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How community adaptation affects biodiversity-ecosystem functioning relationships

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Summary

It is increasingly recognized that evolutionary dynamics impact biodiversity-ecosystem functioning (BEF) relationships, as evidenced by recent experimental studies. However the nature of such impacts remains poorly understood. Here we use a modelling approach to compare random communities, with no trait evolutionary fine-tuning, and co-adapted communities, with traits at co-evolutionary equilibrium, in terms of emerging biodiversity-productivity, biodiversity-stability, and biodiversity-invasibility relationships. Community adaptation impacted most BEF relationships, causing as much as slope inversions compared to random communities. Biodiversity-productivity relationships were generally less positive among co-adapted communities, and less driven by sampling effects. The effect of community-adaptation, though modest regarding invasion resistance, was striking regarding invasion tolerance: co-adapted communities retained greater invasion tolerance at high diversity. BEF relationships are thus contingent on the history of ecosystems and their degree of community adaptation. Observations from short-term experiments or recent perturbations may not be safely extrapolated into the future, once eco-evolutionary feedbacks have taken place.

Introduction

Diversity, most classically defined as the number of constituent species in a community, plays an essential role in many aspects of ecosystem functioning (Hooper *et al.*, 2005, 2012; Isbell *et al.*, 2011). Understanding how species composition affects ecosystem properties is a fundamental question in basic and applied ecology, and renewed practical importance given the accelerating biodiversity crisis (Pimm *et al.*, 2014).

Observational data, controlled experiments and theoretical developments have converged in identifying ecosystem properties that exhibit systematic responses to diversity. Three types of so-called biodiversity-ecosystem functioning (BEF) relationships are most commonly described, even though all three are seldom considered in the same study. (i) First, the biodiversity-productivity relationship has sustained a long and fruitful line of research, and it is often considered that more diverse ecosystems are also more productive, in agreement with theoretical predictions (Loreau, 1998; Tilman, 1999). Biodiversity-productivity relationship studies were historically conducted in grassland communities (Tilman *et al.*, 1996; Loreau & Hector, 2001) but they have been extended to several other taxa and ecosystems (Abramsky & Rosenzweig, 1984; Naeem *et al.*, 1994; Hooper *et al.*, 2005; Gamfeldt *et al.*, 2015). (ii) Second, the biodiversity-stability relationships has also received a lot of attention (Elton, 1958; Tilman, 1999; McCann, 2000), both theoretically (May, 1973; Loreau & Mazancourt, 2013) and experimentally (Gross *et al.*, 2014; Renard & Tilman, 2019). The classical and intuitive view that more diverse ecosystems are more stable in the face of environmental fluctuations appeared contradicted by theoretical models suggesting the opposite (McCann, 2000). A consensus has emerged that the sign of the biodiversity-stability relationship hinges critically on how stability is defined (May, 1973; Tilman *et al.*, 1996; McCann, 2000; Ives & Carpenter, 2007). In particular, predictions differ importantly depending on whether stability is measured at the level of individual species (dynamical stability: May, 1973; Tilman *et al.*, 1996;

Ives & Carpenter, 2007) or on multi-species metrics (ecosystem stability: May, 1973; Tilman *et al.*, 1996; Ives *et al.*, 1999; Barabás & D'Andrea, 2016; Pennekamp *et al.*, 2018). Therefore the relationship may be negative in the former case but positive in the latter. (iii) Last, the biodiversity-invasion relationship has also attracted much attention, since native (resident) diversity has long been regarded as a key attribute determining the susceptibility of communities to invasion from alien species. It is generally considered that more diverse ecosystems should be less susceptible to invasions, and, should an invasion occur, that they should suffer from fewer adverse impacts (such as secondary extinctions) following an invasion (Levine, 2000; Hector *et al.*, 2001; Davis, 2009).

BEF relationships are driven, beyond the sheer number of species, by community composition in terms of key functional traits. Species traits influence their ability to exploit resources (Gagic *et al.*, 2015), and their interactions with one another. Species traits thus provide a mechanism through which different communities, even at a given species richness, might possess different functioning characteristics. Species trait composition can vary not only under the influence of ecological processes such as competition, extinction, recolonization and environmental filters, but also because of natural selection and evolutionary dynamics. Communities may harbor very different traits depending on whether they are recent assemblages randomly drawn from the regional pool, or if species had time to adapt to the local environmental conditions and to the presence of other species (Hendry, 2016). The time required for such community adaptation may often be quite short even by ecological standards, considering the mounting evidence that species can adapt rapidly to environmental changes and to the presence of competitors or predators (Thompson, 1998; Faillace & Morin, 2016; Hart *et al.*, 2019). By altering species trait composition, community adaptation should thus impact BEF relationships, and control their existence, magnitude and shape.

Even though studies of BEF relationships are traditionally conducted from an

ecological perspective, without explicit consideration of adaptation and evolutionary dynamics, long term grassland experiments (Reich *et al.*, 2012; Meyer *et al.*, 2016) and microbe experiments (Bell *et al.*, 2005) found that biodiversity-yield relationships change through time. The most recent studies have explicitly highlighted a role of evolution in modifying biodiversity-yield relationships, in grasslands (Zuppinger-Dingley *et al.*, 2014; van Moorsel *et al.*, 2018) and with microbes, using experiemental evolution (Fiegna *et al.*, 2014, 2015). However, results have proven quite variable, prompting a plea for more theoretical investigations (Fiegna *et al.*, 2015).

Here we propose a theoretical evaluation of the consequences community adaptation may have on BEF relationships. We use a general modeling approach to address the three types of BEF relationships highlighted above (biodiversity-productivity, biodiversity-stability, and biodiversity-invasibility). We compare two contrasted types of communities: (i) random communities, in which only ecological processes control species trait composition, with no evolutionary dynamics, and (ii) co-adapted communities, in which species traits composition have further been shaped by evolutionary dynamics (species adaptation to the environment and to other species). Specifically, species have gradually adjusted their traits to reach an evolutionary equilibrium (Christiansen, 1991). In real-life, natural communities may harbour various degrees of co-adaptation, although purely random communities or communities at a stable evolutionary equilibrium probably do not exist. Real communities in practice lie somewhere between these two limiting cases. Communities recently founded or strongly perturbed, such as recently colonized habitats, artificially assembled communities, and ecosystems having just faced a major environmental perturbation or a wave of biological invasions, are probably closer to random assembly. On the opposite side, ecosystems that have remained in relatively constant conditions for a sufficient time, such as primary old-growth forests, may be better represented by co-adapted communities.

