

Thanks to Tom, Katja, and Jacob for persevering and providing such useful and comprehensive reviews. They have once again improved the manuscript. I have addressed the majority of their concerns. There are one or two I disagree with and have not modified the text to address. I do hope that is OK.

This manuscript by Coulson previously called "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", presents a thorough revision which addresses most of the previous comments by two reviewers and myself adequately. The two reviewers have a number of remaining remarks, which in my view can almost all be addressed with some rewording or the addition of references.

Thank you. I have addressed the vast majority of comments raised via wording changes, and via the deletion of one section that Katja Räsänen found overly speculative.

In my view, this manuscript in a way provides a generalization of the concept of "resource holding power" to a broader eco-evolutionary context.

I found this comment interesting. I agree that when resources are defensible, resource accrual traits could evolve to increase resource holding power. However, I see this as a particular possible outcome of the arguments I make, rather than something underpinning the entire paper. I think this is something that would be worth exploring in an additional paper, rather than being explored here. I have made no changes in response to this comment.

On line 555 the manuscript cites a redefinition of fitness in terms of energy, but there are usually several resources required to complete a life cycle and as L561 states, there can be several primary causes of death and failure to breed. I would appreciate it if the manuscript could give a bit more attention to situations where there are several primary causes or limiting resources, or stress the conditionality of an argumentation on there being a single primary cause or limiting resource when that is the case.

This is a really interesting comment. I think that there will, in general, only be one **primary** cause of death, and that will be the cause that kills the highest proportion of individuals. However, it is true that different age classes, or size classes may experience different causes of death. An example of this comes from Yellowstone elk. The young and old almost exclusively die in the jaws of predators, and predation is the primary cause of death killing the highest proportion of individuals. The prime-aged individuals rarely die. The things that kill them, primarily accidents or the occasional pathogen, do not cause a high proportion of death, and are consequently unlikely not a major driver of evolutionary change. A really interesting case would be where one age-class is predator-limited, and another is food-limited, as evolution then has two problems to solve. Interestingly, I am not aware of any systems where this has been described. Nonetheless the point is a good one and I now include the following statement: "Within in a population there is usually one dominant

cause of death that kills the largest proportion of individuals. However, individuals of different ages, or sizes, may experience different causes of death. Nonetheless, at the level of the population there is usually a primary cause of death associated with the limiting factor. Individuals within a population compete for energy in the presence of a limiting factor that determined the primary cause of death and failure to breed (Berryman 2004).”

Best regards, Tom Van Dooren

Reviewed by Katja Räsänen, 2020-03-24 14:20

Reviewer comments on “Environmental perturbations and transitions between ecological and evolutionary equilibria: an eco-evolutionary feedback framework”

This comprehensive, revised manuscript provides a conceptual and mathematical framework for understanding equilibria of ecological and evolutionary processes. The manuscript aims to link processes regulating population growth and community dynamics with evolution of species interactions and resource accrual & life-history traits. Overall, I find the manuscript very useful and interesting – and it was an enjoyable read for the majority of the individual sections. Even for a “modelling dummy” like myself, it really managed to explain the processes and models in a comprehensive and intuitive way.

Thank you for the complimentary comments; I am pleased you enjoyed reading it.

At the same time, there are some aspects that I think still could be improved to make it an easier read. Particularly is it is a very long ms and the topic complex. The core comments relate to better addressing & acknowledging the pertinent literature at places, clarify some conceptual points and to further structure it (e.g. by add subheadings in few places) to facilitate reading also for non-experts. The figures are clear and useful.

I followed the majority of comments, but as I explain below, I do not add in another level of sub-headings, as I felt this would add an additional level of complexity. However, I have tried to improve the flow between paragraphs where subheadings were proposed.

Below I make an overview (to guide also myself through the complexity of the text), some major and some more specific (including many minor) suggestions. I hope these are helpful and aid in further improving the manuscript.

#### Overview

As the manuscript is long and covers many core concepts and processes, I find it useful to provide an overview of the sections as follows. (I would recommend the author also to consider such overview before going into the actual text to give the reader a frame to follow). It starts from introducing the classic empirical case of the high and low predation adapted Trinidadian guppies, and asking what determines ecological and evolutionary (quasi)-equilibrium in either a high or low predation state. It then introduces the paradox of

stasis and the paradox of maintenance of genetic variance and touches upon species co-existence theory – and different levels of biological organization. The focus is on several places on resource accrual traits (i.e. traits that influence ability to detect and acquire resources). After the introduction section, the manuscript covers (with some notes):

