Dear Chris Klausmeier,

We appreciate the detailed review of our manuscript “Indirect effects of environmental change in resource competition models”. The comments from you and Dr. Meszéna have been constructive in revising the manuscript and we think in making it a better paper overall. We especially thank Dr. Meszéna for the close reading of our mathematical arguments and suggestions for better linking our work to previous theory. We have made extensive changes to the mathematical presentation including a section—at your suggestion—where we derive a general definition of net, direct and indirect effects from the chain rule and the definition of the total derivative. Putting these general equations up front helps organize the rest of the mathematical steps for the mechanistic models. Given the large changes in the presentation we have made, we hope you and any other reviewers will scrutinize each step carefully and check all of our equations for errors. We believe the new presentation is easier to follow and more general, but we emphasize that we reach the same conclusions as in the previous submission. We have responded point by point to each comment and suggested change below.

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*“ASSOCIATE EDITOR'S RECOMMENDATION*

*Dear Judie:*

*We've received two reviews of Andrew Kleinhesselink and Peter Adlers's manuscript, "Indirect effects of environmental change in resource competition models" and I've given it a careful reading myself. The manuscript quantifies how niche overlap leads to indirect effects in models of resource competition (essential and substitutable resources). Both reviewers and I found the topic important and the paper basically sound. We all liked how it integrates Chesson's and Tilman's perspectives on competition, which is itself a valuable contribution. I learned some new things about resource competition from reading the paper, which is great. However reviewer 1, Géza Meszéna, raised some issues and I have some of my own that the authors should address in a revision.*

*The first issue is better integration of existing literature. Meszéna points out some of his recent work, which I agree is quite relevant. I also recall an older paper by Petraitis (1989, The representation of niche breadth and overlap on Tilman’s consumer-resource graphs. Oikos, 56, 289–292) that suggests a different measure of niche overlap in Tilmanian models; could the authors address how their newer Chessonian measure relates to Petraitis's?*

* We agree that Meszéna’s recent work is extremely relevant. Meszéna’s recent paper on sensitivity of community coexistence (Barabas et al. 2014) was published just as we were submitting this manuscript. We are reassured that the expression determining strength of indirect effects in our analysis contains within it the determinant of the community interaction matrix—which is key to understanding community sensitivity in Barabas et al. (2014). In the revision we now make an effort to connect our conclusions more explicitly to their sensitivity framework on lines 170 – 173, line 259 and line 383. At your suggestion, we also provide figures showing resource consumption vectors (figure 2 & figure A1) and discuss how the angle between resource consumption vectors defines Petraitis’ measure of niche overlap and how this relates to Chesson’s measure of niche overlap on line 171 and section 2 of appendix A. As you and Dr. Meszéna point out, our linking of mechanistic resource models to the phenomenological niche difference framework of Chesson is not in itself new. Our contribution is linking this existing theory to current questions in global change ecology. We hope our paper will help guide future global change research by demonstrating to empiricists the utility and relevance of coexistence theory.

*Second, the organization of the paper could be both streamlined and more fully developed. Meszéna noted the unevenness of how the two models are developed in the text and wants more explicit derivations and references to other works. My suggestion is: 1) define direct and indirect effects generally around line 179 using the chain rule; 2) put most of the details of the essential resource model in the appendix (most of lines 185-210); 3) keep equations 12, 13, and 15 in the main text but use rho for niche overlap; 4) describe the equations for substitutable resources in the main text.*

* We had not considered using the chain rule to define direct and indirect effects. After reading your suggestions we found Higashi and Nakajima (1994) and considered their chain rule approach to indirect effects. We also found a useful reference on using the definition of the total derivative to define indirect dependences (Chiang 1984) which allowed us to develop a general definition of indirect effects in terms of partial derivatives in lines 110 through 122. This general derivation of indirect effects between two competing species serves as a guide for our investigations of indirect effects in the more specific instances of essential and substitutable resource competition.
* We have greatly re-organized the equations in the appendix and the main text. We believe our re-organization has resulted in a much more readable and succinct presentation of our analysis. In the main text, we start by introducing a general definition for indirect effects (see response above). We then introduce the essential resource model. We give the definition of niche overlap and show all the partial derivatives required to calculate the indirect effects, and then we give the full equations that define indirect effects in terms of niche overlap. On line 235 we introduce the substitutable resource model, first defining niche overlap in this model (with steps in the appendix), and then showing the full equations for indirect effects in terms of niche overlap. We have greatly simplified the appendix. We reduced the number of equations in the appendix from 66 to 36 and it is now organized into five sections. Section 1 shows how Chesson’s measure of niche overlap can be defined in terms of Tilman’s essential resource model. Section 2 gives additional examples of how Chesson’s measure of niche overlap compares with the geometric definition of niche overlap developed by Petraitis (1989). Section 3 gives the steps for deriving the indirect and direct effects in the essential resource model. Section 4 shows how Chesson’s measure of niche overlap can be defined in the substitutable resource model. In section 5 we show the steps for deriving the indirect and direct effects in the substitutable resource model.

