Response to reviewers 2:

MS #55850R1

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ASSOCIATE EDITOR'S RECOMMENDATION

Dear Judie,

We've received two reviews of this revised manuscript and I've spent a lot of time trying to understand it myself. The authors made good efforts to incorporate most of the changes the reviewers and I suggested in the last round of reviews. I'm afraid that my suggestion in the last round of using the chain rule to decompose sensitivity into direct and indirect effects did not work out as well as I had hoped, which made the revised manuscript actually more confusing to me (echoed by reviewer 1). However I have worked out another approach that seems much clearer (outlined below).

The problems in the section "general definition of competition-mediated indirect effects" are two-fold. First, as reviewer 1 noted, the notation is awkward and confusing.

I can fix this.

Second, there doesn't seem to be a unique way to decompose the equilibrium expressions into direct and competition-mediated parts. For example, when I applied the approach used for the essential resource model to the substitutable resource model, I got a different partition into direct and indirect effects (see my attachment p. 1). It's not clear why this is, and it makes the interpretation difficult.

I see some problems in the equations he used in the substitutable case. I’m not sure whether there is a general problem here. The fact that our analytical solutions match simulation results means we’re on the right track, but of course is no substitute for having the math correct.

Therefore I suggest 1) presenting direct and indirect effects in terms of the Lotka-Volterra model,

I see his example of this and think it works. But it may require a slight change in our definition of direct effects. Is the sensitivity of a species equilibrium abundance in monoculture (by definition K) a direct effect? Or is the sensitivity of the species competitive equilibrium abundance while holding the competitor’s abundance constant the direct effect? The second definition is what we have in the paper, but the derivation that Klausmeier uses depends on the sensitivity of K.

2) converting the resource-competition models to LV parameters,

I don’t love this suggestion because it seems to defeat the purpose of looking at the mechanistic models in the first place. But I need to work this out.

and 3) interpreting the results. See my attachment p. 2-3 for an outline. Only red-starred equations need to show up in the main text, the rest can be in the online appendix.

The LV stuff is helpful, with the caveat about changing the definition of direct—and by extension—indirect effects.

Try to keep the derivations succinct. I hope this plan is correct, makes sense, and satisfies the authors and reviewer 1! You can note that Barabas et al. give a general algorithm for converting resource competition models to LV (in general, this is only a local approximation, which should be noted when interpreting K).

I wish I was fluent in linearizations and local approximations.

Reviewer 1 has suggestions for either dropping the substitutable model or considering more general perturbations. I'd like to keep the substitutable model; if you feel you can easily consider the more general case, that would be OK with me but it's not mandatory.

I think a general case would make this a much better paper. But I’m not confident in the notation or in deciding on a general formula for resource competition. We could try working it out or we could bring on a mathematician.

Reviewer 1 has a number of other comments. In a few places I found myself unable to follow their logic, but this might just be me! Try to address their comments as best you can.

Minor comments:

The substitutable resource model has some traditional use, but I realized it is a bit weird in that there is no conservation of mass (uptake is not tied to resource availability).

I don’t understand this comment about conservation of mass.

While the equilibrium calculations are undoubtedly correct (and simple because of the -qN uptake terms which make consumption vectors always the same slope), I found that resources could be driven negative in the transient dynamics. You might briefly note this oddity.

I don’t understand this comment.

Partial derivative symbol is not delta.

I don’t know which equation he’s talking about – the first few?

eq 1, l 99 - focus on "niche overlap" rho, drop "niche difference = 1- rho:

I can do this.

l 139 - S is a concentration not a rate

Good point. I need to clarify this.

l 142 - a is the resource turnover rate

Good point I need to clarify this.

Could fig 1 come from a real model rather than hypothetical? Perhaps a range of S1 in Fig 3 transcending and going beyond the coexistence region? E0 can be dropped.

I can try and develop this.

Fig 2 could be dropped

I can do this.

l 180-188 not needed?

I like having some examples.

l 189+ - This would be equally clear without the particular example of N and light

I can drop this.

l 249-250 - drop sentence about future studies

I can do this.

l 389 - fix spelling of my first name :) and Jim Powell's last?

I’m an idiot. I will fix.

Chris Klausmeier

Associate Editor

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Reviewer #1:

The Authors made an excellent job to improve presentation quality of the ms. Now it is easy to follow and understand;

Or harder?

references to the literature are sufficiently informative. Unfortunately, I have to conclude that the analysis is not entirely correct.

On which point?

Also, I have to admit that I was wrong in an essential point in my first report.

