THIS IS A PREPRINT VERSION OF THE MANUSCRIPT THAT WAS ACCEPTED FOR PUBLICATION AS

De Meester, L., K.I. Brans, L. Govaert, C. Souffreau, S. Mukherjee, H. Vanvelk, K. Korzeniowski, L. Kilsdonk, E. Decaestecker, R. Stoks & M.C. Urban, 2019. Analyzing eco-evolutionary dynamics - the challenging complexity of the real world. **Functional Ecology** 33: 43-59.

Analyzing eco-evolutionary dynamics - the challenging complexity of the real world

Luc De Meester[1], Kristien I. Brans[1], Lynn Govaert[1,2,3], Caroline Souffreau[1], Shinjini Mukherjee[1], Héléne Vanvelk[1], Konrad Korzeniowski[1], Laurens Kilsdonk[1], Ellen Decaestecker[4], Robby Stoks[5] and Mark C. Urban[6]

[1]Laboratory of Aquatic Ecology, Evolution and Conservation, KU Leuven, Charles Deberiotstraat 32, B-3000 Leuven, Belgium

[2] Eawag: Swiss Federal Institute of Aquatic Science and Technology, Department of Aquatic Ecology, Überlandstrasse 133, CH-8600 D□ubendorf, Switzerland

[3] Department of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstrasse 190, CH-8057 Z□urich, Switzerland

[4]Laboratory of Aquatic Biology, IRF Life Sciences, KULAK, KU Leuven, Campus Kortrijk, E. Sabbelaan 53, B-8500 Kortrijk, Belgium

[5]Laboratory or Evolutionary Stress ecology and Ecotoxicology, KU Leuven, Charles Deberiotstraat 32, B-3000 Leuven, Belgium

[6]Department of Ecology and Evolutionary Biology; Center for Biodiversity and Ecological Risk, University of Connecticut, 75 N. Eagleville road, Storrs CT 06269-3034, USA

Corresponding Author: Luc.DeMeester@kuleuven.be

Abstract

1. The field of eco-evolutionary dynamics is developing rapidly, with a growing number of well-designed experiments quantifying the impact of evolution on ecological processes and patterns, ranging from population demography to community composition and ecosystem functioning. The key challenge remains to transfer the insights of these proof-of-principle experiments to natural settings, where multiple species interact and the dynamics are far more complex than those studied in most experiments.
2. Here we discuss potential pitfalls of building a framework on eco-evolutionary dynamics that is based on data on single species studied in isolation from interspecific interactions, which can lead to both under- and overestimation of the impact of evolution on ecological processes. Underestimation of evolution-driven ecological changes could occur in a single-species approach when the focal species is involved in co-evolutionary dynamics, whereas overestimation might occur due to increased rates of evolution following ecological release of the focal species.
3. In order to develop a multi-species perspective on eco-evolutionary dynamics, we discuss the need for a general definition of 'eco-evolutionary feedbacks' that include any reciprocal interaction between ecological and evolutionary processes, next to a stricter definition of a 'feedback loop' that refers to interactions that directly feed back on the interactor that evolves.
4. We discuss the challenges and opportunities of using more natural settings in eco-evolutionary studies by gradually adding complexity: (i) multiple interacting species within a guild, (ii) food web interactions, and (iii) evolving metacommunities in multiple habitat patches in a landscape. A literature survey indicated that only a few

studies on microbial systems so far developed a truly multi-species approach in their analysis of eco-evolutionary dynamics, and mostly so in artificially constructed communities.

5. Finally, we provide a roadmap of methods to study eco-evolutionary dynamics in more natural settings. Eco-evolutionary studies involving multiple species are necessarily demanding and might require intensive collaboration among research teams, but are highly needed.

An ecologist's perspective on eco-evolutionary dynamics

The recognition that ecological and evolutionary time scales can converge and that evolutionary change might therefore potentially influence the whole spectrum of ecological processes (Thompson 1998) led to the development of the field of eco-evolutionary dynamics, which can be most conveniently defined as evolutionary change in space and time that affects ecological processes and patterns and thus leads to interactions between ecological and evolutionary processes. This field is rapidly growing with a large number of conceptual and review papers (De Meester et al. 2016; Ellner et al. 2011; Fussmann et al. 2007; Hairston et al. 2005; Hendry 2017; Palkovacs & Post 2009; Schoener 2011; Shefferson & Salguero-Gómez 2015; Urban et al. 2008), papers emphasizing applications for conservation and global change (Alberti 2015; De Meester et al. 2011; Merilä & Hendry 2014; Stockwell et al. 2003; Urban et al. 2012), theoretical studies (de Mazancourt et al. 2008; Lion 2018; Loeuille et al. 2013; Loeuille & Leibold 2008; McPeek 2017a; Norberg et al. 2012; Patel et al. 2018; Vanoverbeke et al. 2016), and more and more empirical studies (Bassar et al. 2010; Brunner et al. 2017; Crutsinger et al. 2006; Farkas et al. 2013; Fukami et al. 2007; Gómez et al. 2016; Matthews et al. 2011, 2016; Pantel et al. 2015; Rudman & Shluter 2016; terHorst et al. 2014; Turcotte et al. 2012; Venail et al. 2008; Walsh et al. 2012; Yoshida et al. 2003).

Despite many advances, most experimental studies involve proof-of-principle experiments quantifying the impact of phenotypic variation in highly standardized, simplified environments, using a common gardening design (Matthews et al. 2011). In a common gardening approach, one studies how different phenotypes of focal taxa influence an initially identical environment (the "common garden"; Matthews et al. 2011). Most studies use phenotypically differentiated individuals shown or assumed to be genetically determined and isolated from contrasting habitats (e.g. Walsh et al. 2012) or generated through experimental evolution (e.g. Pantel et al. 2015) and quantify effects on population dynamics, species composition or ecosystem features. Others, mainly studies on microbial and unicellular organisms, quantify eco-evolutionary feedbacks as evolution proceeds

(Becks et al. 2012; Fukami et al. 2007; Gómez et al. 2016; Yoshida et al. 2003). Many of these proof-of-principle experiments demonstrate striking effects of evolutionary trait change on population dynamics and composition (Brunner et al. 2017; Fukami et al. 2007), species interactions (Becks et al. 2011; Friman et al. 2015; Yoshida et al. 2003), community composition (Gómez et al. 2016; Pantel et al. 2015; terHorst et al. 2014) and ecosystem features (Bassar et al. 2010; Harmon et al. 2009).

The current view on eco-evolutionary dynamics

In his scheme on how evolutionary trait change can impact ecological processes, Hendry (2017) emphasizes the pivotal role of the phenotype, i.e. trait values of a species, that can impact population, community and ecosystem features (Figure 1 left). The phenotypes present in a population result from the genotypes present in the population, the environment's influence (phenotypic plasticity), and their interaction (Govaert et al. 2016; Lynch & Walsh 1998; Via & Lande 1985; Via et al. 1995). Both the abiotic environment and interactions with other species can determine selection pressures on the phenotype, and this can result in evolutionary changes in the phenotype if phenotypic variation has a genetic basis (i.e. is heritable). These evolutionary changes in phenotypes can then impact ecological properties of populations, communities and ecosystems, resulting in an eco-evolutionary feedback. The pivotal role of phenotypes in this feedback is in line with the recent upsurge in interest in trait-based ecology (Bolnick et al. 2011) and the relative importance of intra- and interspecific trait variation (Violle et al. 2012). Trait values are the common currency linking evolution to ecology: unless genetic change influences phenotypes, directly through genetic variants coding for different trait values, or indirectly through for example fitness costs linked to inbreeding, evolution will not impact ecology.

While the phenotype is pivotal to eco-evolutionary dynamics, this does not automatically mean that any phenotypic change impacting ecological processes is an example of eco-evolutionary dynamics. Studies on eco-evolutionary dynamics should quantify to what extent the phenotypic change

observed actually reflects evolutionary change or genetic differentiation. Several studies presented in the context of eco-evolutionary dynamics fail to do so. Phenotypic trait change might also be caused by ontogeny or phenotypic plasticity, and such non-genetic trait change can be highly relevant for ecological processes (Bolnick et al. 2011; Lundsgaard-Hansen et al. 2014; Violle et al. 2012). Yet, any study on eco-evolutionary dynamics should at the least document that evolution is involved and that this evolutionary differentiation impacts ecological processes. Assuming that trait differences as observed in the field reflect genetic differences is unwarranted, as it is well-known that the phenotype of individuals in nature is often the combined result of the interaction between genotype and environment. Rarely will the phenotypic differentiation as observed in nature only reflect genetic differences, and assuming so will likely in many cases misrepresent the impact of evolution on ecology (Govaert et al. 2016). Documenting that phenotypic differences as observed in the field reflect evolutionary differentiation involves much work, and hence it might be attractive to take the short cut of only focusing on phenotypic variation. Yet, confounding non-genetic phenotypic variation with genetic trait differences interferes with the core of what eco-evolutionary dynamics is about.

The scheme presented by Hendry (2017) is effective in visualizing how evolutionary changes in phenotypes can influence population, community and ecosystem features. It also reflects how most eco-evolutionary dynamics experiments are performed: the phenotypes of a given species are manipulated (e.g. by using individuals from genetically distinct populations that differ in their phenotype) and the impact of this intraspecific phenotypic variation on population, community and ecosystem characteristics is monitored in a common gardening approach (Matthews et al. 2011). The common gardening approach has been powerful in providing proof of principle that evolution can affect ecology and that eco-evolutionary feedbacks need to be taken into account if we want to understand how populations, communities and ecosystems respond to environmental change, including human impact, through the changes in phenotypes of taxa.

Understanding complexity in real ecosystems

If we want to understand eco-evolutionary dynamics in nature, however, we need to take into account that in reality, species co-occur in diverse communities (Figure 1, right). Each species has its own population features and dynamics, and collectively these species comprise a community. The phenotypes of each species might not only influence population dynamics and other population characteristics of the species itself, but also those of other interacting species (Figure 1; McPeek 2017b). These changes in the population abundances and other population features (e.g. size distribution) of all species collectively determine community characteristics and ecosystem features. While each species can influence population, community and ecosystem features, they do so when interacting: the population features of each species potentially influence or are influenced by the evolution of any member of the community, and it is the joint evolutionary change and its impact on populations that determines community and ecosystem characteristics. While "the phenotype" is still pivotal, it is the phenotypes of all interacting species that is crucial and which captures the more realistic complexities that arise when species can influence each other. This makes a crucial difference in mindset: if we want to understand how eco-evolutionary dynamics play out in nature and go beyond proof-of-principle, we need to move toward understanding evolutionary responses and their ecological impacts in multiple interacting species simultaneously. To our knowledge, no study so far has done in non-microbial systems.

Figure 1 remains an over-simplification, as the community that is depicted only represents one subset of interacting species. In reality, local systems will be characterized by food webs involving predators (Gravel et al. 2011; Poisot et al. 2015), parasites (Lafferty et al. 2006; Thompson 2005) and mutualists (Koskella et al. 2017; Macke et al. 2017) (Figure 2). A body of knowledge exists for predator-prey, host-parasite and host-mutualist co-evolution and how this evolution impacts interaction strengths and population dynamics (Penczykowski et al. 2016). Again, most of these

166 studies quantify evolution either in the host or the parasite and study the impact of this evolution on
167 the other species, with only a limited number of studies incorporating evolution of both partners or
168 three interacting species and how they influence the other partners (Benkman et al. 2001; Brunner et
169 al. 2017; Decaestecker et al. 2013; Ford et al. 2016; Frickel et al. 2016, 2017; Hiltunen & Becks 2014;
170 Masri et al. 2015; Thompson 2005). There are, to our knowledge, so far no empirical studies
171 reporting on how evolution in multiple species of predator and prey, hosts and parasites, or
172 mutualists, simultaneously impacts the dynamics of the populations of each individual species, their
173 community composition, or resulting ecosystem functions.

