

## **RESPONSE TO REVIEWER COMMENTS FOLLOWING REVIEW ON PCI- ECOLOGY**

[response] I would very much like to thank the recommender and the two reviewers for their comments. I am really impressed with how much effort they have put into reading and commenting on the manuscript, and their comments have, I believe, improved the paper.

The vast amount of time between receiving their comments and submission of the revision has occurred because, after deep contemplation over their comments, I have completely restructured the manuscript. I appreciate that the reviewers probably did not intend for their comments to result in such a significant reworking of the paper, I felt it was necessary to robustly capture their primary concerns. The restructuring and rewriting means that many of the comments below have been addressed by removing some sections, and adding in new sections. This means that not all of the references referred to in the reviews are relevant to the arguments I make.

Below, I explain how I addressed the comments, but because of the restructuring it is not possible to point to particular line numbers associated with the changes. I tried, but it came overly complicated. I do hope that the reviewers and recommend find the manuscript improved. I look forward to their new comments, but do hope they don't require another major restructuring of the text!

### **Limiting resources and dominant causes**

[reviewer comment] Coulson proposes a framework to investigate what happens when a change in community composition alters the dominant cause of death (or of failure to reproduce) by changing the limiting resource. This is a topical issue. Immediately, it bears relevance to studies of context-dependent specialization of species, of potential effects of ecosystems going through bifurcations (tipping points), although neither is treated. The manuscript is accessible and reads well. However it is for a large part a very lengthy description of required components of any realistic eco-evolutionary model that would be able to produce predictions for a particular system. These components are rather cursorily covered, none of the equations proposed are linked into a real model. Two reviewers and myself believe that this manuscript presents a relevant topic and that it is potentially worth recommending. However, a number of issues have to be addressed before we can make such a recommendation on behalf of PCI Ecology. Next to the points raised by the reviewers, I want to point out the following:

The guppy example leads us very easily into the issues addressed and I appreciate it very much. However, I believe the manuscript currently has too much focus on removing predators (or consumers, for plants), i.e., on community changes on a different trophic level than a focal species (the guppy). In another relevant scenario, coexisting competitors might each specialize on a different resource, becoming limiting for each of them. A removal of one competitor could then alter the eco-evolutionary feedback drastically.

[response] This comment underpinned the major restructuring I have conducted. Although I still start with the guppy example, I now focus on the paper on ecological and evolutionary quasi-equilibria, and how communities move between different equilibria following an environmental perturbation. Although I do now consider abiotic perturbations, I still primarily focus on biotic ones caused by change in the structure of the community caused by adding or removing species. After introducing the guppies, and providing some definitions and a description of the motivation for the paper, I now consider properties of ecological and evolutionary equilibria. Next, I consider the biological processes required for these equilibria to be realised, including addressing the paradox of stasis. Then, I consider how models of ecological and evolutionary equilibria can be constructed, before considering how environmental perturbations can generate transient eco-evolutionary dynamics as the system moves between equilibria. I do not develop models for a particular system, but I do explain how models can be constructed, and how environmental change impacts functions leading to transient dynamics between contrasting ecological and evolutionary equilibria. I will do this in a much more technical paper that will likely not appeal to non-mathematicians.

[reviewer comment] Here is my most important remark: the manuscript lacks any definition of what a limiting resource is or of a key factor limiting population growth, and how one should define and determine "the dominant cause of death" or a factor controlling reproduction. This needs to be added. When these characteristics are not defined, they cannot be used to generate or assess predictions. I believe the author refers to a method like  $\lambda$ -contribution analysis, but this is not made explicit, so we can't assess whether that approach is entirely defensible for the intended purpose.

[response] I do define limiting resource as a resource the availability of which determines the primary cause of death or failure to reproduce. I do not explicitly explain how to measure it. The reason for this is I do not want to extend the paper to focus on empirical issues. However, I do answer the question here.

First,  $\lambda$ -contribution analysis, elasticity analysis, structured demographic accounting, or any of these approaches do not identify limiting factors. They identify the demographic rate that most strongly influences some measure of population growth (be it  $\lambda$ , the long-run stochastic growth rate, or population size). Such methods are useful, but they do not identify the factors that limit demographic rates. As an example, consider a predator-limited and a food-limited population. One lives at an asymptotic density of 100 individuals, another at an asymptotic density of 50 individuals. Both populations have an average survival rate of 0.7 and an average reproductive rate of 0.3.  $\lambda$ -contribution analysis will give identical results for the two populations even though they are limited by different processes.

So how can you identify the dominant causes of death or failures to reproduce? By far the best way is experimentally – by removing specific causes and observing what happens in different treatments and the control. This is what we did (repeatedly) with the guppies. The second approach is to post-mortem a random sample of individuals to determine causes of death. In some species, this may also provide insight into failures to reproduce. If there is temporal variation in causes of death, statistical

analyses might suggest limiting causes. For example, if predators fluctuate in abundance then you would expect survival and reproductive rates to fluctuate in tandem with predator numbers. However, as with all statistics, this is only suggestive, as other unmeasured causes may be more important. The final approach, is know your system. In many of the systems I have worked in it is quite clear what the primary cause of death or failure to reproduce is. I believe this is normally the case – good empirical field biologists have a feel for their system. In observational systems, one then needs to either design experiments to test the empiricists hunch (my experience is they are often correct), or model the system in such a way to identify the circumstances where the dynamics predicted from the empiricists hypothesis can be generated given a set of model assumptions. I think my framework can help here.

Detecting the primary cause of death or failure to reproduce is challenging. However, just because something is difficult to measure, or hard to do, shouldn't stop us trying to it. If we decide that identifying primary causes of death or failures to reproduce is important in particular systems, we should design ways to do it. I considered adding some text to address this issue in a 'data required' section. However, the section I wrote did not sit well with the structure of the new papers, so I chose to drop it.

[reviewer comment] Recently, a special issue has appeared in *Functional Ecology on eco-evolutionary dynamics* <https://besjournals.onlinelibrary.wiley.com/toc/13652435/2019/33/1> with much attention for community effects of feedback loops in models and empirical systems. Coulson presents a mix of results on age-structured models, of modelling population and evolutionary dynamics in fluctuating environments, mostly using IPM's.

[response] This isn't quite right. I construct trait-structured models that can be age, sex, genotype, or spatially structured. I do, however, now cite papers in this issue, along with other papers that have been published within the last year.

[reviewer comment] Often the presentation does not do justice to the true origin of a concept. For example evolutionary suicide is not due to Rankin and Lopez-Sepulcre, but to Ferriere, Gyllenberg and Parvinen.

[response] Thanks. In the new paper I no longer refer to evolutionary suicide. I have traced back concepts to the mid 20<sup>th</sup> century and now cite these works.

[reviewer comment] Several modelling frameworks are just omitted (physiologically structured population modelling, epidemiological modelling using ODE's). I believe it is undoable to treat them all well. On the other hand, the bias towards IPM's has no obvious merit either.

[response] I have listed other alternative approaches. I have also justified the use of IPMs. IPMs are data-driven models. They are usually significantly easier to parameterise than the other types of model listed. I am an empiricist, and although

this is not an empirical paper – it is a perspective piece – I like there to be a clear link from data to models. I have justified this approach in the section on modelling.

[reviewer comment] I would therefore prefer that the description of all model ingredients is drastically shortened to bring the focus back on the main issue: predict what happens when a sudden species change in an assemblage or community alters the eco-evolutionary feedback drastically.

[response] I have significantly shortened the section on modelling, and instead focused the paper on what happens when a system is perturbed away from an ecological and evolutionary equilibrium. Thanks for this comment. It took time to address, but I think it has improved the manuscript significantly.

[reviewer comment] The manuscript stays a bit unclear on what the timescale is where limiting resources will usually change. Is adaptation really relevant if species composition changes often? How often does a switch in key-factor occur? What with organisms that have a metamorphosis?

[response] This is a good point. I have added paragraphs about this into the final section.

[reviewer comment] The manuscript treats the specialization of traits to environmental conditions. However, there is no mention of trade-offs. They need to be discussed, the focus is too much on single traits now (such as body size).

[response] This is a good point. I now discuss trade-offs, and particularly life history trade-offs. I link these to resource acquisition, and discuss why they can be so difficult to detect. I now focus on resource accrual traits, and life history traits, but also I still discuss size-related traits, as these are fundamental to ecological dynamics.

