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How complementarity and selection affect the relationship between ecosystem functioning and stability

Shaopeng Wang ,[1,7] Forest Isbell ,[2] Wanlu Deng,[3] Pubin Hong,[1] Laura E. Dee ,[4]
Patrick Thompson ,[5] and Michel Loreau[6]

[1]*Institute of Ecology, College of Urban and Environmental Science, and Key Laboratory for Earth Surface Processes of the Ministry of Education, Peking University, Beijing 100871 China*
[2]*Department of Ecology, Evolution, and Behavior, University of Minnesota, St. Paul, Minnesota 55108 USA*
[3]*Center for Statistical Science, Department of Industrial Engineering, Tsinghua University, Beijing 100084 China*
[4]*Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, Colorado 80309 USA*
[5]*Department of Zoology and Biodiversity Research Centre, University of British Columbia, Vancouver, British Columbia V6T 1Z4 Canada*
[6]*Centre for Biodiversity Theory and Modelling, Theoretical and Experimental Ecology Station, CNRS, Moulis 09200 France*

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Abstract. The biotic mechanisms underlying ecosystem functioning and stability have been extensively—but separately—explored in the literature, making it difficult to understand the relationship between functioning and stability. In this study, we used community models to examine how complementarity and selection, the two major biodiversity mechanisms known to enhance ecosystem biomass production, affect ecosystem stability. Our analytic and simulation results show that although complementarity promotes stability, selection impairs it. The negative effects of selection on stability operate through weakening portfolio effects and selecting species that have high productivity but low tolerance to perturbations ("risk-prone" species). In contrast, complementarity enhances stability by increasing portfolio effects and reducing the relative abundance of risk-prone species. Consequently, ecosystem functioning and stability exhibit either a synergy, if complementarity effects prevail, or trade-off, if selection effects prevail. Across species richness levels, ecosystem functioning and stability tend to be positively related, but negative relationships can occur when selection co-varies with richness. Our findings provide novel insights for understanding the functioning-stability relationship, with potential implications for both ecological research and ecosystem management.

Key words: biodiversity; complementarity; functioning; invariability; portfolio effect; resilience; resistance; selection; trade-off.

Introduction

The past three decades have seen major progress in understanding the role of biodiversity in the maintenance of ecosystem functioning and stability. A significant number of experiments have shown that biodiversity promotes the functioning and stability of ecosystems (Hector et al. 1999, 2010, Tilman et al. 2001, 2006, Huang et al. 2018; but see Blüthgen et al. 2016), and new theories and hypotheses have been developed to explain the positive effects of biodiversity observed in experiments (Loreau 2010, Tilman et al. 2014). These studies have offered significant insights, both conceptually, by integrating community and ecosystem ecology, and practically, by predicting the functional consequences of biodiversity changes (Loreau 2010, Cardinale et al. 2012).

Although early research on biodiversity and ecosystem functioning (BEF) focused mainly on one specific measure of ecosystem functioning (e.g., productivity; but see Naeem et al. 1994) or stability (e.g., temporal invariability), recent studies have highlighted the multidimensional nature of both functioning (Hector and Bagchi 2007, Isbell et al. 2011) and stability (Pimm 1984, Ives and Carpenter 2007, Donohue et al. 2013). These studies have sought to clarify the intrinsic links and trade-offs between different aspects of ecosystem functioning or stability (Donohue et al. 2013, Meyer et al. 2018), and how these links and trade-offs depend on different ecological factors, for example, biodiversity (Ives and Carpenter 2007, Pennekamp et al. 2018) and disturbance type (Radchuk et al. 2019). Despite this progress, a largely missing but fundamental question is the relationship between ecosystem functioning and stability, particularly when they can be simultaneously maximized and when they exhibit trade-offs (Montoya et al. 2019).

Although ecosystem functioning and stability have both been shown to increase with biodiversity

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[7] Email: shaopeng.wang@pku.edu.cn

generally, experimental data display large variations in both functioning and stability within a given level of biodiversity (Hector et al. 1999, 2010, Tilman et al. 2001, 2006, Isbell et al. 2015, Huang et al. 2018). This raises a key question whether species assemblages that exhibit higher functioning will also exhibit higher stability. In a meta-analysis of 34 experiments, Cardinale et al. (2013) found that biodiversity positively influenced both productivity and temporal invariability (as measured by the ratio of mean productivity to its standard deviation), but the effect of biodiversity on functioning was independent of that on invariability, both within an experiment with fixed species richness and across experiments with varying richness. They thus concluded that knowing the effect of biodiversity on productivity might not help us predict its effect on stability. However, this study did not distinguish the biotic mechanisms underlying functioning and stability and test how these mechanisms could be related.

Both ecosystem functioning and stability are ecosystem-wide properties emerging from species interactions and population dynamics, which underpin the links between these two properties. Biodiversity enhances ecosystem productivity mainly through two groups of processes, niche complementarity and selection (Loreau and Hector 2001). Complementarity occurs if species differ in their resource use or facilitate each other, whereas selection occurs if interspecific interactions lead to the dominance of species with a higher productivity in mixtures (Tilman et al. 1997, Loreau 2010). On the other hand, biodiversity enhances ecosystem stability by providing insurance or portfolio effects when species differ in their responses to environmental fluctuations (Yachi and Loreau 1999, Thibaut and Connolly 2013), or by including species with a higher resistance or resilience to external perturbations (Polley et al. 2007, Grman et al. 2010, Sasaki and Lauenroth 2011, Wilsey et al. 2014, Isbell et al. 2015). During the past decades, the biotic mechanisms underlying ecosystem functioning and stability have been studied extensively but separately (but see Yachi and Loreau 1999), which creates a fundamental gap limiting our understanding of the relationships between ecosystem functioning and stability.

As niche complementarity promotes species coexistence, we should expect that ecosystem stability increases with niche complementarity because of stronger portfolio and overyielding effects (Isbell et al. 2009, de Mazancourt et al. 2013, Thibaut and Connolly 2013). In contrast, selection tends to increase the dominance of more productive species, which reduces species evenness and thus impairs insurance or portfolio effects (Isbell et al. 2009, Wittebolle et al. 2009, Thibaut and Connolly 2013). Moreover, selection can cause a decrease in trait diversity and thereby reduce the resistance of ecosystems in the face of external perturbations (Norberg et al. 2001, Pfisterer and Schmid 2002). That said, an integrated theoretical framework clarifying the explicit links between the biotic mechanisms that underlie ecosystem functioning and stability is still lacking.

