



HAL
open science

Biodiversity as insurance: from concept to measurement and application

Michel Loreau, Matthieu Barbier, Elise Filotas, Dominique Gravel, Forest Isbell, Steve Miller, Jose M Montoya, Shaopeng Wang, Raphaël Aussenac, Rachel Germain, et al.

► **To cite this version:**

Michel Loreau, Matthieu Barbier, Elise Filotas, Dominique Gravel, Forest Isbell, et al.. Biodiversity as insurance: from concept to measurement and application. *Biological Reviews*, 2021, 96 (5), pp.2333-2354. <10.1111/brv.12756>. <hal-03372772v2>

HAL Id: hal-03372772

<https://cnrs.hal.science/hal-03372772v2>

Submitted on 23 Nov 2021










HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons CC BY-NC-ND 4.0 - Attribution - Non-commercial use - No Derivative Works - International License

Biodiversity as insurance: from concept to measurement and application

Michel Loreau^{1*} , Matthieu Barbier¹ , Elise Filotas², Dominique Gravel³ , Forest Isbell⁴ , Steve J. Miller⁵, Jose M. Montoya¹ , Shaopeng Wang⁶, Raphaël Aussenac⁷ , Rachel Germain⁸, Patrick L. Thompson⁸ , Andrew Gonzalez⁹  and Laura E. Dee¹⁰ 

¹*Theoretical and Experimental Ecology Station, CNRS, 2 route du CNRS, Moulis, 09200, France*

²*Center for Forest Research, Université du Québec (TELUQ), 5800 Saint-Denis, Montreal, QC, H2S 3L5, Canada*

³*Département de Biologie, Université de Sherbrooke, 2500 Boulevard de l'Université, Sherbrooke, QC, J1K 2R1, Canada*

⁴*Department of Ecology, Evolution and Behavior, University of Minnesota, 1479 Gortner Ave, St. Paul, MN, 55108, U.S.A.*

⁵*Environmental Studies Program, University of Colorado, Boulder, 4001 Discovery Drive, Boulder, CO, 80303, U.S.A.*

⁶*Institute of Ecology, College of Urban and Environmental Sciences and Key Laboratory for Earth Surface Processes of the Ministry of Education, Peking University, Beijing, 100871, China*

⁷*Université Grenoble Alpes, INRAE, LESSEM, St-Martin-d'Hères, F-38402, France*

⁸*Biodiversity Research Centre and Department of Zoology, University of British Columbia, 6270 University Blvd., Vancouver, BC, V6T 1Z4, Canada*

⁹*Department of Biology, McGill University, 1205 Dr. Penfield Avenue, Montreal, QC, H3A 1B1, Canada*

¹⁰*Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, 1900 Pleasant St., Boulder, CO, 80303, U.S.A.*

ABSTRACT

Biological insurance theory predicts that, in a variable environment, aggregate ecosystem properties will vary less in more diverse communities because declines in the performance or abundance of some species or phenotypes will be offset, at least partly, by smoother declines or increases in others. During the past two decades, ecology has accumulated strong evidence for the stabilising effect of biodiversity on ecosystem functioning. As biological insurance is reaching the stage of a mature theory, it is critical to revisit and clarify its conceptual foundations to guide future developments, applications and measurements. In this review, we first clarify the connections between the insurance and portfolio concepts that have been used in ecology and the economic concepts that inspired them. Doing so points to gaps and mismatches between ecology and economics that could be filled profitably by new theoretical developments and new management applications. Second, we discuss some fundamental issues in biological insurance theory that have remained unnoticed so far and that emerge from some of its recent applications. In particular, we draw a clear distinction between the two effects embedded in biological insurance theory, i.e. the effects of biodiversity on the mean and variability of ecosystem properties. This distinction allows explicit consideration of trade-offs between the mean and stability of ecosystem processes and services. We also review applications of biological insurance theory in ecosystem management. Finally, we provide a synthetic conceptual framework that unifies the various approaches across disciplines, and we suggest new ways in which biological insurance theory could be extended to address new issues in ecology and ecosystem management. Exciting future challenges include linking the effects of biodiversity on ecosystem functioning and stability, incorporating multiple functions and feedbacks, developing new approaches to partition biodiversity effects across scales, extending biological insurance theory to complex interaction networks, and developing new applications to biodiversity and ecosystem management.

Key words: biodiversity, ecosystems, stability, insurance, portfolio, theory, management

* Address for correspondence (Tel: +33561040578; E-mail: michel.loreau@gmail.com)

CONTENTS

I. Introduction	2334
II. Insurance and portfolio theories in economics	2336
(1) Portfolios	2337
(2) Options	2338
(3) Insurance	2338
III. Insurance and portfolio theories in ecology	2338
(1) Similarities and differences between insurance and portfolio theories in ecology	2339
(2) Mechanisms of biological insurance	2339
(3) Distinguishing between the effects of biodiversity on the mean and variability of ecosystem properties	2340
(4) Spatial insurance	2341
IV. Applications of biological insurance in ecosystem management	2342
(1) Agriculture	2342
(2) Fisheries	2343
(3) Forestry	2344
V. Synthesis	2345
(1) Shared features across disciplines	2345
(2) Contrasts between ecological and economic concepts	2347
VI. Future challenges	2348
(1) Linking the effects of biodiversity on ecosystem functioning and stability	2348
(2) Incorporating multiple functions and feedbacks	2348
(3) Developing new approaches to partition biodiversity effects across scales	2349
(4) Extending biological insurance theory to complex interaction networks	2349
(5) Developing new applications to biodiversity and ecosystem management	2350
VII. Conclusions	2350
VIII. Acknowledgements	2350
IX. References	2351

I. INTRODUCTION

The idea that biodiversity can buffer ecosystem functioning against the disruptive effects of environmental fluctuations has been the focus of decades of research in ecology (MacArthur, 1955; Patten, 1975; McNaughton, 1977). Yachi & Loreau (1999) formalised this idea mathematically and introduced the insurance hypothesis, which posits that, in a variable environment, aggregate ecosystem properties (e.g. total biomass or production) will vary less in more diverse communities because declines in the performance or abundance of some species or phenotypes will be offset, at least partly, by smoother declines or increases in others. As a consequence, biodiversity has been viewed as insuring against extreme lows in ecosystem functioning.

