities will be equally robust for large species pools. In other words, no fine-tuning of the species pool is needed to ensure that a large fraction of

species persist. Regardless of how large the species pool becomes, and regardless of the details of how this pool is sampled, community assembly typically finds a persisting subset of species that is about half the size of the pool.

(4) *I am also curious about the statement that infinite re-invasions one-at-a-time would lead to the same outcome as invasion all at once (L111-122). This result is not generally true with priority effects (Song et al. [10]), for example with the existence of a compositional cycle. I guess that this result relies on the special structure of GLV model imposed by Eq. 3, which seems similar to the setup of Servan et al. [11]. I am curious whether the key results (B(n, 1/2) and assembly equivalence) fundamentally rely on this property, or they can be generalized in more general GLV structures.*

Yes, the Reviewer is correct that this result is due to the fact that the competition-colonization trade-off model is equivalent to a GLV model with a diagonally stable interaction matrix. As we show in the Supplementary Information, there is a unique attractor for each set of species, and consequently no "true" priority effects (e.g. given the same set of species initially present at non-zero abundances, there cannot be multiple distinct long-term outcomes of the dynamics). To avoid confusion, we now better clarify this point regarding priority effects at lines 140-142.

Minor comments:

(1) *Figure resolutions are low.*

Thank you for noting this; we have produced higher resolution versions of the figures.

(2) *I am wondering if the results would remain consistent if the colonization rates were obtained from a mixed distribution. For instance, if there were an equal likelihood of the colonization rate being sampled from an exponential distribution or a uniform distribution. If this were true, this would further strengthen the argument in the paper about the universality of the results. To be clear, I am not seeking an analytical outcome; simulation results would suffice*

Yes, our results are robust to more complex distributions, such as mixtures. Our approximation approach, developed in S2.5, applies very broadly to a large class of distributions (essentially, those which are smooth and do not have $f(a) = 0$ and $f(b) > 0$ for some $b > a$). However, it is a very interesting suggestion to consider a mixture of uniform and exponential distributions, as these are two cases that can be treated more rigorously. While we agree with the Reviewer that extending the results of S2.2 and S2.3 to the mixture of the two cases would strengthen the evidence for universality, it is not clear to us that this analysis would be a straightforward extension. Because each species's colonization rate could be a sampled from either distribution (uniform or exponential), we would need to sum over all possible combinations of this choice, yielding a large number of integrals, each with a different form. While there may be some way to simplify the calculation, we have not been able to perform it. Instead, we have added one set of additional simulations showing that our results do in fact hold for this mixture distribution (Fig. S7). We believe this new addition strengthens the manuscript by showing that our results hold for

more complex distributions. Moreover, this mixture distribution is actually discontinuous, but still produces assembly patterns consistent with our theory, suggesting even further generality.

Reviewer #2

(1) *The manuscript "Coexistence of many species under a random competition-colonization trade-off" explores the coexistence under competition-colonization trade-off using a slightly different and more realistic approach. It employs randomly assembled communities and a probabilistic approach rather than a traditional C-C model. Moreover, the manuscript explores the outcomes when species are introduced one at a time or through de novo speciation. Results highlight that rich communities might arise through ecological assembly under competition colonization trade-off. The question is interesting and timely, theoretical approach is different than classical CC models, which adds value for further use of the methods. Results are well communicated and discussed.*

We thank the Reviewer for highlighting the value and timeliness of this approach.

(2) *The manuscript could be more convincing in that the randomly assembled communities are closer to the real world than the models with fine-tuned species traits. For example, how would the approach be challenged with parameterization using real species traits?*

We agree with the Reviewer that it would be ideal to consider whether real-world trait distributions are consistent with the randomly-assembled communities we study. Unfortunately, though, this kind of direct comparison is presently quite difficult. Only a few studies have estimated the empirical trait distribution of communities putatively shaped by a competition-colonization trade-off (for example, Cadotte *el al.* [12] and later Livingston *et al.* [13]). While it might be possible to assess some of our predictions using such data, other predictions would require before and after estimates over the course of community assembly. Additionally, our quantitative results rely on the assumption that species experience equal mortality/extinction rates; thus, we would need to consider appropriately normalized empirical colonization rates, further complicating the task.

In light of these challenges, we choose to focus on making a theoretical contribution to the literature. Our probabilistic approach is one way – we believe a powerful way – to understand the typical behavior of communities governed by the competition-colonization trade-off, given the difficulty of estimating empirical model parameters. Rather than focus on specific parameter choices, which may or may not reflect real-world communities, we attempt to consider a very broad range of a possible parameter distributions, showing that the model structure – and not the specific parameterization – leads to the surprising result of convergence to the binomial distribution, and other community properties.