[reviewer comment] I believe the statement on p. 35 that no model combines all ingredients of Figure 5 is an overstatement. Please consult for example the models by Gavrillets and coworkers in the group of papers called "CASE STUDIES AND MATHEMATICAL MODELS OF ECOLOGICAL SPECIATION". I believe the link between the issue treated here and such models is strong and insufficiently treated. Consider Rundle and Schluter (2004. Natural selection and ecological speciation in sticklebacks), box 9.5: They use results of eco-evolutionary modelling to predict scenarios where speciation does not occur, but repeated invasions instead. The same trick can be applied for species removals. Hence I believe much of the framework needed exists and has been used to predict effects of changes in community composition, with results maybe needing a different interpretation in view of the questions asked here.

[response] I have removed these statements, and clarify that the complete feedback loops have not been incorporated into structured population models that are the focus of this paper. I did read the papers highlighted, but these do not, in fact, do this either, and referring to them would be distraction. The papers are impressive,

but they do not include the complete feedback loop I develop in Figure 5. For example, they do not focus on limiting resources, or on how a change in limiting resources might impact ecology, evolution, or eco-evolution. The model that comes closest to doing this Bhat et al. 2019 which is cited.

[reviewer comment] The Emu example: I would use it to propose colonization and evolution on islands as a general scenario where changes in limiting factor are relevant. For an overview of patterns of selection on small and large body size, please consult Blanckenhorn, W. U. (2000). The evolution of body size: what keeps organisms small?. *The Quarterly review of biology*, 75(4), 385-407.

[response] This is now cited as requested. I have also significantly altered the emu section following the extensive restructuring following the reviewer comments.

[reviewer comment] Best regards, Tom Van Dooren

## Reviews

[reviewer comment] *Reviewed by Jacob Johansson, 2019-02-15 21:21*

I have read the manuscript "Causes of death and failures to reproduce, limiting resources, ecological dynamics, and selection: how to evolve a low predation guppy, and cause a trophic cascade" by Tim Coulson.

### OVERALL COMMENTS

This manuscript is about the ecological and evolutionary consequences of removing a species from, or adding a species to, an interactive community. In particular the manuscript focuses on limiting resources and the possibility that adding or removing species might affect which resource becomes the most limited resource. As an illustrating example the manuscript starts out discussing how in the case of guppy communities, the presence of a predator could imply change the dominating selection pressures from being mainly determined by competition for food to being mainly determined by competition for predator-free space.

The manuscript is very well written and uses an efficient combination of theory and illustrative empirical examples to guide the reader through the many dynamical effects of biotic perturbations occurring at different levels, from birth and death processes and demography to population dynamics and evolutionary outcomes. Further the manuscript discusses how processes occurring at different levels may interact with each other and cause more or less surprising feedbacks. The paper culminates in the proposal of a modelling framework which integrates these multi-level dynamics.

I suppose the manuscript is intended as a forward-looking review or perspective article with the main aim of pointing out new research areas which becomes possible to study with an integrative approach to study eco-evolutionary responses. In its current form I think the manuscript provides many interesting thoughts, but I also think it could be improved if it would be linked more deeply to previous theory and modelling of eco-evolutionary dynamics in interacting communities.

[response] Thanks for these thoughtful comments. They nicely summarise the objectives of the paper.

[reviewer comment] Firstly, several papers not cited here have been devoted to the study of ecological and evolutionary consequences of species removal. These includes models which are simpler than the framework proposed here, e.g. Lotka-Volterra community models and adaptive dynamics (with much less genetic detail for example). I will provide some examples below. For this reason I think the manuscript would benefit from (A) outlining more precisely which aspects of species-removal responses require further study, and back this up with references and (B) provide more precise arguments why the study of these phenomena require the use of the rather complex model framework proposed here. I am thinking of Occam or perhaps Einstein (?): "Everything should be made as simple as possible, but not simpler". An

advantage of simpler models is that they are more transparent and often lend themselves to analytical treatments.

[response] I have significantly restructured the paper such that figure 5 in the previous version is now figure 2. This makes it easier to stress all the processes that contribute to eco-evolutionary dynamics. Each of these processes has been shown to be important in some situations, so I believe a general framework that captures all of them is a useful step towards identifying the general circumstances when each process should be incorporated into models, and when they can be ignored. The focus of the paper is now less about modelling (although there is a section on this as it helps readers formalise the challenges), but much more about transient dynamics between equilibrium states in the face of environmental change.

This is not to say that simple models are not useful. Of course, they are of enormous utility, and I have developed many myself. Both simple, and more complex models are central to gaining biological understanding. The objective of this paper is not to review all possible modelling approaches, but rather to consider how a change in limiting factor of a population can result in communities moving from one stationary ecological and evolutionary equilibrium to another via the processes outlined in Figure 2.

In restructuring the paper, I have updated the reference list. However, the restructuring means that all not citations listed below are relevant to the revision.

[reviewer comment] Secondly, and following up on point (B) above, there already exists some model frameworks (e.g. eco-genetic models, see below). which have a similar scope as the one proposed here. Thus, I think it is questionable if we actually need a new framework, or if potentially eco-genetic models (or other existing frameworks) could be used with some adaptations. If the conclusion is that existing frameworks might work equally well, then the manuscript could be shortened in this regard and perhaps end in another way, e.g. further ideas and suggestion for systems and questions that would be interesting to study.

[response] There are indeed several modelling frameworks, and I now highlight a few of them. To date, none of them capture the full feedback loop in Figure 2. I also now explain how a number of these modelling frameworks have arrived at similar conclusions. However, as explained above, the aim is not to compare or contrast particular modelling frameworks, it is to consider how biotic perturbations generate ecological and evolutionary dynamics as systems move from one equilibrium state to another.

[reviewer comment] My overall feeling however, is that the manuscript has a big point in highlighting that changes in which resource type is limiting might be likely to define eco-evolutionary responses to species loss or other perturbations. More precisely I think that most theory on evolutionary responses to environmental change in ecological communities mainly has considered adaptation to shifts in "substitutable" resources as opposed to "essential" resources. For example, quite some theory considers evolution in which species shift from one food resource to

another, or shift from using one habitat to using another (substitutable resources). In contrast, a shift from food limitation to predator limitation represents imply a shift from one essential resource (food) being limiting to another essential resource (predator-free space) being limiting. Similarly, both nest holes and food are essential resources for many bird species. Shifts in which essential resource is limiting may have more profound effects than shifts in substitutable resources.

[response] This is an excellent point, and I have moved this aspect of the paper to the fore. Indeed, the paper now focuses on how an environmental perturbation can change the limiting resource of a focal population, leading to the community it is a part shifting from one stationary state to another, particularly if “keystone” species are impact. I found this criticism really useful in restructuring the paper.

[reviewer comment] But if the manuscript would make an argument that shifts in limiting resources is a neglected theme in eco-evolutionary responses, that might need some support. Ground-breaking theory resource limitation in essential as opposed to substitutable resources by Tilman (e.g. 1980) could be cited. Some eco-evolutionary consequences (in terms of optimization and co-existence) of essential/substitutable resources are discussed by Vincent et al. (1996). A review by McGill et al (2006) which argues that community ecology has focused a bit too much on pair-wise interactions and distinct preferences (for substitutable resources) might also be relevant. A recent paper by Higginson (2017) discusses how nest sites in birds and pollinators is now becoming a more limited resource and leading to competitive exclusion in systems which were previously more structured around competition for food.

Resource limitation plays a role also in controlling the outcome of competition when resources are substitutable. For example, if two predators compete for two prey species, the predators which can suppress the population abundances of the prey species to the lowest level and yet survive will win the competition. The predator can co-exist if they have different preferences however and each suppress their preferred prey. This occurs in Lotka-Volterra-style food web models for example, and is fairly well studied. I suppose the manuscript is not about that, but perhaps this is worth clarifying?

References:

Higginson, Andrew D. 2017. "Conflict over non-partitioned resources may explain between-species differences in declines: the anthropogenic competition hypothesis." *Behavioral ecology and sociobiology* 71.99.

Tilman, D. (1980) Resources: a graphical-mechanistic approach to competition and predation. *Am. Nat.* 116, 362–393

Vincent, T. L. S., et al. 1996 Trade-offs and coexistence in consumer-resource models: it all depends on what and where you eat. *The American Naturalist* 148:1038-1058.