As species co-existence and eco-evolutionary dynamics depend on the type of

ecological interactions considered (Mouquet *et al.*, 2002; Chave *et al.*, 2002; Calcagno *et al.*, 2017), we model communities governed by four contrasted scenarios of ecological interactions, representative of classical coexistence mechanisms (Calcagno *et al.*, 2017): two scenarios of ecological interactions based on resource competition (one symmetric, one asymmetric), one life-history trade-off scenario, and a trophic-chain scenario. In each case, several functioning metrics are computed to evaluate BEF relationships. This general approach allows to evaluate the extent to which the consequences of community adaptation are general or depend on particular types of metrics and ecological interactions.

We report clear influences of community adaptation on each of the three BEF relationships investigated, highlighting how co-adaptation impacts species trait distribution, which in turn, impacts functioning properties. Although conclusions may depend importantly on the type of ecological interaction scenario considered, some general predictions regarding the consequences of community adaptation are formulated, and discussed in light of available experimental evidence.

Material and methods

Ecological scenarios and traits

In natural ecosystems species are involved in several types of interactions, within the same trophic level (horizontal interactions) and among different trophic levels (vertical interactions), at different temporal and spatial scales. The dominant form of species interaction may differ depending on the type of community considered (Chave *et al.*, 2002), and some studies have argued that generalist predation, exploitative competition and simple three-species food chains compose the common backbone of interaction networks (Mora *et al.*, 2018). To reflect this diversity, we here considered a set of four contrasted ecological scenarios, based on classical species coexistence models and spanning the range from completely horizontal and

symmetric interactions (resource competition) to completely vertical and asymmetric interactions (trophic chains; Fig. 1a). For the first scenario (*Niche*) we used the classical model of resource competition along an axis of niche differentiation (Dieckmann & Doebeli, 1999). A second scenario (*Body-size*) introduces interference competition and competitive asymmetries, based on *e.g.* body size differences (Rummel & Roughgarden, 1985). The third scenario (*LH-tradeoff*) models a life-history trade-off, describing the strongly asymmetric competition between species good at colonizing empty habitat and species locally dominant, along a competitive hierarchy (Calcagno *et al.*, 2006, 2017). Last, the fourth (*Trophic*) scenario describes a size-structured trophic chain based on the model introduced by Loeuille & Loreau (2005).

In all four interaction scenarios, species are characterized by one key trait, denoted x (see Fig. 1a). In the *Niche* scenario, the trait represents niche position along the continuum of resources (for instance beak size, determining which seed sizes are consumed). In the *Body-size* scenario, species trait is body size, and inter-specific competition depends on size difference: bigger species have a competitive advantage, but the inter-specific interaction decreases with increasing size difference. As a result species are most negatively impacted by species slightly bigger than themselves. In the *LH-tradeoff* scenario, species trait is the colonization rate (per occupied patch), and species with lower colonization rate are more susceptible to win local competition within patches (Calcagno *et al.*, 2006). Last, in the *Trophic* scenario, species trait is body mass, and species preferentially consume species that are smaller, with some optimal mass difference (Loeuille & Loreau, 2005). After some reformulations (Section 1 in supporting information, S.I.), these models can be set in the common Lotka-Volterra form:

$$\frac{dn_i}{dt} = n_i r(x_i) \left(1 - \sum_j \frac{n_j a(x_i, x_j)}{k(x_i)} \right) \tag{1}$$

with n_i the abundance of species i, that denotes, depending on scenario, either a

number of individuals (*Niche*), a biomass (*Body-size* and *Trophic*) or a fraction of occupied sites (*LH-tradeoff*).

The three functions included in equation (1) allow to describe species demography and inter-specific interactions: $r(x_i)$ is the intrinsic growth rate of species i that governs the ecological timescale; $a(x_i, x_j)$ is the impact that a variation in species j abundance has on the per capita growth rate of species i, normalized by the intra-specific interaction (see S.I., section 1.1); and $k(x_i)$, usually called the carrying capacity, quantifies the resistance to density dependence of species i. In all scenarios but the *Trophic* one, it is also the equilibrium abundance reached by the species if growing alone in the community, or in other words the mono-culture abundance (Loreau & Hector, 2001). The shape of the functions for each scenario are represented in Fig. 1a. They differ importantly, and for example, inter-specific interactions $a(x, x_s)$ can be either symmetric (*Niche*) or completely asymmetric (*Trophic*). See S.I. section 1 for a complete description of each scenario.

Evolution would often favor certain trait values that are better adapted to the current habitat; this is described by the mono-specific abundance function $k(x)$, which defines the optimum trait value, as represented by the red dots in Fig. 1a. The relationship between trait value and mono-specific abundance may have an intermediate optimum (*Niche*, *Body-size* and *Trophic*) or be open-ended (*LH-tradeoff*), see red dots positions in Fig.1a. However, inter-individual interactions and competition may counteract evolution towards optimal trait values, in particular in the *LH-tradeoff* scenario, in which evolution effectively results in traits with comparatively low mono-specific abundances (Calcagno *et al.*, 2017).

Species traits, through functions r, k and a, thus determine species interactions and overall ecosystem and evolutionary dynamics. For each scenario, one or two parameters controlling the details of the interaction patterns were systematically varied. All details and parameter values used are presented in S.I. section 2. In the results, for the sake of clarity, only a representative part of the parameter sets

studied are presented.

Random and co-adapted communities

The process of community formation is sketched in Fig. 1b. For different species richness levels, from 1 to 10, sets of species were drawn randomly from a regional pool with a given trait distribution. The latter was chosen in order to minimize the information in the assemblage of species into communities, while being representative of the typical trait values expected for a given ecological scenario and parameter value. The procedure was based on entropy maximization (Jaynes, 1957) (see S.I. section 3). From the N randomly drawn species, the ecological equilibrium obtained from equation (1) was computed, and the community was retained if all N species persisted at equilibrium (see S.I. section 3 for details). The process was repeated until, for each species richness level, 1,000 such random communities were obtained. Note that for some scenarios and parameter values, communities may not be feasible at all species richness levels.

Whereas random communities are only constrained by ecological processes (regional pool and local competitive exclusion), co-adapted communities must meet the additional constraint that species trait values are at evolutionary equilibrium. We thus computed the selection gradient operating on each species trait value in the community (Christiansen, 1991; Metz *et al.*, 1995). Note that fitness is density- and frequency-dependent and depends on the composition (trait values and abundances) of the entire community. The selection gradient is defined as

$$\nabla(x_i) = \left.\frac{ds(x_m)}{dx_m}\right|_{x_m=x_i} \tag{2}$$

where $s(x_m)$ is the invasion fitness. If $\nabla(x_i) > 0$, larger trait values are selected, while smaller values are selected when $\nabla(x_i) < 0$. When all selection gradients are simultaneously cancelled in a community, species have reached an evolutionary

attractor and are at equilibrium with respect to first-order selection (Christiansen, 1991).

