






Analysing eco-evolutionary dynamics—The challenging complexity of the real world

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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 broad-sense definition of “eco-evolutionary feedbacks” that includes any reciprocal interaction between ecological and evolutionary processes, next to a narrow-sense definition 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: (a) multiple interacting species within a guild, (b) food web interactions and (c) 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

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in their analysis of eco-evolutionary dynamics, and mostly so in artificially constructed communities.

- Finally, we provide a road map 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.

KEYWORDS

cryptic eco-evolutionary dynamics, eco-evolutionary dynamics, evolving metacommunities, food web interactions, multi-species guild, nature, regional dynamics

1 | 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, Vanoverbeke, Kilsdonk, & Urban, 2016; Ellner, Geber, & Hairston, 2011; Fussmann, Loreau, & Abrams, 2007; Hairston, Ellner, Geber, Yoshida, & Fox, 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, Doorslaer, Geerts, Orsini, & Stoks, 2011; Merilä & Hendry, 2014; Stockwell, Hendry, & Kinnison, 2003; Urban, De Meester, Vellend, Stoks, & Vanoverbeke, 2012), theoretical studies (Lion,

2018; Loeuille, Barot, Georgelin, Kylafis, & Lavigne, 2013; Loeuille & Leibold, 2008; de Mazancourt, Johnson, & Barraclough, 2008; McPeck, 2017a; Norberg, Urban, Vellend, Klausmeier, & Loeuille, 2012; Patel, Cortez, & Schreiber, 2018; Vanoverbeke, Urban, & De Meester, 2016) and more and more empirical studies (Bassar et al., 2010; Brunner, Anaya-Rojas, Matthews, & Eizaguirre, 2017; Crutsinger et al., 2006; Farkas, Mononen, Comeault, Hanski, & Nosil, 2013; Fukami, Beaumont, Zhang, & Rainey, 2007; Gómez et al., 2016; Matthews, Aebischer, Sullam, Lundsgaard-Hansen, & Seehausen, 2016; Matthews et al., 2011; Pantel, Duvivier, & De Meester, 2015; Rudman & Schluter, 2016; terHorst, Lennon, & Lau, 2014; Turcotte, Corrin, & Johnson, 2012; Venail et al., 2008; Walsh, DeLong, Hanley, & Post, 2012; Yoshida, Jones, Ellner, Fussmann, & Hairston, 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

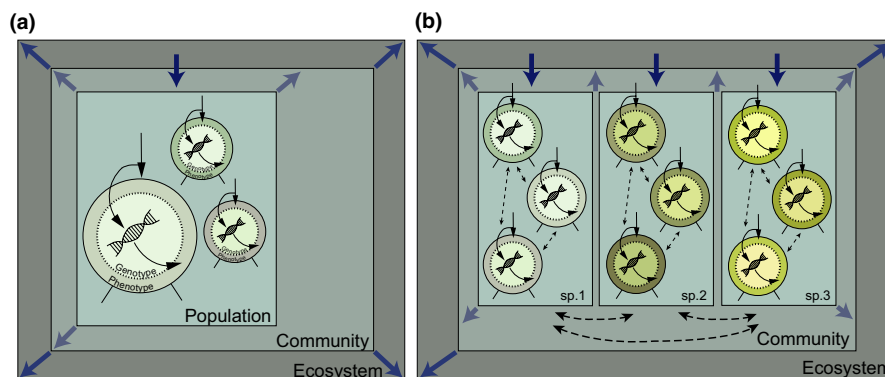


FIGURE 1 Schemes of eco-evolutionary dynamics depicting how evolution of one or multiple species can influence population, community and ecosystem features. Panel (a) shows the traditional focal species perspective, in which evolution of one species is considered (influenced by the environment, indicated by inward-oriented blue arrows), and its impact on population, community and ecosystem features (visualized as outward oriented blue arrows) 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

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, Ellner, Jones, & Hairston, 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., 2012; Friman, Guzman, Reuman, & Bell, 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).

1.1 | 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, that is, 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, Pantel, & De Meester, 2016; Lynch & Walsh, 1998; Via et al., 1995; Via & Lande, 1985). 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, Matthews, & Seehausen, 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 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 are 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 dynamic 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.