174 Even Figure 2 is still an over-simplification, as local food webs interact with food webs in
175 other patches in the landscape (Figure 3). In this spatial context, local selection and evolution in
176 response to abiotic environments and species interactions are linked by regional dispersal and gene
177 flow. Thus the same tension exists in ecology and evolution between the sorting of species and
178 genotypes locally and the regional remixing of species and genotypes. Regional mixing is often
179 maladaptive because a poorly adapted species or genotype lands in a suboptimal habitat, but it also
180 can provide a match to optimal habitats or create novel, more fit genotypes or more diverse
181 communities of species that provide diversity for selection to act upon. The dynamics of these so-
182 called evolving metacommunities (Urban & Skelly 2006; Urban et al. 2008) are poorly studied.
183 Exceptions include the elegant proof-of-principle experiment with “communities” represented by
184 different *Pseudomonas fluorescens* strains evolving in a landscape of food sources in multi-well
185 plates (Venail et al. 2008), the evolution-mediated priority effects experiments of Fukami et al.
186 (2007) again using *P. fluorescens* strains, and the community rescue experiments with bacterial
187 communities carried out by Low-Décarie et al. (2015). While these excellent experiments grasp key
188 features of evolving metacommunities, they all involve highly artificial settings. Given that theory
189 shows that the levels of regional dispersal can strongly influence how evolution affects community
190 assembly (Loeuille & Leibold, 2008; Urban & De Meester 2009; Urban et al. 2012; Vanoverbeke et al.

2016), there is a need to develop methods and approaches to study the features of evolving metacommunities in sufficiently realistic settings, through experimentation and field surveys.

Obviously we do not suggest that studies on eco-evolutionary dynamics that fail to address the full complexity depicted in Figure 3 would be uninformative. Rather, we argue that (1) we should be aware of the fact that most of the studies so far are focusing on the consequences of evolution in single species, and this can result in biases, and (2) we should focus efforts on including some complexities typical of natural systems to make more realistic assessments of the importance of eco-evolutionary feedbacks in nature. At each level of complexity emphasized in Figures 1-3, important properties might emerge that change the impact of evolution on ecology. For instance, studies on the ecological consequences of evolution in a guild of species might be reversed if a predator adapts in response to the novel setting that results from the evolution of competing prey. In another example, the capacity to evolve might be hampered or increased in a landscape setting because of gene flow, co-determined by metapopulation and metacommunity structure. Within a landscape, local eco-evolutionary feedbacks might spill over to influence ecological processes (e.g. community assembly), evolutionary trajectories, and eco-evolutionary dynamics in nearby patches by modulating the numbers and types of dispersing individuals.

These suggestions correspond with an ecologist's perspective on eco-evolutionary dynamics. Evolutionary biologists, in contrast, are often biased towards studying species in isolation or strictly co-evolving species pairs. We need to move beyond demonstrating that the evolution of just a single focal species impacts ecological processes. We argue that it is time to incorporate more ecology in eco-evolutionary dynamics, not only as response variables, but also by incorporating an explicit multi-species context both in the eco-to-evo as well as in the evo-to-eco side of the feedback.

A note on definitions: eco-evolutionary dynamics and eco-evolutionary feedbacks

Given the explicit multi-species perspective that we here advocate, we need to revisit the definition of an eco-evolutionary feedback. Researchers differ in what they mean by an "eco-evolutionary feedback". The strict definition is that the feedback has to involve the same species and traits (cf. the narrow definition listed by Hendry 2017): evolution in a focal species impacts ecological processes, which subsequently impact the further evolution of the focal species. There is empirical evidence for feedbacks that involve the same actors (Becks et al. 2012; Brunner et al. 2017; Bull et al. 2006; Chitty 1967). In a multi-species context, however, it is difficult to maintain this strict definition, because this would imply that we either have to develop a new term for all other feedbacks between ecological and evolutionary processes, or miss most of the relevant interactions between ecological and evolutionary dynamics. We argue that it is preferable to define an eco-evolutionary feedback as any feedback between an ecological and an evolutionary process (cf. the broad definition listed by Hendry 2017). Key to documenting such a feedback is that one needs insights into both the impact of ecology on evolution and of evolution on ecology in the same (multi-species) system. To empirically illustrate an eco-evolutionary feedback in a given system (i.e. a local population, local community or local ecosystem, or a metacommunity or meta-ecosystem), a researcher would want to show that ecological processes impact evolution and that this evolutionary change impacts one or more ecological processes or their resulting patterns. The feedback does not necessarily need to involve the same species or traits and if it does, might do this through multiple intermediate steps (Figure 4). For example, imagine that climate change causes trait evolution in a predator, and this evolution affects prey community composition. This situation would conform to an eco-evolutionary feedback even though the ecology of the prey species may then perhaps not affect the evolution of the predator. The key point is that ecology affects evolution and evolution affects ecology, regardless if the same species are involved. If the feedback does result in additional evolutionary changes of the species that evolved in the first place, this can be specified and would be an example of a feedback loop in the narrow sense, resulting in a broad-sense and narrow-sense definition of eco-evolutionary feedbacks (Figure 4; following Hendry 2017).

A key reason to adhere to a broad definition of eco-evolutionary feedbacks is that many of the impacts of evolution on ecology that matter for our understanding and prediction of ecological processes do not involve feedbacks in the narrow sense. Some of the more important influences of evolutionary on ecological processes might involve feedbacks on very different members of the food web or even on communities in different localities. The importance of eco-evolutionary feedbacks should be quantified by the effect size of evolutionary change on ecological processes, not by the subject of its influence. Moreover, multiple steps in a cascade of effects might eventually result in a feedback in the narrow sense, even though it was not studied originally because too many steps were involved. For instance, evolution in response to climate change in a lizard might influence community composition of the guild of prey species, which might result in a change in vegetation structure, so that the sparser vegetation imposes selection on body colour in the predator linked to thermoregulation. This example involves only four steps, but it is likely that such cascades might involve many more steps. In some cases it might at any of the intermediate steps even lead to the local extinction of species or to qualitatively entirely different ecological trajectories. Especially in a multi-species context, such complexities are likely to be common and need to be considered. By adhering to a narrow definition only, we would limit eco-evolutionary feedbacks to the simplest examples of it.

Our bias to more simple contexts is driven by the ease of its modelling and of experimentation. We argue that there is no intrinsic problem in constructing simplified models and experimental settings, but we need to be careful that the resulting low-dimensional settings do not bias our definitions of what eco-evolutionary feedbacks are and our appreciation of their impact. Much of the impact of eco-evolutionary dynamics for the fields of ecology and evolutionary biology lies in their potential for indirect, multiplicative effects. It is important that we always attempt to understand how far we can simplify a complex system while still retaining its characteristic dynamics and structure. To do that, however, one also needs to study the more complex settings or nature itself.

The need for a multi-species context

Above we argued that the complexities of multi-species contexts and evolving metacommunities should be more often included in studies on eco-evolutionary dynamics. Otherwise we risk introducing biases by focusing on the impacts of a single, focal species. We see three main risks. First, species are expected to strongly differ in how their evolution affects ecological processes. This may be the result of (i) differences in evolutionary potential, (ii) differences in abundances, (iii) differences in dispersal capacity, and (iv) differences in interaction strength, linked to variation in effect traits. Eco-evolutionary studies focusing on a single focal species are likely biased towards abundant species, strong interactors, and species known to evolve. Indeed, many eco-evolutionary feedback studies use species that are abundant in the system studied (e.g. Bassar et al. 2010; Farkas et al. 2013; Urban 2013), use key-stone species (Matthews et al. 2016) or use species that are known to be strong competitors (Pantel et al. 2015; Walsh et al. 2012). There is nothing intrinsically wrong with these choices if one wants to explore how strong eco-evolutionary feedbacks can be. The resulting proof-of-principle studies should, however, not be used to infer how strong eco-evolutionary feedbacks are on average. For instance, in zooplankton communities, *Daphnia* are generally assumed to be strong competitors and keystone grazers. All else being equal, one might thus expect that eco-evolutionary feedbacks on community structure and on top-down control of algae might be smaller for the other community members, yet no such comparative data exist. Conversely, while our focal species approach might in many cases result in a stronger than average impact of evolution on ecological processes, we might also miss cases of strong impacts because understudied species might show a particularly strong evolutionary response or evolve in unexpected ways that elicit strong ecological responses. If we want to move toward predicting eco-evolutionary effects, we will need to know for which species they are important and for which ones they are not.

291 Therefore, we will require comparative data on species in the same guilds, including those with
292 limited impact.

293 Second, studies that manipulate genetic trait values of a focal species to study the
294 community and ecosystem consequences of evolution often do not test this impact of evolution in
295 communities consisting of co-evolved populations. This experimental artifact could result in stronger
296 community and ecosystem consequences than would be obtained in a truly multi-species context
297 where evolution of the other species would partly buffer the effect of evolution of the focal species.
298 For instance, in their mesocosm study on how evolution of the water flea *Daphnia magna* influences
299 zooplankton community composition, Pantel et al. (2015) did not use zooplankton species that were
300 allowed to co-adapt to the same treatments as the focal species *D. magna*. The impact of evolution
301 that they reported might potentially have been smaller if all other species had been co-evolved. The
302 reduced impact of evolution would then result from additional evolution of other species. This would
303 be an interesting case of cryptic eco-evolutionary dynamics (defined as "*eco-evolutionary dynamics*
304 *that are at risk to be overlooked because the resulting pattern is consistent with pure ecological or*
305 *evolutionary theory*"; Kinnison et al. 2015), where evolution in all species in combination might result
306 in a reduced net ecological effect. The ecological consequence of evolution in one species would then
307 be a reduction of the ecological consequences of evolution in another species.

308 Third, one also needs to consider the community context of the evolutionary response itself.
309 Evolutionary trajectories can be very different depending on whether a species is kept in isolation
310 compared to when it is exposed to selection pressures in the presence of a community (Barraclough
311 2015). Simulations showed that evolution of response traits can be reduced in the presence of other
312 species (de Mazancourt et al. 2008), while in other settings the presence of other species can
313 enhance evolutionary responses, especially for traits important in species interactions (Osmond & de
314 Mazancourt 2013). Community context can thus lead to different evolutionary trajectories compared
315 to the ones predicted from single-species studies, with important ecological consequences (Lawrence

et al. 2012). Barraclough (2015) emphasized that evolutionary biologists should carefully take the community context into consideration if they want to obtain insights into how species will evolve in response to specific selection pressures, and this will obviously also impact the ecological consequences of evolution. Community context may even determine whether evolution will occur. If the community harbors species that are pre-adapted to the environmental change that is imposed, changes in species composition through species sorting might occur so fast that a given species is driven to local extinction before it has the time to evolve in response to the environmental change (De Meester et al. 2016; Vanoverbeke et al. 2016). This might be common, even for species that have a high evolutionary potential. If common, then studies that use experimental evolution on species in isolation to first generate populations that are adapted to different conditions (e.g. Pantel et al. 2015) risk over- or under-estimating the impact of eco-evolutionary dynamics, as the species would have shown less or more evolution if embedded in the natural community. In this context, one might argue that genetic constraints for evolution in the first place might be important in a community context, as they alter the rate of adaptation and may thus increase or decrease the likelihood that species sorting dominates and impedes evolution (De Meester et al. 2016).

Finally, a key reason to include a multi-species perspective in a landscape context is that the exchange of species and genotypes among food webs in a landscape (Figure 3) will affect local evolutionary responses, either through the immigration of pre-adapted genotypes or species (De Meester et al. 2016; Vanoverbeke et al. 2016) or through maladaptive gene flow (Richardson et al. 2014). This stresses the importance of taking spatial and evolutionary processes as well as species interactions into account (Thompson 2005; Urban et al. 2016), and stresses that the evolving metacommunity concept provides an integrative framework for carrying out eco-evolutionary dynamics research (De Meester et al. 2016; Urban et al. 2008, 2011, 2016).