To minimize computation time, for each ecological scenario and species richness level, we numerically identified all feasible evolutionary attractors and tracked them continuously in parameter space using continuation methods (Calcagno *et al.*, 2017). Detailed methods are provided in S.I. section 3. We thus obtained exhaustive sets of co-adapted communities (subsets of the random communities previously defined) in the sense of eq. (1) and (2).

Biodiversity-functioning relationships

For each generated community, we computed several properties of interest (full list and description in S.I. section 4) to investigate the three BEF relationships. We present results based on the properties (Fig. 1c) described below (conclusions were qualitatively similar based on other properties described in S.I. section 4). First, community productivity (Tilman, 1999; Loreau & Hector, 2001) was measured as the average rate of production (positive contributions to net growth rate) in the community. Second, ecological stability was assessed at two levels. We computed the classical asymptotic resilience (May, 1973; Arnoldi *et al.*, 2016), *i.e.* the asymptotic rate of return to equilibrium of the community after a perturbation. In addition, we also quantified community stability (May, 1973; Ives *et al.*, 1999), defined as the inverse of the coefficient of variation of the total abundance in the community under sustained environmental noise, and computed by solving the continuous-time Lyapunov equation (May, 1973; Ives *et al.*, 1999). Finally, to study the response to invasions, we also used two properties. The first is the resistance to invasion (Elton, 1958; Hector *et al.*, 2001), defined as the probability that an alien species (randomly drawn from the regional pool and introduced at low initial abundance) does not successfully establishes in the community. Second, the tolerance to invasion (Elton, 1958) was quantified as the proportion of species, following a successful invasion,

that were not driven to extinction by the invader. Details on the mathematical computation of each metric are presented in S.I. section 4.

For each metric, diversity level and parameter set, we recorded the mean value over the 1,000 random communities, and the mean of the few (or possibly the unique) co-adapted communities. To verify that co-adapted communities differed from most random communities, and not just on average, we further computed the percentile in the distribution of values over random communities corresponding to the value observed in the co-adapted communities. Result, given in S.I. section 5, showed that co-adapted communities often lie in the tail of the distribution of random communities, for each metric, indicating that co-adapted communities were quite atypical, relative to the variability of random communities. For this reason we only present mean differences in the following sections.

The above metrics were correlated to species richness to produce BEF relationships, and these were compared between random and co-adapted communities. Since the impacts of co-adaptation are mediated by changes in the trait composition of communities, we summarized trait compositions using two additional quantities (Fig. 1c). The first was the minimum distance to the optimum trait (the trait value that maximizes monoculture abundance; red dots in Fig. 1a), which reflects how well the more performing species is adapted to the habitat. The second was the average interval between species trait values (distance between closest neighbours), which indicates how "packed" or concentrated species are in trait space.

Results

Biodiversity-Productivity

Random and co-adapted communities differed in productivity at low diversity levels, but at higher diversity levels, the difference was very modest on average (Fig. 2). Moreover, in all scenarios except the *LH-tradeoff*, the effect of community adaptation

was to increase productivity. Those two observations explain the quantitative differences in biodiversity-productivity relationships between random and co-adapted communities.

Qualitatively, co-adaptation affected the biodiversity-productivity relationship (Fig. 2) in all four scenarios. The impact could be as spectacular as a slope inversion. For instance, the *LH-tradeoff* scenario, unlike the other scenarios, generated mildly negative biodiversity-productivity relationships in random communities (see also Loreau, 2010). However, in co-adapted communities, the biodiversity-productivity relationship was markedly positive for all parameter sets (Fig. 2c). Conversely, the *Trophic* scenario generated a classical positive biodiversity-productivity relationship in random communities, but the relationships switched to negative (with parity effects caused from trophic cascades) in co-adapted communities (Fig. 2d). In the other two scenarios, based on exploitative competition, biodiversity-productivity relationships were positive irrespective of co-adaptation (Fig. 2a,b). However, the shape of the relationships were markedly different between random and co-adapted communities: in random communities, the increase in productivity with diversity was close to linear, whereas in co-adapted communities, the relationship was saturating with high productivity even at low species richness level, especially in the *Body-size* scenario (Fig. 2b).

Species trait composition

Species trait composition covaried differently with species richness in random and co-adapted communities (Fig. 3). In random communities, the chance to draw a highly performing species mechanically increased with the number of species, so that the minimum trait distance to the optimum decreased with diversity in all scenarios (Fig. 3a-d). Concomitantly, the average distance between species decreased sharply with species richness (Fig. 3e-h), reflecting the fact that species were more and more packed. In contrast, a close-to-optimal species was always present in co-

adapted communities (constant minimum distance to optimum trait Fig. 3a,b,d), except for the *LH-tradeoff* scenario in which evolution did not drive species to the optimum trait (Fig. 3c). Co-adaptation also made the level of species packing virtually constant irrespective of species number (Fig. 3e-h).

Biodiversity-Stability

Asymptotic resilience, in all four ecological scenarios, declined with diversity (Fig. 4a-d). Moreover, the biodiversity-stability relationships were similarly negative, regardless of community adaptation, even though co-adapted communities were generally more stable than random ones.

Ecosystem stability, was also higher overall in co-adapted than in random communities (Fig. 4e-h). However, unlike asymptotic resilience, it had different responses to diversity depending on ecological scenario. Ecosystem stability increased with species richness in the two scenarios strongly based on exploitative competition (*Niche* and *Body-size*), but decreased with species richness in the *LH-tradeoff* and *Trophic* scenarios. In all cases, unlike asymptotic resilience, the variation of ecosystem stability with species richness was strongly affected by co-adaptation, and the patterns were quite consistent with those observed for total productivity (Fig. 2), except for the *LH-tradeoff*.

Biodiversity-Invasibility

Resistance to invasion (Fig. 5a-d) presented consistent trends in the four ecological scenarios. First, it increased with species richness, reflecting classical expectations. Second, co-adapted communities were generally more resistant to invasion than random ones, at any species richness level, reflecting the concentration of species around trait optima, which leaves only more peripheral niches available for potential invasive species. This difference was also quite in line with common expectations, but it could vanish, or even reverse for some parameter values, in the *LH-tradeoff* scenario

(Fig. 5c). Overall, the biodiversity-invasion relationships were thus similar regardless of co-adaptation.