Here we explore the mechanistic links between ecosystem functioning and stability, as quantified by mean community biomass and the response (invariability, resistance, and resilience) of community biomass to external perturbations, respectively. Using a Lotka-Volterra competition model, we explore how complementarity and selection—the two major processes known to enhance ecosystem functioning—affect ecosystem stability, and how they generate synergies or trade-offs between ecosystem functioning and stability. Our analyses and simulations reveal contrasting effects of complementarity and selection within a given level of species richness: While complementarity tends to promote stability, selection tends to impair it. As a consequence, ecosystem functioning can exhibit either a synergy or trade-off with ecosystem stability, depending on the relative importance of complementarity and selection processes. We then extend our models to investigate ecosystem functioning-stability relationships along the species richness gradient. We find that across species richness levels, ecosystem functioning and stability tend to be positively related, but negative relationships can occur when selection covaries with species richness. By clarifying when and why ecosystem functioning and stability can exhibit synergies and trade-offs, our findings provide implications for both ecological research and ecosystem management.

METHOD

The model

Our analysis is based on a Lotka-Volterra model of competitors that are influenced by external perturbations and immigration:

$$\frac{dN_j}{dt} = \left[r_j\left(1 - \frac{N_j + \alpha_{\mathrm{ji}} \sum_{\mathrm{i} \neq \mathrm{j}} \mathrm{N}_\mathrm{i}}{K_j}\right) + E_j\right]\mathrm{N}_j + m_j \qquad (1)$$

where N_j is the population size or biomass of species j, r_j and K_j are the intrinsic growth rate and carrying capacity, respectively, and α_{ji} is the interspecific competition coefficient that measures the per capita effect of species i on j relative to the competitive effect of species i on itself (α_{ii}, which is set to 1). E_j captures the per capita response of species j to external perturbations, which mimic either stochastic environmental fluctuations or a catastrophic, pulse perturbation (Appendix S1: Fig. S1). m_j represents a small immigration of species j from the regional community, which is included simply to maintain species richness when species cannot coexist in a closed system (Norberg et al. 2001). To facilitate analytic solution and interpretations, we focus on symmetric interspecific competition in the main text (i.e., $\alpha_{\mathrm{ji}} = \overline{\alpha}$ for any $i \neq$

j), but relax this assumption using simulations in the Appendix S1.

In our model, the species' dynamical parameters determine their potential contributions to ecosystem functioning and stability. For example, species with a higher carrying capacity (K) can reach a higher biomass, such as plant species with a stronger nutrient uptake capacity (e.g., plant root volume). In contrast, species with a higher population growth rate (r) can recover faster from disturbance, thus exhibiting a higher resilience. Many studies have suggested a trade-off between the species' carrying capacity (K) and population growth rate (r) (MacArthur and Wilson 1967, Kurihara et al. 1990). Under such trade-offs, species with a higher productivity have a slower recovery (referred to as risk-prone species, analogous to such strategies in financial investment), and species with a lower productivity have a faster recovery (referred to as risk-adverse species; Pfisterer and Schmid 2002). Such an r–K trade-off between species can potentially result in a trade-off between functioning and stability at the ecosystem level. To explore this, we assume that $r_j = r_0 \cdot (K_0/K_j)^{\theta}$, where K_0 is the species-averaged carrying capacity in the community and r_0 is the population growth rate for a species with carrying capacity equal to K_0. θ determines the strength of the r–K trade-off among species. A strong trade-off between r_j and K_j exists for a large positive value of θ, no trade-off exists when $\theta = 0$, and there is a positive association between K_j and r_j if θ is negative. We test the robustness of our results under different scenarios of r–K trade-offs. Another potential trade-off is between species' carrying capacity (K_j) and their tolerance to external perturbation (E_j); for example, more productive species can be more vulnerable to droughts or fire (MacGillivray et al. 1995, Norberg et al. 2001). In this paper, we present only results for the r–K trade-off, but models with a K–E trade-off lead to similar results (results not shown).

Quantifying complementarity and selection

We measure the strength of complementarity and selection using two sets of metrics. First, the model parameter $\overline{\alpha}$ captures the average strength of interspecific competition (e.g., due to interspecific niche overlap) relative to intraspecific competition, so a higher $\overline{\alpha}$ suggests a lower potential for interspecific niche complementarity. K_j characterizes species' capacity in nutrient uptake and biomass production, so a larger variation in K_j ($\delta_K \triangleq (K_{\max} - K_{\min})/2\overline{K}$, where $K_{\max}$, $K_{\min}$, and $\overline{K}$ represent the maximum, minimum, and average of carrying capacities across all species) suggests a higher potential for selection. Therefore, $\overline{\alpha}$ and δ_K provide one way to capture complementarity and selection processes. We note that in the two-species case of our model, these two parameters ($\overline{\alpha}$ and δ_K) determine the niche overlap and fitness difference, respectively, in the framework of modern coexistence theory (Chesson 2000; see Appendix S2).

We also measure complementarity and selection using the Loreau and Hector (2001) additive partitioning approach. This approach, which has been widely applied in biodiversity experiments, partitions the total biodiversity effect into two components that represent complementarity (CE) and selection (SE) effects, respectively. Specifically, the net biodiversity effect (NBE) is defined as the difference between mixture biomass and the average of monoculture biomass, which is then partitioned into two additive components (Loreau and Hector 2001): $\mathrm{NBE} = \mathrm{CE} + \mathrm{SE} = n\overline{M}\overline{\Delta \mathrm{RY}} + n\mathrm{COV}(M_j, \Delta \mathrm{RY}_j)$. In this equation, n is the number of species in the mixture, M_j is the monoculture biomass of species j, and $\Delta \mathrm{RY}_j$ is the difference between observed relative yield (i.e., the ratio of species j's biomass in the mixture to its monoculture biomass) and expected relative yield (i.e., planted proportion). $\overline{M}$ and $\overline{\Delta \mathrm{RY}}$ are averages across all species.

We use both sets of measures because they both have advantages and disadvantages. The former measures ($\overline{\alpha}$ and δ_K) can be easily manipulated, but they are model specific and can be difficult to parametrize empirically. The latter measures (i.e., CE and SE) can be easily estimated from experimental data, but they capture aggregate effects that emerge from lower-level interactions and thus they cannot be directly manipulated. Thus, these two sets of measures can be regarded as the "cause" ($\overline{\alpha}$ and δ_K) and "consequence" (CE and SE) of their respective processes, following Barry et al. (2019). Although previous studies showed that $\overline{\alpha}$ and δ_K do not precisely match CE and SE, they are strongly related (Carroll et al. 2011, Loreau et al. 2012).