Key studies on eco-evolutionary dynamics in a community context

To evaluate to what extent empirical studies so far addressed the multi-species context in which eco-evolutionary dynamics operate in nature, we provide an overview of eco-evolutionary dynamics studies that focus on feedbacks at the community level in Table S1 (Supplemental Information). We selected studies documenting how evolution, genetic differentiation or genetic diversity impacts community assembly and community features, because they do incorporate an explicit multi-species context at least in their endpoints. The table illustrates the degree to which these studies fulfill three criteria that are linked to the above highlighted multi-species context, and lists whether (i) the study involved evolutionary change embedded in a natural or multi-species context (i.e. evolution as it occurred in nature or in a multi-species experimental evolution set-up), (ii) the study involved an analysis of evolution in multiple species (rather than just one focal species), and (iii) the endpoint community involved co-evolved populations (i.e. whether the species of the responding community were allowed to co-evolve with the evolving focal species in the experimental evolution trial or came from the same habitats as from which the genetic variants in the focal species were isolated). In defining communities as an endpoint, we refer to communities of guild members, i.e. species that can potentially compete with each other. The endpoint community can be guild members of the same trophic level as the evolving focal species or can be a community of guild members that is affected by evolution of species that interact with the community. An example of the latter is the study of terHorst et al. (2014), in which the impact of evolution of a plant to drought stress was studied on community composition of soil bacteria. The table excludes studies that address interaction modules such as predator-prey interactions (e.g. Becks et al. 2012; Hiltunen & Becks 2014; Yoshida et al. 2003), host-parasite interactions (Brunner et al. 2017; Decaestecker et al. 2013; Frickel et al. 2016; Masri et al. 2015) and host-mutualist interactions (Ford et al. 2016; Macke et al. 2017), unless they involved whole communities of predators, prey, hosts, parasites or mutualists. Most eco-evolutionary studies of predator-prey and host-parasite interactions involve one species of each type of interactors (predator and prey, host and parasite) and thus while taking a two-species approach they do not allow estimating the degree to which evolution of competing predator or prey

influence dynamics. We also excluded studies from the table that show that genetic variation in a host species can influence gut microbiome composition (Macke et al. 2017). Because the gut microbiome develops internally in a particular host individual, incorporating a multi-species context with respect to the host might be less pressing, although the presence of other species might influence patterns by modulating environmental source bacteria in case the microbiome is horizontally acquired.

The conclusion of the overview given in Table S1 (Supplemental Information) is that an increasing number of studies are quantifying the impact of evolution on community features, but that so far none of the published studies on non-microbial systems full-filled all three of our criteria linked to the multi-species context in which eco-evolutionary dynamics operate in nature. Several studies, however, do incorporate one or two of the relevant multi-species dimensions, and thus build towards a more comprehensive picture. Quite a few studies (e.g. Fridley & Grime 2010; Bassar et al 2010; Walsh et al. 2012; Farkas et al. 2013; terHorst et al. 2014: Pantel et al. 2015) used isolates or populations that evolved in a natural or multi-species context. However, only three of the non-microbial studies (Fridley & Grime 2010; Rudman et al. 2015; Faillace & Morin 2016) evaluated the impact of evolution in multiple species at once, hence supporting our claim that a key frontier in eco-evolution is the effect of multi-species evolution on ecology. The study that comes closest to the most realistic experiment is the work of Fridley and Grime (2010) on how genetic variation in multiple species affected species diversity in a grass community. Here, they found that genetically variable populations of each species decreased competition and promoted more evenly diverse communities. The researchers manipulated genetic diversity rather than evolutionary endpoints, but at least they did it in multiple species. With respect to our third criterion, Table S1 shows that quite a few studies used co-adapted communities in evaluating how evolution in a focal species affects community composition. Overall, the list of studies suggest a wide range of effects of evolutionary divergence of plants, zooplankton, insects, salamanders, and fish on community diversity, composition, and biomass, but usually evaluated in microcosms or mesocosms and not in natural

393 settings (Table S1). Exemplars of studies under more natural conditions include the manipulation of
394 maladaptation of stick insects to demonstrate how maladapted and uncamouflaged prey attract
395 predators which eat more prey in the community (Farkas et al. 2013) and how a plant in a
396 manipulated, but natural, setting evolved less herbivore resistance and higher competitive ability,
397 with effects on interacting populations (Agrawal et al. 2012).

398 Overall, the studies that come closest to grasping the key dimensions of the multiple species
399 context of eco-evolutionary dynamics involve microbial systems, but these studies most often involve
400 very artificial conditions, as they involve experimental evolution of multiple species embedded in
401 reconstructed communities in artificial laboratory settings. Some very elegant studies that make
402 inferences on community features are not listed in the table because they involve different strains of
403 the bacterium *Pseudomonas fluorescens* rather than multiple species and thus in essence involve
404 only one species (Fukami et al. 2007; Venail et al. 2008). By excluding these or any other studies from
405 the table, we do not want to suggest that their results are irrelevant to the theory of community
406 assembly, but rather do not meet the criteria of this particular literature review.

407

408 **How to embrace a multi-species perspective in eco-evolutionary dynamics**

409 As mentioned, it is often impractical to incorporate the full complexity of natural systems in eco-
410 evolutionary feedback studies. Yet, there is a need to explicitly study and quantify the emergent
411 features that result from including more complexity and exploring to what extent a multi-species
412 context changes our predictions on the strength and direction of eco-evolutionary impacts on
413 ecological processes. A lot of progress could be achieved if there would be a strong effort towards
414 incorporating specific aspects of the complexity sketched in Figures 1-3 in eco-evolutionary research.
415 While at times challenging, important progress can be obtained through collaborative work with
416 different research teams focusing on different organism groups in the same systems. Alternatively,
417 eco-evolutionary insights for a given system can be built up over time. For instance, a researcher

might begin with understanding the evolution of one species and its effects on ecology and then add insights on the effects of evolution in other species of the same system. We here outline a few approaches on how specific dimensions of the complexity resulting from a multi-species and evolving metacommunity framework could be tackled in empirical work.

Experiments

In experimental studies, there are a number of complexities linked to the multi-species features highlighted in Table S1 (Supplemental Information) that can relatively easily be incorporated, and Table S1 lists some studies that have partially done so. While these complexities might result in more challenging experiments, they can still be feasible when designed in a reasoned way, and would have strong added value. The following is not intended to be an exhaustive list of possibilities on how to implement aspects of a multi-species perspective in eco-evolutionary experiments, but rather is intended to serve as a source of inspiration for the many ways in which a multiple species perspective can be approached:

(1) *Community context of evolution*. In studies that use experimental evolution, quantifying evolution in the presence of other community members should be more often considered (Barraclough 2015). Studies that compare eco-evolutionary feedbacks upon evolution in isolation versus in a community context might reveal how important this aspect can be, and studies on microbial systems hint on its potential importance (Fiegna et al. 2015; Lawrence et al. 2012). Studies based on genetic differences as observed in nature can often be assumed to incorporate this relevant multi-species evolutionary context. However, even in these cases, researchers should be careful to understand how communities co-vary with selective factors. If community context varies with selection, then the chance exists that evolution is modified not just by the focal selective factor, but by coexisting species as well.

(2) *Co-adaptation of other species*. In quantifying ecological consequences of evolution in response to environmental change, it is important to also study settings in which populations of other species equally have had the opportunity to adapt to the environmental change. This is an especially important consideration in the design of follow-up experiments of experimental evolution. Experiments that directly use samples from natural communities to initiate the gardens for a common gardening approach will naturally incorporate these interactions. However, many such experiments create communities from whatever local community is easiest to sample rather than the appropriately co-evolved community. One interesting way to explore the importance of these interactions is a double transplant, where genetically differentiated populations of a focal species are transplanted in two types of common gardens, i.e. seeded with the communities of the two source habitats of the focal species. Again, studies comparing eco-evolutionary impacts in the presence and absence of co-adapted species might provide us with crucial insight into the importance of such co-adaptation. In a context of host-parasite (; Brunner et al. 2017; Decaestecker et al. 2013; Frickel et al. 2016; Masri et al. 2015) and mutualistic (Ford et al. 2016; Macke et al. 2017) interactions, there is already a quite large number of studies that take co-evolution into account in their analysis of joint dynamics of the two interacting species. Recently, co-evolution was also shown to impact invasion success of exotic species (Faillace & Morin 2016). Yet, we know of no empirical studies that compared the strength and direction of eco-evolutionary feedbacks on community members that were either allowed or not to co-evolve in response to the same experimental conditions together with the focal species. Such experiments might reveal strong cases of cryptic eco-evolutionary dynamics.

(3) *Resurrecting communities for reciprocal transplants*. The resurrection ecology approach (Decaestecker et al. 2007; Franks et al. 2018; Stoks et al. 2016; Sultan et al. 2013) applied to multiple species simultaneously might provide a powerful way to obtain insight into the impact of evolution as it occurred in nature on ecological processes. Here again one could test the impact of evolution of every species separately and in combination, and carry out “transplants”

over time (Houwenhuyse et al. 2018; Penczykowski et al. 2015), replacing evolved populations by representatives of their ancestors either for the whole community or for each of the member species, and quantify its feedback on ecological processes. Resurrection ecology can be applied on layered archives of dormant stages (mainly in aquatic systems, e.g. Stoks et al. 2016) or when dormant stages have been collected at different moments of a population's history (Franks et al. 2018).

(4) *Field transplants with adapted / non-adapted species sets*. In field transplant experiments, an interesting avenue might be to carry out "community transplants", in which entire co-evolved communities are reciprocally transplanted (Alexander et al. 2015) and compared to treatments in which community composition is maintained but in which the populations of all dominant species or a selection of key species is replaced by members of the same species but using genotypes isolated from the other habitat. The latter approach is only possible if community composition is not too divergent among habitats, but would provide an integrated analysis of the impact of the joint evolution of all species.

Ultimately, we want to understand natural systems. Therefore, a critical, but often missing, step is comparing eco-evolutionary impacts between experiments and wild systems. For example, a common gardening experiment might reveal a strong feedback from the evolution of increased grazing on primary productivity. The next step should be to evaluate if primary productivity is lower in natural systems in which higher grazing rates have evolved (Walsh et al. 2012). If not, then some critical ecological or evolutionary feature is likely missing from the common gardening experiments, including co-evolved species that could moderate the effects. For instance, the evolution of increased foraging rates of an intermediate consumer in response to selection from an apex predator increased prey diversity and decreased density in mesocosms (Urban 2013). Across ponds differing in the evolution of the focal species, prey diversity and density differed in the same ways as the experiments, suggesting an important eco-evolutionary dynamic had been captured by the simplistic experiments. While such comparisons do not provide solid proof, because similar patterns might in

494 principle also be generated by ecological, processes, their results can be suggestive of the potential
495 importance of the eco-evolutionary feedback in nature. Overall, we should not lose sight of the main
496 reason to study eco-evolutionary interactions: to understand natural dynamics and patterns.