The effects of co-adaptation were much more dramatic and consistent when looking at tolerance to invasion (Fig. 5e-g). In random communities tolerance to invasion steeply declined with species richness, meaning that successful invasions were more and more harmful (in terms of diversity loss) as diversity increased (Fig. 5e-g). In contrast, co-adapted communities were in all cases more tolerant to invasion than random communities: they retained their high tolerance to invasion as diversity increases, the biodiversity-invasion relationship being essentially flat (*Niche*, *Body-size* and *LH-tradeoff* scenarios) or slightly negative (*Trophic*).

Discussion

Natural and anthropized ecosystems present tremendous variation in their diversity and composition (species richness and trait values), and also in the degree to which component species are adapted to the local environmental conditions and to one another, here referred to as community adaptation. While it is clear that diversity is an important determinant of ecosystem functioning, we still know little about how the level of community adaptation might impact BEF relationships (Fiegna *et al.*, 2015; Hendry, 2016). In this study we addressed this question with a general modelling approach, systematically comparing random and co-adapted communities with respect to three BEF relationships (biodiversity-productivity, biodiversity-stability and biodiversity-invasibility) and across four classical scenarios of ecological interactions.

We found that community adaptation had an impact on all BEF relationships, but that the nature and extent of the impact depend on both the metrics and the scenarios considered for species interactions. Overall, the biodiversity-productivity and biodiversity-invasibility relationships were strongly impacted by community ad-

aptation, while the biodiversity-stability relationships were much less so. Indeed, co-adapted communities, at any species richness, tended to be more dynamically stable in terms of asymptotic resilience than random ones, but there was little interaction with diversity: BEF relationships looked qualitatively very similar in random and co-adapted communities. This suggests that the connection between diversity and dynamical stability is a rather universal property in such systems of interacting species, largely insensitive to the details of species interactions and to community adaptation. Co-adapted communities were more dynamically stable, which likely reflects the fact that co-adaptation brings traits closer to optimal values (Fig. 3a-d), entailing faster returns to equilibrium (see also Loeuille, 2010). Consistent with this interpretation, the only case where co-adapted communities were on average less dynamically stable than random ones occurred at low diversity in the *LH-tradeoff* (Fig. 4c), a case where co-adaptation pushes traits away from the optimum (Fig. 1a). When looking at ecosystem stability (May, 1973; Ives *et al.*, 1999; Arnoldi *et al.*, 2016), BEF relationships differed more importantly between co-adapted and random communities, but these differences closely mirrored those observed for biodiversity-productivity relationships (Fig. 4e-h). This suggests that variation in ecosystem stability were linked to variation in total productivity and the total biomass of species, but, beyond that, were little impacted by community adaptation in a direct manner (see Ives *et al.*, 1999), especially for the *Niche*, *Body-size* and *Trophic* scenarios. Consistent with this interpretation, overall Spearman correlation coefficients between productivity and ecosystem stability were, across all communities, 0.99, 0.97, 0.65 and 0.79 for the *Niche*, *Body-size*, *LH-tradeoff*, *Trophic* scenarios, respectively.

Biodiversity-productivity relationships were both quite variable across ecological scenarios and strongly impacted by community adaptation. The impact could be as pronounced as a slope inversion when moving from random to co-adapted com-

munities, from positive to negative (*Trophic* scenario) or from negative to positive (*LH-tradeoff* scenario; Fig. 2c). In all cases, changes in the shape of biodiversity-productivity relationships were mostly driven by low diversity levels, at which co-adapted communities differed importantly for random ones, while at higher diversity levels community adaptation had modest impact on average (Fig. 2). Theoretical (Mazancourt *et al.*, 2008) and experimental (terHorst *et al.*, 2018) studies have found that biodiversity inhibits the evolution of species traits (but see Jousset *et al.* (2016)). This can be attributed to the strong constraints on species trait distributions in rich communities, due to species interactions and persistence conditions ("ecological filter"), which leaves adaptive evolution much less room to alter species traits. As a result, co-adapted communities are more and more similar to random communities as the number of species increases: the added constraint of an "evolutionary filter" makes less and less of a difference. In most ecological scenarios (*Niche*, *Body-size* and *Trophic*), co-adapted communities at low diversity levels were more productive than random ones on average (Fig. 2a,b,d). Therefore, community adaptation weakened the positive biodiversity-productivity relationships observed in random communities, making those shallower, or even reversing them to negative (*Trophic*). In the *LH-tradeoff* scenario, low diversity co-adapted communities were on the contrary less productive than random ones, so that the effect of community adaptation was opposite: co-adapted communities exhibited a positive biodiversity-functioning relationships, whereas a slightly negative relationship is predicted in random communities (see also Loreau, 2010). The qualitative effect of community adaptation on biodiversity-productivity relationships could thus be determined, to a large extent, from the overall direction of selection in isolated species (monocultures), either towards higher productivity (*Niche*, *Body-size*, *Trophic* scenarios) or towards lower productivity (*LH-tradeoff* scenario).

Community adaptation also affected the mechanisms underlying biodiversity-productivity relationships. In the two scenarios describing competition for resources

(*Niche* and *Body-size*) and in the *Trophic* scenario, low diversity co-adapted communities were more productive because adaptive evolution favoured traits that were close to the optimum (Fig. 3a,b,d). At higher diversity levels, more and more species were kept farther away from the optimal trait value, and thus intrinsically less productive. Such a change in the intrinsic productivity of species as diversity increases is often called a "selection effect" (Loreau & Hector, 2001), but here, following Zuppinger-Dingley *et al.* (2014), we will call it a "sampling effect" to avoid confusion. In random communities, this sampling effect was positive, as usually expected, and contributed importantly to the positive biodiversity-productivity relationship: richer communities were more likely, by chance, to harbor species that were intrinsically more productive in the habitat (Fig. 3a,b,d, blue curves). In co-adapted communities, the sampling effect was much reduced or entirely absent, owing to the effect of co-adaptation explained above. In contrast, the average trait distance between adjacent species (the level of niche packing) declined sharply with diversity in random communities, but much less so in co-adapted communities (Fig. 3e-h). Therefore, the level of species trait complementarity was less sensitive to diversity with community adaptation. Altogether, this suggests positive biodiversity-productivity relationships should be more driven by complementarity effects, and less by sampling effects, in co-adapted communities compared to random communities.