Quantifying ecosystem stability

We quantify ecosystem stability by its ability to maintain constancy in a fluctuating environment and resist, and recover from, a large catastrophic disturbance (Appendix S1: Fig. S1; Donohue et al. 2016, Pennekamp et al. 2018). In the first case, the ecosystem experiences continuous environmental stochasticity, that is, E_j represents Gaussian white noises. We define ecosystem invariability as the reciprocal of the squared coefficient of variation, that is, the ratio of the squared mean to the variance of total community biomass (B_T), that is, $S_{\mathrm{inv}} = (\mathrm{Mean}(B_T)^2)/(\mathrm{Var}(B_T))$ (Wang et al. 2017). In the second case, the ecosystem is exposed to a catastrophic perturbation, which lasts for a short period of time and reduces the biomass of all species (Appendix S1: Fig. S1). Resistance is then calculated by the ratio of the minimum value of community biomass following the perturbation ($B_{T_{\mathrm{pert}}}$) to the initial value before perturbation ($B_{T_{\mathrm{eq}}}$), that is, $S_{\mathrm{resist}} = B_{T_{\mathrm{pert}}}/B_{T_{\mathrm{eq}}}$ (Ingrisch and Bahn 2018). Resilience is calculated by the recovery rate or the reciprocal of the time needed for the community to reach a half recovery (Pimm et al. 2019); that is

$$S_{\mathrm{resil}} = 1/\min_{\mathrm{t}}\left\{\frac{B_T(t) - B_{T_{\mathrm{pert}}}}{B_{T_{\mathrm{eq}}} - B_{T_{\mathrm{pert}}}} > 0.5\right\}.$$

These two metrics are scaled to the preperturbation state and to the impact after the perturbation, respectively, which makes them comparable across scenarios (Ingrisch and Bahn 2018).

Analytic investigations

In the absence of environmental fluctuations ($E = 0$) and immigration ($m = 0$), the coexistence of all species requires

$$\delta_K < \frac{1-\overline{\alpha}}{(n-1)\overline{\alpha}+1}$$

where n is the number of species (Appendix S2). Under this coexistence condition, we first analyze a two-species model, in which we obtain analytic solutions for species diversity, ecosystem functioning, and invariability. Specifically, we define species diversity as the inverse Simpson index, i.e., $D = 1/\sum p_i^2$, where p_i denotes the relative abundance of species i. For comparisons within levels of richness, this diversity index is a metric of evenness (Smith and Wilson 1996). We also calculated the community-averaged carrying capacity to capture community trait composition: $\overline{K} = \sum K_i p_i$. A higher (lower) $\overline{K}$ suggests that the community is dominated by risk-prone (risk-adverse) species when r–K trade-offs exist. We then derive the ecosystem functioning measured as total community biomass ($B_{T_{\mathrm{eq}}}$) and obtain the CE and SE. Lastly, we use a linearization approach to derive the temporal invariability of community biomass (Appendix S2; Wang and Loreau 2016).

We then consider communities with a higher richness ($n > 2$). We derive analytic solutions of total biomass in general cases and ecosystem invariability under a symmetric case where all species have same carrying capacity (i.e., $\delta_K = 0$) (Appendix S2).

Simulations

We perform simulations of our model (eq. 1) to explore the relationship between ecosystem functioning and stability both within and across levels of species richness. We first fix the number of species ($n = 5$) to exclude the confounding effect of species richness and examine how ecosystem functioning and stability change along a gradient of complementarity and/or selection processes. By “gradient,” we mean a set of communities with varying strengths of complementarity (e.g., increasing average competition strength, $\overline{\alpha}$) or selection (e.g., increasing variation in carrying capacity, δ_K). The carrying capacities of the five species are regularly distributed within the interval $[K_0{*}(1 - \delta_K),\ K_0{*}(1 + \delta_K)]$. We simulate seven levels of average interaction coefficient ($\overline{\alpha} = 0.2, 0.3, \ldots, 0.8$) and six levels of variation in carrying capacity ($\delta_K = 0, 0.1, \ldots, 0.5$). To quantify species diversity and ecosystem functioning, we first simulate the model (Eq. 1) without external perturbations until the community reaches an equilibrium. For each community, we simulate parallel monocultures with the same life-history parameters (e.g., r_i and K_i) as those in the mixture and apply the additive partitioning to derive CE and SE (Loreau and Hector 2001). We then simulate two types of perturbations to quantify stability. We first simulate communities experiencing a continuous environmental stochasticity, where species' environmental responses (E_j) follow a Gaussian white noise, with variance $\sigma_E^2 = 0.16$ and interspecific correlation $\rho = 0$ or 0.5. For each combination of $\overline{\alpha}$, δ_K, and ρ, we simulate 500 replicates and record the median ecosystem invariability (S_{inv}). We then simulate a catastrophic perturbation ($E_j = -0.5$) that lasts for a short period of time (0.5 time unit in our simulation). Resistance (S_{resist}) and resilience (S_{resil}) are calculated following the catastrophic perturbation. To test the robustness of our results to the r–K trade-off and variation in competition coefficients, we repeated the above simulations with different θ values and asymmetric competition coefficients (α_{ji}), respectively.

We then simulate communities with species richness (n) that varies between 2 and 8. Along the richness gradient, we consider different scenarios describing how competition strength ($\overline{\alpha}$) and interspecific variation in carrying capacity (δ_K) change with richness. For a local community, an increased richness can cause a higher niche overlap between species and a larger interspecific variation in life-history parameters, leading to increased $\overline{\alpha}$ and δ_K with n. But when comparing communities across sites (Cardinale et al. 2013), competition strength and interspecific variation in life-history parameters can also be influenced by the species pool and the environmental conditions, leading to idiosyncratic relationships between species richness (n) and model parameters ($\overline{\alpha}$ or δ_K). For instance, biodiversity experiments usually have a species pool representing the surrounding biota (Hector et al. 1999, Tilman et al. 2001, Huang et al. 2018), so different sites contain species with different life-history traits, which corresponds to varying $\overline{\alpha}$ and δ_K in our model. Thus, we simulate a broad range of scenarios to cover different possibilities. Specifically, given a lower or higher value of δ_K (i.e., $\delta_K = 0.1, 0.5$), we consider three scenarios where $\overline{\alpha}$ increases, remains unchanged, or decreases with n; given a lower or higher value of $\overline{\alpha}$ (i.e., $\overline{\alpha} = 0.2, 0.8$), we also consider three scenarios where δ_K increases, remains unchanged, or decreases with n.