497 *Field data*

498 Ideally, we would like to be able to quantify the impact of evolution on ecological processes directly
499 in the field, as this would capture natural complexity in a real metacommunity setting instead of in
500 isolated, artificial settings typically constructed in the laboratory. The key problem with field surveys
501 is, however, that they yield patterns from which processes need to be inferred, and that similar
502 patterns might result from many processes. This imposes an important limitation on the degree to
503 which mechanisms can be disentangled, including making the distinction between evolutionary and
504 ecological processes as drivers of a particular pattern or change. To make strong inferences, it will
505 often be necessary to tap into additional sources of information. Partnering field surveys with
506 experiments is a particularly valuable approach. Below we suggest some approaches that can provide
507 insight into the role of evolution in structuring natural metacommunities, each with their own
508 limitations:

509 (1) *Contribution of evolution to community trait values in a metacommunity*. If one has data on a
510 spatial survey in which not only the species composition but also genetically determined trait
511 values of local populations of key species have been measured, one can use either local or
512 regional averages of trait values of one or more of those species to quantify how local trait
513 variation affects community trait values across the metacommunity (Brans et al. 2017). This can
514 be done using regression-based methods (Lajoie & Vellend 2015) or using methods that partition
515 ecological and evolutionary contributions to community trait change (as in Govaert et al. 2016,
516 but adapted to spatial data; Govaert et al. unpublished). In order to be able to apply eco-
517 evolutionary partitioning metrics or to apply the regression-based method on data reflecting
518 evolution, one needs genotypic trait values for local populations of the (multiple) focal species

519 (Brans et al. 2017). This requires common garden experiments on representative isolates of local
520 populations of the studied species. If one wants to do this in a multi-species metacommunity
521 context, this would involve extensive common garden experiments on isolates of multiple
522 species from multiple sites in a metacommunity. To our knowledge there are, so far, no
523 published studies that have done this.
524 (2) *Quantifying the evolving metacommunity structure*. A potentially promising approach to quantify
525 the impact of evolution on ecological features of natural metacommunities involves applying a
526 metacommunity-type of analysis to data-sets on both communities and populations of the same
527 set of habitats in a landscape. If one collects data on species composition and on genetically
528 determined trait values of local populations of multiple species, one can quantify to what extent
529 species composition (traditional metacommunity ecology), trait variation based on species
530 composition (trait-based metacommunity ecology; trait values of species are calculated as
531 metacommunity averages or derived from literature), and trait variation within species are linked
532 to environmental (species sorting, natural selection) and spatial (dispersal) drivers (Cottenie
533 2005; Leibold et al. 2004). Again, in order to be able to link these patterns to evolutionary trait
534 change, the intraspecific trait variation needs to be quantified in common garden experiments,
535 isolating the genetic component of trait variation. In the resulting data-set, one can, in addition
536 to linking variation in species composition, community trait distribution, and intraspecific trait
537 variation in the focal species to local (environmental) and regional (spatial) drivers, also explore
538 to what extent intraspecific trait variation in the focal species is associated to deviations of the
539 expected community trait variation. In these analyses, one cannot only quantify the structure of
540 the evolving metacommunity (Urban et al. 2008), but also obtain insight in the likelihood that
541 evolutionary trait change contributed to metacommunity structure and community trait
542 distribution.
543 (3) *Population genomics in an evolving metacommunity context*. In the future, population genomics
544 (Rudman et al. 2018) will likely be key to reduce the amount of work while still being able to link

545 genetic differences to ecological responses (e.g. community composition, population density,
546 etc.). For this approach to be powerful, we will need further insights in how genomic data link to
547 trait values in target species. Given that these links might be complex and not necessarily
548 strongly repeatable (e.g. Becks et al. 2012; Gompert et al. 2014; Nosil et al. 2018), there is still a
549 long way to go for population genomics to translate in reliable estimates of trait variation, except
550 for some well-studied cases that involve major effect loci or gene clusters (Jones et al. 2012;
551 Lamichhaney et al. 2016). As the link between genomic variation and trait values becomes more
552 reliable, however, it will open tremendous opportunities for studying eco-evolutionary dynamics
553 in the field (Rodríguez-Verdugo et al. 2017; Rudman et al. 2018).

554 A key limitation of all the analyses highlighted in the previous paragraphs when based on field
555 surveys is that they only reveal the current pattern, implying that important transient changes that
556 might have been caused by evolution but leave no trace in the current metacommunity cannot be
557 quantified. This is very different from how we quantify eco-evolutionary dynamics in an experimental
558 approach such as common gardening experiments. In a common gardening set-up, one starts with
559 standardized "gardens" to which different genotypes of one or more species are added to then
560 monitor how the garden changes as a function of the manipulated genotype (Matthews et al. 2011).
561 In such settings, one quantifies the impact of evolution as the differentiation of the garden among
562 treatments developing from a common starting point. In most field surveys, however, one only has a
563 snapshot view of the resulting pattern. There is no guarantee that initial environmental conditions or
564 initial community composition of the different sites were identical, and it is actually very unlikely that
565 they were. So there is no common reference point to which the impact of evolutionary
566 differentiation can be scaled. In addition, the impact of evolution can only be quantified for the
567 observed set of species in the different sites. While it is possible that evolution of a given species
568 might have caused extinction of another species at the site or might have allowed a given species to
569 colonize the site, such impacts of evolution cannot be quantified in a snapshot survey. It is therefore
570 important to realize that field surveys documenting the impact of evolutionary change on ecology

quantify different aspects of this impact than the typical laboratory or mesocosm experiments. More specifically, snapshot field survey data can quantify the contribution of evolutionary differentiation in trait values of species among sites to community differentiation in trait values (cf. Govaert et al. 2016) and to the extent that there are well-established links between trait values and ecological processes, there might be a possibility to infer the potential impact of evolutionary differentiation in trait values on ecosystem functions (cf. Ellner et al. 2011).

(4) *Multiple time points*. As highlighted in the previous paragraph, the impact of evolution on transient ecological dynamics such as the local extinction of species cannot be detected in snapshot surveys. To some extent, this limitation is alleviated if one has access to multiple surveys spread in time. Even if only two or a few time points are available, it might be possible to infer more on the dynamics and processes underlying these dynamics. One would at least have insight into species that were lost from or gained by the local communities during the period over which one collected samples. Yet, linking this disappearance to evolution might not be straightforward. Conducting repeated common garden and common gardening experiments in these systems over time might be powerful to reveal evolution and its impact on ecology. Along the same lines, combining survey data with resurrection ecology (Decaestecker et al. 2007; Franks et al. 2018; Houwenhuyse et al. 2018; Stoks et al. 2016; Sultan et al. 2013) might prove very powerful. As having temporal series of data is important, we here make a plea to develop research programs on eco-evolutionary dynamics that involve long-term ecological research (LTER) sites (Knapp & Smith 2001) and/or sites amenable to resurrection ecology approaches (Franks et al. 2018). If one has very consistent and detailed time series, one can apply process-oriented approaches such as, in the case of population dynamics, integral projection modeling (IPM; Coulson et al. 2010; Easterling et al. 2000; Smallegange & Coulson 2013). Several of IPM-inspired analyses have been published on a number of unique data-sets on trait values and population dynamics of mammals to show that evolutionary trait change impacts population dynamics in the field (Ozgul et al. 2010; Pelletier et al. 2007, 2009). Extending this approach to

include multiple species would open important opportunities. The availability of the necessary data will, however, be an important obstacle for such an approach, especially because most LTER sites collect valuable ecological data, while neglecting evolutionary data.

(5) *Natural experiments*. The power of field surveys can be strongly increased by designing the work such that some of the shortcomings are reduced and specific hypotheses are tested using "natural experiments". One may, for instance, identify cases of a well-documented arrival of an exotic species, the application of specific nature management actions (creation of new habitats, assisted migration, clearings, …) or any other well-documented change (fire, recent urbanization, other land use change, pollution event). These well-documented cases of environmental change could then be used to design field work to test the impact of evolution, knowing that prior to the change community composition was similar. The latter can be achieved by pairing sites that are impacted or not but are nearby and used to belong to the same system, or for which data exist on the situation prior to the environmental change. Moreover, repeated sampling (i.e. prior and following the environmental impact, or multiple times following the environmental change) will also increase the strength of the inferences. These type of surveys can provide information on both the ecological and evolutionary (through common garden experiments or genomics) responses to the environmental change, quantify the contribution of evolutionary trait change to community trait change, and determine the likelihood that evolutionary change contributed to changes in species abundances (including extinction). Such survey studies should preferably be combined with the experimental approaches outlined in the previous section, such as field transplant experiments of populations or entire communities. The existence of samples prior to the environmental change can in some cases be provided by studying museum samples or through a resurrection ecology approach. The resurrection ecology approach is especially useful in this regard, as it allows the use of both old and recent populations of the different species in experiments.

622 The most powerful approaches to multispecies eco-evolutionary dynamics studies would be the
623 combination of well-designed field studies that identify cases of particular interest, which are then
624 combined with the appropriate experimental approaches (such as field transplants, common garden
625 experiments, resurrection ecology, or experimental evolution) to test particular hypotheses. To our
626 knowledge, no study so far engaged in such an endeavor in a truly multiple species context. While
627 this will no doubt be a huge effort, it would be worth it, as it would allow quantifying the importance
628 of eco-evolutionary dynamics in ecologically relevant settings, and would likely reveal several cases
629 of cryptic eco-evolutionary dynamics (Kinnison et al. 2015).

630

631 **Using complexity to make things simple again: emergent patterns and rules**

632 A key problem with increasing study complexity is that the results are often contingent on starting
633 conditions and that apparent minor differences can lead to strongly deviating patterns and
634 trajectories (Fukami 2015; Losos et al. 1998; Scheffer et al. 2001). This contingency results in reduced
635 power to derive generic laws (Lawton 1999) or to make predictions on responses to future change
636 (Urban et al. 2016). In the case of evolving metacommunities, there is the additional complexity that
637 the results and dynamics are not only strongly contingent on environmental conditions, but also on
638 the properties of the interacting species. There are ~8 million species globally, each with their own
639 set of traits, histories and evolutionary strategies responding to the environment and to interactions
640 with other species. Even if there is a great deal of redundancy in species traits, it is clear that the
641 dynamics of interactions as studied in the field and in experiments is often very strongly dependent
642 on the specific traits of the interacting species. The mere observation that evolutionary trait change
643 can so strongly impact ecological dynamics (e.g. Becks et al. 2012) testifies to the importance of trait
644 values and thus the specificity of interactions on ecological dynamics. It would, however, be unwise
645 to derive from this level of contingency that it is not useful to study the impact of evolution on
646 ecological processes in complex settings and that it is therefore preferable to stick to proof-of-

principle experiments. It is true that context-dependency can lead to high levels of contingency on environmental conditions and the nature of species and communities that are considered, but the resulting emergent patterns of adding levels of complexity such as including evolutionary dynamics or including multiple species can be so strong that studying isolated modules will simply lead to the wrong conclusions.

We thus need to obtain insight in the importance and the resulting patterns of eco-evolutionary dynamics in a multi-species context for two reasons. First, ignoring complexity may lead to erroneous judgments on the importance or even the direction of eco-evolutionary dynamics, so that relying on proof-of-principle experiments in highly simplified settings is risky, for instance when making predictions on responses to human-induced change (Urban et al. 2016). Adding a community or metacommunity context might change dynamics in a spectacular way (Kinnison et al. 2015), but has not been systematically explored. Second, while the results of studies that add a multi-species context might depend on the systems, species and environmental conditions studied, investment in a large number of eco-evolutionary dynamics analyses in a community context or in nature might reveal patterns that can be translated into “rules” that we can apply to estimate the likely effect of evolution on ecological processes given certain conditions.

Potential rules are for example, the suggestion made by Bailey et al. (2009) that the impact of evolution might fade as one moves from populations to communities to ecosystems, because of an increasing number of potential sources of variation as complexity increases. While this seems a logical rule, it might be challenged in the case of evolution in traits that directly might impact ecosystem functioning. Another potential rule is that the amount of eco-evolutionary dynamics might scale with body size, because of shorter generation times enabling higher rates of evolutionary change. Many processes scale with body size (Peters 1986), and there is evidence for such a scaling in metacommunity ecology (De Bie et al. 2012). Moreover, for microbial organisms it has indeed been shown that a few days of difference in time of establishment is sufficient for evolutionary

672 diversification to impact ecological dynamics (Fukami et al. 2007; Venail et al. 2008; Zee & Fukami
673 2018). So there are indications that eco-evolutionary feedbacks might be more prevalent in
674 organisms with short generation times (De Meester et al. 2016), even though it has not been
675 systematically analyzed and clear cases of eco-evolutionary feedbacks have been reported for many
676 long-lived species too (Hendry 2017). We also note that when eco-evolutionary feedbacks are
677 studied across community types (e.g. gut microbiota or microbial communities that are eaten upon),
678 time scales differ among interacting partners, enhancing the potential of organisms with short
679 generation time to have a strong impact on ecological processes through trait evolution. This has
680 been well-established in studies on host-parasite interactions (Gandon et al. 2008) but also applies in
681 a broader context for all co-evolutionary and eco-evolutionary dynamics (Dercole et al. 2006). Other
682 potential rules might be that evolutionary dynamics might be more important in species-poor (Urban
683 et al. 2008) and more isolated systems (De Meester et al. 2016; Vanoverbeke et al. 2016). Developing
684 insights in such rules might involve the combined effort of empirical work and targeted modelling.
685 Theoretical modelling can help to identify instances where eco-evolutionary feedbacks could
686 potentially be important (Govaert et al. this volume), or to test the strength of these feedbacks in
687 more complex systems (de Andreazzi et al. 2018). Further development of theory will be crucial in
688 order to be able to incorporate eco-evolutionary dynamics in predictions (Urban et al. 2016) and
689 management beyond the specific settings that have been empirically documented.