I start with correcting myself. I wrote that the R\* values remains constant during perturbation in case of essential resources, but not in case of the substitutable ones. As the Authors pointed out correctly in their response, this was wrong. In both cases the equilibrium resource concentrations, R1\* and R2\*, are unequivocally determined by the crossing point of the two isoclines. They perturbs the resource supply values S1 and S2. It does not affect the physiology of the species, therefore does not affect the isoclines and their crossing point. The origin of my mistake was, that the R1\*, R2\* values are just the single species R\* values with respect to the single limiting resources of the corresponding species for essential resource. THIS is not true for substitutable resources, where both quantities are affected by both physiologies. Still, R1\*, R2\* remain constant PROVIDED that only S1 and S2 are perturbed and the physiologies are not affected.

And assuming that both species can respond to the perturbation in resource supply.

However, constancy of R1\* and R2\* has an important consequence. If the resource point does not change during perturbation, dependence on resource concentrations is irrelevant.

Our analysis and simulations are focused exclusively on what happens when the resource point (S1,S2) is perturbed.

It does not matter, what are the shapes of the isoclines, it does not matter, what are the w values describing the resource dependences. The only thing that matters is the crossing point and the performance of the species at this specific resource point.

Therefore, there should be no any difference between the two model versions in their responses to the perturbation of the resource supply.

The models do respond the same way in terms of niche overlap. However, the essential resource model is a more limited example of the type of response that can occur. The substitutable model shows that a wider range parameters play a role in the indirect effect.

The Authors point to page 77 of Tilman (1982) as the origin of their eq. (10), which is their basis of analyzing the essential resources model. However, Tilman does NOT restrict the scope of this specific analysis to essential resources. Eq. (15) of Tilman in p. 77 is an immediate consequence of his eq. (14) on the previous page, which is just the resource equilibrium equation, independent of the physiologies. Actually, this eq. (14) is repeated as eqs. (9) and (10) of Appendix (p. 271), where Tilman discusses specifically the case of substitutable resources. The whole analysis of the current Authors that is based on their eq. (10) is applicable irrespective to the shape of the isoclines. All of their results stated for essential resources are equally valid for substitutable resources.

I need to think about what this means. So there is no reason to work up the substitutable example?

There is nothing wrong with their calculations for substitutable resources, either. I convinced myself that their "substitutable" formulas give the very same S-dependences as the "essential" ones. This is surprising, because one can expect the very similar dependence on the resources, i.e., very similar isoclines, makes the coexistence very sensitive. So the irrelevance of the w-s seems paradoxical. The resolution of the paradox is that similar resource-dependences implies that any perturbation of the resource supply affects the two species very similarly and does not induces a significant push for competitive exclusion. The issue resembles to Chesson's "equalizing effect" in some extent. Again, the important thing is that we perturb only the resource supplies.

So, what is the real difference between the two analyses by the Authors? The "essential" one uses from the very beginning that the R\*s are fixed and considers them as a parameter. The "substitutable" one follows Tilman's Appendix, which calculates the R\*s from the isoclines.

We agree that this is a key distinction between the two models. It also makes thinking about indirect effects in the substitutable model more difficult.

As the R\*s are affected by the w-s, the w-s do appear in the formulas, even if the S dependences will turn out to be independent of the w-s, when everything is calculated and the formulas are properly simplified.

To see the full picture, assume now a perturbation that DOES affect the physiologies. Then we must calculate, how the R\*s affected and how this change propagates. To simplify our job, assume that the q-s are independent of the resource concentrations, so they do not change as a result of changing R\*s. Then we should repeat the second, "essential" type of calculation. Only the very last step will differ: the only difference is that we are interested now in dependence on the perturbation parameter, instead of the resource supply. The response will be high, when the niche overlap is high, i.e., if rho, containing the w-s and the q-s, approaches 1. Consider now essential resources in the same context. For small perturbation the L shape of the isoclines does not matter. One of the isoclines is vertical, the other one is horizontal; therefore w12=w21=0. Substituting this into eq. (32) leads to eq. (13), as it should be.

I like the suggestion here of using the same form of the equation to explain the essential resource model but simply changing the parameters (in this case w12 and w21 to zero). The math underlying the two models should be the same.

That is: the Authors' distinction between niche overlap for essential and for substitutable resources is correct if (1) we consider a perturbation that affects the physiologies, not only the resource supply, and (2) assume that the change of R\*-s do not affect the q-s. Unfortunately, the second condition is not met in Tilman's model.