Results

Analytic solutions for ecosystem functioning and invariability

In the absence of immigration and under the coexistence condition, we derive full analytic solutions for species diversity, ecosystem functioning, and invariability in two-species systems (Appendix S2). Species diversity (i.e., evenness) is

$$D=\frac{2}{1+\frac{\delta_K^2(1+\overline{\alpha})^2}{(1-\overline{\alpha})^2}}$$

and the community-averaged carrying capacity ($\overline{K}$) is

$$\overline{K}=K_0\left(1+\delta_K^2\cdot\frac{1+\overline{\alpha}}{1-\overline{\alpha}}\right).$$

Thus, species diversity or evenness (D) decreases with $\overline{\alpha}$ and δ_K, and the community-averaged value of carrying capacity ($\overline{K}$) increases with $\overline{\alpha}$ and δ_K. In other words, as interspecific competition and/or variation in carrying capacities increase, the community becomes increasingly uneven and dominated by species with higher carrying capacity (i.e., risk-prone species). Total community biomass ($B_{T_{\text{eq}}}$) and complementarity (CE) and selection (SE) effects can also be derived (Appendix S2):

$$B_{T_{\text{eq}}}=\frac{2K_0}{1+\overline{\alpha}} \tag{2}$$

$$\text{CE}=\left[\frac{1+\overline{\alpha}}{1-\overline{\alpha}}-\frac{4\overline{\alpha}}{(1-\overline{\alpha}^2)(1-\delta_K^2)}\right]K_0 \tag{3}$$

$$\text{SE}=\frac{4\overline{\alpha}\delta_K^2K_0}{(1-\overline{\alpha}^2)(1-\delta_K^2)}. \tag{4}$$

These equations show that total community biomass decreases with $\overline{\alpha}$ but does not change with δ_K (note that these solutions are derived under the coexistence condition). Moreover, CE decreases, and SE increases, as $\overline{\alpha}$ and δ_K increase.

In two-species cases, we also derive the approximate solution for ecosystem invariability (S_{inv}; Appendix S2). When the growth rates of both species are identical (denoted as r), the solution can be simplified:

$$S_{\text{inv}}=\frac{4r}{\sigma_E^2}\cdot\frac{1}{1+\rho+(1-\rho)\delta_K^2\left[\frac{(1+\overline{\alpha})}{(1-\overline{\alpha})}+\frac{4\overline{\alpha}^2}{(1-\overline{\alpha})\left[1-\overline{\alpha}-\delta_K^2(1+\overline{\alpha})\right]}\right]}. \tag{5}$$

Eq. 5 shows that ecosystem invariability generally increases with complementarity (a lower $\overline{\alpha}$) and decreases with selection (a higher δ_K), except when species respond to environmental fluctuations in a perfectly correlated manner ($\rho = 1$). Eq. 5 also indicates an interaction between $\overline{\alpha}$ and δ_K. In the special case of symmetric communities (i.e., $\delta_K = 0$), $\overline{\alpha}$ has no effect on invariability, consistent with previous findings using discrete-time models (Ives et al. 1999, Loreau and de Mazancourt 2013).

In diverse communities ($n > 2$), we can derive total community biomass under the coexistence condition (Appendix S2):

$$B_{T_{\text{eq}}}(n)=\frac{nK_0}{(n-1)\overline{\alpha}+1}. \tag{6}$$

Moreover, we derive invariability in completely symmetric communities, that is, all species have same life-history parameters (Appendix S2):

$$S_{\text{var}}(n)=\frac{2r}{\sigma_E^2}\cdot\frac{n}{1+(n-1)\rho}. \tag{7}$$

Eq. 6 shows that ecosystem functioning increases with richness (n) unless species are completely overlapping in their niches (i.e., $\overline{\alpha}=1$). Eq. 7 shows that the invariability increases with richness (n) unless species' responses to environmental fluctuations are perfectly synchronous (i.e., $\rho = 1$). In other words, ecosystem functioning and stability both tend to increase with richness and thus exhibit a positive relationship along the richness gradient. Such a prediction is made under the assumptions of symmetric and fixed life-history parameters, which will be relaxed in our simulations.

Ecosystem functioning and stability in simulated ecosystems with fixed species richness

Our simulations of five-species communities generate qualitatively similar results to our analytic solutions, but for a broader set of conditions (e.g., coexistence maintained by immigration and asymmetric competition coefficients) and stability metrics. Across simulated communities, total community biomass ($B_{T_{\text{eq}}}$) decreases with $\overline{\alpha}$ but does not change with δ_K when species can coexist locally (Fig. 1a; below the dashed line), as our analytic solution (Eq. 2) predicts. However, $B_{T_{\text{eq}}}$ increases with δ_K when coexistence is maintained by immigration (Fig. 1a; above the dashed line). Our simulations show that CE decreases largely with $\overline{\alpha}$ and changes only moderately with δ_K, whereas SE increases largely with δ_K and changes only moderately with α. In other words, although $\overline{\alpha}$ and δ_K both affect CE and SE (as predicted by eqs. 3 and 4), CE is mainly influenced by $\overline{\alpha}$ and SE is mainly influenced by δ_K (Fig. 1b,c). Furthermore, $\overline{\alpha}$ and δ_K exhibit significant interactive effects on both $B_{T_{\text{eq}}}$ and CE, though not on SE (Appendix S1: Table S1). Consistent with the analytic solutions, our simulations also show that species evenness decreases