690

691 **Conclusions**

692 In the past, ecologists ignored evolution, whereas evolutionary biologists ignored ecological
693 interactions in multi-species communities. The field of eco-evolutionary dynamics is starting to alert
694 ecologists to the substantial impacts of evolutionary change in their models and empirical work. We
695 hope that this opinion paper together with other recent reviews and synthesis papers (e.g.
696 Barraclough 2015; Kinnison et al. 2015) will encourage researchers working on eco-evolutionary

feedbacks to not focus on single species in isolation but to consider realistic ecological contexts in their work. While integrating evolution into ecology can revolutionize ecology, we predict that having a multi-species ecological context built into our eco-evolutionary models and empirical framework may be equally important in revolutionizing the field of eco-evolutionary dynamics. At this stage, we do not know to what extent the multi-species context hinders rapid evolution or promotes it, and how evolutionary change impacts ecological features that are the result of the interaction of multiple species beyond the simplest of modules (one single predator and prey species, or one host and one parasite species). Simple species interaction modules for the most abundant species and strongest interactors might perhaps capture dominant eco-evolutionary processes sufficiently to understand key features of some natural communities. However, in other cases, indirect effects and cryptic eco-evolutionary dynamics will necessitate a more sophisticated understanding. There is a need for a research framework to tackle eco-evolutionary dynamics in a truly multi-species context. Obviously, responses will vary widely, but the question is whether we can detect emergent patterns that allow us to predict how the dynamics will be influenced as we build in more realism. Combining this realism with the rigor in testing hypotheses in eco-evolutionary dynamics, might be the key challenge in the field of eco-evolutionary dynamics in the coming decade.

References

Alberti, M. (2015). Eco-evolutionary dynamics in an urbanizing planet. Trends in Ecology & Evolution, 30(2), 114–126. https://doi.org/10.1016/J.TREE.2014.11.007

Alexander, J. M., Diez, J. M., & Levine, J. M. (2015). Novel competitors shape species' responses to climate change. Nature, 525(7570), 515–518. https://doi.org/10.1038/nature14952

Agrawal, A. A., Hastings, A. P., Johnson, M. T. J., Maron, J. L., & Salminen, J.-P. (2012). Insect herbivores drive real-time ecological and evolutionary change in plant populations. Science, 338(6103), 113–116. https://doi.org/10.1126/science.1225977

Bailey, J. K., Schweitzer, J. A., Ubeda, F., Koricheva, J., LeRoy, C. J., Madritch, M. D., … Whitham, T. G. (2009). From genes to ecosystems: a synthesis of the effects of plant genetic factors across levels of organization. Philosophical Transactions of the Royal Society of London. Series B. Biological Sciences, 364(1523), 1607–1616. https://doi.org/10.1098/rstb.2008.0336

Barraclough, T. G. (2015). How do species interactions affect evolutionary dynamics across whole communities? Annual Review of Ecology, Evolution, and Systematics, 46(1), 25–48. https://doi.org/10.1146/annurev-ecolsys-112414-054030

Bassar, R. D., Marshall, M. C., López-Sepulcre, A., Zandonà, E., Auer, S. K., Travis, J., … Reznick, D. N. (2010). Local adaptation in Trinidadian guppies alters ecosystem processes. Proceedings of the National Academy of Sciences of the United States of America, 107(8), 3616–3621. https://doi.org/10.1073/pnas.0908023107

Becks, L., Ellner, S. P., Jones, L. E., & Hairston, N. G. (2012). The functional genomics of an eco-evolutionary feedback loop: linking gene expression, trait evolution, and community dynamics. Ecology Letters, 15(5), 492–501. https://doi.org/10.1111/j.1461-0248.2012.01763.x

Benkman, C. W., Holimon, W. C., & Smith, J. W. (2001). The influence of a competitor on the geographic mosaic of coevolution between crossbills and lodgepole pine. Evolution; International Journal of Organic Evolution, 55(2), 282–294. https://doi.org/10.1111/j.0014-3820.2001.tb01293.x

Bolnick, D. I., Amarasekare, P., Araújo, M. S., Bürger, R., Levine, J. M., Novak, M., … Vasseur, D. A. (2011). Why intraspecific trait variation matters in community ecology. Trends in Ecology & Evolution, 26(4), 183–192. https://doi.org/10.1016/j.tree.2011.01.009

Brans, K. I., Govaert, L., Engelen, J. M. T., Gianuca, A. T., Souffreau, C., & De Meester, L. (2017). Eco-evolutionary dynamics in urbanized landscapes: evolution, species sorting and the change in zooplankton body size along urbanization gradients. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 372(1712). https://doi.org/10.1098/rstb.2016.0030

Brunner, F. S., Anaya-Rojas, J. M., Matthews, B., & Eizaguirre, C. (2017). Experimental evidence that parasites drive eco-evolutionary feedbacks. Proceedings of the National Academy of Sciences of the United States of America, 114(14), 3678–3683. https://doi.org/10.1073/pnas.1619147114

Bull, J. J., Millstein, J., Orcutt, J., & Wichman, H. A. (2006). Evolutionary feedback mediated through population density, illustrated with viruses in chemostats. The American Naturalist, 167(2), E39-51. https://doi.org/10.1086/499374

Chitty, D. (1967). The natural selection of self-regulatory behaviour in animal populations. Proceedings of the Ecological Society of Australia, 2, 51–78.

Cottenie, K. (2005). Integrating environmental and spatial processes in ecological community dynamics. Ecology Letters, 8, 1175–1182. https://doi.org/10.1111/j.1461-0248.2005.00820.x

Coulson, T., Tuljapurkar, S., & Childs, D. Z. (2010). Using evolutionary demography to link life history theory, quantitative genetics and population ecology. The Journal of Animal Ecology, 79(6), 1226–1240. https://doi.org/10.1111/j.1365-2656.2010.01734.x

Crutsinger, G. M., Collins, M. D., Fordyce, J. A., Gompert, Z., Nice, C. C., & Sanders, N. J. (2006). Plant genotypic diversity predicts community structure and governs an ecosystem process. Science, 313(5789), 966–968. https://doi.org/10.1126/science.1128326

de Andreazzi, C. S., Guimarães, P. R. & Melián, C. J. (2018). Eco-evolutionary feedbacks promote fluctuating selection and long-term stability of antagonistic networks. Proceedings of the Royal Society B: Biological Sciences, 285, 20172596. https://doi.org/10.1098/rspb.2017.2596

De Bie, T., De Meester, L., Brendonck, L., Martens, K., Goddeeris, B., Ercken, D., … Declerck, S. A. J. (2012). Body size and dispersal mode as key traits determining metacommunity structure of aquatic organisms. Ecology Letters, 15, 740–747. https://doi.org/10.1111/j.1461-0248.2012.01794.x

de Mazancourt, C., Johnson, E., & Barraclough, T. G. (2008). Biodiversity inhibits species' evolutionary responses to changing environments. Ecology Letters, 11(4), 380–388. https://doi.org/10.1111/j.1461-0248.2008.01152.x

De Meester, L., Van Doorslaer, W., Geerts, A., Orsini, L., & Stoks, R. (2011). Thermal genetic adaptation in the water flea *Daphnia* and its impact: an evolving metacommunity approach. Integrative and Comparative Biology, 51(5), 703–718. https://doi.org/10.1093/icb/icr027

De Meester, L., Vanoverbeke, J., Kilsdonk, L. J., & Urban, M. C. (2016). Evolving perspectives on monopolization and priority effects. Trends in Ecology & Evolution, 31(2), 136–146. https://doi.org/10.1016/J.TREE.2015.12.009

Decaestecker, E., De Gersem, H., Michalakis, Y., & Raeymaekers, J. A. M. (2013). Damped long-term host-parasite Red Queen coevolutionary dynamics: a reflection of dilution effects? Ecology Letters, 16(12), 1455–1462. https://doi.org/10.1111/ele.12186

Decaestecker, E., Gaba, S., Raeymaekers, J. A. M., Stoks, R., Van Kerckhoven, L., Ebert, D., & De Meester, L. (2007). Host–parasite 'Red Queen' dynamics archived in pond sediment. Nature, 450(7171), 870–873. https://doi.org/10.1038/nature06291

Dercole, F., Ferrière, R., Gragnani, A., & Rinaldi, S. (2006). Coevolution of slow-fast populations: evolutionary sliding, evolutionary pseudo-equilibria and complex Red Queen dynamics. Proceedings of the Royal Society B: Biological Sciences, 273(1589), 983–990. https://doi.org/10.1098/rspb.2005.3398

Easterling, D. R., Meehl, G. A., Parmesan, C., Changnon, S. A., Karl, T. R., & Mearns, L. O. (2000). Climate extremes: observations, modeling, and impacts. Science, 289(5487), 2068–2074. https://doi.org/10.1126/science.289.5487.2068

Ellner, S. P., Geber, M. A., & Hairston, N. G. (2011). Does rapid evolution matter? Measuring the rate of contemporary evolution and its impacts on ecological dynamics. Ecology Letters, 14, 603–614. https://doi.org/10.1111/j.1461-0248.2011.01616.x

795 Endler, J. A. (1986). Natural selection in the wild. Princeton University Press. New Jersey.

796 Faillace, C. A., & Morin, P. J. (2016). Evolution alters the consequences of invasions in experimental
797 communities. Nature Ecology & Evolution, 1(0013). https://doi.org/10.1038/s41559-016-0013

798 Farkas, T. E., Mononen, T., Comeault, A. A., Hanski, I., & Nosil, P. (2013). Evolution of camouflage
799 drives rapid ecological change in an insect community. Current Biology, 23(19), 1835–1843.
800 https://doi.org/10.1016/j.cub.2013.07.067

801 Fiegna, F., Scheuerl, T., Moreno-Letelier, A., Bell, T. and Barraclough, T.G. (2015). Saturating effects of
802 species diversity on life-history evolution in bacteria. Proceedings of the Royal Society B: Biological
803 Sciences, 282, 1815.

804 Ford, S. A., Kao, D., Williams, D., & King, K. C. (2016). Microbe-mediated host defence drives the
805 evolution of reduced pathogen virulence. Nature Communications, 7, 13430.