There is good experimental evidence that biodiversity-productivity relationships can indeed change over time. In grassland experiments, the positive biodiversity-productivity relationships were reported to become steeper (Reich *et al.*, 2012), or sometimes flatter (Meyer *et al.*, 2016, for most of its biomass-related metrics), over several years. A study of decomposing microbial communities observed a decline in productivity and a flattening of the biodiversity-productivity relationship over several days (Bell *et al.*, 2005). These studies deal with relatively short timescales and are not directly relevant to evaluate the consequences of community adaptation, since observed changes are generally attributed to transient ecological mech-

anisms, such as below-ground feedbacks or depletion of most profitable resources. Direct comparison with our modelling results is thus difficult, in which transient dynamics have been sorted out and communities have reached a state of equilibrium. Fortunately, more recent analyses of the longest grassland experiments have looked for, and found, evidence of character displacement and evolution of niche differentiation, even on such relatively short timescales (Zuppinger-Dingley *et al.*, 2014; van Moorsel *et al.*, 2018). This suggests that the evolutionary effects analyzed in this work might have begun to play a role. Interestingly, it was observed that biodiversity-productivity relationships assembled from co-selected species were higher at low diversity, but saturated faster with diversity, thus being more concave (van Moorsel *et al.*, 2018). This is strikingly reminiscent of our predictions in the standard "resource competition" scenarios (*Niche* and *Body-size*; see Fig. 2a,b). Furthermore, it was found that species evolving in mixture assemblages (thus approaching a state of community adaptation) elicited more complementarity effects, and less sampling effects, than assemblages of non-co-adapted species (Zuppinger-Dingley *et al.*, 2014). This too is quite consistent with our findings. In a more direct approach, Fiegna *et al.* (2014, 2015) used experimental evolution to demonstrate that biodiversity-productivity relationships are impacted by co-adaptation in bacteria. They further showed that these changes involved an evolutionary component in species interactions, not just of individual species performances, even though the overall impact on biodiversity-productivity relationships was quite variable among experiments. These studies thus clearly support a role for community adaptation in the dynamics of BEF relationships as highlighted here.

Regarding the biodiversity-invasibility relationships (Fig. 5), the effects of community adaptation were much more consistent across ecological scenarios than for biodiversity-productivity relationships. Resistance to invasion increased, and tolerance to invasion decreased, with diversity under all scenarios, which conforms well to general expectations (Levine, 2000; Hector *et al.*, 2001; Davis, 2009). The

impact of community adaptation was very consistent across scenarios. It was moderate for resistance to invasion (probability of establishment) but spectacular for tolerance to invasion (number of secondary extinctions) (Fig. 5e-h). Indeed, resistance to invasion was only slightly impacted by community adaptation, the latter generally increasing resistance, but with almost no interaction with of diversity: alien species thus had a lower probability to invade co-adapted communities, but otherwise biodiversity-resistance relationships were pretty much parallel in random and co-adapted communities. In contrast, biodiversity-tolerance relationships we markedly differed with community adaptation (Fig. 5e-h): while tolerance to invasion gradually decreased with species diversity in random communities, it remained virtually constant in co-adapted ones, in which successful invaders almost never caused any secondary extinctions. This can be understood in terms of changes in the species trait distributions. In co-adapted communities, species traits were more concentrated around the optimal trait (Fig. 3e-h orange curves) and more evenly spaced (see S.I. section 6), so that successful invaders tended to occupy peripheral niches at either tail of the trait distribution, which did not cause resident extinctions. However, this is not the case in random communities in which an invader might find vacant niche space anywhere along the trait spectrum, possibly very close to a resident species, thus potentially excluding the latter and triggering further secondary extinctions. Empirical evidence is even scarcer regarding the role of community adaptation for invasion properties than it is for productivity. Most studies focus on documenting the impact of invasions on the evolutionary dynamics of communities, rather than the other way round ; yet, evolutionarily immature (e.g. insular) communities or recently assembled ecosystems such as anthropized habitats are known to be more sensitive to invasions than old species assemblages such as primary forests. Although this is suggestive of a protective role of co-evolution, the diversity-invasibility relationship is difficult to relate to evolutionary history, as most long-co-evolved communities are highly diverse while recently assembled ones

are usually species-poor (David *et al.*, 2017).

Overall our work highlights some potentially important consequences of evolutionary dynamics for biodiversity-functioning relationships. Through its action on species trait values, community adaptation can profoundly change the expected relationship between diversity and various ecosystem functioning properties, even in qualitative terms. This occurs because of the differential magnitude and direction of species trait evolution in poor versus rich communities, so that the ecological impact of species number interacts with the evolutionary history of communities. Therefore, BEF relationships derived from short-term experiments or observed following recent habitat perturbations might not be safely extrapolated into the future, once eco-evolutionary feed-backs have played out. This may have consequences for our understanding and prediction of the way ecosystems respond to species loss or environmental perturbations, and for ecosystem management and restoration. Ecological theory definitely calls for more long-term or evolution-oriented studies of BEF relationships.