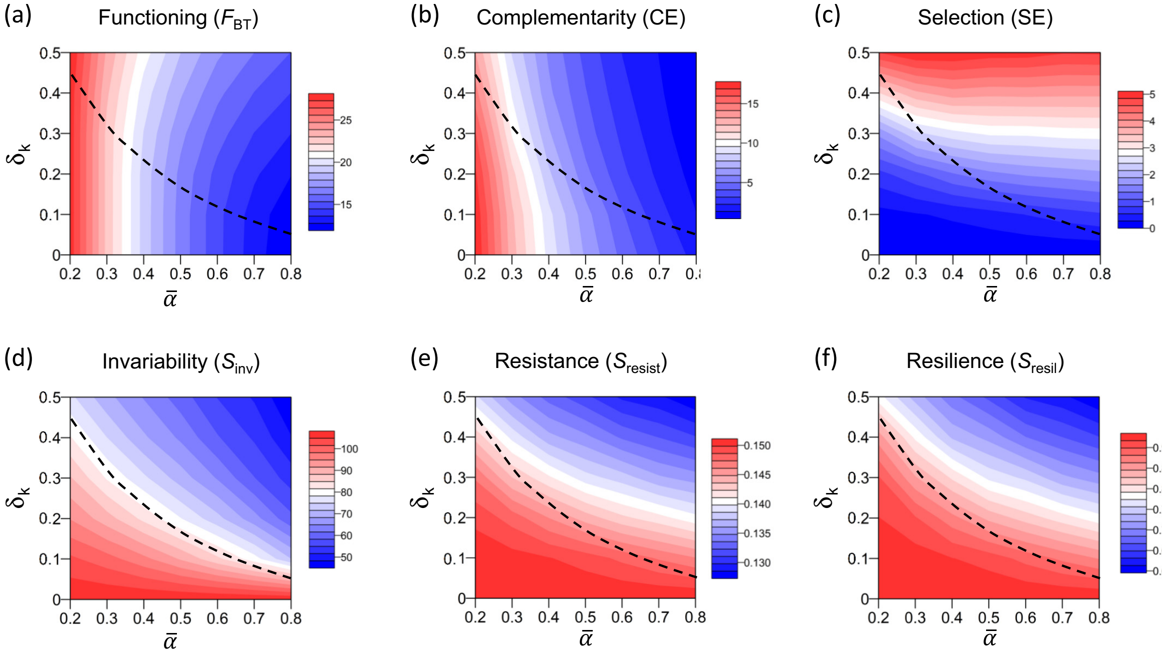

FIG. 1. Ecosystem functioning and stability as functions of two model parameters: the interspecific interaction coefficient ($\bar{\alpha}$) and variation in carrying capacity (δ_K). The black lines show the threshold condition for coexistence; below this line species can coexist locally but additional processes (e.g., immigration) are needed for coexistence above this line. Parameters: $n = 5$, $K_0 = 10$, $m = 10^{-4}$, $\theta = 1$, $E_j \sim N(0, \sigma_E^2 = 0.16)$ for environmental stochasticity (where $\rho = 0$) and $E_j = -0.5$ for the catastrophic perturbation.

with $\bar{\alpha}$ and δ_K, caused by an increase in the dominance of species with a high productivity (i.e., *K*, Appendix S1: Fig. S2).

All three stability metrics decrease with both $\bar{\alpha}$ and δ_K, and the stabilizing effect of a lower $\bar{\alpha}$ is stronger when δ_K is large and weaker when δ_K is small (Fig. 1d–f; Appendix S1: Table S1), consistent with analytical predictions for invariability (eq. 4). Similarly, all three stability metrics exhibit positive relationships with CE and negative relationships with SE (Fig. 2). Thus, overall, stability increases with complementarity (i.e., a low $\bar{\alpha}$ or a high CE) and decreases with selection (i.e., a high δ_K or SE). These relations are robust for all stability metrics in simulations with asymmetric competition coefficients (Appendix S1: Fig. S3), and for invariability in the absence of *r–K* trade-offs (Appendix S1: Fig. S4) or under a strong correlation in species' environmental responses (Appendix S1: Fig. S5). For resistance and resilience, these relations hinge on the *r–K* trade-off assumptions, such that in the absence of *r–K* trade-offs ($\theta = 0$), neither resistance nor resilience is related to either CE or SE (Appendix S1: Fig. S4).

The contrasting relationships between stability and complementarity (i.e., a low $\bar{\alpha}$ or high CE) or selection

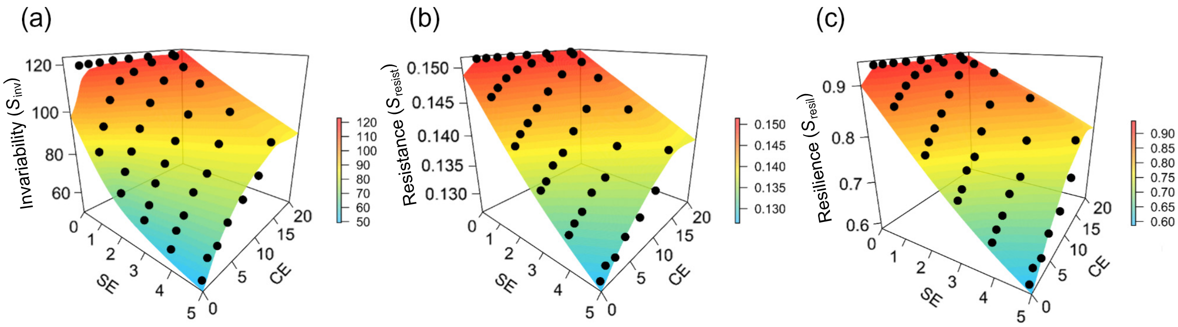

FIG. 2. Ecosystem stability as a function of the complementarity effect (CE) and selection effect (SE) derived from the additive partitioning: (a) invariability, (b) resistance, (c) resilience. The black points show simulated data across a gradient of competition coefficients ($\bar{\alpha}$) and variation in species' carrying capacities (δ_K). The surfaces are fitted using the generalized additive model using *mgcv:gam* in R. Parameters are same as in Fig. 1.

(i.e., a high δ_K or SE) lead to context dependence of the functioning-stability relationship. Specifically, ecosystem stability exhibits positive relationships with ecosystem functioning along a gradient of complementarity (i.e., varying $\overline{\alpha}$ with a fixed δ_K), especially when selection processes are strong (i.e., large fixed δ_K). In contrast, stability exhibits negative relationships with ecosystem functioning along a gradient of selection (i.e., varying δ_K with a fixed $\overline{\alpha}$), especially when complementarity processes are weak (i.e., large fixed $\overline{\alpha}$) (Fig. 3). If the two gradients of complementarity and selection are mixed, the statistical relationship between stability and functioning will be masked (Fig. 3a, d, g).