806 Franks, S. J., Hamann, E., & Weis, A. E. (2018). Using the resurrection approach to understand
807 contemporary evolution in changing environments. Evolutionary Applications, 11(1), 17–28.
808 https://doi.org/10.1111/eva.12528

809 Frickel, J., Sieber, M., & Becks, L. (2016). Eco-evolutionary dynamics in a coevolving host-virus
810 system. Ecology Letters, 19(4), 450–459. https://doi.org/10.1111/ele.12580

811 Frickel, J., Theodosiou, L., & Becks, L. (2017). Rapid evolution of hosts begets species diversity at the
812 cost of intraspecific diversity. Proceedings of the National Academy of Sciences of the United States
813 of America, 114(42), 11193–11198. https://doi.org/10.1073/pnas.1701845114

814 Fridley, J. D., & Grime, J. P. (2010). Community and ecosystem effects of intraspecific genetic
815 diversity in grassland microcosms of varying species diversity. Ecology, 91(8), 2272–2283.
816 https://doi.org/10.1890/09-1240.1

817 Friman, V.-P., Guzman, L. M., Reuman, D. C., & Bell, T. (2015). Bacterial adaptation to sublethal
818 antibiotic gradients can change the ecological properties of multitrophic microbial communities.
819 Proceedings of the Royal Society B: Biological Sciences, 282(1806), 20142920.
820 https://doi.org/10.1098/rspb.2014.2920

821 Fukami, T. (2015). Historical contingency in community assembly: integrating niches, species pools,
822 and priority effects. Annual Review of Ecology, Evolution, and Systematics, 46, 1-23.
823 https://doi.org/10.1146/annurev-ecolsys-110411-160340

824 Fukami, T., Beaumont, H. J. E., Zhang, X.-X., & Rainey, P. B. (2007). Immigration history controls
825 diversification in experimental adaptive radiation. Nature, 446(7134), 436–439.
826 https://doi.org/10.1038/nature05629

827 Fussmann, G. F., Loreau, M., & Abrams, P. A. (2007). Eco-evolutionary dynamics of communities and
828 ecosystems. Functional Ecology, 21(3), 465–477. https://doi.org/10.1111/j.1365-2435.2007.01275.x

829 Gandon, S., Buckling, A., Decaesteckerà, E., & Day, T. (2008). Host–parasite coevolution and patterns
830 of adaptation across time and space. Journal of Evolutionary Biology, 21(6), 1861-1866.
831 https://doi.org/10.1111/j.1420-9101.2008.01598.x

832 Gómez, P., Paterson, S., De Meester, L., Liu, X., Lenzi, L., Sharma, M. D., … Buckling, A. (2016). Local
833 adaptation of a bacterium is as important as its presence in structuring a natural microbial
834 community. Nature Communications, 7, 12453. https://doi.org/10.1038/ncomms12453

Gompert, Z., Comeault, A. A., Farkas, T. E., Feder, J. L., Parchman, T. L., Buerkle, C. A., & Nosil, P. (2014). Experimental evidence for ecological selection on genome variation in the wild. Ecology Letters, 17(3), 369–379. https://doi.org/10.1111/ele.12238

Govaert, L., Fronhofer, E. A., Lion, S., Eizaguirre, C., Bronte, D., Egas, M., Hendry, A. P., De Brito Martins, A., Melián, C. J., Raeymaekers, J. A. M., Ratikainen, I. I., Saether, B.-E., Schweitzer, J. A., Matthews, B. (2018). Eco-evolutionary feedbacks - theoretical models and perspectives. Functional Ecology (this special issue).

Govaert, L., Pantel, J. H., & De Meester, L. (2016). Eco-evolutionary partitioning metrics: assessing the importance of ecological and evolutionary contributions to population and community change. Ecology Letters, 19, 839–853. https://doi.org/10.1111/ele.12632

Gravel, D., Massol, F., Canard, E., Mouillot, D., & Mouquet, N. (2011). Trophic theory of island biogeography. Ecology Letters, 14(10), 1010–1016. https://doi.org/10.1111/j.1461-0248.2011.01667.x

Hairston, N. G., Ellner, S. P., Geber, M. A., Yoshida, T., & Fox, J. A. (2005). Rapid evolution and the convergence of ecological and evolutionary time. Ecology Letters, 8(10), 1114–1127. https://doi.org/10.1111/j.1461-0248.2005.00812.x

Harmon, L. J., Matthews, B., Des Roches, S., Chase, J. M., Shurin, J. B., & Schluter, D. (2009). Evolutionary diversification in stickleback affects ecosystem functioning. Nature, 458(7242), 1167–1170. https://doi.org/10.1038/nature07974

Hendry, A. P. (2017). Eco-evolutionary Dynamics. Princeton University Press, New Jersey.

Hiltunen, T., & Becks, L. (2014). Consumer co-evolution as an important component of the eco-evolutionary feedback. Nature Communications, 5(1), 5226. https://doi.org/10.1038/ncomms6226

Houwenhuyse, S., Macke, E., Reyserhove, L., Bulteel, L., & Decaestecker, E. (2018). Back to the future in a petri dish: Origin and impact of resurrected microbes in natural populations. Evolutionary Applications, 11(1), 29–41. https://doi.org/10.1111/eva.12538

Jones, E. I., & Gomulkiewicz, R. (2012). Biotic interactions, rapid evolution, and the establishment of introduced species. The American Naturalist, 179(2), E28-36. https://doi.org/10.1086/663678

Kinnison, M. T., Hairston, N. G., & Hendry, A. P. (2015). Cryptic eco-evolutionary dynamics. Annals of the New York Academy of Sciences, 1360(1), 120–144. https://doi.org/10.1111/nyas.12974

Knapp, A. K., & Smith, M. D. (2001). Variation among biomes in temporal dynamics of aboveground primary production. Science, 291(5503), 481–484. https://doi.org/10.1126/science.291.5503.481

Koskella, B., Hall, L. J., & Metcalf, C. J. E. (2017). The microbiome beyond the horizon of ecological and evolutionary theory. Nature Ecology & Evolution, 1(11), 1606–1615. https://doi.org/10.1038/s41559-017-0340-2

Lafferty, K. D., Dobson, A. P., Kuris, A. M., & Tilman, G. D. (2006). Parasites dominate food web links. Proceedings of the National Academy of Sciences of the United States of America, 103(30), 11211-11216.

Lajoie, G., & Vellend, M. (2015). Understanding context dependence in the contribution of intraspecific variation to community trait–environment matching. Ecology, 96(11), 2912–2922. https://doi.org/10.1890/15-0156.1

Lamichhaney, S., Han, F., Berglund, J., Wang, C., Almén, M. S., Webster, M. T., … Andersson, L. (2016). A beak size locus in Darwin's finches facilitated character displacement during a drought. Science, 352(6284), 470–474. https://doi.org/10.1126/science.aad8786

Lawrence, D., Fiegna, F., Behrends, V., Bundy, J. G., Phillimore, A. B., Bell, T., & Barraclough, T. G. (2012). Species interactions alter evolutionary responses to a novel environment. PLoS Biology, 10(5), e1001330. https://doi.org/10.1371/journal.pbio.1001330

Lawton, J. H. (1999). Are there general laws in ecology? Oikos, 84(2), 177. https://doi.org/10.2307/3546712

Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F., … Gonzalez, A. (2004). The metacommunity concept: a framework for multi-scale community ecology. Ecology Letters, 7, 601–613. https://doi.org/10.1111/j.1461-0248.2004.00608.x

Lion, S. (2018). Theoretical approaches in evolutionary ecology: environmental feedback as a unifying perspective. The American Naturalist, 191(1), 21–44. https://doi.org/10.1086/694865

Loeuille, N., Barot, S., Georgelin, E., Kylafis, G., & Lavigne, C. (2013). Eco-evolutionary dynamics of agricultural networks: implications for sustainable management. Advances in Ecological Research, 49, 339-435. https://doi.org/10.1016/B978-0-12-420002-9.00006-8

Loeuille, N., & Leibold, M. A. (2008). Evolution in metacommunities: on the relative importance of species sorting and monopolization in structuring communities. The American Naturalist, 171(6), 788–799. https://doi.org/10.1086/587745

Losos, J. B., T. R. Jackman, A. Larson, K. de Queiroz, and L. Rodriguez-Schettino. (1998). Contingency and determinism in replicated adaptive radiations of island lizards. Science, 279, 2115-2118. https://doi.org/10.1126/science.279.5359.2115

Low-Décarie, E., Kolber, M., Homme, P., Lofano, A., Dumbrell, A., Gonzalez, A., & Bell, G. (2015). Community rescue in experimental metacommunities. Proceedings of the National Academy of Sciences of the United States of America, 112(46), 14307–14312. https://doi.org/10.1073/pnas.1513125112

Lundsgaard-Hansen, B., Matthews, B., & Seehausen, O. (2014). Ecological speciation and phenotypic plasticity affect ecosystems. Ecology, 95(10), 2723–2735. https://doi.org/10.1890/13-2338.1

Lynch, M., & Walsh, B. (1998). Genetics and analysis of quantitative traits. Sinauer.

Macke, E., Tasiemski, A., Massol, F., Callens, M., & Decaestecker, E. (2017). Life history and eco-evolutionary dynamics in light of the gut microbiota. Oikos, 126(4), 508–531. https://doi.org/10.1111/oik.03900

Masri, L., Branca, A., Sheppard, A. E., Papkou, A., Laehnemann, D., Guenther, P. S., … Schulenburg, H. (2015). Host–pathogen coevolution: the selective advantage of *Bacillus thuringiensis* virulence and its CRY toxin genes. PLOS Biology, 13(6), e1002169. https://doi.org/10.1371/journal.pbio.1002169

Matthews, B., Aebischer, T., Sullam, K. E., Lundsgaard-Hansen, B., & Seehausen, O. (2016). Experimental evidence of an eco-evolutionary feedback during adaptive divergence. Current Biology, 26(4), 483–489. https://doi.org/10.1016/j.cub.2015.11.070

Matthews, B., Narwani, A., Hausch, S., Nonaka, E., Peter, H., Yamamichi, M., … Turner, C. B. (2011). Toward an integration of evolutionary biology and ecosystem science. Ecology Letters, 14(7), 690–701. https://doi.org/10.1111/j.1461-0248.2011.01627.x

McPeek, M. A. (2017a). The ecological dynamics of natural selection: traits and the coevolution of community structure. The American Naturalist, 189(5), E91–E117. https://doi.org/10.1086/691101

McPeek, M. A. (2017b). Evolutionary community ecology. Princeton University Press. New Jersey.

Merilä, J., & Hendry, A. P. (2014). Climate change, adaptation, and phenotypic plasticity: the problem and the evidence. Evolutionary Applications, 7(1), 1–14. https://doi.org/10.1111/eva.12137

Norberg, J., Urban, M. C., Vellend, M., Klausmeier, C. A., & Loeuille, N. (2012). Eco-evolutionary responses of biodiversity to climate change. Nature Climate Change, 2. https://doi.org/10.1038/NCLIMATE1588

Nosil, P., Villoutreix, R., de Carvalho, C. F., Farkas, T. E., Soria-Carrasco, V., Feder, J. L., … Gompert, Z. (2018). Natural selection and the predictability of evolution in *Timema* stick insects. Science, 359(6377), 765–770. https://doi.org/10.1126/science.aap9125

Osmond, M. M., & de Mazancourt, C. (2013). How competition affects evolutionary rescue. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 368(1610), 20120085. https://doi.org/10.1098/rstb.2012.0085

Palkovacs, E. P., & Post, D. M. (2009). Experimental evidence that phenotypic divergence in predators drives community divergence in prey. Ecology, 90(2), 300–305. https://doi.org/10.1890/08-1673.1

Pantel, J. H., Duvivier, C., & De Meester, L. (2015). Rapid local adaptation mediates zooplankton community assembly in experimental mesocosms. Ecology Letters, 18, 992–1000. https://doi.org/10.1111/ele.12480

Patel, S., Cortez, M. H., & Schreiber, S. J. (2018). Partitioning the effects of eco-evolutionary feedbacks on community stability. The American Naturalist, 191(3), 381–394. https://doi.org/10.1086/695834

Pelletier, F., Clutton-Brock, T., Pemberton, J., Tuljapurkar, S., & Coulson, T. (2007). The evolutionary demography of ecological change: linking trait variation and population growth. Science, 315(5818), 1571–1574. https://doi.org/10.1126/science.1139024

Pelletier, F., Garant, D., & Hendry, A. P. (2009). Eco-evolutionary dynamics. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 364(1523), 1483–1489. https://doi.org/10.1098/rstb.2009.0027

Penczykowski, R. M., Laine, A.-L., & Koskella, B. (2016). Understanding the ecology and evolution of host-parasite interactions across scales. Evolutionary Applications, 9(1), 37–52. https://doi.org/10.1111/eva.12294

Peters, R. H. (1986). The ecological implications of body size. Cambridge University Press.