1.2 | 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 influence those of other interacting species (Figure 1; McPeck, 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 towards understanding evolutionary

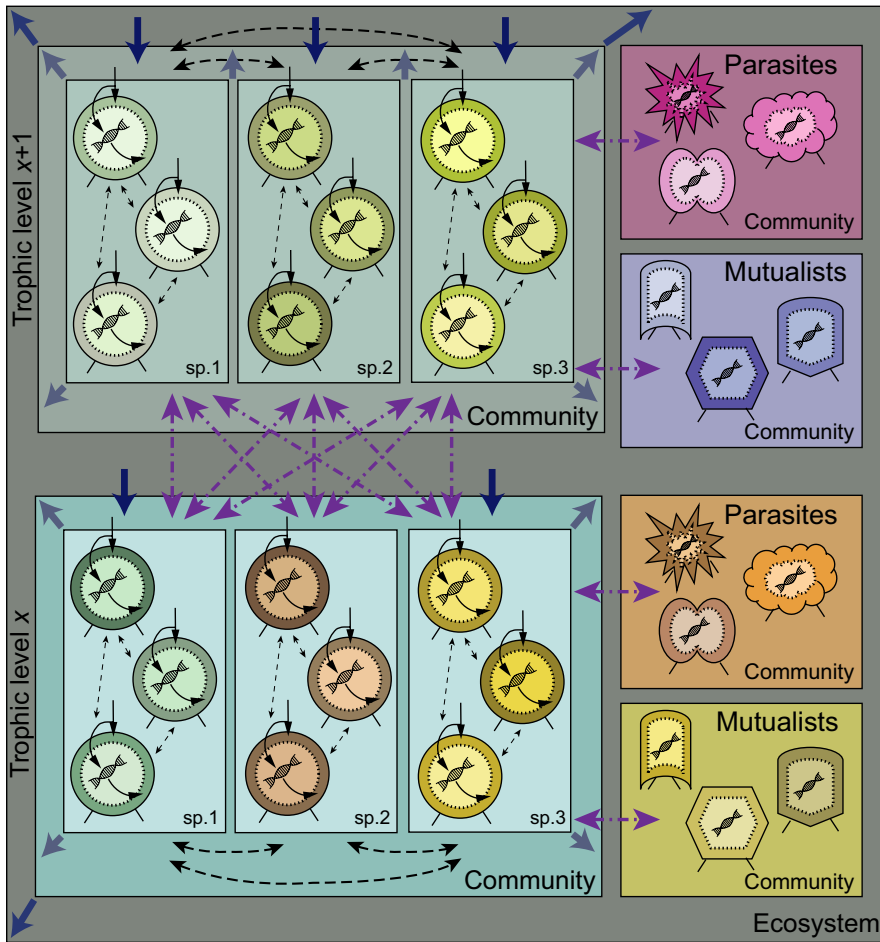


FIGURE 2 The scheme depicted in Figure 1 refers to only one module of interacting communities in a food web. Species groups interact with each other, among others through predator–prey interactions. The central set of arrows depict that interactions are network-like. The small boxes referring to parasites 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

responses and their ecological impacts in multiple interacting species simultaneously. To our knowledge, no study so far has done this in nonmicrobial systems.

Figure 1 remains an oversimplification, 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, Massol, Canard, Mouillot, & Mouquet, 2011; Poisot, Stouffer, & Gravel, 2015), parasites (Lafferty, Dobson, Kuris, & Tilman, 2006; Thompson, 2005) and mutualists (Koskella, Hall, & Metcalf, 2017; Macke, Tasiemski, Massol, Callens, & Decaestecker, 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, Laine, & Koskella, 2016). Again, most of these studies quantify evolution either in the host or in the parasite and study the impact of this evolution on the other species, with only a limited number of studies incorporating evolution of both partners or three interacting species and how they influence the other partners (Benkman, Holimon, & Smith, 2001; Brunner et al., 2017; Decaestecker, Gerssem, Michalakis, & Raeymaekers, 2013; Ford, Kao, Williams, & King, 2016; Frickel, Sieber, & Becks, 2016; Frickel, Theodosiou, & Becks, 2017; Hiltunen & Becks, 2014; Masri et al., 2015; Thompson, 2005). There are, to our knowledge, so far no empirical studies reporting on how evolution in

multiple species of predators and prey, hosts and parasites, or mutualists, simultaneously impacts the dynamics of the populations of each individual species, their community composition or resulting ecosystem functions.