*Some more comments to the authors from me:*

*1) You should emphasize more that these results are valid only when species coexist. Maybe present some numerical results of equilibrium abundance vs. supply point that transcend the coexistence region (showing both direct and indirect effects within the coexistence region).*

* We have more explicitly and formally defined the conditions for coexistence in the main text. Please see equation 10 and inequality 13. We have also added notation to indicate that the partial derivatives 14 – 19 and A26 – A31 are to be evaluated at the coexistence equilibrium.

*2) How about a couple ZNGI-style diagrams showing how the size of the coexist region depends on the consumption vectors (rho).*

* We agree that the ZNGI style diagram is a nice way to visualize niche overlap and the sensitivity of the species to indirect effects. We have added figure 3 to show this and discuss how the region of niche overlap relates both to the angle between consumption vectors and area of the parallelogram formed from their sides (lines 170 to 173). Interestingly, we found that niche overlap defined by Chesson can change even when the angle between resource consumption vectors is held constant. This is a bit beyond the scope of our current analysis but we include a figure in the appendix to demonstrate this (figure A1).

*3) In the essential-resource model, light is used as an example but is treated as a nutrient in a chemostat in the model. In reality light behaves differently due to its asymmetric supply, which has important implications for modeling competition (Huisman & Weissing 1994, 1995). Either mention that this or switch the example to two nutrients like N&P?*

We agree that there are many caveats that come with treating light competition with a diffusion model. Our use of light and nitrogen as our example was inspired by Dybzinski and Tilman (2007), who had some success explaining coexistence among terrestrial plants competing for these resources. Their study stands out as one of the very few field experiments, and probably the most complete for terrestrial plants, to test for coexistence based on essential resource partitioning. They indeed have a section in the paper where they discuss the problem of light competition and cite Huisman and Weissing. They make the case that light can still be modeled using the R\* framework much like other resources. We don’t think our paper is a good place to get into all the problems with modeling light or any other resource mechanistically. We do believe that Dybzinski and Tilman (2007) is a good place to direct a reader interested in real world tests of this model. There are more studies of chemical essential resource competition among phytoplankton, but we thought that including a terrestrial plant example would be a better tie into global change research and specifically the impacts of nitrogen deposition. That said we are happy to switch this to a different example if you think it would be more appropriate. We indicate that there are problems with modeling light competition next to the citation of Dybzinski and Tilman.

*4) The substitutable-resource model is justified as more applicable to animals eating food, but the resource supply is chemostat-based, not logistic as perhaps more appropriate for biotic resources. Again, at least mention it or better yet, change to logistic?*

We agree here that biological resources might be better modeled with some kind of logistic growth, or some other form of population model. We note in the text that a diffusion based model has been used before for zooplankton competition see line 250, but we added text to alert readers that this may be an unrealistic assumption (lines 250 to 251). Extending our analysis to a more complicated competition model with logistic resource supply would be a valuable avenue for future work. Introducing a logistic function in the resource supply equation could potentially alter the relationship with Lotka-Volterra competition coefficients (see Tilman 1982 pp. 197-198) and thus could make defining niche overlap more difficult.

*5) I had a few concerns about the argument for implications for real systems (lines 313-335). First, 2 of the 3 studies that measured rho empirically are currently unpublished, therefore impossible to judge the correctness of. I personally have serious concerns about the methodology of the third. Second, the theory here assumes coexistence is due to competition for two essential resources, but coexistence in the field may be due to other unknown mechanisms. It's not clear that the empirical measure of niche overlap due to some unknown coexistence mechanism would work the exact same way in the formulas derived here as the measure of niche overlap defined by consumption vectors. So I am not convinced of the conclusion drawn in lines 331-333.*

* Good points. Chu and Adler (2015) is now available online and we have updated this reference. We have removed the reference to Narwani et al. 2013 and the unpublished data of HilleRisLambers and Levine. We have also hedged our interpretation of the niche overlap value in field studies a bit. We agree that our analysis can only support conclusions about indirect effects when coexistence is determined solely by resource partitioning. When other coexistence mechanisms are at work, our conclusions about the effects of a change in resource supply might not hold. We added some more specific caveats about using phenomenological niche overlap to infer indirect effects on lines 338 - 344.

*6) In (17), should S\_N be S\_1?*

* Thanks for catching this. We ultimately removed that entire equation.