The stabilising role of diversification in ecosystem functioning has older roots in economics, cybernetics, and ecology. In economics, a diversification of assets in a portfolio is known to reduce the risk arising from the volatility inherent to fluctuations in the value of each asset (Markowitz, 1952; Roy, 1952). In cybernetics, Ashby (1958) postulated that the regulation of a cybernetic system requires that it has a large enough variety of responses to counter disturbances. In ecology, MacArthur (1955), Patten (1975) and McNaughton (1977) provided various theoretical and empirical arguments why a diversity of species responses should be expected to buffer ecosystems against environmental

fluctuations, and thereby enhance the stability of ecosystem functioning.

Biodiversity can affect not only the temporal variability of ecosystem properties, but also their temporal mean. This is why biological insurance theory identified two ways in which biodiversity can enhance ecosystem functioning in fluctuating environments: (i) a ‘buffering effect’, i.e. an increased temporal stability or reduced variability of aggregate ecosystem properties that arises from species’ differential responses to environmental variations (Yachi & Loreau, 1999; Loreau, 2010; Loreau & de Mazancourt, 2013), and (ii) a ‘performance-enhancing effect’, i.e. an increase in the mean level of ecosystem properties, which occurs when the best-performing species are favoured under each environmental condition (Table 1) (Yachi & Loreau, 1999). Similarly, in economics, portfolio theory considers the dual effects of asset diversification on the mean and variance (or risk) of portfolio returns (Markowitz, 1952; Roy, 1952).

Economic portfolio theory inspired other ecologists, who dubbed the buffering effect of biodiversity on ecosystem properties the ‘portfolio effect’ (Doak *et al.*, 1998; Tilman, Lehman & Bristow, 1998; Tilman, 1999). The buffering and portfolio effects of biodiversity are essentially identical since they describe the same ecological phenomenon. Unfortunately, the existence of two different terms to denote the stabilising effect of biodiversity on ecosystem functioning and of two different theoretical derivations of this effect has created

Table 1. Definition of the main concepts used in ecology and economics, parallels between them, and applications in ecosystem management

Ecology (Point of view: observer of ecosystem property ^a)	Economics (Point of view: economic agent)	Applications in ecosystem management (Point of view: manager optimising ecosystem output)
<p>Variability: variations of an ecological property (e.g. plant biomass or production) through either time or space. Classic measures of variability include the variance, standard deviation or coefficient of variation^b of the ecological property.</p> <p>Stability: a broad concept, which we use here to denote a reduced variability of an aggregate ecosystem property, usually through time.</p> <p>Biological insurance^c: general concept used to denote the fact that aggregate ecosystem properties vary less in more diverse communities because of compensatory changes between species or phenotypes across time, space, or both.</p> <p>Buffering/portfolio effect: the increased temporal stability or reduced variability of aggregate ecosystem properties that results from increasing biodiversity.</p> <p>Selection effect: occurs when species that have the best individual features (mean or variability) in monoculture become dominant in multispecies communities. A larger biodiversity in the initial or regional species pool enables selection effects to operate across time, space, or both.</p> <p>Performance-enhancing effect: a type of selection effect that applies specifically to the mean, when environmental conditions vary and the best-performing species are favoured under each environmental condition.</p> <p>Mean-stability trade-off: occurs when increased stability or reduced variability is associated with reduced mean.</p> <p>Spatial insurance: concept used to denote the fact that aggregate ecosystem properties vary less in more diverse metacommunities because of compensatory changes between species or communities across space, or across both time and space.</p> <p>Delayed selection effect: ecological equivalent of economic option, in which biodiversity maintenance comes at the expense of reduced ecosystem functioning in the short run but allows enhanced functioning in the long run through selection of the best-performing species under future conditions.</p> <p>Catastrophe avoidance: ecological equivalent of economic insurance, in which biodiversity maintenance comes at the expense of reduced ecosystem functioning in the short run but prevents</p>	<p>Risk: chance that an outcome or return will differ from an expected outcome or return. Risk is typically associated with a high temporal variance; more variable economic assets have higher risk.</p> <p>Portfolio: set of assets with uncertain returns. Basic portfolio theory focuses on avoiding unnecessary mean–variance trade-offs, identifying portfolios that maximise expected returns for a given level of risk (e.g. though the efficiency frontier^d).</p> <p>Mean–variance trade-off: occurs when reduced variance or risk comes at the cost of lower expected return.</p> <p>No economic equivalent of spatial insurance. The closest analogy is spatial equilibrium, whereby people can move across space to choose locations that best match their skills and preferences, thereby reducing variation in individual welfare across space.</p> <p>Option: grants an individual the right to wait (up to an expiration date) before making a decision about whether or not to buy or sell an asset at a given price. Option value reflects the ability to exploit fluctuations in asset value.</p> <p>Insurance: paying an insurance premium lowers mean wealth, but the coverage that premium buys lowers potential variance in wealth. Insurance has strong similarities with portfolios of asynchronous assets, but</p>	<p>From a manager's point of view, increased variability in ecosystem output (e.g. crop yield) is often detrimental as it comes with episodes of extreme lows.</p> <p>Species diversity enhances the stability of food production across multiple spatial scales in both agro-ecosystems and fisheries.</p> <p>Fish diversity maintains high aggregate levels of fisheries catch and revenue against fluctuating and shifting conditions in both environment and market through a performance-enhancing effect.</p> <p>Application of the efficiency frontier approach helps reveal the best management strategy that maximises average forest stand productivity for a given level of risk.</p> <p>Crop pollination in large-scale natural systems requires a much higher number of bee species than in small-scale experiments because of spatial complementarity between species.</p> <p>A potential application would be growing seedlings of two crop types (which is costly), but planting only one type later in the season once weather forecasts are refined.</p> <p>Private land managers may use biological insurance as a partial substitute for economic crop insurance to avoid the deleterious effects of climate extremes, such as droughts.</p>

Table 1. (Cont.)

Ecology (Point of view: observer of ecosystem property ^a)	Economics (Point of view: economic agent)	Applications in ecosystem management (Point of view: manager optimising ecosystem output)
catastrophic declines in ecosystem functioning in the long run through the maintenance of species that resist major disturbances (e.g. fires or biological invasions).	it generally applies to risk incurred by the purchaser, who often has some control over their own risk factors.	Another potential application would be selecting a crop whose yield is lower on average but less variable across different environmental conditions.
Bet hedging: evolutionary equivalent of economic insurance, in which organisms have lower fitness under typical conditions but lower fitness reduction under stressful conditions through strategies such as dormancy.		
Complementarity effect: occurs when a mixture of species performs better than would be expected based on their performance in isolation because of niche differentiation among species.	Economic diversification: complementarity may occur when more diversified assets span more market niches and lead to larger overall economic productivity (e.g. at the regional scale).	Intercropping and crop rotations often enhance crop yields and help suppress weeds because of complementarity in resource use among species.