Mcgill, B. J., Enquist, B. J., Weiher, E., & Westoby, M. (2006). Rebuilding community ecology from functional traits. *TRENDS in Ecology and Evolution*, 21: 178-185.

[response] I have agonised over this comment for some time. Although I agree there is a literature on essential and substitutable resources, I have decided that this distinction is not central for the arguments I make. I have consequently not cited these papers. Nonetheless, if the reviewer is adamant that this distinction has to be made, then I can add in a section describing the difference between the two resource types.

[reviewer comment] MORE SPECIFIC POINTS

Following up my points above I will provide some specific suggestions below regarding literature which I think the manuscript should be related to and which in some cases may require some larger adjustments of the text. The manuscript already has a lot of references, which is natural since it covers so many areas. I do not suggest all the below references need to be cited. Rather, I hope that these suggestions would help defining the novelty in the manuscript a bit more and make it possible to shorten sections where previous work has been done.

#### 1. Eco-genetic modeling and individual based eco-evolutionary models

The so called “eco-genetic” model framework presented by Dunlop et al (2009) bears many similarities with the framework proposed here (Fig. 5). Similar to here that model describes processes at many scales. Specific building blocks include: evolving traits, inheritance model, individual growth model, density dependence, environmental variation, phenotypic plasticity, sex structure, mating systems and more. I have not done a detailed comparison, but it seems to me that the proposed framework in principle corresponds to such an eco-genetic model. Potentially the genotype-phenotype mapping is not included in the Dunlop et al framework, but on the other hand that framework includes a nice take on plasticity (via reaction norms) which seems generic and not discussed here. In Dunlop et al there are further references to applications of eco-genetic models (in fisheries). These studies give some idea of the strengths and potential weaknesses of this approach.

A recent review of individual-based eco-evolutionary models of different complexity is further provided by Romero-Mujalli et al. 2019.

References:

Dunlop ES, Heino M & Dieckmann U (2009). Eco-genetic modeling of contemporary life-history evolution. *Ecological Applications* 19: 1815–1834

Romero-Mujalli, Daniel et al. 2018 Individual-based modeling of eco-evolutionary dynamics: state of the art and future directions. *Regional Environmental Change* 1:1-12.

[response] The focus of the revised paper is much less on which modelling approaches to use, but is now on transitions between ecological and evolutionary states. However, I do now cite these two papers.

[reviewer comment] 1. Evolution in species interactions

The manuscript discusses evolution in species interactions (e.g. last para on page 22 to top of page 24 and page 30). There are relatively few citations here in spite of this being a huge research area, especially within the field of adaptive dynamics, and addresses many issues including community evolution, speciation and diversification (see refs below). I think this should be acknowledged, however I also think it might be possible to argue that there has been little focus on resource limitations and essential resources here (I think, but I am not 100%). Another reason to link the manuscript more to the field of adaptive dynamics and related frameworks is that the manuscript once published then could become more easily accessed to a broader modelling community, which I think will be inspired by the ideas in this manuscript.

Some references:

Loeuille, N. and Loreau, M. 2005. Evolutionary emergence of size-structured food webs. *Proc. Natl. Acad. Sci. USA*, 102: 5761–5766.

Dieckmann U & Doebeli M (1999). On the origin of species by sympatric speciation. *Nature* 400: 354–357

Van Dooren, TJM, M Durinx and I Demon 2004 Sexual dimorphism or evolutionary branching? *Evolutionary Ecology Research* 6: 857-871.

Abrams P. A. 2001. Modelling the adaptive dynamics of traits involved in inter- and intraspecific interactions: An assessment of three methods. *Ecology Letters* 4:166-175.

Ripa J., L. Storlind, P. Lundberg & J. S. Brown. 2009. Niche co-evolution in consumer-resource dynamics. *Evol. Ecol. Res.* 11: 305-323.

Brännström Å et al. 2012. Modeling the ecology and evolution of communities: A review of past achievements, current efforts, and future promises. *Evolutionary Ecology Research* 14: 601–625

[response] I have completed removed the section on the evolution of species interactions. Not because it is not interesting, but in the new structure of the paper I do not discuss this aspect. I am preparing another manuscript on this topic, where I will cite these papers. Thanks!

[reviewer comment] 2. Theory regarding ecological and evolutionary consequences of species removal

The ecological consequences of species removal from an interactive community has been studied quite a lot. The classic study by Paine (1966) could be cited as it identifies keystone species, i.e. species which if removed have a large impact on the community structure, relevant for present manuscript. Theoretical studies have tried to identify keystone species in model food webs. One interesting phenomena which may occur when removing species from a community is “community closure”, i.e. once you have removed some species they cannot reinvade again, i.e. the community has changed irreversibly (Lundberg et al. 2000). That in turn links to the idea of “alternative stable states” and “attraction domains” in ecological systems where removal of species can lead to irreversible changes and trophic cascades (i.e. when a significant perturbation or removal of important (keystone) species moves the system from one domain of attraction to another).

Johansson & Dieckmann (2009) introduces the Evolutionary Domain of Attraction (EDA) as an evolutionary analogue to the ecological concept. The idea there is that if you perturb an evolutionarily stable community (an ESS community), for example by temporarily subject it to a new selection regime, ensuing evolutionary responses may or may not restore the original community after the perturbation. Some ESS communities may have a large EDA meaning that it will return to the original ESS also after large perturbations. In some cases, a system may have multiple possible evolutionary equilibria (several locally stable ESS solutions). In such systems a perturbation may cause a transition from one ESS to another. The guppy system discussed in this manuscript could be thought of as a system with two evolutionarily stable states. The addition/removal of predators causes the evolutionary transition from one ESS to another. It is conceivable that the removal of a guppy prey species instead would not cause such drastic changes. Perhaps the lost prey species may over time be replaced by a similar one, by speciation or invasion and the original system be restored. Such a perturbation would hence not cause a transition to another ESS: the community would stay within the evolutionary domain of attraction of the original ESS community and be restored after the perturbation.

There is also a connection between the guppy discussion and the concept of “evolutionary keystones” introduced by Brown and Vincent (1992). In their model, removal of the predator caused evolutionary convergence in the niche positions of their prey, resulting in competitive exclusions. Hence the presence of the predator was key to maintain coexistence among the prey. Similarly, Johansson & Dieckmann studied the removal predator species from a slightly more complex food web of 5 species including two predators. After removal of one of the predators, the original system is restored, but when removing the other triggers evolutionary responses which collapses the food web. In this system there are thus two alternative evolutionary stable states. An evolutionary keystone species can thus be seen as one which if removed causes the system to enter another evolutionary domain of attraction.

For the section of trophic cascades caused by evolutionary change, it might be relevant to cite theoretical work dealing with the issue of evolutionary change in one species causing severe changes in population densities of other species. One model studied by Bronstein et al (2004) considers co-evolutionary extinction cascades in

mutualistic networks. Another theoretical study (Georgelin et al 2015) considers plant-pollinator-herbivore communities and shows that evolutionary changes in herbivores triggered by environmental change (pesticide use) may cause extinctions among pollinator species.

These studies are generally based on more minimalistic models than the framework proposed in the present manuscript. Many of them consist of Lotka-Volterra population dynamic models where the interaction coefficients are trait-dependent and selection gradients derived directly from the population dynamic models. Therefore, they cannot make predictions regarding for example population structure. They nevertheless show that many aspects of eco-evolutionary responses to species removal can be studied using relatively simple approaches.

## References

Bronstein, Judith L., Ulf Dieckmann, and Régis Ferrière. "Coevolutionary dynamics and the conservation of mutualisms." (2004).

Brown J. S. & T. L. Vincent. 1992. Organization of predator-prey communities as an evolutionary game. *Evolution* 46:1269-1283

Georgelin, E et al 2015 Eco-Evolutionary Dynamics of Plant–Insect Communities Facing Disturbances: Implications for Community Maintenance and Agricultural Management. *Advances in Ecological Research*. 52: 91-114.

Lundberg, Per, E. Ranta, and V. Kaitala. 2000. Species loss leads to community closure." *Ecology Letters* 3: 465-468.

Johansson, J., & Dieckmann, U. (2009). Evolutionary responses of communities to extinctions. *Evolutionary Ecology Research*, 561–588.