Even, Figure 2 is still an oversimplification, as local food webs interact with food webs in other patches in the landscape (Figure 3). In this spatial context, local selection and evolution in response to abiotic environments and species interactions are linked by regional dispersal and gene flow. Thus, the same tension exists in ecology and evolution between the sorting of species and genotypes locally and the regional remixing of species and genotypes. Regional mixing is often maladaptive because a poorly adapted species or genotype lands in a suboptimal habitat, but it also can provide a match to optimal habitats or create novel, more fit genotypes or more diverse communities of species that provide diversity for selection to act upon. The dynamics of these so-called evolving metacommunities (Urban et al., 2008; Urban & Skelly, 2006) are poorly studied. Exceptions include the elegant proof-of-principle experiment with “communities” represented by different *Pseudomonas fluorescens* strains evolving in a landscape of food sources in multiwell plates (Venail et al., 2008), the evolution-mediated priority effects experiments of Fukami et al. (2007) again using *P. fluorescens* strains, and the

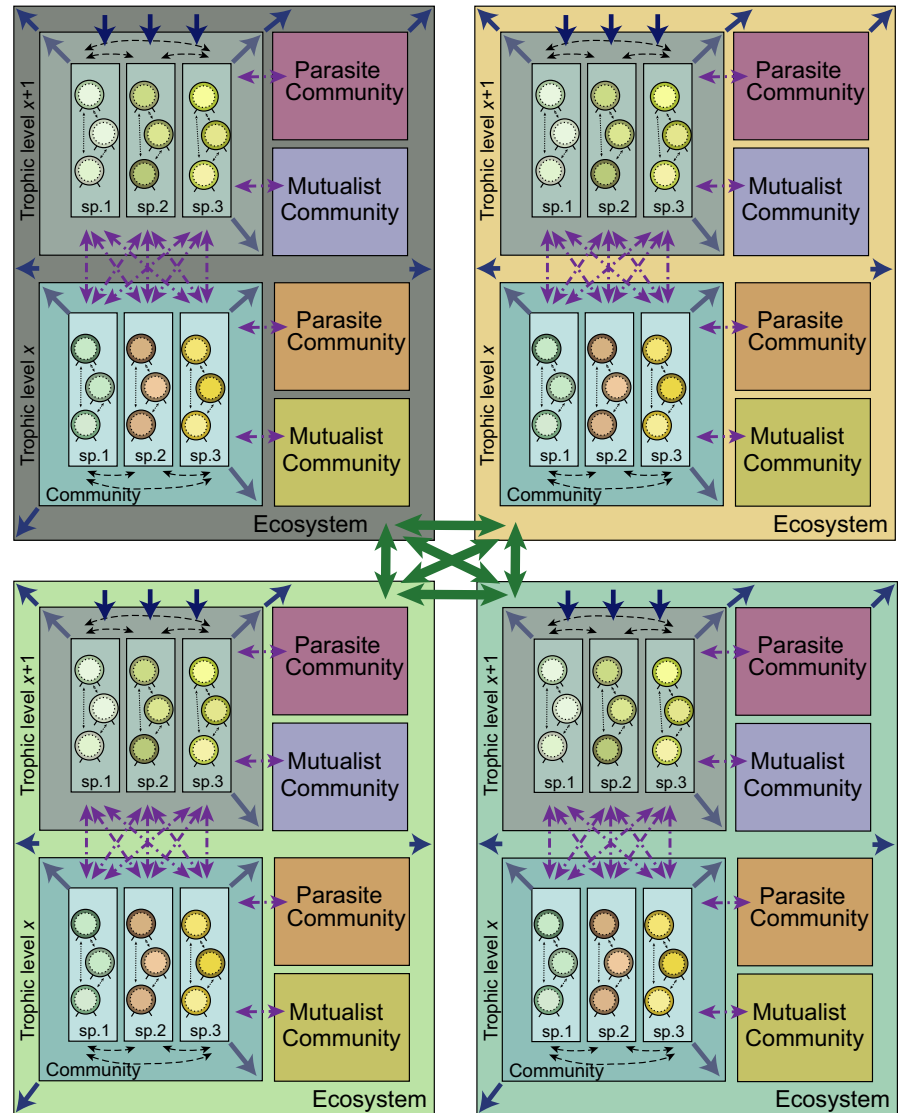


FIGURE 3 In an evolving metacommunity, the interacting local communities forming local food webs inhabiting specific habitat patches can interact through the dispersal (green arrows) of genotypes/species with other such local communities. This results in a regional group of interacting communities comprised 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