^aThe ecosystem property is determined by the observer. By selecting species and shaping their fluctuations, ecological dynamics may result in the same effects as those of strategic economic agents, but the parallels between ecological and economic concepts do not imply any intentionality from either the ecosystem or its observer.

^bThe coefficient of variation is traditionally used to remove or reduce the effect of the mean on variability in comparisons of systems with different means, but it generally does not remove this effect completely.

^cFollows the common-language usage of 'insuring' as 'guaranteeing safety'.

^dIn ecological terms, economic portfolio theory thus encompasses both buffering and selection effects.

confusion in the ecological literature as to the particular domain of phenomena each is referring to (Loreau, 2010).

Biological insurance and portfolio theories have been particularly influential in ecology during the past two decades. They have led to the development of a whole body of new theoretical and empirical work that is changing our views of ecological stability and its relationships with biodiversity (Tilman, 1999; Loreau, 2010; Arnoldi, Loreau & Haegeman, 2019). They have inspired a large number of empirical and experimental studies, which have largely confirmed the theoretical prediction that biodiversity can buffer ecosystem functioning against environmental variations (Tilman, Reich & Knops, 2006; Jiang & Pu, 2009; Leary & Petchey, 2009; Hector *et al.*, 2010; de Mazancourt *et al.*, 2013; Isbell *et al.*, 2015), although in most cases biodiversity stabilises ecosystem functioning through changes in both the mean and variability of ecosystem properties, making it often difficult to separate the two effects. Further, biological insurance theory has been extended in several directions. In particular, it has been expanded to include the spatial dynamics of biodiversity and ecosystem functioning and the role played by species dispersal in maintaining the benefits of biodiversity at large spatial scales – this is known as spatial insurance theory (Loreau, Mouquet & Gonzalez, 2003a). It has also inspired new methods to partition the buffering (Wang *et al.*, 2019a; Hammond *et al.*, 2020) and performance-enhancing (Isbell *et al.*, 2018) effects of biodiversity across multiple scales in empirical data. Lastly, it has been applied in biodiversity and ecosystem management, and has even fed back into economics through the development of new approaches to quantify the insurance value of biodiversity (Baumgärtner, 2007).

As biological insurance theory is reaching the stage of a mature theory that is both supported by experimental tests and branching into new basic and applied directions, we believe it is critical to revisit and clarify its conceptual foundations to guide future developments, applications and measurements. Herein, we do not wish to duplicate previous reviews of the use of the insurance and portfolio concepts in ecology (Loreau, 2010; Schindler, Armstrong & Reed, 2015). Instead, we first seek to clarify the connections between these concepts and the economic concepts that inspired them. Doing so points to gaps and mismatches between ecology and economics that could be filled profitably by new theoretical developments and new management applications. Second, we discuss some fundamental issues in biological insurance theory that have gone unnoticed so far and that emerge from some of its recent applications. In particular, we draw a clear distinction between the two effects embedded in biological insurance theory, i.e. the buffering and performance-enhancing effects. We also discuss the potential for inherent trade-offs between the mean and stability of ecosystem processes and services. Lastly, we suggest new ways in which biological insurance theory could be extended to address new issues in ecology and ecosystem management.

II. INSURANCE AND PORTFOLIO THEORIES IN ECONOMICS

Both biological insurance and portfolio theories in ecology found inspiration from several related but distinct concepts

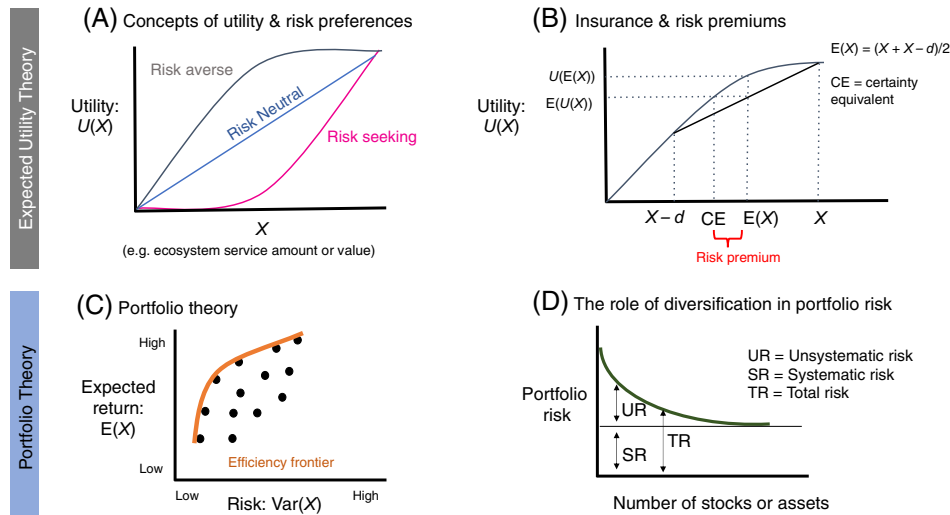


Fig 1. Main economic concepts related to biological insurance and portfolio theories in ecology. (A) Utility and utility functions for risk-averse, risk-neutral, and risk-seeking preferences as the building blocks for the economic concept of insurance. (B) Why risk aversion leads people to buy insurance. The x -axis shows the amount of something (e.g. dollar value, wealth, or amount of an ecosystem service) and the y -axis represents the utility of that amount for a risk-averse person. The outcome is risky, potentially taking on the values X or $X-d$, where d measures damage (here with equal probability in this simple illustration). The expected outcome is then $E(X)$. Because the person is risk-averse, the utility of a lower amount of X with certainty is equal to the higher expected value: $E(X) = (X + X-d)/2$. This point of equivalence is known as the ‘certainty equivalent’ (CE), and the difference between CE and the expected value is the risk premium, or the amount someone is willing to pay to obtain a lower value of X but with certainty. (C) Portfolio theory: when there are trade-offs between the expected return and its variance (a so-called ‘risk–return trade-off’), an efficiency frontier indicates the best expected return possible for a given risk-tolerance level. (D) Role of diversification of stocks or assets in economics. Diversification reduces unsystematic risk, i.e. risk that differentially affects some stocks or assets more than others when those assets are uncorrelated in their response, but it does not reduce systematic risk, i.e. the risk of shocks that affect all stocks simultaneously (e.g. a market collapse).

in economic theory: portfolios, options, and insurance (Table 1). Uses of these concepts in ecology, however, have been largely metaphorical, and there are significant differences in their uses between the two disciplines. In this section, we revisit the definition of these concepts in economics to help clarify the scope and limitations of their usage in ecology.