Paine, R. 1966. Food web complexity and species diversity. *Am. Nat.* 100: 65-75.

Solé, R.V., Montoya, J.M. and Erwin, D.H. 2002. Recovery after mass extinction: evolutionary assembly in large–scale biosphere dynamics. *Philos. T. Roy. Soc. B.* 357: 697-707.

[response] The heavily restructured paper actually draws more heavily on these ideas. I have consequently cited the majority of these papers in the revision. Thank you for pointing me to these papers.

[reviewer comment] DETAILS:

Page 4, middle

"Obviously, when  $a = 0$ ,  $E(\lambda) = VE$ ."

This is not really obvious from the approximation  $a = \log(\lambda_{dat}) - VE$ . If one linearizes  $\log(\lambda_{dat})$  one gets  $\log(\lambda_{dat})$  approximately equal to  $\lambda_{t-1}$ . Perhaps I am missing something.

[response] Oops – well spotted! There was a typo in this equation. It has been corrected and now enters the paper towards the end.

[reviewer comment] Page 12

"More generally, in such cases some heritable phenotypes will have long-run stochastic population growth rates that are greater than 0, others will necessarily have rates that are less than zero, but the average long-run stochastic growth rates across competing phenotypes will be 0."

Here you could cite Ripa & Dieckman 2013 who considers evolution in stochastic environments (both for clonal and sexual (diploid) inheritance) Ripa, J., & Dieckmann, U. (2013). Mutant invasions and adaptive dynamics in variable environments. *Evolution*, 67(5), 1279–1290. <http://doi.org/10.1111/evo.12046>

[response] I have removed the offending text. But I do cite Ripa and Dieckmann as requested when I make an equivalent comment.

[reviewer comment] Page 14

"This is most easily achieved by assuming that competing strategies are clonally inherited with (near) perfect fidelity (Metz et al. 1995). For sexually reproducing species this assumption is violated."

With sexually reproducing species it becomes trickier to study evolution of competing strategies. But the adaptive dynamics approach (i.e. Metz et al. 1995) has been extended to sexually reproducing species and can thus be used in this context:

Metz J. A. J. & C. G. F. de Kovel. 2013. The canonical equation of adaptive dynamics for Mendelian diploids and haplo-diploids. *Interface Focus* 3: 20130025.

See also Ripa & Dieckmann above.

[response] I have altered the wording. I do have a paragraph where I discuss adaptive dynamic approaches. I am actually a fan of adaptive dynamics, but this is not really what this paper is about. I have added a number of adaptive dynamic citations to acknowledge the important work that has been conducted in the field. A key new paragraph is:

"Biologists are often interested in the evolution of life histories, without focusing on evolution of the resource accrual traits that influence energy acquisition and the optimal life history (Stearns 1976). To do this, life history strategies are assumed to be clonally and near perfectly inherited, rather than as arising as a consequence of underlying resource accrual traits (Childs et al. 2004). Under this assumption, the

reproductive value of a life history will be associated with its long-run stochastic growth rate when measured in the presence of competing, clonally inherited, life histories.  $R_0$  can usually (but not always) also predict which clonally inherited life history will grow to dominate all others (Metz et al. 1992, Metz et al. 1995, Ripa and Dieckmann 2013). Adaptive dynamics and game theory consequently rely on the assumption of clonal inheritance. The approach is useful as invasion approaches can be used to identify the evolutionarily stable life history strategy, and in particular the optimal value of life history trade-offs such as those between offspring size and offspring number. However, genetic architecture significantly influences ecological and evolutionary dynamics (Schreiber, Patel, and terHorst 2018), except in very specific cases (Geritz and Kisdi 2000, Metz and de Kovel 2013), and I consequently focus on cases where inheritance is not assumed to be clonal.”

[reviewer comment] Page 27

"A third route to large body size is the ability to access resources that may be unavailable to smaller individuals."

Perhaps trees fit in here as well? Evolutionary arms race to access light and suppress competitors. I am just curious.

[response] This is almost certainly true. However, I am not a sufficiently competent plant ecologist to stray into discussion of trees.

[reviewer comment] Page 30

" Such a process will occur in systems where resources are limiting, where density- and frequency-dependent selection operates, or where coevolution is observed (Roughgarden 1971, Thompson 1999). "

Here is a good place to cite adaptive dynamics papers mentioned above, because most of them considers frequency and density dependent selection.

[response] I have now removed this paragraph, and section. I do cite adaptive dynamic papers elsewhere in the text.

[reviewer comment] Fig. 1.

It would be good with worded titles of the top panels, just like in the bottom panels and the mathematical symbol in the top panel looks odd. What = 1.046? Perhaps also colour the population dynamics in B with red to get a consistent coloring scheme which can be immediately appreciated from the figure.

[response] Figure 1 has been removed and replaced with a new figure.

[reviewer comment] Figure 3.

Here I think it would be good with some more details about the simulations (for reproducibility). It seems like the original distribution of traits (the  $z_i$ s) are drawn from a normal distribution. How are the offspring generated?

[response] The old version of Figure 3 has been removed.

[reviewer comment] Signed by Jacob Johansson

[response] Thanks Jacob!

[reviewer comment] *Reviewed by anonymous reviewer, 2019-02-03 21:18*

Review on 'CAUSES OF DEATH AND FAILURES TO REPRODUCE, LIMITING RESOURCES, ECOLOGICAL DYNAMICS, AND SELECTION: HOW TO EVOLVE A LOW PREDATION GUPPY, AND CAUSE A TROPHIC CASCADE' by Coulson T

This manuscript describes the case how structural models can aid in understanding ecological population dynamics and natural selection – particularly Integrative Population Models and Individual Based models.

[response] For clarity, I focus on integral projection models rather than integrative population models. I understand this was simply a typo, but thought it worth clarifying for the record.

[reviewer comment] The manuscript first describes well in detail the components of life-history-fitness linkages and how these may be implemented in a modelling framework. In particular, the author discusses the role of various sources of 'resource limitation' in driving fitness and selection. For most parts the manuscript is clear and pleasant read and would be a valuable contribution.

[response] Thank you.

Your comments were extremely valuable, and made me realise I needed to restructure the paper. They reveal that I have made assumptions about the level of theoretical background that readers will have that are clearly misplaced. As you will see, my responses to your questions run to many pages, and this would result in making the manuscript even longer than it currently is. I have significantly refocused the paper, and in doing so have tried to make things clearer and use less technical language.

[reviewer comment] However, the sections (starting page 31) on how to implement these models, left me wanting. I would like to see a discussion how we can better integrate empirical data collection with implementing such models – as it seems that some of the short comings of our ability to use these in natural populations come from lack of right kind of temporal population size, demographic and life-history/trait data, and data on the key limiting resources in any given system. Currently it would seem to be possible to apply such models to a limited number of model systems. I think the field would progress more if we could aim to collect more of relevant long-

term data in nature (in addition perhaps to implementing similar data on more controlled but manipulative systems on organisms with sufficiently fast generation times). Would be great if the 'data needed' aspect was explicitly covered and the non-modeller readers among us would be advised on what type of data would be useful to collect for increasing inferential power and rigour of such structured models – so that they could be implemented on a wider range of natural systems.

[response] I have reduced the focus on models as I never intended the paper to be about a particular modelling approach.

One of the great strengths of Integral Projection Models is they can be data driven. What this means is that the types of statistical analyses that empiricists so often conduct results in equations that can be directly used to parameterise this class of model that I do describe. I should also note here that just because something is difficult to measure, or hard to do, shouldn't stop us doing it. If we decide that identifying primary causes of death or failures to reproduce is important in systems, we should design ways to do it.

[reviewer comment] Sometimes the use of references is insufficient, and the manuscript is rather long and could be shortened somewhat – I make some suggestion below to this end. I hope my comments help to improve it further, as I think it would be a useful paper for many evolutionary ecologists.

[response] Thank you. Your comments have definitely helped improve the manuscript. I appreciate the time you have spent on my paper.