*Chris Klausmeier*

*Associate Editor*

*xxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxx*

*Reviewer #1:*

*The authors investigate direct and indirect, competition-mediated, consequences of an environmental change on a species. They conclude that the indirect effect becomes very strong when niche-difference diminishes. I am sure that they are right in this. I am not satisfied however with the extent the Authors integrate their work into the existing literature and with the clarity of their math.*

* We try in the revision to make a much stronger connection to previous literature on indirect effects (see reference to Higashi and Nakijima (1994)) and to previous work on niche overlap and community sensitivity. We found Barabas et al. 2014 especially useful and relevant to our work and have cited it (see response to editor above).
* We have greatly streamlined the mathematical presentation—see response to editor above. We have also been more explicit in defining the conditions for coexistence in each model.

*The proper reference point is the principle of competitive exclusion: without niche segregation competitive exclusion applies; coexistence is possible only when species are tuned to be equally fit. Then, an arbitrarily small environmental change leads to immediate extinction of one, or the other, species. This drastic competition-mediated effect becomes more and more moderate with stabilization induced by niche segregation. Such understanding was implicitly present already in Vandermeer (1975, Science, 188:253). Chesson's equalizing vs. stabilizing is the same story, as the Authors point out correctly. Meszena et al. (2006, TPB 69:68) developed the formal theory of community robustness based on niche segregation; several other papers followed the line. Recently Barabas et al. (Ecol. Lett. 17:1479) discussed the issue in context of several, relatively complicated, models. The main conclusion of this approach is that species must differ both in environmental impact and in environmental sensitivity for stabilization to operate; the mathematical formalization is independent of the specific model assumptions.*

* We agree. More than developing a completely novel theory we hope that this paper can introduce empirical researchers to the theory that might help them interpret the indirect effects in studies of environmental change. We clarify the purpose of our contribution at lines 105 to 109.

*The current paper fit into this picture perfectly. The Authors discuss two Tilmanian resource competition models: one with essential and one with substitutable resources. For essential resources they assume that the two species are limited by two different resources. Consequently, the "sensitivity" niches of the two species are distinctly different by model definition; they investigate the overlap of the "impact" niches. For substitutable resources both species are limited by both resources in some extent. Therefore they have to study segregation both in sensitivity (described by their matrix w) and in impact (their matrix q) niches - and they do so correctly. Based on Chesson (2013) the Authors use a niche overlap parameter rho, which becomes 1 for complete niche overlap. The formulas contains a factor rho^2/(1-rho^2), which is the proportional to the inverse of the determinant of the community matrix. As expected, this factor diverges for rho=1, representing the complete loss of stabilizing feedback when niche overlap is complete.*

* It is reassuring that our conclusions mesh with previous work, especially Barabas et al. (2014). We try to link our work with the sensitivity framework developed in that paper on lines 170 – 173, line 259 and line 383.

*My other point is lack of presentation clarity. The structure of the paper is confusing. The model with essential resources is discussed formally both in the main text and in the Appendix. The separation of roles between the two texts is unclear. In contrast, the main text cites only the final result for substitutable resource; both the model definition and the calculations are relegated to the Appendix. Structure of the Appendix does not represent the fact that it presents two different models.*

* We agree that the equations in the previous draft were hard to follow. We outline our reorganization of the equations in our response to the editor above. We hope that by presenting a more general definition of indirect effects (eqq. 2 through 5) at the outset of the main text we provide the reader with a roadmap for the more specific equations further on in the paper. For the essential and substitutable resource models, we introduce the main equations and their assumptions in the main text. Then we show in the main text how niche overlap and indirect effects are linked. We have re-organized the appendix into five sections: one, two and three dealing with the essential resource model, and the four and five dealing with the substitutable resource model. The reader should only need to refer to the appendix for two reasons, first in order to see exactly how we have done the work of translating Chesson’s niche overlap measure into the parameters of the resource competition models (appendix sections 1 and 4). And then to see exactly how we applied the general formula for net and indirect effects (eqq. 3 and 4) to the more specific cases of essential and substitutable resource models (appendix sections 3 and 5).

*More importantly, the mathematical arguments are often unclear. For instance, the equilibrium condition (6), as an example is derived from dynamics (2-3). This is correct only with the assumption, that one of the species is limited by one of the resources, while the other species is limited by the other resource. (Moreover: what do indices i and j mean in this formula?) Coexistence would not exist without this condition, so the Authors seem to take it for granted. However, validity of this assumption depends on the parameter values in eqs (2-3). (The fact that each species is limited by a single resource is a direct consequence of the Liebig law, represented by the MIN operation in eqs. (2-3). However, the formulation itself would allow both species to be limited by the same resource.) Unfortunately, the Authors address this issue nowhere in the main text. Instead, the assumption is stated twice in p. 2 of the Appendix, where it is not really needed: eqs. (A12-A15) are just rearrangements of eqs. (A7-A8).*

* Again we have greatly reorganized the appendix—see responses above. Also in the revision we are careful to more explicitly define the conditions for coexistence and stable equilibrium abundances (lines 150 to 156; and inequality [10]). We also use more specific notation to show that the partial derivatives of interest are evaluated near the equilibrium (equations 14-19, and A26-A31).