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Figures

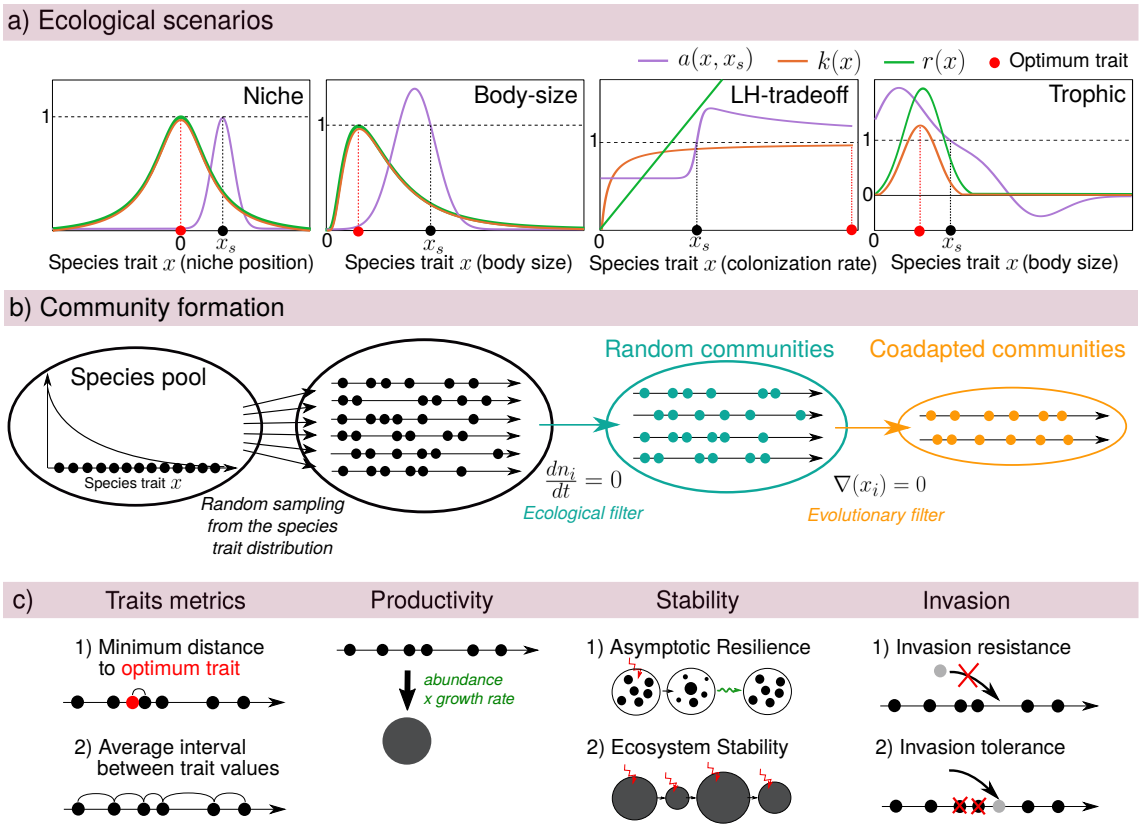

Fig. 1

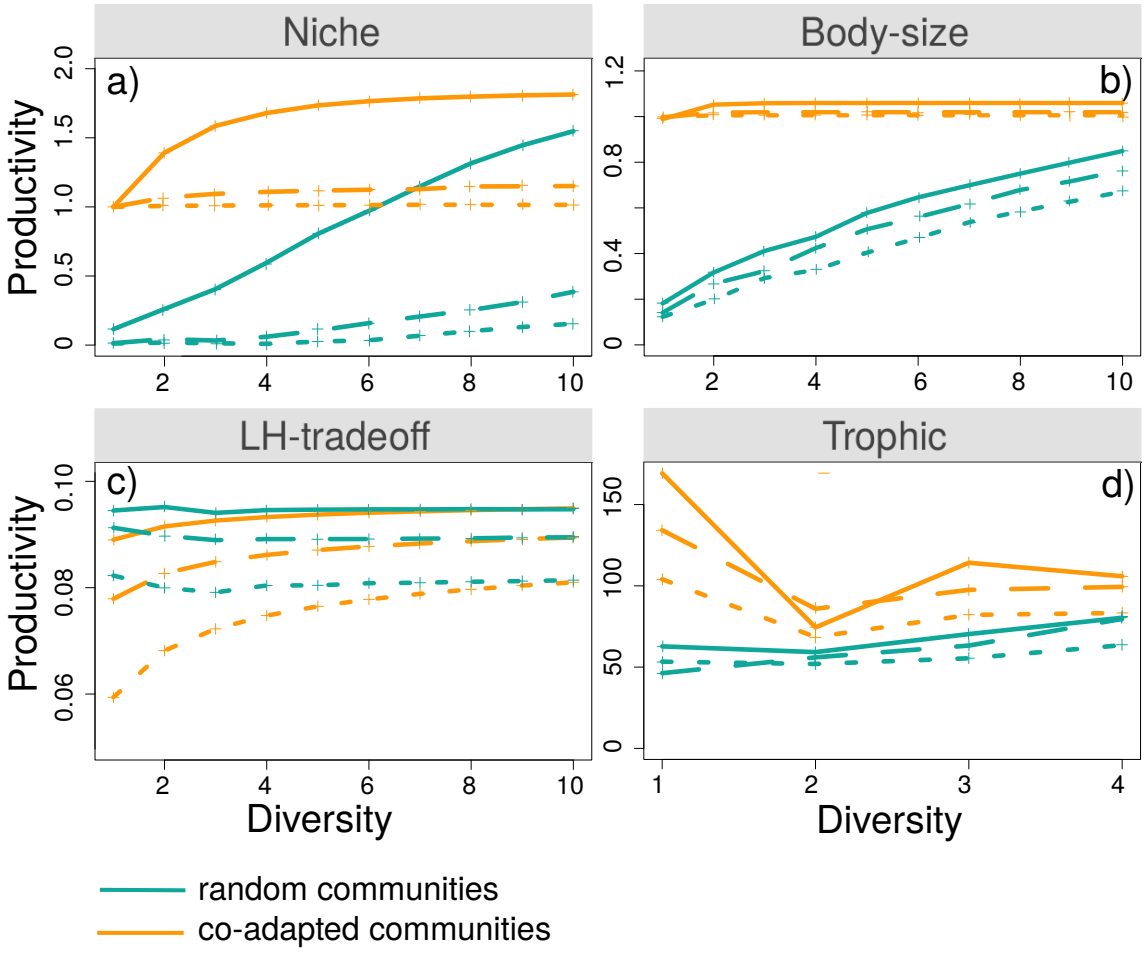
Niche
Body-size
LH-tradeoff
Trophic
a)
b)
c)
d)
Productivity
Productivity
Diversity
Diversity
random communities
co-adapted communities