Poisot, T., Stouffer, D. B., & Gravel, D. (2015). Beyond species: why ecological interaction networks vary through space and time. Oikos, 124(3), 243–251. https://doi.org/10.1111/oik.01719

Richardson, J. L., Urban, M. C., Bolnick, D. I., & Skelly, D. K. (2014). Microgeographic adaptation and the spatial scale of evolution. Trends in Ecology & Evolution, 29(3), 165–176. https://doi.org/10.1016/j.tree.2014.01.002

953 Rodríguez-Verdugo, A., Buckley, J., & Stapley, J. (2017). The genomic basis of eco-evolutionary
954 dynamics. Molecular Ecology, 26(6), 1456–1464. https://doi.org/10.1111/mec.14045

955 Rudman, S. M., Barbour, M. A., Csilléry, K., Gienapp, P., Guillaume, F., Hairston, N. G., … Levine, J. M.
956 (2018). What genomic data can reveal about eco-evolutionary dynamics. Nature Ecology & Evolution,
957 2(1), 9–15. https://doi.org/10.1038/s41559-017-0385-2

958 Rudman, S. M., Rodriguez-Cabal, M. A., Stier, A., Sato, T., Heavyside, J., El-Sabaawi, R. W., &
959 Crutsinger, G. M. (2015). Adaptive genetic variation mediates bottom-up and top-down control in an
960 aquatic ecosystem. Proceedings of the Royal Society B: Biological Sciences, 282(1812), 20151234.
961 https://doi.org/10.1098/rspb.2015.1234

962 Rudman, S. M., & Schluter, D. (2016). Ecological impacts of reverse speciation in threespine
963 stickleback. Current Biology, 26(4), 490–495. https://doi.org/10.1016/j.cub.2016.01.004

964 Scheffer, M., Carpenter, S., Foley, J. A., Folke, C., & Walker, B. (2001). Catastrophic shifts in
965 ecosystems. Nature, 413(6856), 591–596. https://doi.org/10.1038/35098000

966 Schoener, T. W. (2011). The Newest Synthesis: understanding the interplay of evolutionary and
967 ecological dynamics. Science, 313(616), 426-429. https://doi.org/10.1126/science.1193954

968 Shefferson, R. P., & Salguero-Gómez, R. (2015). Eco-evolutionary dynamics in plants: interactive
969 processes at overlapping time-scales and their implications. Journal of Ecology, 103(4), 789–797.
970 https://doi.org/10.1111/1365-2745.12432

971 Smallegange, I. M., & Coulson, T. (2013). Towards a general, population-level understanding of eco-
972 evolutionary change. Trends in Ecology & Evolution, 28(3), 143–148.
973 https://doi.org/10.1016/j.tree.2012.07.021

974 Stockwell, C. A., Hendry, A. P., & Kinnison, M. T. (2003). Contemporary evolution meets conservation
975 biology. Trends in Ecology & Evolution, 18(2), 94–101. https://doi.org/10.1016/S0169-
976 5347(02)00044-7

977 Stoks, R., Govaert, L., Pauwels, K., Jansen, B., & De Meester, L. (2016). Resurrecting complexity: the
978 interplay of plasticity and rapid evolution in the multiple trait response to strong changes in
979 predation pressure in the water flea *Daphnia magna*. Ecology Letters, 19(2), 180–190.
980 https://doi.org/10.1111/ele.12551

981 Sultan, S. E., Horgan-Kobelski, T., Nichols, L. M., Riggs, C. E., & Waples, R. K. (2013). A resurrection
982 study reveals rapid adaptive evolution within populations of an invasive plant. Evolutionary
983 Applications, 6(2), 266–278. https://doi.org/10.1111/j.1752-4571.2012.00287.x

984 Terhorst, C. P., Lennon, J. T., & Lau, J. A. (2014). The relative importance of rapid evolution for plant-
985 microbe interactions depends on ecological context. Proceedings of the Royal Society B: Biological
986 Sciences, 281(1785), 20140028. https://doi.org/10.1098/rspb.2014.0028

987 Thompson, J. N. (1998). Rapid evolution as an ecological process. Trends in Ecology & Evolution,
988 13(8), 329–332. https://doi.org/10.1016/S0169-5347(98)01378-0

989 Thompson, J. N. (2005). The geographic mosaic of coevolution. University of Chicago Press.

990 Turcotte, M. M., Corrin, M. S. C., & Johnson, M. T. J. (2012). Adaptive evolution in ecological
991 communities. PLoS Biology, 10(5), e1001332. https://doi.org/10.1371/journal.pbio.1001332

Urban, M. C. (2013). Evolution mediates the effects of apex predation on aquatic food webs. Proceedings of the Royal Society B: Biological Sciences, 280(1763), 20130859. https://doi.org/10.1098/rspb.2013.0859

Urban, M. C., Bocedi, G., Hendry, A. P., Mihoub, J.-B., Pe'er, G., Singer, A., … Travis, J. M. J. (2016). Improving the forecast for biodiversity under climate change. Science, 353(6304), aad8466. https://doi.org/10.1126/science.aad8466

Urban, M. C., & De Meester, L. (2009). Community monopolization: local adaptation enhances priority effects in an evolving metacommunity. Proceedings of the Royal Society B: Biological Sciences, 276(1676), 4129–4138. https://doi.org/10.1098/rspb.2009.1382

Urban, M. C., De Meester, L., Vellend, M., Stoks, R., & Vanoverbeke, J. (2012). A crucial step toward realism: responses to climate change from an evolving metacommunity perspective. Evolutionary Applications, 5(2), 154–167. https://doi.org/10.1111/j.1752-4571.2011.00208.x

Urban, M. C., Leibold, M. A., Amarasekare, P., De Meester, L., Gomulkiewicz, R., Hochberg, M. E., … Wade, M. J. (2008). The evolutionary ecology of metacommunities. Trends in Ecology and Evolution, 23(6), 311–317. https://doi.org/10.1016/j.tree.2008.02.007

Urban, M. C., & Skelly, D. K. (2006). Evolving metacommunities: toward an evolutionary perspective on metacommunities. Ecology, 87(7), 1616–1626. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/16922313

Vanoverbeke, J., Urban, M. C., & De Meester, L. (2016). Community assembly is a race between immigration and adaptation: eco-evolutionary interactions across spatial scales. Ecography, 39(9), 858–870. https://doi.org/10.1111/ecog.01394

Venail, P. A., MacLean, R. C., Bouvier, T., Brockhurst, M. A., Hochberg, M. E., & Mouquet, N. (2008). Diversity and productivity peak at intermediate dispersal rate in evolving metacommunities. Nature, 452(7184), 210–214. https://doi.org/10.1038/nature06554

Via, S., Gomulkiewicz, R., De Jong, G., Scheiner, S. M., Schlichting, C. D., & Van Tienderen, P. H. (1995). Adaptive phenotypic plasticity: consensus and controversy. Trends in Ecology & Evolution, 10(5), 212–217. https://doi.org/10.1016/S0169-5347(00)89061-8

Via, S., & Lande, R. (1985). Genotype-Environment interaction and the evolution of phenotypic plasticity. Evolution, 39(3), 505. https://doi.org/10.2307/2408649

Violle, C., Enquist, B. J., McGill, B. J., Jiang, L., Albert, C. H., Hulshof, C., … Messier, J. (2012). The return of the variance: intraspecific variability in community ecology. Trends in Ecology & Evolution, 27(4), 244–252. https://doi.org/10.1016/j.tree.2011.11.014

Walsh, M. R., DeLong, J. P., Hanley, T. C., & Post, D. M. (2012). A cascade of evolutionary change alters consumer-resource dynamics and ecosystem function. Proceedings of the Royal Society B: Biological Sciences, 279(1741), 3184–3192. https://doi.org/10.1098/rspb.2012.0496

Yoshida, T., Jones, L. E., Ellner, S. P., Fussmann, G. F., & Hairston, N. G. (2003). Rapid evolution drives ecological dynamics in a predator–prey system. Nature, 424(6946), 303–306. https://doi.org/10.1038/nature01767

Zee, P. C., & Fukami, T. (2018). Priority effects are weakened by a short, but not long, history of sympatric evolution. Proceedings of the Royal Society B: Biological Science, 285(1871), 20171722. https://doi.org/10.1098/rspb.2017.1722

Acknowledgements

We acknowledge financial support from the KU Leuven Research Fund (project C/16/17/002) and from National Fund for Scientific Research – Flanders (FWO) projects G0C3818 and G0B9818. MCU received support from NSF grants DEB-1555876 and PLR-1417754. We thank two reviewers, associate editor Martijn Egas and senior editor Charles Fox for their feedback on a previous version of the manuscript.

Author contributions

LDM wrote the first version of the text, inspired by discussions with all co-authors. KIB, LG, SM, CS KK, HV and LDM made the first versions of Table S1. MU and LG made the final version of the figures. All authors contributed substantially through multiple rounds of editing of the manuscript.

Competing interests

The authors declare no competing interests.

Figure legends

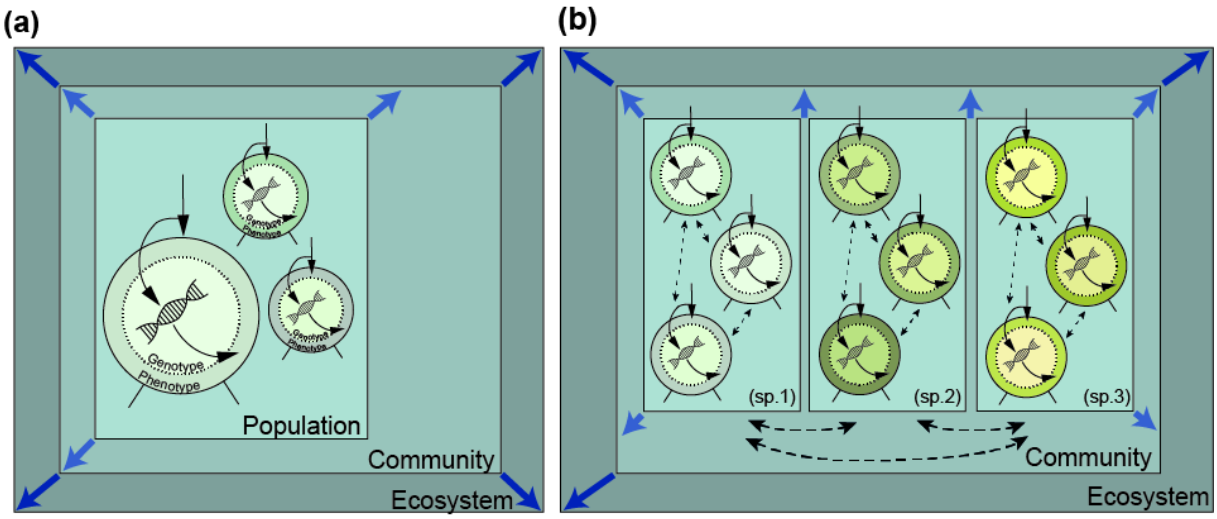

Figure 1. Schemes of eco-evolutionary dynamics depicting how evolution of one or multiple species can influence population, community and ecosystem features. Panel (a) shows the traditional focal species perspective, in which evolution of one species is considered and its impact on population, community and ecosystem features is quantified. Panel (b) depicts a multi-species perspective, in which evolution of the different interacting species that build up a community can influence their own and the other species' population characteristics, and collectively influence community and ecosystem features. We illustrate the pattern for three interacting species, and each species is represented by three individuals. The schemes also visualize that the phenotype, in part determined by the genotype and in part by the environment (cf. arrows within individuals), is central to eco-evolutionary dynamics, as it is phenotypes that are subject to selection and that can influence population, community and ecosystem characteristics.