[reviewer comment] Specific comments that I hope help to increase readability & value further:

P2: I found the start of the introduction, using the empirical guppy example a bit lengthy – before coming to the main goal of the manuscript. It is nice to illustrate with an empirical case the biological relevance, but I think the first 2 paragraphs could be condensed to essential. Particularly since the guppy example is repeatedly returned to in different places. In fact, it might work best if the guppy system, to the parts relevant to the topic at hand, was described in a separate box – to which one could refer to in the text. (The first 3 lines on page 3 “The guppies...factors that limit the population's growth” could in fact be moved earlier on, for a sharper start)

[response] The comment made me realise that the manuscript started rather abruptly with a specific observation, and that this observation might confuse readers given the title and abstract. However, it was the guppy observations that motivated me to develop the ideas described in the manuscript, so it is an appropriate point to start with. I tried putting the text in a box as proposed, but it didn't work well. I have consequently altered the abstract, but still start the paper with reference to the guppy system.

[reviewer comment] P5: As a non-modeller I had to check the word 'moments' used in this context. Might be useful (if also empiricists are targeted) to clarify such jargon.

[response] I have removed this jargon from the revised manuscript.

[reviewer comment] P5: I found the reasoning for the use of clonal versus sexually reproducing species in different aspects a bit confusing. May be useful to explicitly state why in some place clonal reproduction and in other sexual reproduction is assumed (= why is not one or the other used for the different section – or more interestingly both compared).

[response] I have removed the offending text. I do now refer to clonality in relation to adaptive dynamics and game theory that rely upon these assumptions.

[reviewer comment] P6-1st line P7: I would like to see clear mentioning of the caveats of making inferences about historical determinants of selection – else this statement seems rather trivial, at least for within species comparisons.

[response] I have removed the offending statement from the new version of the manuscript.

[reviewer comment] P7, last 3 lines: The relevance of comparing the scenario of two different equilibria, with both  $a = 0$ , is not clear. Perhaps provide empirical example to illustrate this. Neither is it clear why the shift between the two equilibria is expected to last only a few generations. Is there a basis for this?

[response] In the Trinidadian guppies, high predation populations are limited by predation. Their population fluctuates in size, but does not show any persistent temporal trend. The long-run stochastic growth rate is consequently zero. If we now remove all the predators, the population will grow until it is limited by food availability. Low predation guppy populations live at a higher density than high predation ones. Their populations fluctuate in size, but once an equilibrium is reached, they too show no long-term temporal trend in numbers. Their long-run stochastic growth rate is equal to 0. It only takes a generation or two before for the population size of guppies to increase from being predator-limited, to being food-limited, once predators are removed. The switch between the two equilibria consequently does not take long. This pattern is likely general when a population's limiting factor changes. Figure 1 now demonstrates this point.

[reviewer comment] P13, 2nd paragraph. This paragraph seems to me to be linked to traits that allow adjustments to buffer against environmental variation = phenotypic plasticity in physiology, behaviour, morphology etc. Does this refer to phenotypic plasticity only or are there other forms of traits that allow resilience in face of environmental variation? Or does it not matter for how selection operates whether the 'resilience increasing' traits are plastic?

[response] Great comment, and this is exactly right. I have added the following text to the end of the last paragraph: -- anything that helps buffer populations from environmental variation. I discuss plasticity and adaptive evolution and refer to both processes in the new Figure 1.

For interest, i) the trait itself could be plasticity, ii) a trait that helps individuals cope with environmental variation could be plastic, but iii) it could also be entirely genetically determined. Selection can act on traits regardless of how they are determined.

[reviewer comment] P14, 1st paragraph: I would imagine that in several empirical study systems, it would be possible to compete the different life-history strategies against each other empirically also. Would be useful to state (for those who work on such malleable systems) how this could be empirically directly tested (also to confirm results of simulations). Also, state more explicitly why this assumption is violated for sexually reproducing species and what difference it makes. Can we only test clonally reproducing species? If so, how strong are our inferences?

[response] Models always make simplifying assumptions, much in the same way that experiments are simplifications of nature, consisting of only one or two treatments that are varied while everything else is controlled as best as possible. One frequently made simplifying assumption is clonality. Clonal systems have indeed been used to test predictions from some models that assume clonality.

So why do theoreticians assume clonal reproduction in many models? The primary reason is this allows a life history strategy to have long-term fitness – something I now mention. For example, imagine that you have a yellow and a blue life history strategy that are competing against one another. Blue individuals always produce offspring following the blue life history strategy, while yellow individuals always produce offspring following the yellow life history strategy. You now compete them against one another in a particular environment, and you see whether one outcompetes the other. The best strategy will win out, potentially driving the other one to extinction. You could do this in an experiment if you have blue and yellow strategies in real life, or you could use virtual individuals and do it on the computer in a simulation.

In sexually reproducing species you cannot assess fitness in this manner. This is because the genotypes, and consequently the life history strategy, of an offspring is expected to be half way between that of its parents, plus some variation (the reason (non-identical twin) siblings do not perfectly resemble one another in diploid species). In sexually reproducing species each individual is consequently genetically unique, while in clones they are not. Lineages also mix. In sexually reproducing blue and yellow strategies, a blue male and yellow female might mate, producing a green offspring. How can you measure lineage fitness in such a case? It is much harder than in the case of clonality, but that is how sexual reproduction works.

The difference the sexually reproducing and the clonal strategies is genetic inheritance, and the question becomes how do you measure fitness in sexually

reproducing species? One way, is you assign fitness to alleles (population genetics). Another way is you assign it to individuals (quantitative genetics and much empirical behavioural ecology). There is a significant literature on the definition of fitness in different contexts and I now discuss this in the paper.

In fact, the appropriate definition of fitness is always the genetic representation of an entity at time  $t$  in the descendent population at some time point in the future. The entity could be an allele, a genotype, an individual, or a strategy. The challenge is that the way you calculate this depends upon how each entity is inherited. I also discuss this in the new version of the manuscript. Assuming clonality make life easier.

Interestingly, most modellers favour one particular approach. It is usually the one they feel most comfortable with. Jacob Johansson, who was reviewer 1, nearly exclusively cites adaptive dynamics papers that assume clonal inheritance in his review. My preference is for non-clonal models, and I tended to cite those papers in the original version of the paper. The choice of model framework really depends upon the biological question being asked, or the reason for constructing a model. Like experiments, all models simplify the real world. The choice of simplifying assumptions to make to address a particular question takes practice.

[reviewer comment] P14, 2nd paragraph: you mean variation in developmental plasticity / ontogeny? Would be useful to clarify and exemplify.

[response] Not necessarily. The trait could be developmentally plastic. Or it could be genetically determined. For example, in quantitative genetics, it is sometimes assumed that a trait like body size measured at one age is actually a different trait from body size measured in the following year. The argument is that a different set of genes can contribute to different traits at different ages. If some of the genes that contribute to the traits at different ages are shared, the traits are said to be genetically covary. Because I go on to talk about genotype-phenotype maps, I do not provide examples.

[reviewer comment] P15: I think this is a bit thin argument for what we can do (and should do) to build better genotype-phenotype-fitness maps, such as could be achieved by investing G-P maps in more detail and via high throughput phenotyping (e.g. Houle et al. 2010 review on Phenomics) and accounting for gene-phenotype network structure.

[response] I have removed the offending paragraph from the text.

[reviewer comment] P17, 3rd paragraph, line 3: this would seem to me to assume that the food source productivity (e.g. grass or algal production) is stable and does not evolve in response (which in many cases of biotic interactions of herbivory or predator-prey does not hold). How does the scenario change in eco-evolutionary feedbacks where the food source may evolve? Same holds for p 18, 2nd paragraph: failure could also be if assumed that the food does not evolve in response to consumption?

[response] I did not make this assumption. The statement holds regardless of eco-evolutionary feedbacks or evolution of the resource. If a trait is determined by resource availability, then individuals that acquire many resources will express a larger phenotypic trait value compared to those that express smaller phenotypic trait value. The feedback between evolving resources and their evolving consumers is really exciting, and I now discuss this throughout the paper. I have also rewritten this section, and hopefully it is clearer.

[reviewer comment] P18-19. I found the heading of 'Inheritance – genetic and otherwise' intriguing but the content somewhat disappointingly not covering the recent discussions on non-genetic inheritance. How this matters for our inferences on evolution, for example via cross-generational effects of resource limitation, would be a useful addition. Right now the content covers standard population genetic/quantitative genetic ( $V_a$ ) based inferences. P19: earlier in the text evolution was defined as either allele frequency change or heritable phenotypic change. Here only allele frequency changes are covered primarily and the linkages with different inferences based on heritable phenotypic change could be better covered.

[response] I have removed this section in the revised version of the manuscript.