community rescue experiments with bacterial communities carried out by Low-Décarie et al. (2015). While these excellent experiments grasp key features of evolving metacommunities, they all involve highly artificial settings. Given that theory shows that the levels of regional dispersal can strongly influence how evolution affects community 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 (a) 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 (b) 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, codetermined 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 coevolving 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 and in the evo-to-eco side of the feedback.

2 | 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, Millstein, Orcutt, & Wichman, 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 the impact 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 that 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.

3 | 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 (a) differences in evolutionary potential, (b) differences in abundances, (c) differences in dispersal capacity and (d) 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 keystone species (Matthews

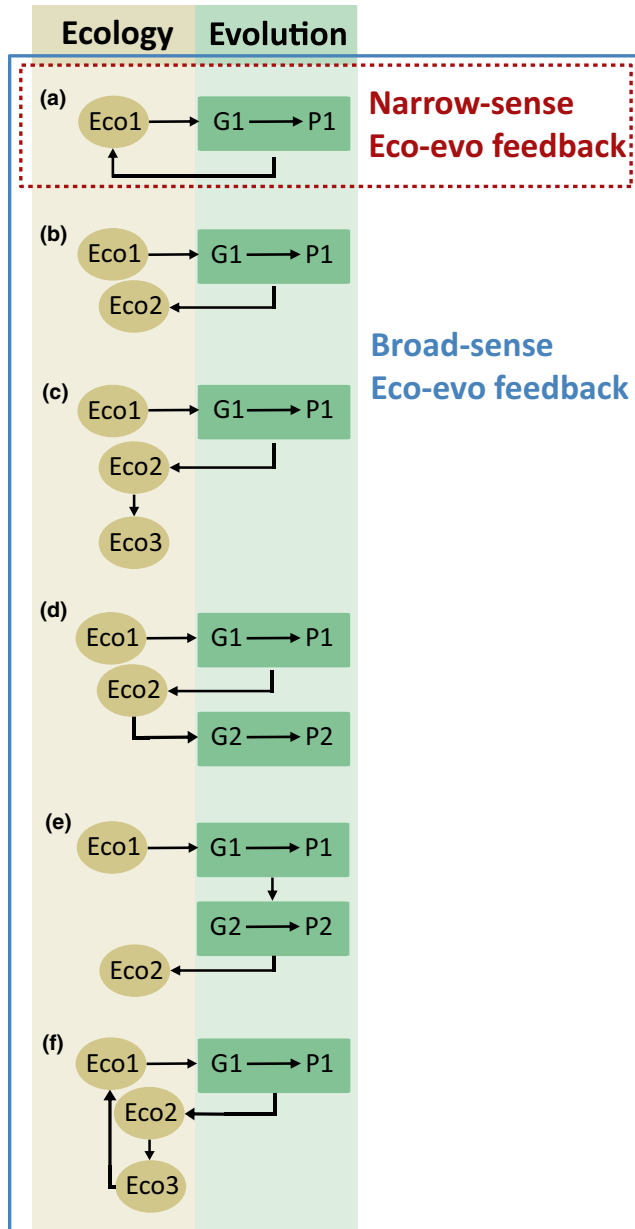


FIGURE 4 A schematic representation of different types of eco-evolutionary feedbacks. Evolutionary change is depicted as G influencing P in green boxes (right part of each panel), whereas ecological responses are depicted as Eco1/Eco2/Eco3 (left part of each panel). In each scheme, there is at least 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. The red (dotted line) and blue (full line) boxes emphasize the narrow- and broad-sense definition of eco-evolutionary feedbacks, respectively

move towards predicting eco-evolutionary effects, we will need to know for which species they are important and for which ones they are not. Therefore, we will require comparative data on species in the same guilds, including those with limited impact.