Ecosystem functioning and stability in simulated ecosystems across species richness levels

Across richness levels, ecosystem functioning and invariability are positively related if model parameters ($\overline{\alpha}$ and δ_K) do not change with richness (Fig. 4), consistent with our analytic solutions (eqs. 6, 7). But if model parameters change with richness, the relation between functioning and invariability becomes idiosyncratic. When competition coefficients ($\overline{\alpha}$) increase strongly with richness, the CE can first increase (because of higher richness) and then decrease (because of increased niche overlap; Appendix S1: Fig. S7), resulting in an initial

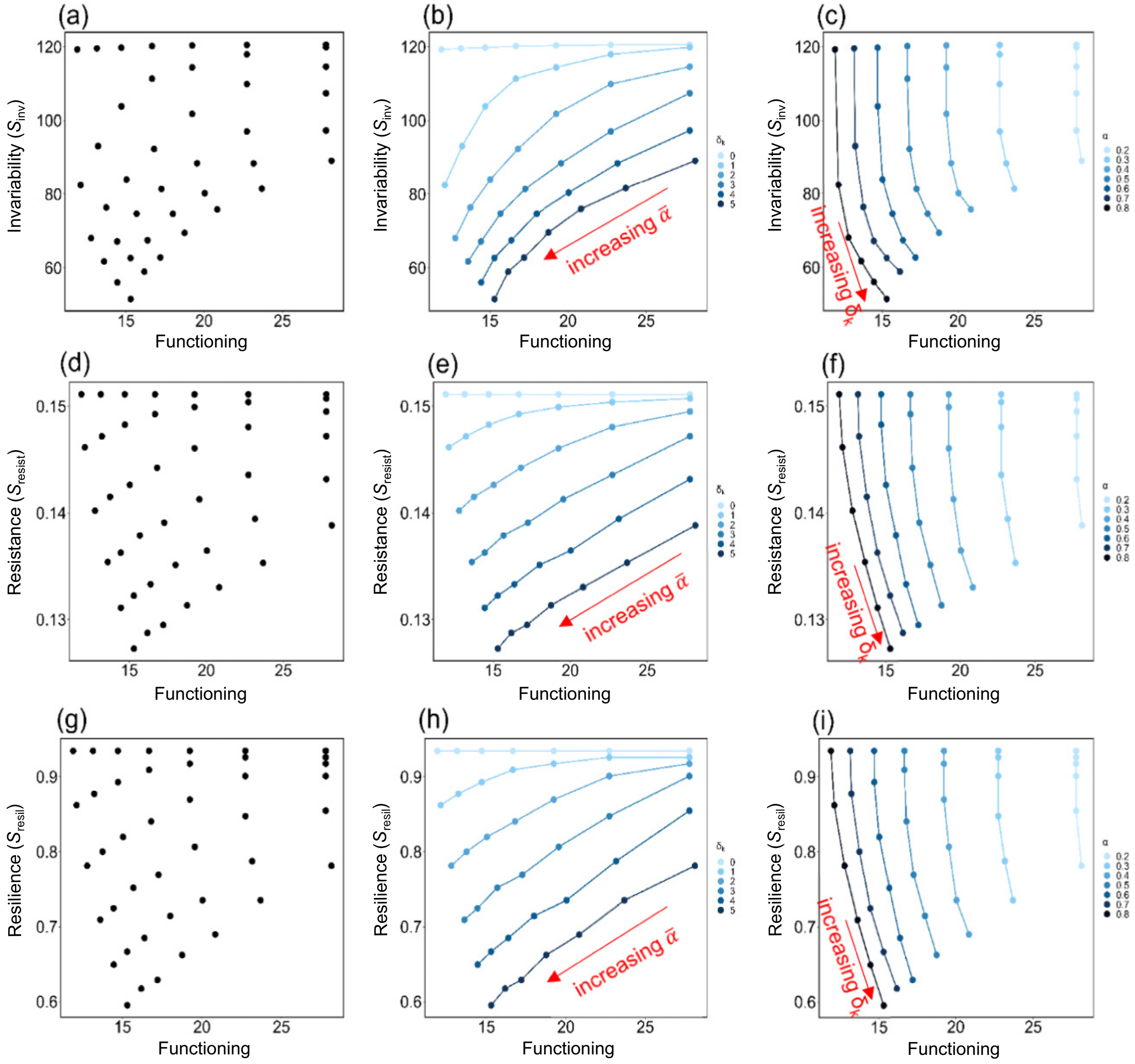

FIG. 3. Relationships between ecosystem stability and functioning. Each row shows results for a different stability metric: invariability (a–c), resistance (d–f), and resilience (g–i). The three panels in a row show the same functioning and stability data points in three ways: original scatters (a, d, g), points connected within each level of variation in carrying capacity (δ_K) (b, e, h), and points connected within each level of the competition coefficient ($\overline{\alpha}$) (c, f, i). Parameters are same as in Fig. 1.