[reviewer comment] P21, 1st paragraph. The forms of non-genetic inheritance is rather poorly covered here. It would be useful to more explicitly state the main types, as well as how (if) it affects our inferences about ecological and evolutionary processes. The recent book by Bonduriansky and Day on "Extended heredity" could be a useful reference here. And perhaps at least briefly touch on under the structural models section how these could be implemented and what information is needed for us to be able to infer the relevant contribution of different modes of inheritance on direction and magnitude of eco-evo feedbacks.

[response] I have removed this paragraph. In fact, I have written an entirely new paper on this topic using some of the arguments in the previous version of this paper, and intend to submit it imminently.

[reviewer comment] P22: how does the within species variance (rather than mean distance) affect our inferences and predictions on co-evolution? Also P23: The concept of individual specialization and how it links to eco-evolutionary feedbacks could be better covered here.

[response] In rewriting the manuscript, I have removed this section. I do discuss individual specialisation as a potential mechanism to maintain additive genetic variance.

[reviewer comment] P26: I could not quite follow from all that was written earlier, why we now focus on body size – comes abit out of the blue- Of course body size is a key life-history trait and typically a strong fitness determinant, as well as intimately linked to resource mediated selection (via metabolic requirements) – but this could be made more explicit to make clear why body size receives this extended treatment

in the manuscript. References for metabolic theory of ecology should be better covered in here.

[response] A good comment. I do still focus on body size in part of the manuscript, but linkages between sections are hopefully now clearer.

[reviewer comment] P27, 2nd paragraph: the island rule comes out of the blue and relevance is not clear for the general goal of the manuscript. Seems to take away attention from the core. In general, I find the body size evolution section in need of streamlining and condensing. It just seems to bring different alternatives for body size evolution and some seem rather peripheral – yet is not explicit enough how this will help us with those structural models...and evolution of life-histories / eco-evo feedbacks in general. Would be good to streamline this and link better to the goal of the manuscript.

[response] I no longer discuss the island rule, but do include a section on body size as a resource accrual trait.

[reviewer comment] P30: In general, unless we are talking of population dynamics (of one focal species or of two interacting species) I am not sure we expect the dynamics to continue 'ad infinitum'. I think such continuous process takes place under certain assumptions (the same factors feeding back on each other, the continued ability of the target species to evolve etc...).

[response] I don't follow the logic here. If two species interact in a way that can generate feedbacks with one another, why would embedding them in a broader community prevent feedback loops occurring? Community dynamics are often more unstable than population dynamics. Indeed, a key debate in community ecology is how are they stable at all. However, this text has also been altered in the rewrite.

[reviewer comment] P30: 2nd paragraph, line 5: It would be perhaps useful to consider the potential for indirect eco-evolutionary feedbacks – that may be much harder to both track. Also, how predictable would we expect such feedbacks to be (i.e. when the ecological selective agent and the phenotype determining fitness may not influence each other directly) ?

[response] I do consider these explicitly now.

[reviewer comment] P31, 2nd paragraph: I am convinced that we would require significant amounts of data – much more, and much more detailed, than is available for most empirical systems. However, not stating how we could overcome this challenge, seems a bit unsatisfactory. Also, that we are not able to measure eco-evo feedbacks in many systems with currently available data, does not mean that they do not occur in nature. Hence the last statement could be modified to something 'Although it is empirically difficult to demonstrate eco-evolutionary dynamics in nature, in some cases eco-evo feedbacks have the potential to generate pronounced eco-evo dynamics'. I would like to see a clear definition for eco-evo feedbacks versus eco-evo dynamics, references to empirical work that has been able to show

such consequences, as well as suggestions (if possible to make) under which situations we expect eco-evo feedbacks to lead to dynamics. (I think that for the field to advance, we should be more consistent in separating feedbacks and dynamics, although other seems to put all under the umbrella of dynamics.)

[response] I have removed the offending text. You are right, that many data are required, but that should not prevent us considering dynamics of entire communities.

[reviewer comment] P31, 'Tying strands together'.

I would have liked to see a lead here to the complexity of the real world (see also Hendry 2019 'Critique of eco-evolutionary dynamics', Functional Ecology Special Issue), the type of data needed to do so, and how making sense/tracking the dynamics can be aided by understanding the processes and models laid out in this manuscript.

[response] I don't understand this comment. Which key processes is figure 2 missing? Indeed, in some ways this paper is a critique of existing eco-evolution, but it is more than that. It describes a possible way forward.

[reviewer comment] The importance of mating system could be made more explicit and be an interesting part of the discussion in context of eco-evo dynamics

[response] I would be happy to provide a further example but I do not understand why this is singled out. What the mating system does is determine the distribution of genotypes given the alleles contained in gametes of selected parents. These feed through to influence the distribution of the new generation's phenotypes via development.

[reviewer comment] P33: I found the set-up of the paragraphs for the different functions somewhat confusing – yet these components (functions of survival, reproduction, development, inheritance) are really important for predictions of eco-evolutionary feedbacks as well as understanding the models. Would be good to structure the text for clarity (perhaps also numbering the functions by 1,2, 3, 4 would be helpful for the reader, see minor comments below).

[response] I have removed this section, and considerably simplified the modelling texts.

[reviewer comment] As to function 3 (development) – this seems to me reflecting plasticity (including developmental plasticity) of the phenotype. This could be more explicitly stated. In general, I think we need more attention to this component in understanding eco-evolutionary feedbacks (e.g. given that the plastic components of the phenotype can be an important determinant of speed and magnitude of ecological change, and these can change over the course of the ontogeny or life-time of the organisms).

[response] A good comment, and correct. I now explain how this component captures phenotypic plasticity. I have added a new figure that should demonstrate this (I hope).

[reviewer comment] P34. To me the treatment of the inheritance function is rather narrow. Most standard approaches to eco-evo feedbacks only consider additive genetic effects, whereas non-genetic inheritance, or genetically determined parental (typically maternal) effects can strongly affect evolutionary speed and direction – and on the same token, we would expect also effects on eco-evo feedbacks. Any detailed treatment to this end is not needed for the current manuscript, but I think it would be useful to make the point explicit that these other forms of cross-generational effects may alter the scenarios based on additive genetic inheritance.

[response] Indeed the inheritance function is exactly where genetic and non-genetic inheritance is captured. I have explicitly explained this now. The inheritance function consequently captures both genetic and non-genetic inheritance, and the non-genetic component can capture parental effects.

[reviewer comment] P35-36: 2nd paragraph. As noted in my general comment above, it would be useful to state what we (empiricists) need to do to be able to use these models – more explicitly state the type of data needed.

[response] Please see earlier responses. I have toned down the modelling text extensively and in doing so hope this comment is no longer relevant.

[reviewer comment] Which ecologically relevant eco-evo model systems are possibly suitable for this? I find the long list of different models conducted a bit too abstract to be useful – it does illustrate the many different aspects, but perhaps would work better as an overview table? Can we say something more about when each type of model is best used or how they can be integrated - to create that 'single model' that captures better the organization of the different components influencing eco-evo processes? Do we not need the data that allows building the details of these models?

[response] I am afraid I disagree with this comment. The list of work is required as it shows that each of the steps in Figure 2 has been developed within the framework I propose. I appreciate that this paragraph might not appeal to empiricists, but I think it is crucial to theoreticians so they understand that each of the steps has been developed, peer-reviewed and published.

[reviewer comment] P38, 1st paragraph. Saying that such models are 'frequently not analytically tractable' begs the question of what should we do then? Can we overcome this? Or what do we do with the models at all if they are not tractable?? Perhaps the last paragraph – using models that do not have to capture all feedbacks, but still can be informative about core processes, is meant to be one solution. Which is fine, but could be better stated.

[response] Analytically tractable has a well-defined meaning. It does not mean that a model cannot be analysed. An analytically tractable model can be understood without iterating the model. You can look at the model and completely understand the dynamics it will predict for any set of parameter values without actually running the model. Such models are typically very simple – like the logistic model of population growth. Models that are not analytically tractable, perhaps because they are frequency-dependent or contain eco-evolutionary feedbacks, need to be iterated, with each simulation having a different set of parameters. In some cases, a single iteration can be used to make more general inference. They are semi-analytically tractable. Many stochastic models in ecology and evolution are like this. A model that is not analytically tractable does not mean they are not tractable. They can still be analysed. In the worst-case scenario, insights will only hold in the vicinity of the set of parameter values, however this is still useful. Most models can be analysed in ways that provide more general insight than this worst-case scenario.