1) A mathematical break down of demographic population models in the context of Eco and Evo equilibria (which is very nicely done). 2) Conditions that are required for stasis in Eco and Evo processes. 3) Potential solutions to the paradox of stasis in the context of quantitative genetics • This is a rather lengthy and complex section (including various processes from life-history theory to stabilizing selection and frequency dependent selection) – but informative (see specific comments below). 4) Focus on body size as a major resource accrual trait and how body size links to population growth rate and its dependence on environmental sources of variance 5) Population models, focusing on structural and individual based models -particularly IPMs • suggesting that models based on demographic, developmental and inheritance functions can aid in understanding eco-evolutionary dynamics (broadly speaking). It explains the IPMs in more detail in this context. 6) Exploration on how systems can transition between different equilibria states – as a consequence of abrupt environmental change. 7) The ms then ends with speculating on processes that may have been driving the evolution of the emu (to a large bodied, flightless bird via resource and predation mediated selection) and returns briefly to the Trinidadian guppies and trophic cascades.

On lines 162-170 I inserted the following paragraph that replaced the previous description of the structure of the paper. “In the remainder of this paper I provide 1) a description of the conditions required for a system to be at ecological and evolutionary equilibria, 2) discussion of how these conditions can be achieved in nature, and the observation of two paradoxes that need to be addressed: the paradox of stasis for size-related phenotypic traits, and the paradox of standing additive genetic variation, 3) solutions to the paradoxes, 4) a more detailed treatment of the evolution of life history and body size, which I consider to be central to solving the paradox of stasis, 5) an examination of models that can describe systems in ecological and evolutionary equilibrium, 6) a focus on how systems transition between different equilibria states as a consequence of abrupt environmental change, and 7) a brief concluding section.”

Major comments:

In several locations, I still feel there is a jump in the logic – I indicate below (by JMP) where I noticed it. Perhaps it will help to make some simple adjustments with concrete statements that link across paragraphs in these situations. For this case, using some subheadings in select long paragraphs where there is a topic shift might most easily solve the issue. In several cases also core references should be given - I indicate those below by REF. Where wording should be corrected or checked, I use RWD for “reword”

Thank you. This was a very useful way of structuring your review.

I still think the section on Emma-Steve is too speculative. No references are given what the current hypotheses are for the evolution of body size and flightless ness in ratites – or if there is any evidence that would support body size as an resource accrual trait (L895-896). I

am by no means either a phylogeneticist or phylogeographicist – but it seems to me (by a brief check of recently published literature, such as Faux & Field 2017, Yonazewa et al. 2017; Thomson et al. 2018) that there is much discussion about what drove the evolution of flightless ness and large body size of ratites, and body size evolution of emu’s. To write this section without that context in mind, is not in my opinion useful – neither really appropriate. So either the context of open questions – and to what extent there is evidence for resources and/or predation to have influenced their evolution – should be widened (briefly), or then this section should be left out. As fun as it is and as cute – I am sure – Emma-Steve was, the current treatment is a bit “lose”.

I have removed the section on the emu.

Detailed comments

P3: I still struggle a bit to get at the core of the paper when we start by a general description of the Guppy system. But this may be a matter of style.

This is indeed a matter of style. I am keen to start the paper with an empirical observation.

L45-46 would more logically be moved after L33-34.

I disagree, and once again, consider this a matter of style.

Core general REFs should be provided at L33-34 already.

Done.

In general, the way that I write is to combine insights from a number of papers and from personal observations or discussions, and I like to reference papers that contributed to the narrative towards the end of a paragraph. Often, no single paper provides an explicit statement to support each sentence in the narrative. For example, in this case, aspects of the high and low predation guppy environments are gleaned across the papers cited, yet no one paper covers all aspects of these environments.

In some of the REF requests below, this is the case, and this is why the references from which the narrative is constructed are cited towards the end of paragraph, often just before the concluding, synthesising, sentence that concludes the paragraph.

L60: REF needed

I am not aware of any reference that actually states this for guppies. This is synthesising sentence of a paragraph where numerous references are provided. No additional reference has been added.

L68-69: There is something odd with the wording here. Perhaps RWD to “The genetic, phenotypic trait, xxx and sex structure of all populations...” ?

L71: RWD “This means that there may be...”

L74 – I do not follow the logic here from L71-73 to L74 about species going extinct.