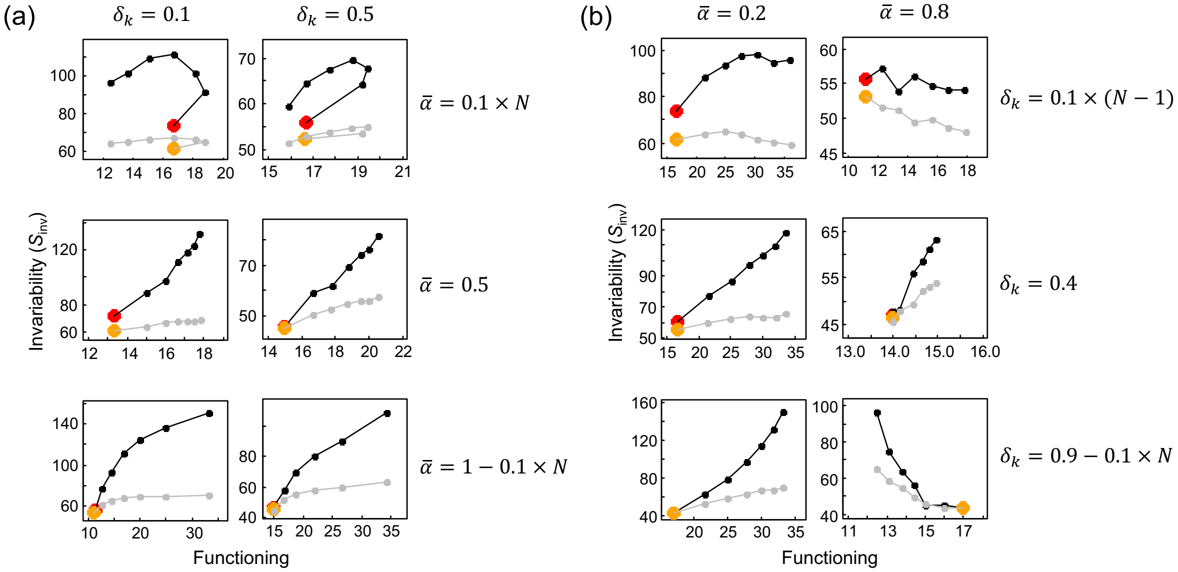

Fig. 4. Relationships between invariability and functioning across communities with increasing species richness: (a) communities have a fixed low or high variation in carrying capacity ($\delta_K = 0.1$ or 0.5) but varying competition coefficient ($\bar{\alpha}$) with richness; (b) communities have a fixed low or high competition coefficient ($\bar{\alpha} = 0.2$ or 0.8) but varying δ_K with richness. In (a) and (b), top panels correspond to increasing trends of $\bar{\alpha}$ or δ_K with richness, middle panels correspond to constant $\bar{\alpha}$ or δ_K, and bottom panels correspond to decreasing $\bar{\alpha}$ or δ_K with richness. The red and orange points in (a) and (b) indicate the lowest richness (i.e., $n = 2$), from which the corresponding lines connect communities with increasing richness (up to 8). Two levels of correlation in species' response are considered: $\rho = 0$ (red and black points) and 0.5 (orange and gray points). Other parameters: $K_0 = 10$, $m = 10^{-4}$, $\theta = 1$, $\sigma_E^2 = 0.16$.

increase followed by a decrease in both ecosystem functioning and invariability (Fig. 4a). Moreover, given a large competition coefficient ($\bar{\alpha} = 0.8$), changes in the variation of carrying capacities (δ_K) with richness can result in a negative relation between ecosystem functioning and invariability (Fig. 4b). Specifically, ecosystem functioning increases but invariability decreases if δ_K increases with richness, because SE increases dramatically across richness levels but CE changes only moderately thanks to the high competition coefficient (i.e., $\bar{\alpha} = 0.8$; Appendix S1: Fig. S8b). Similarly, functioning decreases but invariability increases if δ_K decreases with richness. However, when the competition coefficient is fixed to be small ($\bar{\alpha} = 0.2$), CE increases strongly with richness (Appendix S1: Fig. S8a), which can overwhelm the effect of SE and increase both functioning and invariability (Fig. 4b).

Resistance and resilience exhibited similar patterns as invariability in many scenarios, but not always (Appendix S1: Figs. S6–S8). When the competition coefficient is low ($\bar{\alpha} = 0.2$) and δ_K increases with richness, the resulted increase in CE does not lead to an increase in resistance and resilience (though it does for invariability) because $\overline{K}$ or the fraction of risk-prone species increases with the increasing δ_K (Appendix S1: Fig. S8a). Consequently, resistance and resilience exhibit negative relationships with ecosystem functioning in such a scenario. Besides, when model parameters are kept constant, while ecosystem invariability increases with richness (Fig. 4), both resistance and resilience change slightly across species richness levels (Appendix S1: Figs. S7, S8).

DISCUSSION

Our theoretical results demonstrate that complementarity and selection—the two major classes of mechanisms underlying effects of biodiversity on ecosystem functioning—generally have opposite effects on ecosystem stability. Complementarity processes tend to increase ecosystem stability, whereas selection processes tend to decrease it (Figs. 1, 2). These findings provide new insights for understanding the relationship between ecosystem functioning and stability, which has both theoretical and practical implications.

Contrasting effects of complementarity and selection on stability

Although complementarity and selection processes both increase the amount of biomass production, they have contrasting effects on ecosystem stability, which can be understood from their opposite effects on species diversity and community trait composition (Fig. 5). Our analyses suggest two ways in which selection processes can impair stability. First, selection can reduce species diversity (including evenness) and thus weaken insurance

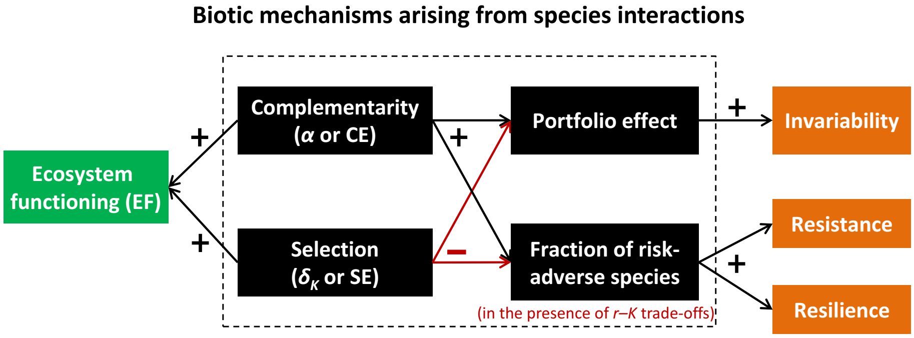

FIG. 5. Conceptual illustration on how biotic mechanisms underlying ecosystem functioning and stability are linked. All mechanisms (black boxes) are driven by lower-level species interactions, and they are interrelated either positively (black lines) or negatively (red lines) as our model shows. In particular, complementarity processes increase the portfolio effect and proportion of risk-adverse species (in the presence of *r*–*K* trade-offs), whereas selection processes decrease them. As a consequence, stability and functioning are positively (negatively) related if species interactions result in stronger complementarity (selection).

or portfolio effects (Appendix S1: Fig. S2a; Yachi and Loreau 1999, Thibaut and Connolly 2013, Wang and Loreau 2016), which decreases ecosystem invariability whether or not *r*–*K* trade-offs exist (Appendix S1: Fig. S4). Second, when there is a life-history trade-off between species carrying capacities (K) and growth rates (r), selection for species that produce a lot of biomass in monoculture but have a low rate of recovery after perturbations (“risk-prone” species), results in a low fraction of species that are more perturbation-tolerant but less productive (“risk-adverse” species; see Appendix S1: Fig. S2b), which weakens the resistance and resilience of the whole ecosystem in the face of catastrophic perturbations. In contrast, complementarity tends to increase species evenness and maintain the relative abundance of risk-adverse species, which contribute to a higher stability. Classic models predict that local stability (i.e., asymptotic resilience) decreases as the strength of species interactions increases (May 1973, Berlow et al. 2004, Allesina and Tang 2012). Our findings of a positive relationship between stability and complementarity (i.e., low α) are in line with these predictions, but extend them to a broader set of stability metrics (i.e., invariability, resilience, and resistance).