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

Third, one also needs to consider the community context of the evolutionary response itself. Evolutionary trajectories can be very different depending on whether a species is kept in isolation compared

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

to when it is exposed to selection pressures in the presence of a community (Barraclough, 2015). Simulations showed that evolution of response traits can be reduced in the presence of other species (de Mazancourt et al., 2008), while in other settings, the presence of other species can enhance evolutionary responses, especially for traits important in species interactions (Osmond & de Mazancourt, 2013). Community context can thus lead to different evolutionary trajectories compared 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 harbours species that are preadapted 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 underestimating 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 preadapted genotypes or species (De Meester et al., 2016; Vanoverbeke et al., 2016) or through maladaptive gene flow (Richardson, Urban, Bolnick, & Skelly, 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 points to the evolving metacommunity concept provides as an integrative framework for carrying out eco-evolutionary dynamics research (De Meester et al., 2016; Urban et al., 2008; Urban et al., 2012; Urban et al., 2016).

4 | 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 dynamic studies that focus on feedbacks at the community level in Supporting Information Table S1. 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 fulfil three criteria that are linked to the above highlighted multi-species context, and lists whether (a) 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 setup), (b) the study involved an analysis of evolution in multiple species (rather than just one focal species) and (c) 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, that is, 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 predators 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 Supporting Information Table S1 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 nonmicrobial systems fulfilled 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., Bassar et al., 2010; Farkas et al., 2013; Fridley & Grime, 2010; Pantel et al., 2015; terHorst et al., 2014; Walsh et al., 2012) used isolates or populations that evolved in a natural or multi-species context. However, only three of the nonmicrobial studies (Faillace &

Morin, 2016; Fridley & Grime, 2010; Rudman et al., 2015) 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, Supporting Information 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 suggests 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 settings (Supporting Information Table S1). Exemplars of studies under more natural conditions include the manipulation of maladaptation of stick insects to demonstrate how maladapted and uncamouflaged prey attract predators which eat more prey in the community (Farkas et al., 2013) and how a plant in a manipulated, but natural, setting evolved less herbivore resistance and higher competitive ability, with effects on interacting populations (Agrawal, Hastings, Johnson, Maron, & Salminen, 2012).

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

5 | HOW TO EMBRACE A MULTI-SPECIES PERSPECTIVE IN ECO-EVOLUTIONARY DYNAMICS

As mentioned, it is often impractical to incorporate the full complexity of natural systems in eco-evolutionary feedback studies. Yet, there is a need to explicitly study and quantify the emergent features that result from including more complexity and exploring to what extent a multi-species context changes our predictions on the strength and direction of eco-evolutionary impacts on ecological processes. A lot of progress could be achieved if there would be a strong effort towards incorporating specific aspects of the complexity sketched

in Figures 1–3 in eco-evolutionary research. While at times challenging, important progress can be obtained through collaborative work with different research teams focusing on different organism groups in the same systems. Alternatively, 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 into 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.

5.1 | Experiments

In experimental studies, there are a number of complexities linked to the multi-species features highlighted in Supporting Information Table S1 that can relatively easily be incorporated, and Supporting Information 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, Scheuerl, Moreno-Letelier, Bell, & Barraclough, 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 covary 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, that is, 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, Hamann, & Weis, 2018; Stoks, Govaert, Pauwels, Jansen, & Meester, 2016; Sultan, Horgan-Kobelski, Nichols, Riggs, & Waples, 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, Macke, Reyserhove, Bulteel, & Decaestecker, 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/nonadapted 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, Diez, & Levine, 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 whether 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 principle also be generated by ecological processes, their results can be suggestive of the potential importance of the eco-evolutionary feedback in nature. Overall, we should not lose sight of the main reason to study eco-evolutionary interactions: to understand natural dynamics and patterns.