Portfolios, options, and insurance are three approaches used in economics and finance to manage risk arising from an uncertain future. In each case, an individual may pay to reduce variability in their income or wealth, giving up a higher mean in exchange for a lower variance. In economics, individuals are assumed to decide whether or not paying to reduce risk is worthwhile by maximizing their expected well-being or ‘utility’ (von Neumann & Morgenstern, 1944). How risk factors into well-being (‘risk preferences’) varies across individuals (Fig. 1A): some dislike risk (‘risk averse’), some enjoy it (‘risk seeking’), and others are ambivalent (‘risk neutral’). These preferences determine what level of certain wealth an individual would value the same as a risky gamble (‘certainty equivalent’; Fig. 1B), and, as a result, how much an individual is willing to give up to avoid risk entirely (‘risk premium’).

Portfolios, options, and insurance operationalize the trading off of mean and variance in slightly different ways. In portfolios, investors accept lower average returns (changes

in value) from a group of assets (e.g. stocks) in exchange for lower variance in those returns. Options permit an investor to purchase the right to delay making a decision about whether to buy or sell an asset until more information becomes available. Finally, insurance allows a policy holder to pay an insurer to assume some or all of the risk stemming from an uncertain future (e.g. the possibility of a flood). In what follows, we provide more details on each approach.

(1) Portfolios

Economic portfolio theory deals with optimal financial investment in sets of assets (portfolios) with uncertain returns. A portfolio with lower risk can be constructed by choosing assets (e.g. stocks) that do not have highly positively correlated changes in price, thereby reducing the potential for all assets to plummet in value at the same time. However, reducing variance in returns is often assumed to come with the cost of lower average returns, yielding a risk–return or mean–variance trade-off. Basic portfolio theory focuses on avoiding unnecessary mean–variance trade-offs, identifying portfolios that maximise expected returns for a given level of risk (Fig. 1C) (Markowitz, 1952, 2010). Those portfolios trace out an ‘efficiency frontier’ of the best choices for each level of variance; which ‘efficient’ portfolio an investor should

select depends on how much that individual likes or dislikes risk. Even efficient portfolios cannot eliminate risk entirely; portfolios limit exposure to unsystematic or idiosyncratic risk, but systemic risks such as the recent Covid-19 pandemic can negatively affect all assets at once (Fig. 1D).

Economic portfolio theory has many conceptual analogues in biological insurance and portfolio theories. Diverse portfolios in which each asset has a price that responds differentially to external conditions resemble biodiverse collections of species that may respond differently to environmental drivers. The use of efficiency frontiers to evaluate trade-offs is widespread in multi-objective conservation planning and ecosystem management (Armsworth & Roughgarden, 2003; Nelson *et al.*, 2008; Polasky *et al.*, 2008; Ando & Mallory, 2012; White, Halpern & Kappel, 2012; Halpern *et al.*, 2013; Lester *et al.*, 2013; Runting *et al.*, 2018), but this concept has not yet been applied to evaluate potential mean–variance trade-offs in ecosystem functioning (Section III).

(2) Options

Financial options grant an individual the right to wait (up to an expiration date) before making a decision about whether or not to buy or sell an asset at a given price. By waiting, the option owner can see if the asset price has risen above or fallen below the agreed-upon sale price (the ‘strike’ or ‘exercise’ price) before making a trade (‘exercising the option’), reducing risk of a loss. The resulting ‘option value’ of that delayed decision is reflected in the purchase price of that option (‘option price’) (Black & Scholes, 1973). Because the option value arises from improved information, options are valuable to investors even if those investors are risk neutral.

While the prices and contractual details of financial options do not have exact analogues in ecology, the concept of option value is used directly in applied ecology and conservation. In fact, prominent economic theory on option value was motivated by the decision about whether to preserve or develop natural landscapes when the benefits provided by an intact ecosystem are uncertain (Arrow & Fisher, 1974; Henry, 1974; Dixit & Pindyck, 1994). If economic development is irreversible, preserving a natural landscape maintains the option to benefit from that ecosystem in the future while permitting learning about potential benefits before revisiting the development decision (Traeger, 2014). Option value compares the benefits from preserving and learning to the benefits of development, and plays the role of the option price should one choose not to develop (Dixit & Pindyck, 1994).

Similar logic explains the option value in preserving biodiversity. We do not perfectly know the values of species or their future role in the provision of ecosystem services, and maintaining biodiversity preserves the option to enjoy those future benefits (Polasky, Costello & Solow, 2005; Leroux, Martin & Goeschl, 2009; Traeger, 2014; Dee *et al.*, 2019). If the species needed to support ecosystem services in the future were known to be lost irreversibly or persist with certainty, this option value of biodiversity would vanish. Dee

et al. (2017) provided a general application of this concept by showing that there is an added value of protecting more species than presumed to be critical to ecosystem services today, because of uncertainty over which species are needed for ecosystem services and whether they will be the ones lost in the future (Isbell *et al.*, 2011; Reich *et al.*, 2018; Dee *et al.*, 2019).

There is also another way in which biodiversity may have option value. In an ecosystem, the loss or decrease in abundance of species ill-suited to environmental conditions may give rise to a performance-enhancing or selection effect (Section III). Similarly, in economics, an option owner can choose the best investment alternative (e.g. buy an asset or not) once future market conditions are known. The ability to invest in an asset only if it is performing well yields an increase in mean returns for the option owner akin to the performance-enhancing effect in ecology.

(3) Insurance

Insurance contracts offer the most direct way for individuals to reduce exposure to risk. Specifically, paying an insurance premium lowers mean wealth, but the coverage that premium buys lowers potential variance in wealth from accidents and disasters in the future. The insurance company assumes the associated risk but is compensated for doing so *via* the premium, and may pass along that risk through reinsurance markets (Borch, 1962). Insurance companies also manage risk by constructing portfolios of insurance policies across many customers, which act as assets from the insurer’s perspective. Individuals can also self-insure (e.g. through the purchase of a fire sprinkler system), which may substitute for insurance purchased through the market (Ehrlich & Becker, 1972).