These three comments refer to a paragraph that has now been substantially revised. It now reads: “What characterises the Trinidadian freshwater ecosystems when they are at ecological and evolutionary (quasi)-equilibrium in either the high- or low-predation state? The size and genetic-, phenotypic trait-, size-, age-, and sex- structure of all populations in

the community show no persistent temporal trends with time. I consequently use the term 'equilibrium' to describe a stochastic but stationary state of populations and the community. This means there may be temporal fluctuations in the sizes and structures of populations within the community, but none will exhibit a long-term temporal trend (Lundberg, Ranta, and Kaitala 2000). I use the prefix 'quasi' to acknowledge that some slow temporal patterns in genotype frequencies may occur in cases of slow co-evolution between species, but, that in general, natural systems frequently achieve states where statistics describing each population with the community remain within bounds for protracted periods of time (Figure 1; (Lewontin 1969, Bronstein et al. 2004). A consequence of this is there will also be no persistent temporal trends in community size and structure, or energy and nutrient flows."

L84 – JMP in logic from evolutionary equilibrium to definition of phenotypic traits.

I had used phenotypic traits in the previous sentence, but I understand the link wasn't clear. I have now rewritten this sentence to: "When I refer to phenotypic traits, I define them as any attribute that can be characterised at the individual level, ranging from molecules within cells to lifetime reproductive success."

L88 – RWD to "...under directional selection, and heritable, but do not evolve..."

Unchanged – the grammar is correct.

L90 – is this full sentence needed?

Unchanged – I believe it is logical, and relates the reader back to the quasi-equilibrium definition above.

L99-100 – I am missing some of the logic here. If phenotypic traits are at optimum, presumably there would be no selection and additive genetic variation would be maintained? (Else I see the "no paradox" in additive genetic variation being maintained in presence of selection – be it directional or stabilizing).

If there is an optimum phenotypic trait value, there is a fitness peak – i.e. a phenotypic trait value where fitness is maximised. Over time, we would expect alleles associated with all sub-optimal phenotypic traits, i.e. those that are not at the optimum, to be eroded. If all individuals have optimal phenotypic trait values, then there will be no phenotypic variation within the population. In most evolutionary models, an absence of phenotypic variation translates to an absence of underlying additive genetic variation. The paradox is we observe significant amounts of additive genetic variance within most populations, even though their phenotypic traits are at their equilibrium, and often assumed to be at their optimum value. I have not addressed this concern in the text at this point, as the argument is rehearsed later in the manuscript.

L117-118: JMP across paragraphs

I have moved the text "Second, I introduce the concept of resource accrual traits." To the beginning of the following paragraph.

L120 – Here I assume you refer to the "selective environment" within which an individual performs. What about the developmental environment which may influence phenotypic

variation in resource accrual traits? I see this comes later in the text, but might be useful here to clarify which aspect of the environment you refer to.

Sentence rewritten to state “These traits determine individual abilities to acquire resources from the ecological environment in which they find themselves, which in turn determines continued rates of development and chances of survival, reproduction and dispersal at each age and size.”

L125: Add REF

Although personally I am not persuaded a reference is needed to support a concept that is so central to evolutionary biology, I have added a reference to Crow and Kimura.

L131: Add REF. The role of transgenerational plasticity (TGP) is not addressed – although you refer to non-genetic inheritance. Would TGP possibly affect the potential for ecological or evolutionary stasis (for example)? I don’t see a need to dwell in this in any length – but given theoretical and empirical work indicating that TGPs can drive/influence population dynamics – it may be useful to briefly refer to such work.

I have removed the end of the sentence that stated “via non-genetic inheritance” here as it is a distraction away from the main message. The complete sentence now reads: “These interacting individuals include its parents, who can use their attributes to influence offspring phenotypes via controlling the developmental environment”.

L142: State (see REF above) or provide couple of REFs as a reminder to the reader.

I have provided a citation to Reznick and Endler (1982).

L147: RWD. Should this be “...evolution also optimizes ..” ?

Good spot – corrected.

L155 – RWD. Something missing in the logic/wording relating to the limiting factor.

The sentence now reads “I primarily focus on the guppies as they provide a well-characterised example of a general phenomenon: if the primary causes of death or failures to breed in a population are altered by a biotic or abiotic perturbation, so too is the limiting factor, the population dynamics (Schindler 1974, Sibly and Hone 2002, Rohr et al. 2003), selection, and the course of evolution (Walters and Juanes 1993, Fishman and Willis 2008).”

L157 – This rapid change in population size and selective regimes would presumably require rapid environmental change also. Clarify.

Reworded to state “Such a perturbation results in rapid change in population size and selective regimes in a focal species and the species with which it interacts. The new regime selects for phenotypic traits and trait values that allow organisms to optimally detect, acquire, and utilize food given the primary causes of death and failures to breed in the new environment in which they find themselves.”

L188 – RWD to ..”there may be 23 individuals..”

Changed.

L211 – What about environmental effects on gene expression – which would possibly influence genetic inheritance?

Genetic inheritance is the transfer of alleles from parents to offspring. I do not follow how environmental effects on gene expression can alter the inheritance patterns of DNA. Is this not non-genetic inheritance?