We have manipulated the strength of complementarity and selection processes in two different ways: (1) by varying model parameters directly, and (2) by using the Loreau and Hector (2001) additive partitioning of biodiversity effects (i.e., CE and SE). Although CE and SE represent emergent effects combining different lower-level processes of species interactions (eqs. 3, 4; see also Loreau et al. 2012), they match variations in lower-level dynamical parameters relatively well in our model (i.e., $\overline{\alpha}$ and δ_K; see also Carroll et al. 2011, Loreau et al. 2012). Because CE and SE can be easily derived in biodiversity experiments, our predictions between stability and complementarity or selection could be tested empirically by deriving CE and SE with experimental data. To our knowledge, the Isbell et al. (2009) is the only study that has examined the relationship between ecosystem invariability and CE and SE with experimental data, and it shows patterns that are consistent with our theoretical predictions.

Functioning-stability relationships: synergy or trade-off

Our results suggest that ecosystem functioning and stability can exhibit either synergy or trade-off, both within and across levels of species richness. For a given species richness, ecosystem stability can either increase or decrease with ecosystem functioning, depending on whether complementarity or selection is the major driver of biodiversity effects on ecosystem functioning. Specifically, stability and functioning are positively related across ecosystems when complementarity prevails, and they are negatively related when selection prevails. When both complementarity and selection vary simultaneously, however, the relationship between stability and functioning can be masked (Fig. 3). This may explain the lack of relationship between the net effects of biodiversity on ecosystem functioning and invariability observed in experiments with a fixed richness level (Cardinale et al. 2013). Therefore, although knowing the total effect of biodiversity on ecosystem functioning may be insufficient to predict stability (Cardinale et al. 2013), additional information on the underlying mechanisms (e.g., complementarity and selection) allows for better predictions.

Across species richness levels, ecosystem functioning and stability tend to be positively related, but negative relationships can still occur when selection co-varies with richness (Fig. 4; Appendix S1: Fig. S6). In cases where average competition strength and trait variation between species remain relatively constant with increasing species richness (but see Levine et al. 2017), both ecosystem functioning and invariability increase with species richness (Fig. 4), as widely reported in biodiversity experiments (Cardinale et al. 2013, Tilman et al.

2014). This causes a positive functioning-stability relationship across the richness gradient. But when comparing ecosystems from different sites (Cardinale et al. 2013), differences in the species pool lead to different strengths of complementarity and selection processes, which complicates the relationship between ecosystem functioning and invariability (Fig. 4). In addition, ecosystems from different sites can also differ in the magnitude of environmental fluctuations they experience, which has a strong effect on ecosystem invariability but a weak effect on ecosystem functioning (eqs. 6, 7; see also Gonzalez and Loreau 2009). Therefore, variations in the species pool and environmental conditions may explain the lack of correlation between ecosystem functioning and invariability across sites (Cardinale et al. 2013).

Resistance and resilience can exhibit different patterns with richness and thus different relationships with ecosystem functioning across richness levels. In particular, when interspecific variation in carrying capacity increases with richness, more diverse communities will be increasingly dominated by risk-prone species, leading to a higher ecosystem functioning but a lower resistance and resilience (Appendix S1: Fig. S6). This may explain the contrasting effects of biodiversity on productivity and resistance observed in plant and microcosm experiments (Pfisterer and Schmid 2002, Pennekamp et al. 2018).

Implications and future directions

Our findings have implications in both theory and practice. Theoretically, the insurance hypothesis has been proposed to explain the effects of biodiversity on ecosystem functioning and stability (Yachi and Loreau 1999, Isbell et al. 2018). Our results show that the two insurance effects originally introduced by Yachi and Loreau (1999), that is, the performance-enhancing effect, which increases the mean level of ecosystem functioning, and the buffering effect, which reduces its variance, can exhibit trade-offs. Thus, future studies should clearly distinguish between these two effects. Practically, ecosystem management aimed at optimizing the benefits from ecosystems should recognize the potential trade-off between functioning and stability. For instance, in forestry and agriculture, monocultures of a particular species may lead to a higher biomass production and pollination services, compared to more diverse mixtures (Cardinale et al. 2012, Kleijn et al. 2015, Huang et al. 2018). Thus, an artificial selection on such monocultures can maximize the ecosystem productivity and some services. However, such a selection may put the managed systems at risk by reducing the insurance effects of biodiversity that maintains ecosystem stability (Huang et al. 2018, Manning et al. 2019). In such cases, managers need to make a decision to either maximize the expected functioning or minimize its uncertainty in the long run. One useful tool for such decision making is the efficiency frontier approach, which was originally developed in economics and has increasingly been used in ecosystem management (Alvarez et al. 2017).

Our theoretical predictions can be tested empirically with experimental data (Isbell et al. 2009) and extended to more mechanistic models. We have used phenomenological Lotka-Volterra competition models, which are advantageous in terms of generality and tractability but constrained in terms of realism. In particular, our models assume that the processes of complementarity and selection are independent (represented by $\overline{\alpha}$ and δ_K) or weakly dependent (represented by CE and SE), but in natural ecosystems they are emerging properties from complex species interactions and are likely to be interrelated (Fig. 5). Future theoretical and empirical work should clarify the interdependence between complementarity and selection and their implications. Recent studies highlighted trait-based approaches to understand mechanisms underlying species coexistence (Kraft et al. 2015), ecosystem functioning (Díaz and Cabido 2001, Cadotte 2017), and stability (Pillar et al. 2013, Craven et al. 2018). Such approaches may provide promising tools to further integrate the functioning and stability of ecosystems and make mechanistic predictions about their trade-offs in more realistic settings. Lastly, extensions of our models to larger spatial scales (e.g., metacommunity models) will provide an important step forward for transferring theoretical insights to real-world ecosystems (Manning et al. 2019, Gonzalez et al. 2020).

CONCLUSION

Our study provides novel theoretical insights into the relationship between ecosystem functioning and ecosystem stability, and clarifies when and why trade-offs between them may arise. Although trade-offs are a central concept in ecology and in other disciplines such as economics, the trade-off between the mean and variance of benefits from ecosystems (e.g., functioning vs. stability) has largely been overlooked. Our theory takes steps towards closing this gap and generates several predictions that can be tested empirically. Overall, we find that ecosystem stability tends to increase with complementarity but decrease with selection. As a result, ecosystem stability is expected to increase (or decrease) with ecosystem functioning if complementarity (or selection) is the main outcome of species interactions. Across species richness levels, ecosystem functioning and stability tend to be positively related, but negative relationships can occur when selection co-varies with richness. Our findings highlight potential trade-offs in the functioning and stability of ecosystems, which have implications for both ecological research and ecosystem management aimed at optimizing both the amount and stability in benefits from ecosystems.

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