Links between economic insurance and biological portfolio and insurance theories centre primarily on the concepts of risk aversion rather than elements of the financial contract itself (e.g. insurance premiums). The preferences of ecosystem managers and conservation organisations may easily exhibit risk aversion (see e.g. Mouysset, Doyen & Jiguet, 2013; Tulloch *et al.*, 2015; Xiao *et al.*, 2019). Yet most analyses of conservation decisions about biodiversity and/or ecosystem services under uncertainty consider risk-neutral managers and preferences (e.g. Wilson *et al.*, 2006; Dee *et al.*, 2017). Although these economic concepts have not been addressed explicitly by biological insurance theory, they are obviously relevant in applied ecology and biodiversity and ecosystem management (Binder *et al.*, 2018).

III. INSURANCE AND PORTFOLIO THEORIES IN ECOLOGY

The insurance and portfolio concepts have been used in ecology as metaphors rather than as strict applications of their economic counterparts. The shared conceptual basis

between the economic and ecological concepts is simple: much like a diverse set of stocks or assets in a portfolio, an ecosystem process or property may, in principle, be viewed as an aggregate of the contributions of the various species, phenotypes or functional groups that make up the ecosystem to this process or property. For instance, analogous to the summed value of a portfolio of assets, an ecosystem's primary production is the sum of the productions of the various plant species it contains. If different plant species have biomasses or mass-specific productions that do not fluctuate in perfect synchrony, their contributions to primary production will partly compensate for each other (Gonzalez & Loreau, 2009), thereby decreasing fluctuations of total primary production. This is the shared essence of the 'buffering' and 'portfolio' effects in ecology (Doak *et al.*, 1998; Tilman *et al.*, 1998; Tilman, 1999; Yachi & Loreau, 1999).

(1) Similarities and differences between insurance and portfolio theories in ecology

Despite their strong similarity, the insurance and portfolio metaphors have been used in slightly different ways in ecology – and in ways that do not match their usage in economics (Table 1). The term 'portfolio effect' was used initially specifically to define the stabilising effect of biodiversity on ecosystem properties that results from independent fluctuations (zero correlation) of species abundances through time, based on the assumption that independent fluctuations depict a statistical null hypothesis in the absence of biotic interactions (Doak *et al.*, 1998; Tilman, 1999), although some authors adopted a broader view by allowing for non-zero correlations between fluctuations of species abundances (Doak *et al.*, 1998; Thibaut, Connolly & Sweatman, 2012). Economic portfolio theory, however, does not require that fluctuations of the various assets in a portfolio be statistically independent; it only assumes that these fluctuations are determined by external factors and are sufficiently decoupled, i.e. assets do not fluctuate synchronously and do not interact with each other (Section V). Absence of direct interactions between species does not entail statistical independence as fluctuations in species abundances are often partly driven by shared environmental factors that tend to generate positive correlations between them (Loreau & de Mazancourt, 2008).

Instead of focusing on a specific effect of biodiversity, biological insurance theory has sought to identify a broader set of biological processes that generate the stabilising effect of biodiversity on ecosystem functioning, and to explore its various consequences (Yachi & Loreau, 1999). Following from this aim, this theory has included additional features such as: (i) the effects of biodiversity on both the mean (the 'performance-enhancing effect') and variability (the 'buffering effect') of ecosystem properties; (ii) positive, as well as zero or negative, correlations among the fluctuations of species abundances through time; and (iii) spatial variability between patches or locations in heterogeneous landscapes (spatial insurance theory). Biological insurance theory identified

differential responses of species to environmental variations through either time (Yachi & Loreau, 1999) or space (Loreau *et al.*, 2003a) as the key underlying biological mechanism of the buffering effect. It also proposed metrics of synchrony or asynchrony to quantify these differential responses (Loreau & de Mazancourt, 2008).

Although biological insurance theory has been more explicit about its mechanistic underpinning and implications than has biological portfolio theory, it is important to note that the two approaches share the same underpinning. In economics, a portfolio helps to reduce variability in economic returns if and only if it contains assets that fluctuate asynchronously. If assets are subject to the same market forces and fluctuations (e.g. if they are exposed to systemic risk), increasing the number of assets does little to reduce the fluctuations of the portfolio's value (Section II). Similarly, in ecology, ecosystem functioning is stabilised if and only if the ecosystem contains species or phenotypes that fluctuate asynchronously, although not necessarily independently. Thus, it is important to realise that the basic biological insurance and portfolio concepts and theories are fundamentally equivalent, and they are most closely related to portfolio theory in economics.

(2) Mechanisms of biological insurance

While there is consensus on the fact that biological insurance or portfolio effects emerge from asynchronous fluctuations of system components, several hypotheses have been proposed to explain their origin. Biological insurance theory has consistently emphasised differential responses of system components to environmental variations as the key mechanism underlying the stabilising effect of biodiversity on ecosystem functioning (McNaughton, 1977; Yachi & Loreau, 1999; Loreau, 2010). This mechanism is deeply rooted in biology since differential responses to environmental variations are ultimately based on the universal presence of trade-offs in biological systems, which constrain species to evolve towards a species-specific balance between various biological functions, and thus to perform best under a species-specific set of environmental conditions (Chesson, Pacala & Neuhauser, 2001). Differential environmental responses result in temporal complementarity between species at the community level (Loreau, 2000), which echoes the functional complementarity that underlies the effects of biodiversity on mean ecosystem functioning (Loreau & Hector, 2001; Cardinale *et al.*, 2007). Differential species responses to environmental variations were shown to explain the stabilising effect of species diversity on ecosystem functioning in several experiments (Leary & Petchey, 2009; Hector *et al.*, 2010; Allan *et al.*, 2011; Thibaut *et al.*, 2012; de Mazancourt *et al.*, 2013).

By contrast, biological portfolio theory invoked statistical averaging as a purely statistical 'mechanism' underlying the stabilising effect of biodiversity on ecosystem functioning (Doak *et al.*, 1998). Statistical averaging, however, cannot be regarded as a mechanism as it is the statistical outcome

of large numbers of individual events that occur at smaller scales and that tend to average out at larger scales. When the scales considered differ greatly (such as between particle physics and thermodynamics), microscopic events appear as essentially independent, random events at the macroscopic scale. Thus, statistical averaging does not provide a mechanistic explanation for the stabilising effect of diversity at the ecosystem level; it merely describes this effect from a statistical viewpoint (Loreau, 2010). Differential responses of system components to environmental variations are often the basic ingredient that underpins statistical averaging and hence ecosystem stability.