L234 – Clarify how genotype-by-environment interactions and non-genetic inheritance are dealt with in these models. (And if they are).

The models can include these processes, and I cover this in more detail further below. Instead of explaining the details here, I refer the reader to the section later in the paper that covers this.

L243 – JMP in logic between the two sentences.

Reworded to state “In this paper I primarily focus on cases where this assumption is not made, and populations are structured by alleles, genotypes and phenotypic traits (Coulson et al. 2011, Coulson et al. 2017).”

L265-266 – A subheading would be helpful between these two paragraphs.

Although I can see the logic of doing this at one level, it would require introducing a whole new level of sub-headings, something I am not prepared to do.

L283-284 – Provide REF.

I have cited Fisher (1930)

L301- JMP in logic. Add a lead sentence between paragraphs.

I don't see this – the preceding paragraph, and this one, are about life histories. No change made.

L321-326 paragraphs seem to me somewhat repetitive from earlier in the ms. If so, consider shortening given the extensive length of the manuscript.

It is the first time it is stated that these models capture the key concepts described earlier in the paper. I have consequently left it in.

L333-335 – Should this not include “in a density dependent manner” ? For example, when the effects of predation, herbivory or resource availability affect population density and therefore per capita population growth rate?

No, change not necessary: any population that fluctuates within bounds, as stated, will exhibit statistical density-dependence. No change made.

L356 – RWD to... “workS by...”

Done

L406-407 – I think moving this first – and thereby tying the sentences about rotifer-algae system better together would make the reasoning easier to follow. This would seem to call for key REFS for eco-evolutionary dynamics literature (would benefit the broader audience).

I have deleted the second sentence, and made reference to Lotka-Volterra dynamics above. I am also not sure this interpretation of the rotifer-algae dynamics has been expressed before, and do not know of appropriate references to cite.

L408 – RWD to “...rotifer population lagging a half cycle..”

Changed

L409-418 – Calls for a REF. I seem to recall that the mechanisms related to clumping vs soloists in the eco-evolutionary dynamics were considered in a separate paper by Becks et al. 2010 (Ecol. Lett).

Citation added

L423-428 -This section is repetitive to above. Consider shortening.

I don't see this – it makes a novel point about the storage effect, linking two parts of the manuscript together.

L435- A subheading may be useful here given a JMP in the content

See previous comment about a desire to avoid a new level of sub-headings

L437-438 – RWD to “.....observed, for example, in the Trinidadian freshwater streams (See Introduction).

Changed.

L444 – I would state “ determined by the association between phenotypic trait values and fitness (i.e. survival and reproduction)”.

Changed.

L448 – how is the environmentally determined variance (= phenotypic plasticity) considered in this genotype-phenotype map?

It can be specified in any way the modeller desires. The environmental component of the phenotype could be specified to be a function of the weather, the size and structure of the focal population, or of an interacting species, or of the social structure of a group. Such determinants of the environmental component of the phenotype can act in linear or non-linear manners, via interactions with the additive genetic component of the phenotype, or in even more exotic ways if so desired. I have not added this in here, as the manuscript is already long enough, and I have published such mechanistic details previous in Coulson et al. (2017).

L449. RWD to “ ...trait values and fitness.”.

Done.

L452 – RWD to “...where the highest fitness is observed at...”

I have not changed this. Selection is frequently partitioned in viability and fertility selection which means it is appropriate to refer to survival and reproduction rather than fitness on occasion.

L478 – REF to the concept of individual specialization here (papers by Bolnick & co)

Done. I have cited Chesson 1994 as Bolnik papers discuss individual specialisation but not the link to this coexistence mechanism explicitly.

L483 – a reminder of REFs to the storage effect would be useful (given the length of the paper finding the appropriate location for what the “storage effect” is not so quick).  
I cite the relevant papers at the end of the sentence.

L487-488 – RWD perhaps to “When these processes are operating, ....., equilibria can be achieved, whereby each species, and ....has a long-run stochastic growth rate of zero.”  
Changed.

L490 – RWD to “includING”  
Done

L495 – Provide a REF to phenotypic gambit as a reminder for non-experts in the field. Though I am not sure if we need to evoke the phenotypic gambit in this sentence – given that quantitative genetic partitioning in its self does not yet imply that we can use estimates of VA as predictors of evolutionary dynamics. So the gambit part of the usage, perhaps would rather be brought up a bit later when aiming to infer evolutionary processes.  
The relevant citations are included at the end of the sentence. I’m not sure I follow the logic of the argument here. Sorry!