There are a number of reasons for models to be constructed. Models can be developed to clarify ideas on how systems are constructed, or how feedbacks work. Abstract models like this reveal how different forms of linkages might result in particular dynamics at different levels of biological organisation. Alternatively models might be constructed to understand how one particular process might generate a particular type of dynamic. For example, the logistic model of population growth only contains one process – density-dependence. It reveals how density-dependence can generate a range of dynamical patterns. No one believes the world is solely governed by density-dependence, but that does not mean the equation lacks utility. It can be thought of being equivalent to an empirical experiment where everything is kept identical across treatments except for density. The experiment might reveal that density is important, but it might not be the most important driver of dynamics in the field. Models can also be used to make testable predictions – this is often how they are used in management, providing insight into how a particular intervention might impact dynamics.

In this paper I use models to clarify ideas on how different levels of biological organisation are linked. I believe I provide a fairly comprehensive overview of all key processes. I then review how each link in the feedback loop has already been incorporated into simpler models. This provides insights that may or may not hold as more realism is incorporated into models. It is also sometimes possible to build a complex model, and to then simplify it. For example, what happens when we move from diploid genetic inheritance and simplify to clonality. Or what happens when we linearize a frequency-dependent feedback loop? How do dynamics change?

Nonetheless, I have removed the term analytically tractable.

[reviewer comment] P39. 'What can we say without models' section was rather uninformative. It basically seems to present what empiricists can do by hard work and conducting a lot of well-designed field studies and experimental manipulations. What I would like to see is how we best can take the power of both worlds, integrating the models with empirical work to inform each approach of the best way to tackle the core questions at hand (e.g. which life-stage is the most important in

mediating eco-evo feedbacks, how does sexual selection influence eco-evo feedbacks in contrasting ecological environments, which species interactions in a foodweb are likely to result in eco-evo-dynamics, how does the mode of inheritance influence direction and magnitude of eco-evo feedbacks, etc etc).

[response] I found this to be an extremely interesting comment. Empiricists cannot provide generality. They can identify a pattern in a particular empirical system, and such observations might be general. However, without models, it would be impossible to conclude the pattern was general across systems until all systems were tested. Clearly that is impossible. What models do is allow biologists to identify the circumstance required for an empirical pattern to be general. It may then suggest another set of experiments, or observations, that are required.

This logic is at the heart of the physical sciences and is universally accepted. It is not so widely accepted in biology, and I don't understand why – it is after all just the scientific method. Empirical observations are necessary, and theory is necessary. Of course, they should be linked! To suggest otherwise is incredibly surprising to me.

Nonetheless, I have removed this section in revising the manuscript.

[reviewer comment] Page 39

the case of the guppy. Is the most interesting question to be addressed really 'why low predation environments result in parallel evolution of phenotypes'? Wouldn't the simple answer be there is parallel divergent selection (loss of predators)? Wouldn't it be more interesting to understand HOW this parallel selection operates (the eco-to-evo pathway in the feedbacks) and how do these parallel phenotypic changes influence eco-evo feedbacks? Again, some of this text is rather repetitive and adding a box with the guppy system as an example case would help making just the case of relevant points without the need to repeat the text in other places of the manuscript.

[response] I started the paper with an observation on guppies. If I did not return to it, it would be left hanging. This is why I return to it.

[reviewer comment] Although the emu case (I assume the start was not an e-mail chick, Page 39, 2nd paragraph... ..) is somewhat entertaining as a heuristic thought exercise, I did not find the 1.5 page description necessary nor informative for our understanding.

[response] I disagree. I would love the emu example to be a thought experiment that is conducted by empiricists working on a range of different systems, and by modellers who champion particular approaches.

[reviewer comment] Minor (RWD= reword):

At several places it seems original work is not well referenced (statements made without reference) – I indicate those below.

P6, 1st paragraph, 5th line – RWD to ‘increasing survivorship or fertility at any age...’

[response] Changed.

[reviewer comment] P6, line 6: provide the reference for the case of Elk in Yellowstone

[response] I am not aware of any reference that actually says this (I have worked on the system for a decade). That is why I use the word ‘likely’. It is certainly plausible given our understanding, but appropriate have not, to my knowledge, been collected.

[reviewer comment] P7, line 4: State explicitly that this refers to guppies experiencing high predation environments. (Note that this is an example case were it would work perhaps better to have the guppy system presented in a separate box). Same unclarity holds for P8, 2nd paragraph (guppy example). This refers to the case of guppies inhabiting low predation environments?

[response] Text altered in the rewrite.

[reviewer comment] P7, line 5: RWD to ‘Many of the phenotypic...’

[response] Text altered in the rewrite.

[reviewer comment] P7, line 19. This statement about ‘prior to removal of predators’ is confusing. Does this refer to an empirical case study with experimental removal?

[response] Text altered in the rewrite.

[reviewer comment] P9, Line 2: allow who to survive? Check wording of this sentence for clarity.

[response] Text altered in the rewrite.

[reviewer comment] P9, 1st paragraph, last 3 lines. It would be helpful for the naïve empirist to have a reference for selection differentials and need to understand patterns of inheritance already here (I am not that naïve reader, but I think this may be useful for others that may not be familiar with evolutionary inferences – but still may work on relevant empirical study systems).

[response] I now cite Price (1970) here.

[reviewer comment] P9, 3rd paragraph, line 7: RWD to ...’ result in selection on phenotypic traits associated with detection, ....’

[response] Text altered in the rewrite.

[reviewer comment] P9, 3rd paragraph, line 9: I think we can not assume that any population ‘will’ adapt – without making further assumption about trait heritability and

lack of evolutionary constraints. RWD to something like ‘Given sufficient time, and that assumption underlying evolutionary responses (e.g. that traits are heritable), the population may adapt and express adaptive traits ...’ (Else sounds rather deterministic).

[response] Text altered in the rewrite.

[reviewer comment] P11, line 4: clarify that this means the mean fitness of the population.

[response] Wording changed to state this.

[reviewer comment] P11, line 6 RWD to ‘consequence of this is that the...’

[response] Wording changed.

P11, 2nd paragraph, line 6: RWD to ‘non-zero selection differential...’

[response] Text altered in the rewrite.

[reviewer comment] P11, last paragraph: This hole nesting bird sentence is unclear and confusing. RWD.

[response] This section has been removed.

[reviewer comment] P12. State at first mention what the beta’s refer to (beta0 and beta1).

[response] No longer referred to in the new version.

[reviewer comment] P12, lines 1-4: I found these sentences unclear. Why do we expect this and how is this evolutionary suicide manifested in this case ? L 3: RWD to ‘..., evolution will favour fewer, larger individuals...’. Again saying that ‘evolution will result’ sounds too deterministic.

[response] Wording changed, and the evolutionary suicide sentence now reads “with a solitary individual exploiting all available resources”.

[reviewer comment] P13: It was not clear to me what the first alternative of evolution was. RWD perhaps to ‘I now consider how evolution can proceed by reducing VE’.

[response] Sentence changed to read: “I now consider how evolution can proceed via selection to reduce  $V_E$ ”

[reviewer comment] P13, last paragraph: Not clear why ploidy of species matters. State more explicitly.

[response] Please see my answer on the definition of fitness when inheritance mechanisms differ – e.g. clonality or sexual.

[reviewer comment] P16, 2nd paragraph: State for the non-expert reader what the breeding value is – or at least provide reference.

[response] It is now defined and a referenced is provided.

[reviewer comment] P16, 2nd paragraph, line 4-5: RWD the last sentence of gene expression and how environment can affect gene expression. (e.g. what are the 'environmental drivers? Also sentence structure unclear). In general, this section against seems to relate to phenotypic plasticity (via gene expression) yet this link is poorly made.

[response] This is an interesting query. Phenotypic plasticity is defined as the same genotype producing phenotypes in different environments. In the scenario I describe, the same gene expresses a different breeding value in different environments. I am not sure that this is strictly phenotypic plasticity. Nonetheless, I have removed this comment.

[reviewer comment] P17, 2nd paragraph, line 1: you mean developmentally plastic traits – or traits that are expressed at maturity or that are impacted by senescence ? RWD.