Some purely stochastic processes, such as demographic stochasticity and observation error, however, do contribute to statistical averaging and diversity-stability relationships (de Mazancourt *et al.*, 2013). Fluctuations in total biomass due to demographic stochasticity tend to decrease when species diversity increases because the latter often increases mean total abundance and biomass, which reduces the impact of demographic stochasticity at the community level. Observation error is typically independent in different species, and thus it contributes to increase asynchrony in the observed fluctuations of species abundances, thereby inflating the observed stabilising effect of biodiversity on ecosystem properties. An analysis of long-term grassland biodiversity experiments revealed, quite surprisingly, that much of the stabilising effect of biodiversity observed in these experiments was explained by the community-level effects of demographic stochasticity and observation error (de Mazancourt *et al.*, 2013), probably because of the relatively small size of the experimental plots and plant populations in these experiments.

Other factors also come into play. In particular, interspecific competition tends to generate negative temporal covariances between species; accordingly, it has often been assumed to enhance community stability (Tilman, 1999; Klug *et al.*, 2000; Lehman & Tilman, 2000; Ernest & Brown, 2001; Houlahan *et al.*, 2007; Gross *et al.*, 2014). Theory, however, predicts that interspecific competition should rarely stabilise aggregate community- or ecosystem-level properties (Ives, Gross & Klug, 1999; Loreau & de Mazancourt, 2013). The reason is that, while competition does contribute to increase the level of asynchrony of population fluctuations, which has a stabilising effect on ecosystem properties, it simultaneously increases the amplitude of population fluctuations, which has a destabilising effect. The net result of these countervailing effects is often a neutral or negative effect of competition on ecosystem stability, although exceptions are possible (Loreau & de Mazancourt, 2013). Thus, generally speaking, one should expect reduction of competition, i.e. niche complementarity, not competition, to favour ecosystem stability. There is some experimental evidence that increased complementarity does lead to increased ecosystem stability (Isbell, Polley & Wilsey, 2009).

Differences in the speed at which different species or ecosystem components respond to perturbations are another mechanism that can generate asynchronous population

dynamics and thereby promote ecosystem stability (Rooney *et al.*, 2006; Ranta *et al.*, 2008; Fowler, 2009; Rooney & McCann, 2012). This mechanism, however, operates under rather restrictive conditions (Loreau & de Mazancourt, 2013) and has not been tested experimentally so far. More generally, the temporal scale of environmental fluctuations and their degree of autocorrelation play an important role in population and ecosystem stability (Gonzalez & Descamps-Julien, 2004; Gonzalez & De Feo, 2007) as patterns of asynchrony between species depend upon the temporal grain and extent over which the community is measured (Gonzalez *et al.*, 2020).

Lastly, species may differ in their population-level stability, and thus ecosystem stability may increase or decrease simply because communities are dominated by species that have a higher- or lower-than-average level of population stability. This is another variant of the selection effect, which was found in a number of experiments (Gonzalez & Descamps-Julien, 2004; Steiner *et al.*, 2006; Polley, Wilsey & Derner, 2007; Grman *et al.*, 2010; Zhang *et al.*, 2016; Song *et al.*, 2019).

(3) Distinguishing between the effects of biodiversity on the mean and variability of ecosystem properties

By failing to identify clearly their connections and differences with economic theories, biological insurance and portfolio theories in ecology have missed some opportunities to develop to their full potential. In particular, economic portfolio theory does not simply describe the stabilising effect of diversification on a portfolio's return, it also considers the relationship between expected return and risk, which is then used to select the best portfolio for a given risk level (the efficiency frontier, see Section II). Although some empirical ecological work investigated the relationship between the mean level and stability of ecosystem functioning (Cardinale *et al.*, 2013), biological insurance and portfolio theories have not so far considered communities that optimise ecosystem functioning for a given stability level, while some management applications have (Section IV). This is one obvious avenue for the further development of these theories (Section VI).

This development, however, requires clarification of some of the concepts used in biological insurance theory. While the breadth of biological insurance theory has been one of its greatest strengths, for it has allowed extensions in various directions, it is also a weakness in other ways. In particular, merging the performance-enhancing and buffering effects under the joint term of 'insurance effects' (Yachi & Loreau, 1999) was somewhat unfortunate as the two types of effects do not always go hand in hand. Economic portfolio theory is based precisely on the idea that there is often a trade-off between the average return of an investment and risk reduction, i.e. between its mean and stability, such that high-risk investments provide a higher return on average than do low-risk investments (Section II). Biological insurance theory has, until very recently, largely ignored the

trade-offs that may exist between the mean and stability of ecosystem processes or services such as crop yield (Montoya *et al.*, 2019). It has also made an inconsistent usage of the insurance concept since an insurance typically has a cost (i.e. risk-averse people pay risk premiums, see Section II), and thus it implies a reduction in mean performance that one is willing to accept to reduce the risk of a major loss at some unpredictable time in the future.

The mechanism that underlies the performance-enhancing effect of biodiversity is clear: this effect arises when the best-performing species are selected for (i.e. increase in abundance, frequency or yield) in each environment (Yachi & Loreau, 1999). These conditions precisely define an ecological selection effect (Loreau, 2000). Therefore, for clarity's sake, we propose that the performance-enhancing effect be renamed a selection effect, which may operate in time, space, or both (Chesson *et al.*, 2001; Dee *et al.*, 2016; Isbell *et al.*, 2018; Gonzalez *et al.*, 2020). It may be worth recalling here that the selection effect does not conflict with the positive effects of biodiversity. Not only does it require the maintenance of biodiversity at larger spatial and temporal scales (Loreau, 2000), it even turns into functional complementarity when considered at larger scales because selection of the best-performing species under each environmental condition tends to increase the average level of ecosystem properties across space or time (Chesson *et al.*, 2001; Dee *et al.*, 2016; Isbell *et al.*, 2018; Gonzalez *et al.*, 2020).