L503-507. Refer to those “other” – sometimes substantial - sources of phenotypic variance more explicitly than just saying “can be partitioned into various other” ... This over simplification of assuming  $VP = VA + VE$  should be better justified (e.g. from the perspective that it is the narrow sense heritability that is assumed to matter for evolutionary responses – although this is not strictly true).  
Done. I have added in reference to dominance and epistatic variances.

L510 – RWD to “...and the traits are heritable...”  
Done

L511-515 – The jump to body size comes a bit abruptly. Perhaps move L528 lead sentence here and to draw attention to why size related traits are of interest. We should also keep in mind that although size related traits are heritable (in terms of harbouring additive genetic variation), they also are classic examples for traits harbouring substantial phenotypic plasticity.  
There is a subtle difference between stating that size-related traits are under selection but do not evolve and that they vary systematically with life history strategy. I have consequently not moved the sentence up as suggested. I completely agree about plasticity. Indeed, the conclusion of this section is that body size is frequently a consequence of a genotype-by-environment interaction.

L516-517 – I assume it is not the individuals that have  $\alpha = 0$ , but genotypes or populations. RWD sentence for clarity.  
I have modified the sentence to start ‘Groups of individuals....’

L528 – See comment for L511-515.  
Please see previous response

L533 – and also why not individual size in all populations ? (if taking a micro- to macroevolution process thinking).

Certainly all individual adults, but I think that is the same as saying all species.

L571 – A REF would be useful here.

I am not sure I have seen this argument stated anywhere previously.

L571-572 – A subheading would be useful given the lengthy part of this solution to the paradox section

Please see previously comments on subheadings.

L583-587 – Seems somewhat repetitive from the early parts of the manuscript. Perhaps simplify and refer to “as above”.

This is the first time I mention the types of traits associated with detection and acquisition. So it is not repeating anything that has gone before.

L598-601 seems to come as a logic JMP and could be better tied to the text before and after.

I have removed this sentence.

L620-622 – RWD. This sentence of body size not evolving and its link to resource accrual trait and optimal values is unclear. Something like “When body size is heritable and under directional selection, there will be no evolution of larger body size because the mean trait value of this resource accrual trait is at an optimum when the population has achieved an evolutionary equilibrium”. (If I now understand this correctly).

You have indeed understood it correctly! I have reworded the sentence to read “Body size will consequently appear heritable and subject to directional selection (Figure 3), yet will not evolve to larger values because the mean of the resource accrual trait will be at the optimal value once the population has achieved evolutionary equilibrium.”

L650-652 – something missing in logic. You mean “...such that body size  $Z$  is not  $A + E$ , but rather  $A + E/A$ ”. ?

Well spotted! Reworded to “In this section I have argued that body size is determined by an interaction between breeding values  $A_i$  and the environmental component of the phenotype  $E_i$  such that body size is not determined by  $Z_i \neq A_i + E_i$  but rather by  $Z_i = A_i + E_i|A_i$ ”

L655-657. I find this statement not to be well framed to the theory – Modern quantitative genetic approaches and attempts to predict evolutionary responses are increasingly indicating that predictions based on additive genetic variance and  $h^2$  are often not accurate – for example due to the various alternative sources of phenotypic variance and the relative contribution of environmental variance differing in different environments (e.g. populations) and traits. Perhaps I am missing the point here but it would be useful to REF to recent other papers that have aimed to address the issue that  $r = h^2*s$  does not often predict accurately evolutionary changes in traits.

This is a different way to express exactly the same thing. If additivity is correctly assumed, then the Breeders equation will work. If the assumption of additivity is violated, it won't work. There are numerous processes that can lead to the violation of additivity, from unmeasured correlated characters, to various forms of plasticity and non-genetic

inheritance. Strictly speaking, the quantitative genetic framework can only provide accurate predictions of phenotypic evolution if selection on the phenotypic trait is an accurate estimate of selection on the additive genetic variance for that trait. It hardly ever appears to be so for size-related traits in natural settings. However, it often the only genotype-phenotype map we can work with using observational data from free-living populations, and the theory is absolutely correct in its logic.

L656-657 – A logic JMP here between previous and invoking body size. Can this last sentence be left out or tied to the start of the next paragraph (L659 onwards) ?

I have reworded the final sentence as it was a rather clunky linkage.

L662-664 - I don't follow the logic here, RWD needed. You mean body size is a consequence of how aggressive individuals are? If so, you mean their developmental trajectories were influenced by behavioural aggression ? Or there is in fact a genetic correlation between body size and behavioural aggression?

Reworded to: "For example, large lions can prevent smaller members of the pack feeding on a kill, while large individuals of many species may be able to dominate smaller individuals in competition for a territory. Alternatively, it may be aggression that is the resource accrual trait determining the quantity of resources accrued, such that body size is a consequence of how aggressive an individual is, rather than body size per se being the resource accrual trait."