(3) *More biological/empirical support might be needed to justify the rationale behind the framework chosen. What could be the biological reason that the niche shadow reduces with colonization, for instance?*

The basic competition-colonization trade-off model was developed in a series of papers beginning with work by Levins and Culver [14] and including classic papers by Hastings [15] and Tilman [16]. The biological motivations and assumptions behind this framework are widely discussed in this literature, and we prefer to point readers to these papers and others – including critiques of the model framework, such as Adler and Mosquera [5] and Yu and Wilson [17] – rather than attempt to summarize these discussions in great detail. Instead, we take the widely-used framework as a starting place and try to uncover its typical assembly properties.

The fact that niche shadows are reduced by the arrival of a superior competitor is a prediction of the model, rather than an assumption of the framework. As we discuss in lines 65-67, this phenomenon occurs because any given species, which casts a niche shadow of a certain length, will be competitively suppressed by the arrival of a superior competitor. Facing greater competition from the invader, this focal species will have reduced occupancy, and consequently be less able to compete with inferior competitors for patches. The net result is that an inferior competitor that previously would be excluded might now coexist with the others. Intuitively, this indirect effect can be understood as a case where "the enemy of my enemy is my friend", from the perspective of the inferior competitor. To better clarify this point, we have added an additional sentence expanding our intuitive explanation of this phenomenon (line 67).

(4) *Historical contingency has been briefly mentioned but not elaborated on. For example, are there priory effects when the species are introduced in a one-at-a-time manner?*

We thank both Reviewers for noting this ambiguity in the original manuscript. As we explain above, there are no priority effects in this model. This is due to the fact that the competition-colonization trade-off model is equivalent to a GLV model with a stable interaction matrix. As we show in the Supplementary Information, there is a unique attractor for each set of species, and consequently no "true" priority effects (e.g. given the same set of species initially present at non-zero abundances, there cannot be multiple distinct long-term outcomes of the dynamics). There are historical contingencies in the sense that a certain species may be able to invade some communities but not others. Whether that species will become part of the assembling community depends on which species are already present, which of course depends on the history of which species have previously attempted to invade. This kind of historical contingency is only found when species cannot re-invade the community multiple times (our second assembly scenario).

To avoid confusion, we now better clarify this distinction at lines 140-142.

(5) *Another issue is the increased diversity after speciation effects. In a real-world example, generation times would be important for the speciation. How this time to speciate issue was handled is not very clear.*

We agree with the reviewer that the use of word "speciation" might be confusing. We used this term to indicate that, in this scenario, each new invader was sampled with a new colonization rate, and could not re-invade the community. However, this could represent a novel species, a genotype

within an existing species, or an immigrant from a distant patch (outside the focal system). Because we do not explicitly consider the evolutionary dynamics of the community, and to avoid any confusion, we have shifted our terminology to refer to "de novo invasion", rather than "de novo speciation". Regardless of what mechanism drives these invasions, we make the assumption that they are very infrequent, so that the local metacommunity dynamics reach equilibrium between invasions.

Specific comments:

(1) *Title: I wonder if the title would be more appealing if it mentions "randomly assembled communities" and the probabilistic estimations.*

While we appreciate the Reviewer's suggestion, we prefer to retain our original title. This title was chosen in part to highlight the interesting parallel with the results of Serván *et al.* in *Coexistence of many species in random ecosystems* [11]. In addition, we worry that the phrase "randomly assembled communities" might mislead readers, since the assembly process itself is deterministic for most of our analytical results (only the species pool is random), and only some scenarios involve stochastic arrival of species. We hope the phrase "under a random competition-colonization trade-off" communicates the probabilistic aspect of our analysis to potential readers.

(2) *Abstract: The species parameters are clearly defined here. If the manuscript wants to use traits instead of parameters, maybe can define it so with the parameters. it will read better. Exclusion (shadow) is an important part of the manuscript. The abstract can briefly mention that dependency.*

Throughout the manuscript, we use the terms "parameters" and "traits" mostly synonymously, preferring parameters when discussing the mathematical model and traits when discussing real world communities. While the connection between specific species traits and model parameters may be an interesting and complex subject in its own right, we seek to avoid that complexity here. To better clarify our usage, we have revised the abstract slightly to explicitly state that model parameters correspond to species traits.

Additionally, we agree with the Reviewer that niche shadows are an important component of the manuscript, but we avoid using this terminology in the abstract given that this is not a phrase all readers will recognize. Instead, we refer more broadly to conditions necessary for coexistence, and define niche shadows more carefully in the main text.

(3) *Line 51: Maybe highlight the two important results.*

We agree, and we have added a brief preview of the main results in this paragraph (see lines 49-51).

(4) *Lines: 71-72: The manuscript could explain the possible ecological reason for distribution selection.*

We thank the reviewer for this comment and agree that the choice of distributions could be better motivated in the text. We chose to examine the following colonization rate distributions: Uniform, Exponential, Pareto (power law), and Triangular (we additionally consider Half-Uniform distributions in the SI, and we have now added simulations for a mixture distribution, following the comments of Reviewer 1). While there is no direct ecological reason for choosing these distributions, we chose a range

of distributions with different qualitative properties, in order to highlight
the generality of our findings. In particular, we wanted to include some
distributions with both finite and infinite support. This comparison is im-
portant because empirical colonization rate distributions should have an
upper bound. Additionally, the uniform and exponential distributions are
amenable to analytical calculations, which are not possible for other choices.
We have added some additional explanation of these choices at lines 77-78.