(4) Spatial insurance

Scaling-up biological insurance theory is critical to guide policy and management, which typically deal with relatively large spatial scales (Gonzalez *et al.*, 2020). This is the goal of spatial insurance theory (Loreau *et al.*, 2003a), which extends biological insurance theory to metacommunities (Leibold *et al.*, 2004) or meta-ecosystems (Loreau, Mouquet & Holt, 2003b), i.e. to ecological systems that are distributed patchily across space but that are connected by movements of organisms and/or materials. Spatial insurance theory alone has generated a large number of recent theoretical (Gonzalez, Mouquet & Loreau, 2009; Thompson, Rayfield & Gonzalez, 2014, 2017; Shanafelt *et al.*, 2015, 2018; Leibold, Chase & Ernest, 2017) and experimental (France & Duffy, 2006; Matthiessen & Hillebrand, 2006; Staddon *et al.*, 2010; Bouvier *et al.*, 2012; Limberger *et al.*, 2019) and field (Brittain, Kremen & Klein, 2013; Wilcox *et al.*, 2017; Winfree *et al.*, 2018; Lefcheck *et al.*, 2019; Catano *et al.*, 2020) studies.

Spatial insurance implies considering variability in both time and space simultaneously, which adds new dimensions to biological insurance. The stability of aggregate ecosystem properties can be quantified for three types of variability: (i) local temporal variability, i.e. the degree to which local ecosystem properties vary through time, as is the focus of classic biological insurance theory; (ii) spatial variability, i.e. the degree to which local ecosystem properties vary across space at any given time; and (iii) regional temporal variability,

i.e. the degree to which aggregate ecosystem properties at the landscape or regional scale vary through time. Spatial insurance theory shows how these three components of stability are interdependent, how different mechanisms contribute to stability in each case, and how biodiversity and dispersal affect these mechanisms.

Local biodiversity decreases local temporal variability *via* the classic insurance mechanisms discussed in previous sections. Spatial insurance theory further shows how these local mechanisms can be maintained and enhanced by dispersal between local communities. In particular, dispersal can maintain alpha (local) diversity and ensure that species are present when they are favoured by the current environmental conditions (Loreau *et al.*, 2003a), thereby fostering local insurance effects.

Biodiversity decreases spatial variability when species compensate for each other in space because their growth is favoured under different environmental conditions (Fig. 2A) (Wang & Loreau, 2014, 2016; Isbell *et al.*, 2018), thereby generating a form of 'spatial stability' of ecosystem functioning (Wang *et al.*, 2019b). This aspect of spatial insurance is the direct spatial equivalent of the classic temporal insurance effect, but here it is spatial complementarity between species rather than local temporal complementarity that provides spatial insurance. Spatial complementarity arises from the local selection of species that are best adapted to the local environmental conditions, and this can occur through changes across space in species abundance, species composition, or both. Figure 2A illustrates a simple example in which only species abundances change across space, but species composition also changes at large spatial scales, thereby generating beta (between-community) diversity. The importance of spatial complementarity between species in maintaining ecosystem functioning at the regional scale is nicely illustrated by a recent study that showed that the number of bee species needed to provide crop pollination was one order of magnitude higher in large-scale natural systems than in small-scale field experiments because of species turnover across space (Winfree *et al.*, 2018).

Spatiotemporal stability of ecosystem functioning can also arise from the interactive effects of temporal and spatial variations in biodiversity such that different species show compensatory fluctuations across both space and time (Fig. 2B). Spatial insurance theory has focused in particular on how dispersal can then maintain spatiotemporal complementarity between species by allowing them to shift their distributions to track conditions that support their growth (Loreau *et al.*, 2003a). Although not represented explicitly on Fig. 2B, beta diversity generally plays a key role in the spatiotemporal stability of ecosystem functioning by allowing the best-performing species to be present at the right place and time. A small-scale example of spatiotemporal complementarity between species that contributes to stabilising the provision of an ecosystem service is provided by honey bees (*Apis mellifera*) and wild pollinators in California almond orchards; honey bees and wild pollinators preferentially visit different almond tree sections, and thus play complementary

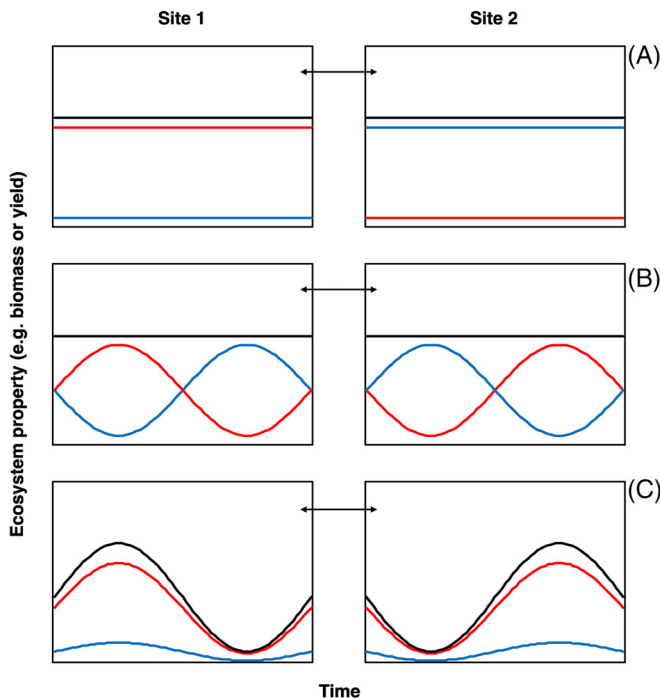


Fig 2. Spatial insurance theory: additional stabilising effects on ecosystem functioning that arise from environmental variations across space (two sites 1 and 2). (A) Biodiversity enhances the spatial stability of total biomass or yield (black curves) when different species (red and blue curves) are favoured under different environmental conditions. (B) Biodiversity enhances the spatiotemporal stability of total biomass or yield when different species show compensatory fluctuations across both space and time. (C) Spatial asynchrony of environmental conditions generates asynchronous fluctuations in ecosystem properties across space, thereby stabilising total biomass or yield at the regional scale (as measured by the sum of the two black curves). Horizontal arrows represent dispersal, which helps maintain rare species in a site when environment conditions are unfavourable. The same red and blue species are shown in the two sites for simplicity, but changes in species composition are expected at large spatial scales. Local fluctuations in species contributions to ecosystem functioning are assumed to be periodic for simplicity, but they could be also stochastic, with similar outcomes.

roles in pollination, but change their preferences depending on wind speed (Brittain *et al.*, 2013).

Finally, at the regional scale, biodiversity contributes to reducing the temporal variability of ecosystem properties through any of the above-mentioned temporal, spatial or spatiotemporal insurance effects. Spatial asynchrony of environmental conditions that generates asynchronous fluctuations in ecosystem properties across space is an additional mechanism that may contribute to stabilising regional ecosystem functioning (Wang & Loreau, 2016). This can be seen from Fig. 2C, where summing the black curves that represent fluctuations in the total biomass or yield at the two sites would show a constant regional-scale aggregate biomass or yield.