L677 – RWD to "...is THAT they may be able to..."

Done

L687 – core original REFs for Bergmann's rule should be provided

Done

L690-691 – I don't follow the reasoning in this sentence. RWD to "In cases where body size...harbours heritable (additive genetic) variation .." – I don't understand the latter part of the sentence – what do you mean "as predated by evolution" ?

Reworded to: "In some cases when body size is a resource accrual trait, it can conform to the additivity assumptions of quantitative genetics, and can evolve as predicted by the Breeder's equation."

L690-700 onwards – I am not sure this predictable evolutionary responses in artificial environments is needed in this length. I think a shorter statement would suffice.

I am quite pleased with this insight, so have left it in.

L704-L705 – I thought above also was about the paradox of stasis? Rather perhaps RWD to "Next I will show how population models can be constructed to address the paradox of stasis".

Woops! Corrected, and it now reads "I now consider how models of the phenomena described above can be constructed."

L716 – RWD? You mean to say that models can be structured (e.g. by size or age class) or individual-based?

Correct. Reworded.

L735 – RWD to “...need to be explicitly combined..”

Changed

L753-755 & L766-769 are partially redundant. Combine. (I suggest removing L753-755).

I disagree, they are making related, but subtly different points. Unchanged.

L775-777 – What about the role of transgenerational plasticity in these transition functions? They may have rather strong impacts on how environmental effects of parental generations influence offspring phenotype and performance in the offspring environment (and hence natural selection).

Indeed, this is captured in the dynamics of the inheritance of environmental component of the phenotype. There is a completely separate paper to be rewritten on non-genetic inheritance processes and the vast, often redundant, vocabulary used to describe them. This paper is not the right place to do this.

L804 – RWD to “...would be TO construct...”

Changed

L806-808 – Just a note: environmental effects on body size can be other than resource related (such as physiological stress that may reduce body size, and organisms due to cellular processes may not be able to compensate even when resources per se would be abundant).

Where does the stress come from? Presumably the environment, and particularly being poorly matched to it. And if you are poorly matched, you are not accruing many resources. So although I am not saying all of the environment is about resource acquisition, many individual aspects do link back to it. Nothing changed.

L820 – which “this” trait?

Changed to state resource accrual trait.

L830 – the sudden shifts that organisms experience as abiotic change due to volcanic eruption is not the volcanic eruption per se, but rather changes that occur as consequence (e.g. elevated toxicants in the air). Perhaps chemical spill would be a more appropriate direct abrupt abiotic example?

I’m not sure I follow. A volcanic eruption is abiotic, and it can result in death via a large number of routes. Unchanged.

L838-840 – I find the argumentation here about role of plasticity in reducing rate of evolution possibly unclear to the non-experts. I suggest stating this more explicitly and referring to pertinent literature. Also, although such novel selection may initially result in changes in trait mean, this may change when plasticity is costly or insufficient – whereby there would be selection at the genetic level when plasticity is not available or sufficient.

(NB. I would also consider transgenerational plasticity as a modifier of phenotypic change and responses to selection).

Trans-generational plasticity is a form on non-genetic inheritance. It is not something I discuss in any detail, as non-genetic inheritance is a more general and inclusive process.

L848 – The argument about considering key stone species is valid, but comes here with a logic JMP. Also RWD to “If a change in A limiting factor, population size, and selection pressure.

Changed. The switch to keystone species is in a new paragraph.

L863 onwards – See my comment (above) about the need to address the open questions in ratite evolution rather than just stating a speculative hypothesis without known context in to the discussion.

Removed. I have removed the section that discusses ratite evolution.

L863 – Change heading to reflect order of text (emu, guppy, innovation)

This section has been deleted, and this addresses all remaining comments.

L870 – you mean individuals ? (e.g. adaptive traits via plasticity and/or a genetic basis)

See response to L863.

L901-902 – provide REFs for these arguments

See response to L863.

L921 – provide some of the core REFs for role of evolutionary innovations as a bridge between micro- and macroevolution

See response to L863.

L925-940 – this section is rather long and could be shortened to the key points, esp given the ms is already very long

See response to L863.

Reviewed by Jacob Johansson, 2020-04-05 08:49

Dear editors,

I have reviewed the manuscript “Environmental perturbations and transitions between ecological and evolutionary equilibria: an eco-evolutionary feedback framework” which is a revised version of a previous manuscript submitted to PCI.