5.2 | Field data

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

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

focal species (Brans et al., 2017). This requires common garden experiments on representative isolates of local populations of the studied species. If one wants to do this in a multi-species metacommunity context, this would involve extensive common garden experiments on isolates of multiple species from multiple sites in a metacommunity. To our knowledge, there are, so far, no published studies that have done this.

2. *Quantifying the evolving metacommunity structure.* A potentially promising approach to quantify the impact of evolution on ecological features of natural metacommunities involves applying a metacommunity-type of analysis to datasets on both communities and populations of the same set of habitats in a landscape. If one collects data on species composition and on genetically determined trait values of local populations of multiple species, one can quantify to what extent species composition (traditional metacommunity ecology), trait variation based on species composition (trait-based metacommunity ecology; trait values of species are calculated as metacommunity averages or derived from literature) and trait variation within species are linked to environmental (species sorting, natural selection) and spatial (dispersal) drivers (Cottenie, 2005; Leibold et al., 2004). Again, in order to be able to link these patterns to evolutionary trait change, the intraspecific trait variation needs to be quantified in common garden experiments, isolating the genetic component of trait variation. In the resulting dataset, one can, in addition to linking variation in species composition, community trait distribution and intraspecific trait variation in the focal species to local (environmental) and regional (spatial) drivers, also explore to what extent intraspecific trait variation in the focal species is associated with the deviations of the expected community trait variation. In these analyses, one cannot only quantify the structure of the evolving metacommunity (Urban et al., 2008), but also obtain insight in the likelihood that evolutionary trait change contributed to metacommunity structure and community trait distribution.
3. *Population genomics in an evolving metacommunity context.* In the future, population genomics (Rudman et al., 2018) will likely be key to reduce the amount of work while still being able to link genetic differences to ecological responses (e.g., community composition and population density). For this approach to be powerful, we will need further insights in how genomic data link to trait values in target species. Given that these links might be complex and not necessarily strongly repeatable (e.g., Becks et al., 2012; Gompert et al., 2014; Nosil et al., 2018), there is still a long way to go for population genomics to translate in reliable estimates of trait variation, except for some well-studied cases that involve major effect loci or gene clusters (Jones & Gomulkiewicz, 2012; Lamichhaney et al., 2016). As the link between genomic variation and trait values becomes more reliable, however, it will open tremendous opportunities for studying eco-evolutionary dynamics in the field (Rodríguez-Verdugo, Buckley, & Stapley, 2017; Rudman et al., 2018).

A key limitation of all the analyses highlighted in the previous paragraphs when based on field surveys is that they only reveal the current

pattern, implying that important transient changes that might have been caused by evolution but leave no trace in the current metacommunity cannot be quantified. This is very different from how we quantify eco-evolutionary dynamics in an experimental approach such as common gardening experiments. In a common gardening set-up, one starts with standardized "gardens" to which different genotypes of one or more species are added to then monitor how the garden changes as a function of the manipulated genotype (Matthews et al., 2011). In such settings, one quantifies the impact of evolution as the differentiation of the garden among treatments developing from a common starting point. In most field surveys, however, one only has a snapshot view of the resulting pattern. There is no guarantee that initial environmental conditions or initial community composition of the different sites was identical, and it is actually very unlikely that they were. So there is no common reference point to which the impact of evolutionary differentiation can be scaled. In addition, the impact of evolution can only be quantified for the observed set of species in the different sites. While it is possible that evolution of a given species might have caused the extinction of another species at the site or might have allowed a given species to colonize the site, such impacts of evolution cannot be quantified in a snapshot survey. It is therefore 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; Houwenhuysen 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 modelling (IPM; Coulson, Tuljapurkar, & Childs, 2010; Easterling et al., 2000; Smallegange & Coulson, 2013). Several of IPM-inspired analyses have been published on a number of unique datasets 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, Clutton-Brock, Pemberton, Tuljapurkar, & Coulson, 2007; Pelletier, Garant, & Hendry, 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.

The most powerful approaches to multispecies eco-evolutionary dynamics studies would be the combination of well-designed field studies that identify cases of particular interest, which are then combined with the appropriate experimental approaches (such as field transplants, common garden experiments, resurrection ecology or experimental evolution) to test particular hypotheses. To our knowledge, no

study so far engaged in such an endeavour in a truly multiple species context. While this will no doubt be a huge effort, it would be worth it, as it would allow quantifying the importance of eco-evolutionary dynamics in ecologically relevant settings and would likely reveal several cases of cryptic eco-evolutionary dynamics (Kinnison et al., 2015).