Not sure how this applies to us because we don’t consider a change in the physiologies.

Considering resource-dependence of the q-s would complicate the formulas further. I have not made the calculation, but my guess is, that the qualitative message would not change.0

There is a more fundamental question behind all of these issues: why does anybody assume that a model, which is significantly different from the Lotka-Volterra competition model, corresponds to a Lotka-Volterra one in some sense? In which sense? Why should the L-V-based concept of niche overlap applicable to any other model? Technically, it does not matter. If we calculate correctly the response of a system to a perturbation, then it is irrelevant whether quantity rho is referred to, as niche overlap, or not. Still, the perceived correspondence between Tilman's model and the Lotka-Volterra model guides our intuition, so it is not just terminology.

Unfortunately, finding the correspondence between the two models is not unequivocal. For substitutable resources, the Authors consider the resource equilibrium equation eq. (14) by Tilman on p. 76 of his book as an analog of the Lotka-Volterra model. After all, eq. (15) is more than reminiscent to the coexistence result for L-V. This is why they identify the q-s with the competition coefficients and calculate niche overlap from q-s in the Chessonian way. Here it is important that the R\*s are considered given, and S-R\*s are seen as an analog of the carrying capacity. I find nothing wrong with this analogy. However, as far as I studied his book, Tilman does not consider his eq. (15), as an L-V analog. Instead, he build the correspondence in the Appendix via calculating the R\*s from the underlying parameters. This way he reached equilibrium equations in the L-V form eqs. (1) and (2) of that Appendix. This is a different way of connect the two types of model; the Authors accept this correspondence for substitutable resources. I find nothing wrong with this, either. It is less clear, what is the point of either of these correspondences.

I have to clarify also, how all of these are related to my work. I think the only robust and generic way to connect a resource competition model with the Lotka-Volterra one is local linearization of the density dependences. With sufficient care, this can always be done (Barabás et al. 2014, EER 14: 361), but it is valid only as a local approximation. This linearization is identical to Tilman's correspondence if, and only if, the q-s are constant. In this case the resource equations of the model are linear and we need not linearize them locally. Then the "impact" niche vectors in my theory corresponds to the q-s and the "sensitivity" ones to the w-s. The analog of the competition matrix is the product of the matrix composed from the four w values and of the matrix of the four q values. The rho of eq. (32) of the current paper is the niche overlap calculated from that competition matrix. (It would be advisable to rewrite the expression of rho by multiplying both its nominator and denominator by wF2 x wC2 to see a more meaningful structure.) From a superficial reading of Tilman long time ago I got the impression that Tilman assumes the constancy of the q-s. This was incorrect: In Tilman's model the w-s depends on the resource concentrations.

I’m not sure about this. I thought that qs and the ws were indeed constant, unless I’m missing something.

Then, Tilman's linear equations (1) and (2) of the Appendix are not the linearizations of the nonlinear original model. However, q-dependence is irrelevant, when only the S-s are perturbed and the resource concentrations are fixed - as discussed above.

Therefore my suggestion for the Authors is to choose one of the following two options:

1. Restrict the paper to the current "essential" calculation with the understanding that it is valid for any kind of resource use, provided that only the resource supplies are perturbed.

Chris doesn’t like this.

1. Consider a general perturbation, which may affect the physiologies also and take into account that the w-s are also perturbed in this way. This will be something resembling to the current "substitutable" calculation, but more complicated than that.

We’d probably need a real mathematician to do this. It might be worth it?

I close my review with a few smaller points.

1. Notations in the Section "General Definition…" in p. 6 are strange. They use f and g as notations for functions and not for variables. Therefore expressions, like "delta f / delta g", are meaningless, even if the reader can figure out the intended meaning. Instead, write "partial f / partial N\*C", etc.

I can do this… if we keep the general equations.

(2) I think that the "-" sign in the first bracket of eq. (20) is in error. Probably the negative sign in eq. (18) - which is correct - was duplicated here.

I’ll need to check the algebra, but I think equation 20 is correct.

(3) Section II of Appendix is unhelpful this way. Either clarify the issue fully, or leave it out. Note that the area of the parallelogram spanned by the consumption vectors is the absolute value of the determinant w11w22-w12w21. The sine of the angle between the vectors is this area divided by the length of the vectors.

I agree. I can leave it out, but I don’t know how Klausmeier feels about this.

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Reviewer #2: The paper was strong before and is stronger now. I only caught that lines 54-55 refer to a "difference" but then go on to mention only one thing.

Thanks. The difference refers to the difference between net effects and direct effects.

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