(5) *Lines 82-83: Maybe a couple of references for coexistence close to n and
exclusion close to 0 are theoretically almost impossible.*

We have added references to two studies that consider the likelihood
of n species coexistence (these are examples of the "existing theoretical
predictions" we refer to). The fact that it is rare to find very few (e.g. one)
species in the assembled community (for large n) is a new result of a our
analysis, rather than a known fact.

(6) *Line 192-195: The manuscript can mention some other trade-off scenarios.*

To make this point more concrete for readers, we now list two examples
of other trade-off scenarios, rather than just citing them (line 201). We
have also added references to two new trade-off scenarios: a competition-
persistence trade-off, recently studied by Ontiveros *et al.* [18], and light
competition trade-offs, analyzed by Detto *et al.* [7]. The latter study, al-
though focusing on very different trade-off models, finds results intriguingly
similar to ours. We now highlight this recent study (lines 205-206), as it
supports our speculation that these qualitative findings may apply more
broadly across different trade-off scenarios.

(7) *Line 233-234: Although c is always higher than m, experiencing the same
mortality rate for all species is a sort of environmental filtering. Justify if
it is not the case.*

We agree with the Reviewer that, by assuming the same mortality rate
for all species, we are effectively focusing on a community of species that
are similarly adapted to the shared environment. This assumption is made
largely to simplify the analysis and its presentation, in order to avoid com-
plexity that might distract readers from the main results. Variation in
m can be handled in this model framework, for example as discussed by
Tilman [16]. Considering random distributions of both m and c values
would be a very interesting extension of this work, but it is beyond the
scope of our current analysis. Instead, we choose to focus on a scenario
where all species have equal $m > c$, and we acknowledge this somewhat
limiting assumption in line 226. Ecologically, this choice can be justified by
our focus on the specific process of competitive exclusion; we aim to avoid
the additional complexity of considering species that are not well adapted
to the environment ($c < m$), or species with very different ability to persist.

(8) *Eq.s 4-5: Is there ecological reasoning that the niche shadow decreases with
increasing c?*

The niche shadow of species i extends from c_i to ℓ_i, and the length of
the niche shadow is $\ell_i - c_i$. ℓ_i, the right upper bound of the niche shadow
(given by eq. 4), necessarily increases with c_i, since it is greater than this
value by definition. However, the length of the niche shadow, $c_i - \ell_i$, does

not obviously increase with colonization rate. In fact, our analysis shows that niche shadows do *not* systematically vary with colonization rate.

(9) *Eq.s 7-8: I wonder if correspondence between random variables K and the final coexisting species can be verbalized in the results with a sentence or two.*

To avoid confusion, we now explicitly define the random variables K_i in line 295. We additionally provide an example of how a certain sequence of K_i values corresponds to a particular set of coexisting species. However, these random variables are essentially a technical device for carrying out the calculations in the methods; for this reason, we think it is better not to mention them in the results, and to avoid too much interpretation of these quantities.

(10) *Figure 1: is there a way to illustrate that the niche shadow of a species reduces when affected by another species?*

While we agree that it would be ideal to communicate this concept graphically, we have not found a clear visualization that fits within the space limitations of the article. Niche shadows are illustrated in Fig. 1b, and examination of this figure shows that the length of each shadow depends on the distance from the species "casting" it to the edge of the proceeding niche shadow. To emphasize this feature of the figure, we have added a new sentence in the caption. Additionally, when niche shadows are explained in the main text (lines 64-65), we include a reference to the work of Kinzig *et al.* [19], which includes a very detailed exploration of niche shadows, as well as additional visualizations (see Figure 1 in Kinzig *et al.*). We hope interested readers will also consult this study for more information.

(11) *Figure 4: I think the spacing between rates could be explained better for a broad audience.*

We have tried to explain this concept in non-technical terms, for example we state "Compared to a random subset of species from the pool, the spacing between consecutive persisting species ... is substantially more even, with fewer small or large gaps." We also represent this idea graphically in Fig. 4, to provide readers with multiple ways to understand the result. While we agree the discussion of the analytical distribution of spacings in the uniform case (lines 105-115) is more technical (in order to be more precise), this discussion only supplements the basic finding – it is not necessary in order for readers to grasp the main message.

(12) *Lines 161-162: It is hard to see connect niche partitioning phenomena to the theoretical results.*

We agree with the Reviewer that it might be hard to connect existing concepts of niche partitioning with the repulsion of colonization rates that we observe. To avoid confusion with existing meanings and connotations of the phrase, we replace "niche partitioning" with "community assembly" in line 169.

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