6 | USING COMPLEXITY TO MAKE THINGS SIMPLE AGAIN: EMERGENT PATTERNS AND RULES

A key problem with increasing study complexity is that the results are often contingent on starting conditions and that apparent minor differences can lead to strongly deviating patterns and trajectories (Fukami, 2015; Losos, Jackman, Larson, Queiroz, & Rodriguez-Schettino, 1998; Scheffer, Carpenter, Foley, Folke, & Walker, 2001). This contingency results in reduced power to derive generic laws (Lawton, 1999) or to make predictions on responses to future change (Urban et al., 2016). In the case of evolving meta-communities, there is the additional complexity that the results and dynamics are not only strongly contingent on environmental conditions, but also strongly contingent on the properties of the interacting species. There are ~8 million species globally, each with their own set of traits, histories and evolutionary strategies responding to the environment and to interactions with other species. Even if there is a great deal of redundancy in species traits, it is clear that the dynamics of interactions as studied in the field and in experiments are often very strongly dependent on the specific traits of the interacting species. The mere observation that evolutionary trait change can so strongly impact ecological dynamics (e.g., Becks et al., 2012) testifies to the importance of trait values and thus the specificity of interactions on ecological dynamics. It would, however, be unwise to derive from this level of contingency that it is not useful to study the impact of evolution on 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 judgements 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 diversification to impact ecological dynamics (Fukami et al., 2007; Venail et al., 2008; Zee & Fukami, 2018). So there are indications that eco-evolutionary feedbacks might be more prevalent in organisms with short generation times (De Meester et al., 2016), even though it has not been systematically analysed and clear cases of eco-evolutionary feedbacks have been reported for many long-lived species too (Hendry, 2017). We also note that when eco-evolutionary feedbacks are studied across community types (e.g., gut microbiota or microbial communities that are eaten upon), time-scales differ among interacting partners, enhancing the potential of organisms with short generation time to have a strong impact on ecological processes through trait evolution. This has been well-established in studies on host–parasite interactions (Gandon, Buckling, Decaestecker, & Day, 2008) but also applies in a broader context for all co-evolutionary and eco-evolutionary dynamics (Dercole, Ferrière, Gragnani, & Rinaldi, 2006). Other potential rules might be that evolutionary dynamics might be more important in species-poor (Urban et al., 2008) and more isolated systems (De Meester et al., 2016; Vanoverbeke et al., 2016). Developing insights in such rules might involve the combined effort of empirical work and targeted modelling. Theoretical modelling can help to identify instances where eco-evolutionary feedbacks could potentially be important (Govaert et al., 2018), or to test the strength of these feedbacks in more complex systems (de Andreazzi, Guimarães, & Melián, 2018). Further development of theory will be crucial in order to be able to incorporate eco-evolutionary dynamics in predictions (Urban et al., 2016) and management beyond the specific settings that have been empirically documented.

7 | CONCLUSIONS

In the past, ecologists ignored evolution, whereas evolutionary biologists ignored ecological interactions in multi-species communities. The field of eco-evolutionary dynamics is starting to

alert ecologists to the substantial impacts of evolutionary change in their models and empirical work. We hope that this opinion paper together with other recent reviews and synthesis papers (e.g., 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 rigour in testing hypotheses in eco-evolutionary dynamics might be the key challenge in the field of eco-evolutionary dynamics in the coming decade.

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CONFLICT OF INTEREST

The authors declare no competing interests.

AUTHORS' CONTRIBUTIONS

L.D.M. wrote the first version of the text, inspired by discussions with all co-authors. K.I.B., L.G., S.M., C.S., K.K., H.V. and L.D.M. made the first versions of Supporting Information Table S1. M.C.U. and L.G. made the final version of the figures. All authors contributed substantially through multiple rounds of editing of the manuscript.

DATA ACCESSIBILITY

All data (journal references) are given in Supporting Information. No other data were used for this review.

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SUPPORTING INFORMATION

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