*For the case of essential resources it is important (e.g., for deriving (A35)) that the R\* values are not affected by the perturbation. This is true, because each R\* is determined solely by the corresponding species via eq. (6). Again, the Authors fail to point this out. The same assumption would not be true for substitutable resources, as both resources are affected by both species and the environmental change affects their coexistence. The Authors do the right thing (hopefully for the right reason), without mentioning the issue.*

* We are glad we did the right thing, and we believe we did it for the right reasons. This might be a bit of confusion over how we define R\*. R\*’s defined in monoculture are not the same as R\*’s defined when two species are competing. In the substitutable model, if we solve for the sensitivity of the focal species to a change in resource supply and hold the competitor’s abundance constant, this will shift the R\* to a new point on the focal species ZNGI. I think this new point is what you are talking about. This indeed does make it trickier to define direct effects in the substitutable resource model. We think we got the answer right here but we do hope you check again to make sure that both our answer and the explanation are sound. We think this shifting R\* is implicit in our analysis of the substitutable resource model. We have changed the presentation of the analyses quite a bit and hopefully the way we have it now circumvents this problem.

*The Authors cite often Chesson (2013) and Tilman (1982) as source for formulas, without explicitly stating, where to look in the book, exactly which formula of the book is relevant there. Sometimes it is easy to find, sometimes it is not. I gave up checking their equations and look up for their original versions in the citations where they introduced the Lotka-Volterra parametrization. Some resource competition models can be reduced to a Lotka-Volterra model, others are not. In the second case one can still introduce a Lotka-Volterra, as a linearization, and use it only for local approximation. It is a known science. Unfortunately, the Authors present it as if it were some black magic: X and Y told us this-and-that formulas. And the formulas are not easy to identify in the source.*

* We have revised our citations of Tilman (1982) and Chesson (2013) to indicate the page number of the equations that we are drawing from. Our derivation of niche overlap from the mechanistic models in the appendix relies on first finding the Lotka-Volterra equivalence for the mechanistic models. We realize this is not novel but simply wanted to give our steps for deriving the definition of niche overlap. Hopefully our presentation of this is more straightforward in the revised version and we have avoided making it seem mysterious.

*Such lack of real mathematical clarity is prevalent for the whole paper. I found only a single mistake: denominator of the second term of eq. (A12) must contain mF, instead of mC. Hopefully, it is just a typo. And a puzzle: Did they perform numerical simulations? The code in Appendix B contains numerical routines; however no such results are presented. It would be a good check.*

* We corrected this typo in the appendix.
* Indeed, we did perform some numerical checks on the analyses with simple scripts in R and these are presented in the Appendix B. We refer to these numerical results in the main text at the end of the substitutable resource model section on line 278.

*I am sure, that their big picture is correct. I hope that all formulas are correct, they look very reasonable. I spent lot of time to understand and check them - but they should write it up more cleanly. The literature I mentioned may be of help.*

* We are greatly reassured by this comment and we hope our revision has indeed presented our arguments more cleanly. We do hope you and the editor can check all our equations again and make sure we have presented them clearly.

*[signed]*

*Géza Meszéna*

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*Reviewer #2:*

*What a pleasure! This paper is extremely well-written and marries two well-established, but previously distinct, modeling frameworks - Chesson's phenomenological equalizing/stabilizing framework and Tilman's mechanistic resource competition framework. That alone seems worth publication, but the authors go on to present a tidy analysis of direct vs. indirect effects of changing resource supply rates, which they couch in terms of environmental change. I only caught a few hiccups in an otherwise flawless paper:*

* Thank you. We greatly appreciate this positive review.

*Line 26: change "competition" to "competitive outcomes"*

* We have made this change.

*Line 234: "S1" should be "S2" (?)*

* Yes. Thanks for catching this we have made the change.

*Line 252: That this beta is different from the previous beta may be a source of needless confusion… why not use gamma or something else?*

* Good suggestion. In our revision we ended up with a slightly different formulation of indirect effects in which we don’t use the beta term in the equation for indirect effects in the essential resource model at all. This allows us to leave the second beta term in the substitutable resource model because now it is the only one in the paper and there should be no ambiguity.

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