[response] Not necessarily. It could be any trait that develops with age. But the trait might have different breeding values at different ages. It does not necessarily need to be developmentally plastic. The reviewer views any developmental process as plastic, but that is not necessarily correct.

[reviewer comment] P17, 2nd paragraph, line 10: RWD to '...they will have large values...'

[response] Wording changed.

[reviewer comment] P18, 3rd paragraph, line 4: RWD to '... is that there is little competition...'

[response] Wording changed.

[reviewer comment] P18, 3rd paragraph, line 2: provide references for these statements about how artificial selection operates, as well as for line 7 on quantitative genetic covariances, and for evidence for these methods working well in absence of the covariances.

[response] I am not aware that anyone has argued this before. I do not know of any appropriate references. Also moved to later in the paper.

[reviewer comment] P20, 3rd paragraph line 2: RWD to 'base pair substitutions...'; line 3: RWD to insertions..' line 6: unclear what is meant by 'such' genes. Clarify. Line 8: provide reference for this insight on mutations

[response] This section has been entirely removed in the rewrite.

[reviewer comment] P20. It would be useful to be more specific here as to which definition of epigenetic inheritance is referred to here (the narrow definition of methylation etc alteration or wider parental effects).

[response] This section has been entirely removed from this manuscript.

[reviewer comment] P21, 2nd paragraph: It would be useful for those not accustomed to think of eco-evo feedbacks to explicitly state that an important difference these biotic resources make (as opposed to non-biotic) is that they can evolve in return.

[response] Surely only biotic things can evolve? I don't really understand this comment. Sorry!

[reviewer comment] P21, last paragraph. Provide reference for interaction coefficients capturing functional responses and conversion rates.

[response] This section has been removed.

[reviewer comment] P22, 2nd paragraph: 'However' seems redundant here. Remove.

[response] Change made.

[reviewer comment] P24: It would be useful to have the subheading f 'Trophic cascades' here. Line 4, provide reference and definition or empirical example of trophic cascades. Last 2 lines on this page could be moved after the 1st full paragraph for easier reading.

[response] I have completely rewritten this section.

[reviewer comment] P25, 2nd paragraph. This is to me generally a very unclear paragraph. For instance, does it mean evolution of any other species altered the dominant causes (and hence selection) of death and successful reproduction in a dominant species – or rather the evolution of the dominant species itself – or either ? RWD for clarity. RWD to 'In such a case, the dominant species was unable...'. Also, what is meant by dominant species? Dominant in numbers? Dominant in role in ecosystem (aka keystone species)?

[response] This whole section has been rewritten.

[reviewer comment] P25, 3rd paragraph: Again I think it would be easier to make these arguments more streamlined if the guppy case would be overviewed in a separate box.

[response] Please see previous comment. The guppy example motivated this paper. Putting in a box would result in poor flow to the ms.

[reviewer comment] P26, 2nd paragraph - 3rd line: Provide reference for 'relative metabolic rate' - 4th line: RWD to ...'than those that are smaller ' - Why is it key that the exponent is less than unity – for the current discussion?

[response] This sentence has been cut in the rewrite.

[reviewer comment] P27, 2nd paragraph - line 6: RWD to 'For example, food-limited populations of...'

[response] Wording changed.

[reviewer comment] P29, Eco-Evolutionary feedbacks

Is the reason that compelling empirical evidence is missing for eco-evo feedbacks that they are poorly defined or that they are difficult to demonstrate? I would rather think the reason is the latter (though I also agree that they are often poorly defined).

[response] Both. They are poorly defined, often simply with a box saying evolution and another saying ecology, and arrows between them. That is not a definition. If they are not well defined, how can there be compelling evidence for them? There are models that define eco-evolutionary feedbacks explicitly, of course, but most are never parameterised for real systems. The few examples of where eco-evolution is well defined and models are parameterised are cited.

[reviewer comment] Here again the contrast in definitions earlier on in the manuscript for evolution defined as change in allele frequencies or heritable phenotypic change. The allele frequency change is the narrowest sense, but given the increased realization that non-genetic (at least non-DNA sequence change) inheritance mechanisms appear common, I would consider these other alternatives. Especially since for ecological relevance of the eco-evo feedbacks any transgenerational effects can be important.

[response] Changing the definition of evolution to include non-DNA sequence change is not a sensible suggestion. This is not to say that processes like non-genetic inheritance and phenotypic plasticity cannot impact the rate, or outcome, of evolution (change in allele frequencies). Of course they can! But they do not need a redefinition of evolution.

[reviewer comment] Line 4: RWD to '...is frequently defined as the dynamics of populations, communities,...'. Or otherwise give a clearer definition (rather than how

they are measured). Also: provide reference for the definitions. Line 5-6 'If we stick with this definition...' seems redundant, delete.

[response] I have completely removed this section.

[reviewer comment] Line 8: I think we need the mediating effect of the phenotype for allele frequency change to have any eco-evo feedbacks.

[response] Except that was not what the models I discussed in that paragraph do. Nonetheless I have removed the offending text.

[reviewer comment] 2nd paragraph, line 2: you mean constant positive trait-fitness association ? I guess we would not expect exponential growth of the population if the association was negative.

[response] We would. In a positive association the phenotype increases in size as the population grows. In a negative association the phenotype decreases in size as the population grows. Nonetheless, this is no longer relevant as this section has been removed.

[reviewer comment] 2nd paragraph – It would be easier to follow this argumentation (biological relevance) if here the reader was reminded of what the denominator and numerator of the selection differential equation represents.

[response] This section has been removed and will be published in another paper.

[reviewer comment] P30, 1st paragraph: The sentence on line 2-3 ('What all this means...') seems repetitive to what as said in the previous paragraph.

[response] I have removed this section from the paper.

[reviewer comment] P30, 3rd paragraph. What type of 'parameters' do the beta's present? Slope of relationships? Any?

[response] Yes, any. I have removed this equation.

[reviewer comment] P31, 1st paragraph, line 4. RWD to 'increasingly'

[response] Wording changed.

[reviewer comment] P32. Would be useful to have a subheading 'Modelling eco-evolutionary feedbacks' –before going into the models.

[response] I disagree with this. Tying it all together requires models. I have not added in the proposed subheading, but the focus of the paper has changed.

[reviewer comment] P32, 3rd paragraph, line 5: I don't understand what this really means '...the number of individuals within a population with each combination of components of the phenotype' ? Be more explicit.

[response] This section has been completely rewritten.

[reviewer comment] If these models are to be generally usable, perhaps refer to statistical packages that are available for users (if there are such)?

[response] Modelers don't typically use statistical packages to construct models. They might use R or SAS to conduct statistical analyses to identify parameters that are then used to parameterise their models. A model does not have to have some R package to make it usable.

[reviewer comment] P33, line 3: which two functions? Which other functions? This becomes clear below but these can be tied together and made easier to read if 'two functions (i.e. survival and reproduction) and two other (i.e. development and inheritance)...')

[response] Wording changed in the rewrite.

[reviewer comment] P38, 1st paragraph, line 10: The sentence of '...have spurred on the modelling approaches I have been involved in developing' is not very informative and can be deleted. The manuscript is lengthy as it is.

[response] Sentence removed.

[reviewer comment] P40, last paragraph, line 8: RWD to '...which phenotypic trait will evolve' (or which phenotype will evolve?)

[response] Sentence removed.

[reviewer comment] P41, 2nd paragraph. Provide references for presumed predation pressure on ground feeding birds. Is the idea that emus lost the ability to fly prior to predation becoming a significant source of mortality based on phylogenetic or historical inferences or some such (in which case references would be appropriate) or only speculation ? In general, I find this emu section rather speculative and also uninformative. In particular the last paragraph could be completely be left out.

[response] It is speculation, and I do not have a reference to support it.

[reviewer comment] Last sentence of conclusion. I do think that the next step would be conduct studies in different populations where the limiting factor differs – or has changed recently so predictions can be made and eco-evolutionary (or ecological and evolutionary) dynamics observed. But it seems to me we generally require more data and, in particular, be able to identify the key limiting factor (which may require substantial data in most system) – to then test whether the framework proposed in this manuscript helps us to make more accurate predictions.

[response] This comment is no longer relevant given the significantly restructured version of the paper following reviewer comments.

[response] Thanks, once again, for the comments. I found them helpful and stimulating.