Fig. 2

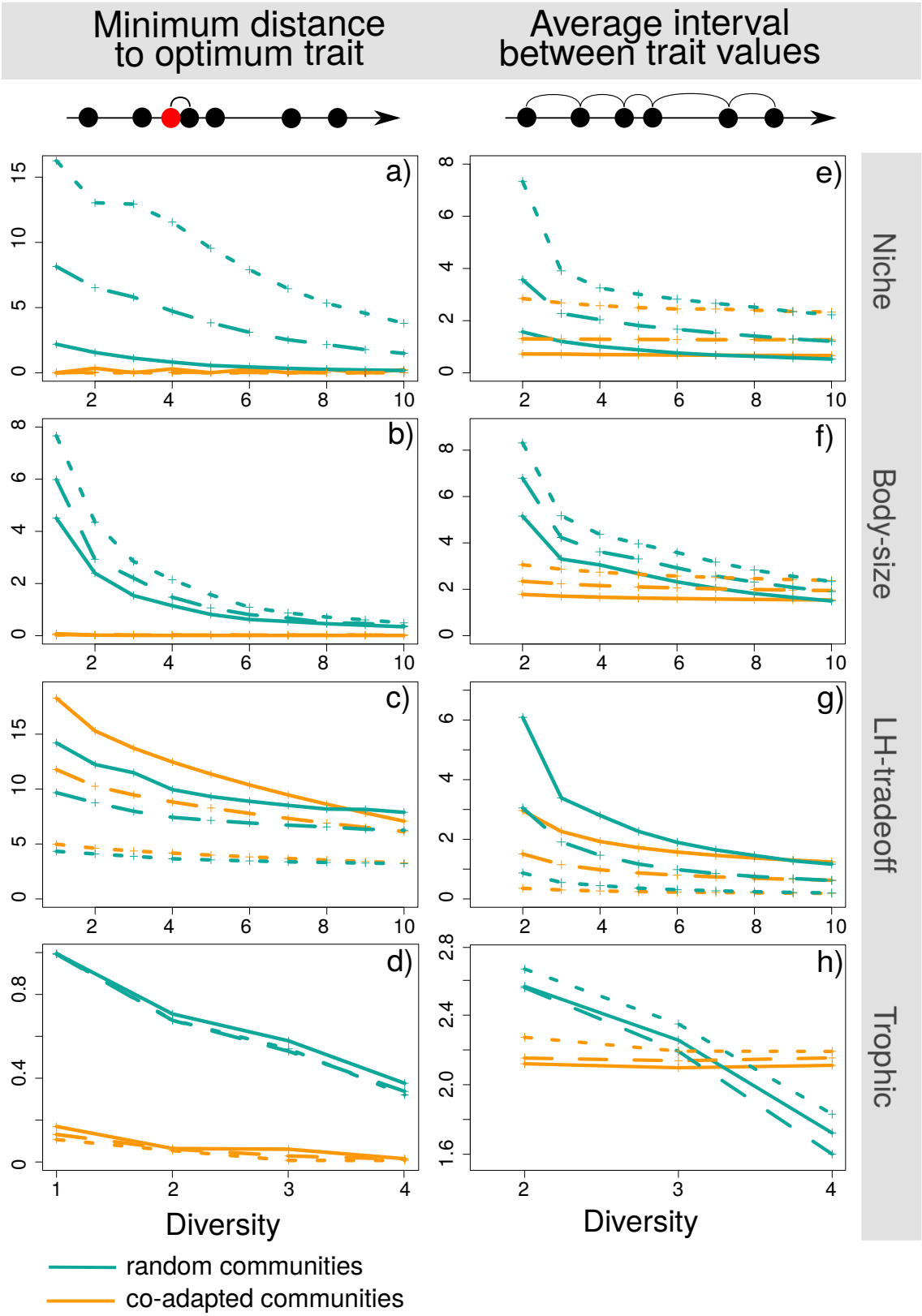
Minimum distance to optimum trait
Average interval between trait values
Niche
Body-size
LH-tradeoff
Trophic
a)
b)
c)
d)
e)
f)
g)
h)
Diversity
Diversity
random communities
co-adapted communities

Fig. 3

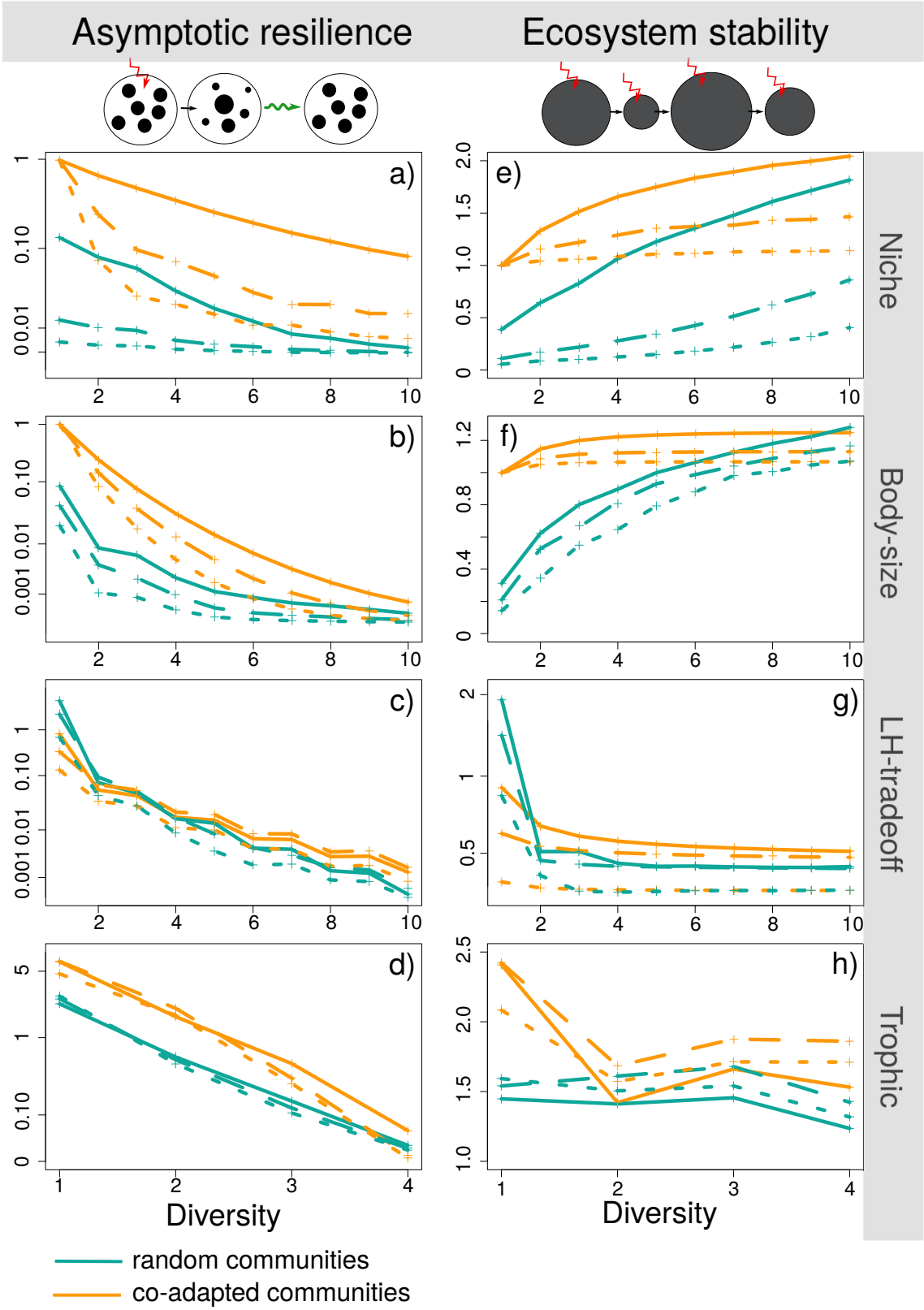
Asymptotic resilience
Ecosystem stability
a)
b)
c)
d)
e)
f)
g)
h)
Niche
Body-size
LH-tradeoff
Trophic
Diversity
Diversity
random communities
co-adapted communities