The manuscript has been thoroughly revised and reworked and I am convinced it would be a valuable contribution to the field of evolutionary ecology and of interest for empiricists and theorists alike. The manuscript provides an interesting overview of how evolutionary and ecological stationarity may arise and be characterized. Just like the previous version, 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. Finally, the ms puts forward an

interesting and novel framework to study ecological and evolutionary processes which combines integral projection models (addressing demographic dynamics and individual development) and a type of quantitative genetic model (I think you may say). The description of the model has been much improved in this version by more clearly describing the role of the transition and inheritance functions, resource accrual traits, a generic equation clarifying the model for theorists (L746) and new and much more instructive figures (figs. 3-5). Hence it should now be clearer to readers how this type of model may be constructed. Previous models/framework with a similar scope have also now been cited making it easier for readers to compare with previous work and related literature. It seems to me that this type of model could have a large appeal to empiricists since both population structure (e.g. size structure) and genetic structure (e.g. trait variance) structure in the model are described as continuous functions which can be related to data obtained in the field or in experiments.

Thank you for the nice words.

I only have a few comments, which I hope can be useful for a final revision. They are a bit tricky to explain and I am sorry if they are a bit lengthy but I am convinced most of them can be addressed by adjusting the wordings and explanations in this review/perspective piece.

According to the abstract energy budgets are integrated into the framework. Then the dynamic energy budget model (DEB) by Kooijman is cited and energy/energy budgets are discussed intensively in the beginning and middle of the MS. However energy budgets seems to be absent in the section where the model framework is outlined. I suspect energy budget are an integrated part of the demographic or resource accrual function but it would not hurt to remind the reader in the model section. The model is outlined on approx. L739-827 but last mention of "energy" is before that on L699.

A great observation. I have now included a paragraph on energy utilisation. It states: "Lachish et al. (in press) have developed a model of a vegetation resource that renews seasonally, and stochastically. The resource is consumed by elk (*Cervus canadensis*), with individuals in each attribute class partitioning the energy they accrue into maintenance, development, and, if individuals have reached sexual maturity, reproduction. A proportion of the maternal energy reserve of breeding individuals is invested into offspring. In this bioenergetic model based on dynamic energy budget theory (Kooijman and Kooijman 2010), the life history is determined by the energy budget at each age and size. This work builds on a previous model of Smallegange et al. (2017) that was the first to incorporate energy budgets into IPMs."

L249 "when genotypes are additive, genotypes within offspring cohorts are expected to have identical reproductive values (Sæther and Engen 2015)". This requires more explanation. I admit I have not consulted the paper by S&E 2015, but I wonder if this is generally true under evolutionary stationarity in a stochastic world. Specifically I am thinking of mutation-selection balance which is an important characteristic of evolutionary stationarity. Under mutation-selection balance, mutants (i.e. genotypes) with fitness/reproductive value below 1 coexist with genotypes alongside those with the optimal phenotype (with  $R_0=1$  or in fact ever so slightly above 1 so that the whole population including maladaptive types has mean  $R_0=1$ ). Without having thought too much about it, I can imagine the statement on L249 is true in a deterministic world but I doubt it is true

when accounting for mutation-selection balance where necessarily some genotypes in the offspring cohorts might be maladaptive mutants. One may perhaps assume this is a very small effect if mutants are rare etc, but frequency and density dependence can generate very flat fitness landscapes (since species evolve towards any resource peaks and thereby press them down) so at evolutionary equilibrium mutants close but not on the optimum phenotype may have only a small fitness disadvantage and take very long time to weed out. As an example, I did some individual-based population genetic simulations under frequency dependent selection in Johansson, J. (2008). *Evolution*, 62: 421–435 where the population had a considerable standing genetic variation at ESS with three species due to mutation-selection balance in a fitness landscape evolution had flattened out in this way (note I don't at all propose that paper should be cited here – it is not about mutation-selection balance and I am sure it is well covered elsewhere). Anyway, my point is that it is not intuitively clear that all offspring have the same reproductive value at an evolutionary stationary state, and if so rewording is needed at L249 and several other places in the MS where this line of thought appears (e.g. L289, 298, 491).

Following up on the point 2, I personally wonder if mutation-selection balance can generate a quite large standing genetic variation especially if you consider genetic variation in many loci, where alleles at each loci has small effects on fitness. We could then have many just slightly maladaptive genotypes that would take ages to weed out.

This is a good point. I did clarify that I was defining reproductive value as an expectation from a model. I am now much more explicit, and state that “in the absence of mutation, expected reproductive value from a model...”. I then refer to expected reproductive value at relevant places in the text that follows. I believe that this addresses the concerns raised.