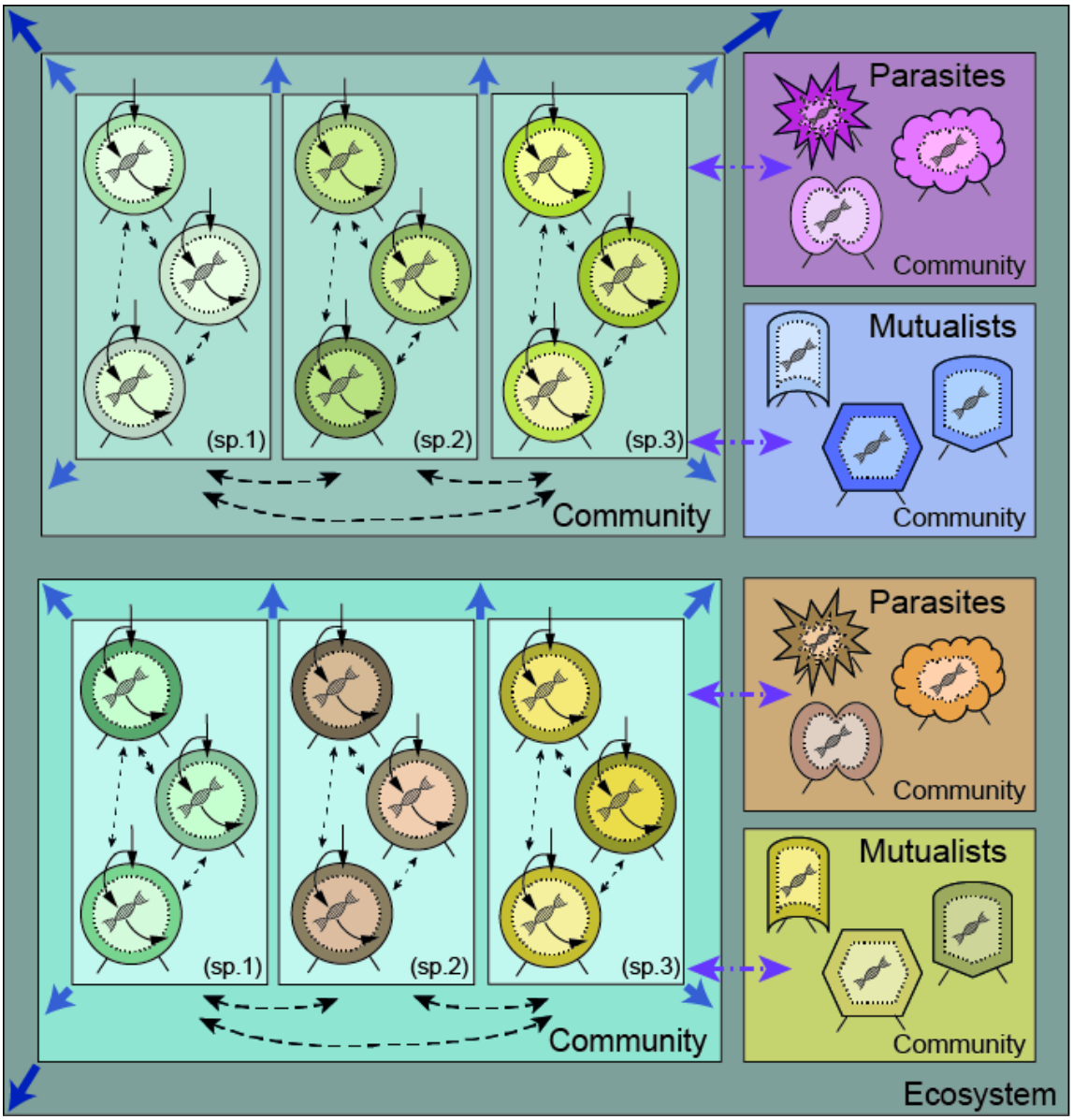

Figure 2. The scheme depicted in Figure 1 refers to only one module of interacting communities in a food web. Species groups interact with each other, amongst others through predator-prey interactions. The central arrows depict that interactions are network-like. The small boxes referring to parasites and mutualists indicate that, in addition to the two trophic levels displayed here (trophic level x and trophic level x+1), there are other groups of species with their own specific interactions with a focal guild.

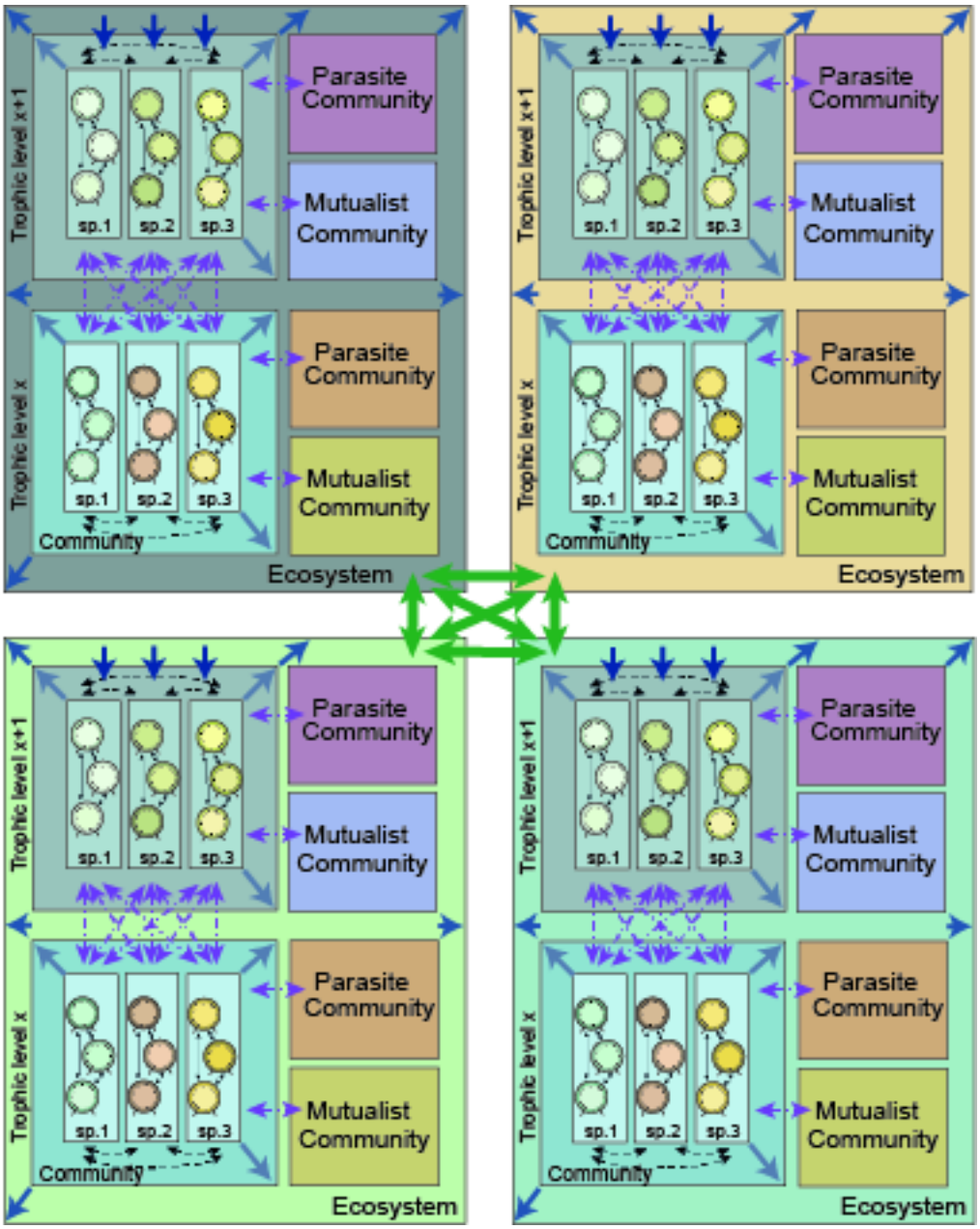

Figure 3. In an evolving metacommunity, the interacting local communities forming local food webs inhabiting specific habitat patches can interact through the dispersal (greenarrows) of genotypes/species with other such local communities. This results in a regional group of interacting communities comprised of evolving or coevolving species (Thompson 2005; Urban et al. 2008). The size of the habitats and the corresponding populations might vary widely in real landscapes, contributing to asymmetries in dispersal rates.

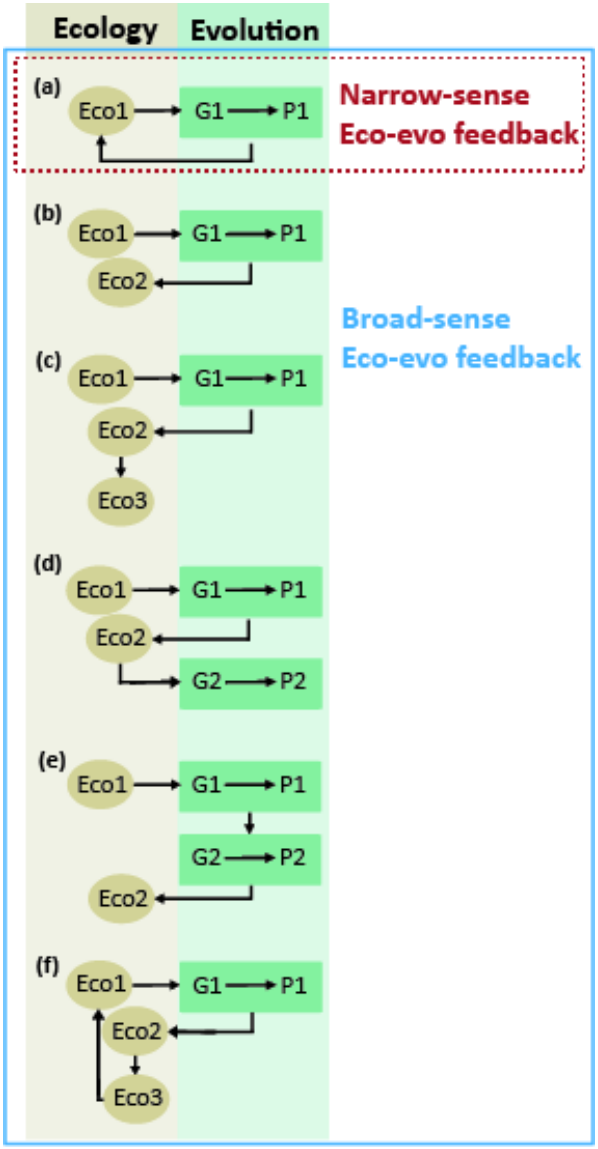

Figure 4. A schematic representation of different types of eco-evolutionary feedbacks. Evolutionary change is depicted as G influencing P in gray boxes (right part of each panel), whereas ecological responses are depicted as Eco1/Eco2/Eco3 (left part of each panel). In each scheme there is at least one arrow from ecological to evolutionary processes and from evolutionary to ecological processes, representing the feedback. (a) narrow-sense eco-evolutionary feedback loop: an environmental change leads to evolutionary trait change, which feeds back to influence further evolutionary change in the focal species; (b)-(f) broad-sense eco-evolutionary feedbacks, representing eco-evolutionary feedbacks that not necessarily feedback to the original actor: (b): environmental change leads to evolution, which impacts an ecological process; (c) same but this ecological change influences a second ecological process; (d) same as (b) but the ecological change influences evolution in another species; (e) evolution in the first species leads to evolution in a second species, which influences an ecological process; (f) as in (c) but the second ecological process influences the evolution of the first species. Case (f) depicts the lizard example in the main text: evolution of thermal tolerance in response to climate change in a lizard influences community composition of its prey, which results in a change in vegetation structure, which influences thermal adaptation in the lizard. Boxes emphasize the narrow- and broad-sense definition of eco-evolutionary feedbacks.