Fig. 4

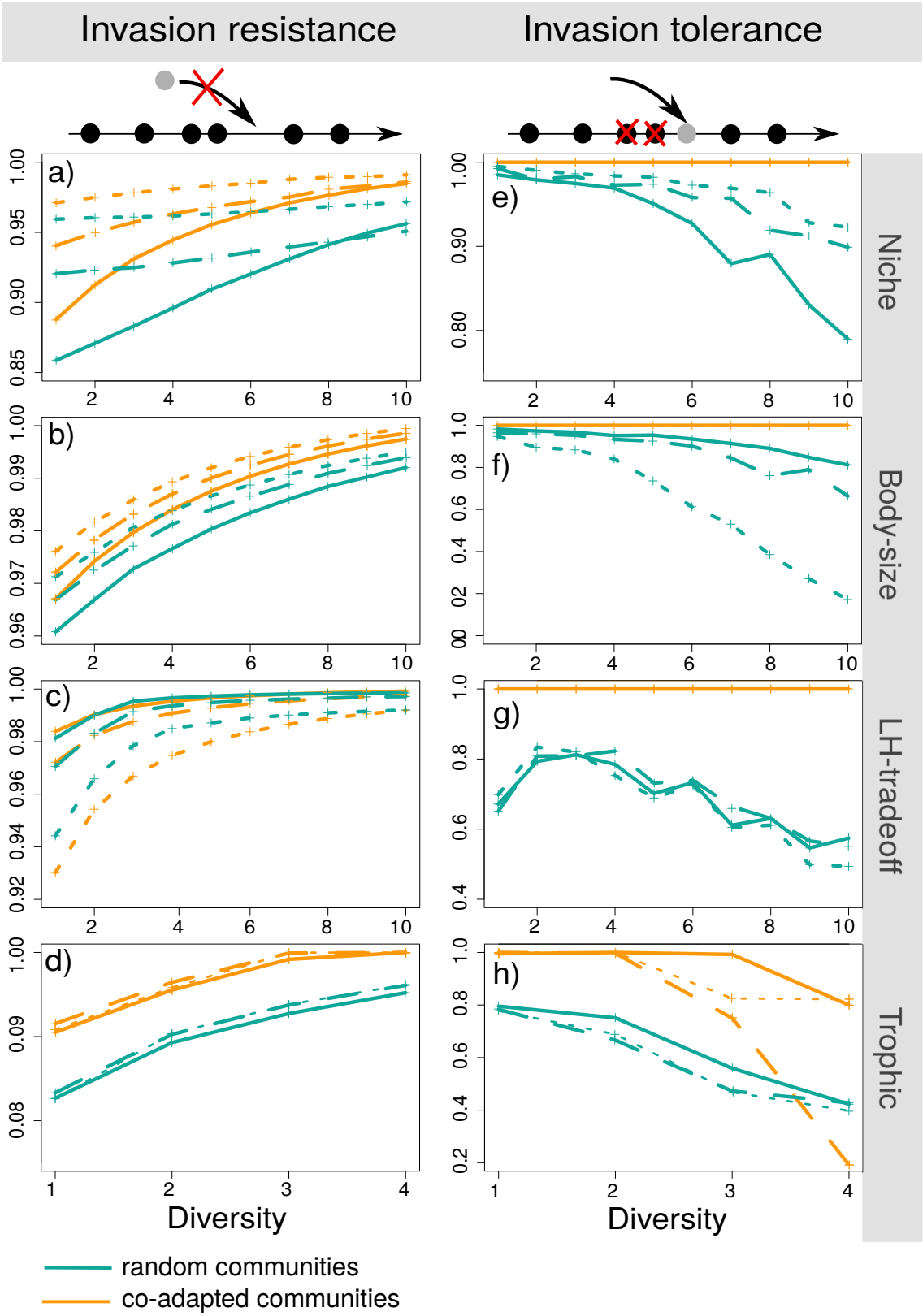
Invasion resistance
Invasion tolerance
a)
b)
c)
d)
e)
f)
g)
h)
Niche
Body-size
LH-tradeoff
Trophic
Diversity
Diversity
random communities
co-adapted communities

Fig. 5

Captions

Fig. 1 (a) Ecological parameters for the four scenarios considered: intrinsic growth rate $r(x)$ (green), mono-specific abundance $k(x)$ (orange) and competitive impact $a(x, x_s)$ (purple) of species x_s over species x as a function of species trait x for the four scenarios. By definition the intra-specific competition is $a(x_s, x_s) = 1$. Red dots indicate the optimum ecological trait, *i.e.* trait that maximizes mono-specific abundances. (b) Community formation. Species are sampled from a species pool within a given distribution. An ecological filter is then applied so that only the ecologically existing communities are kept (with no null abundance), and form the random communities. Then, species evolution towards their evolutionary equilibrium filters out some species, leading to co-adapted communities. (c) For each community (random or co-adapted), we measure two species trait metrics (minimum distance to optimum trait, and average interval between trait values) and the three types of functioning properties: (i) productivity measured by species abundances time species growth rates, (ii) stability, with asymptotic resilience (return rate to equilibrium) and ecosystem stability (reflecting changes in abundances over time), and (iii) response to invasion, with invasion resistance (probability of non-establishment of a foreign species) and tolerance to invasion (probability of non resident extinction following an invasion).

Fig. 2 Productivity as a function of diversity under the the four scenarios and the two community co-adaptation levels. Three sets of parameters are used for each scenario, represented by the three different line types. Parameter values are given in S.I. section 2 together with other explored parameter sets (not shown for the sake of clarity).

Fig. 3 Minimum distance to optimum trait (a-d) and average interval between trait values (e-h) as a function of diversity under the four scenarios and the two

community co-adaptation levels. Three sets of parameters are used for each scenario, represented by the three different line types. Parameter values are given in S.I. section 2 together with other explored parameter sets (not shown for the sake of clarity).

Fig. 4 Asymptotic resilience (a-d) and ecosystem stability (e-h) as a function of diversity under the four scenarios and the two community co-adaptation levels. Asymptotic resilience is represented in log-scale, which does not modify the interpretation on co-adaptation effect and allows to better visualize the consequences of co-adaptation. Three sets of parameters are used for each scenario, represented by the three different line types. Parameter values are given in S.I. section 2 together with other explored parameter sets (not shown for the sake of clarity).

Fig. 5 Probability that a foreign species does not get installed into a community, e.g. resistance to invasion (a-e), and proportion of resident species that do not undergo a secondary extinction, e.g. tolerance to invasion (f-j), as a function of diversity, under the four scenarios and the two community co-adaptation levels. Three sets of parameters are used for each scenario, represented by the three different line types. Parameter values are given in S.I. section 2 together with other explored parameter sets (not shown for the sake of clarity).