L13,L19,L20, L147, L307 and more places. The MS talks about optimization of traits, but whenever you have ecological feedback loops via trait evolution, trait optimization becomes problematic. If a predator trait affect the availability of different prey types, for example, the optimum trait would depend on the current trait values of the predators. Assume for example a novel environment with a lot of large prey and a few small prey. The optimum appears to be to eat large prey. But if all predators eat large prey, large prey would decrease in number and then it might be optimal to eat small prey. So we quickly get game-theory-like situations when ecological feedbacks are operating and game-theory has shown many examples where apparently sub-optimal strategies are viable at evolutionary equilibria (this is by the way of course a main thread in adaptive dynamics and has less to do with clonal inheritance). There may be specific instances where trait optimization is a valid principle, for example the vision trait discussed on. But more generally, I suggest some caution the word optimization being used with caution. There is a lot of tradition in  $R_0$  maximization, but this principle may only be valid in certain circumstances when you have ecological feedbacks, e.g. when population size is constant and regulated by a simple density dependence such as sibling competition. See e.g. Kozlowski Measuring fitness in life-history studies. *Trends in Ecology & Evolution* 8:84–85 and Metz, J. A. J., Mylius, S. D., & Diekmann, O. (2008). When does evolution optimize? *Evolutionary Ecology Research*, 10(5), 629–654 who argues it is very rare for  $R_0$ -maximization to be a justifiable principle.

This is a subtle argument, and one that I don't entirely buy. Of course, the optimum can change with the environment – it can evolve, and indeed this is much of what the paper is about. There can also be frequency-dependence such that there may be multiple optima, or

a flat fitness function at equilibrium, but I never argue against this – in fact it is a mechanism I discuss. Such frequency-dependence can happen with clonal reproduction. I consequently have not edited the paper to address this debate. I think that defining optima as fixed is particular definition of optimisation that is specific to adaptive dynamics and game theory, but is not a definition that most biologists will adhere to. Sorry to disagree!

L307. R0-optimization is extensively used in life history theory but not (or at least very rarely) in adaptive dynamics by Metz 1992, 1995 so this sentence needs rewording.

Done

L309: “Adaptive dynamics and game theory consequently rely on the assumption of clonal inheritance.” This statement is made without references, and not discussed before so they come a bit abruptly. It is also problematic because both these frameworks are quite diverse with many model versions. Game theory is a big area so there may be some games for sexually reproducing organisms out there somewhere and for adaptive dynamics, you perhaps intend to refer to the adaptive dynamics version by Metz and others, where you have the so called canonical equation of adaptive dynamics (Dieckmann and Law 1996) which is defined for asexual inheritance as this is easier (yet not easy...) to derive mechanistically, but in this broader school of thought you also find models with sexual inheritance, and as I pointed out in my previous review adaptive dynamics equations have been derived for sexual inheritance. Also, in an earlier branch of adaptive dynamics inheritance is modelled using quantitative genetics which in turn is often used to model sexual populations (see e.g. Vincent et al "Evolution via strategy dynamics." Theoretical Population Biology 44.2 (1993): 149-176.). I think it is easier to skip labels and simply refer to “approaches assuming clonal inheritance” and cite such papers.

I have reworded this. I have stressed that the canonical equation of adaptive dynamics assumes asexual, clonal, reproduction.

L464. Two species with the same “optimal” fitness may appear able to coexist, but I am not sure it is generally true. Identical fitness rather leads to drift in the two populations and if you have simple density dependence (e.g.  $n_1+n_2$  is constant) then in the long run there would be stochastic extinction of one of them just due to demographic stochasticity. A much stronger argument for coexistence is negative frequency-dependent selection so that the rare genotype bounces back to equilibrium when rare.

Again, this is an expectation. It is true that demographic stochasticity can result in one drifting to extinction. I have clarified this.

L823. Here I wonder whether the model assumes there can only be a single size at maturation that maximizes fitness given this trade-off, or whether the model would be able to account for coexistence of small and large phenotypes, such as fighters and sneakers which differ in size at maturation yet are able to coexist on game-theoretical grounds (the hawk and dove game).

It can indeed, and in fact each attribute class can have its own size and age at sexual maturity. I have not modified the text because this is a rather specific case.

Fig. 4. Here all curves are smooth. But given e.g. interannual variability of the availability of different resources due to changing demographics of several populations I would expect the

population size distributions and trait distributions to become irregular and deviate from smooth normal distributions etc. Or are there some simplifying assumptions here I have missed, for example about population sizes being very large?

Figure 4 is for illustration only. In a stochastic model, the intercepts or slopes of the functions would change with time, generating non-smooth distributions of population size and phenotypic trait distributions. I have not modified the figure.

Extremely minor comments:

Equation numbers needed on L668, L746

Added.

A couple of typos: L147 optimally->optimize L490 included-> including L907 specie->+s

Corrected.

Signed by Jacob Johansson