Note that the same stabilising effect of spatial asynchrony occurs across populations of the same species within a metapopulation (Wang, Haegeman & Loreau, 2015), thereby generating a spatial buffering or portfolio effect at the regional scale. A good example is provided by sockeye salmon (*Oncorhynchus nerka*) subpopulations in Alaska, whose asynchronous fluctuations lead to reduced variability in sockeye salmon total annual catches (Rogers & Schindler, 2008; Schindler *et al.*, 2010).

A growing body of theoretical and empirical work is seeking to disentangle the contributions of the various mechanisms underlying regional ecosystem stability. In particular, theory predicts that alpha diversity, beta diversity and spatial environmental asynchrony all contribute to providing insurance at large spatial scales (Wang & Loreau, 2016; Wang *et al.*, 2017; Delsol, Loreau & Haegeman, 2018). Recent empirical studies have sought to assess the respective roles of these factors in regional ecosystem stability. For instance, Wilcox *et al.* (2017) found that regional ecosystem stability was driven by both local stability and spatial asynchrony in herbaceous plant communities across the world, but these responses could not be directly attributed to alpha and beta diversity. By contrast, Catano *et al.* (2020) found that spatial asynchrony explained three times more variation in the regional stability of total bird biomass across North America than did local stability, and that beta diversity played a key role in spatial asynchrony. Building new integrative approaches to partition biodiversity effects across scales is an active area of current research, which requires further development (Section VI).

IV. APPLICATIONS OF BIOLOGICAL INSURANCE IN ECOSYSTEM MANAGEMENT

Although biological insurance and portfolio theories were developed initially to address issues in fundamental ecology, they are clearly relevant for managing ecosystems. In this section, we review how these theories have been applied in agriculture, fisheries, and forestry, and we suggest potential avenues by which the value of biological insurance could be further leveraged by both public and private natural resource managers.

(1) Agriculture

Most agricultural systems are far less diverse than the natural ecosystems they replaced (Newbold *et al.*, 2015) by design and due to inputs of fertilisers and pesticides. Strategies for diversifying agricultural systems are not new, but there is growing interest in leveraging biodiversity in a variety of ways to provide a partial to complete substitute for many costly agricultural inputs (Isbell *et al.*, 2017). Centuries ago, farmers discovered that combining grasses and legumes, either by sowing them together as an intercrop mixture or by sowing them consecutively in a crop rotation, can enhance crop

yields (Trenbath, 1974; Harper, 1977; Vandermeer, 1989; Sanderson *et al.*, 2004). Intercropping and rotations can also help suppress weeds (Liebman & Dyck, 1993), in part because combining multiple crop species can enhance the exploitation of nutrients, water, and light (Liebman & Staver, 2001). Crop diversity enhances yield and weed suppression because of functional complementarity between species (Loreau, 2000; Loreau & Hector, 2001). As agricultural systems become increasingly diversified over time (e.g. rotations) and space (e.g. intercropping) at multiple spatial scales and multiple levels of biological organisation, local and spatial insurance effects may also arise. For example, increasing the number of crop genotypes can stabilise the production of livestock fodder (Prieto *et al.*, 2015), and planting forbs along field edges can help support crop pollination (Kremen *et al.*, 2007). Crop pollination at regional scales requires an order of magnitude more bees than are needed at very local scales, due to spatial turnover in which bees are providing pollination services at different places (Winfree *et al.*, 2018).

A private land manager may use biological insurance as a partial substitute for economic crop insurance (Quaas & Baumgärtner, 2008). For example, droughts are becoming increasingly frequent and intense in many parts of the world (Alexander *et al.*, 2013). Droughts are often difficult to predict, leading to unrecoverable up-front investments. Options to compensate for the undesirable impacts of droughts, such as irrigation, are often expensive, unfeasible, or unavailable. Consequently, droughts often reduce crop yields below profitable levels. Farmers in many parts of the world purchase crop insurance to recover unavoidable losses due to droughts and other similarly unpredictable and inescapable damages. In some agroecosystems, investments that enhance local biodiversity may provide biological insurance (Schlöpfer, Tucker & Seidl, 2002; Carnus *et al.*, 2014; Isbell *et al.*, 2017; Binder *et al.*, 2018), which could be viewed as a partial substitute for crop insurance. For example, grassland plant diversity enhances the resistance of productivity to extreme climate events, including droughts (Isbell *et al.*, 2015). Specifically, the productivity of low-diversity communities with one or two grassland plant species changes by about 50% during climate events, whereas that of high-diversity communities with 16–32 species changes by only approximately 25%. In rangelands, pastures, and hay-production systems, investing in diverse seed inputs may help reduce the frequency with which droughts, pest outbreaks, and other disturbances reduce profitability (Isbell *et al.*, 2017).

Societies may also use biological insurance to stabilise food production at national, global, or other geopolitical scales. In addition to temporarily affecting yields on individual farms, climate extremes (both droughts and deluges) destabilise food production from 1 year to the next at larger spatial scales, including the national scale. This can create shortages and surpluses, both of which can result in economic inefficiencies. Spatial insurance may help dampen interannual fluctuations in total national harvest, especially if climate events affect yields in some, but not all, parts of a country. Indeed,

countries with greater crop diversity also tend to have greater stability of total national harvest (Renard & Tilman, 2019). Thus, policies that encourage crop diversity, or limit current subsidies for small number of crops, may be economically efficient, if they reduce shortages and surpluses.

(2) Fisheries

The benefits of diversification have been documented for food production from fisheries across multiple spatial scales (Sethi, 2010), from regional (Sethi, Reimer & Knapp, 2014; Anderson *et al.*, 2017; Cline, Schindler & Hilborn, 2017) to global (Dee *et al.*, 2016), and in both marine (e.g. Sethi *et al.*, 2014; Anderson *et al.*, 2017) and freshwater (Matsuzaki *et al.*, 2019) systems. They have also been documented at different levels of biological organisation, from diversity within fish populations to metacommunities, and at different levels of social organisation, from individual fishers and their income variability (Anderson *et al.*, 2017; Holland *et al.*, 2017) to regional management units and aggregate yields (Schindler *et al.*, 2010; Dee *et al.*, 2016). For example, differences in the life-history characteristics of sockeye salmon subpopulations in Alaska lead to asynchrony between these subpopulations, and hence reduced variability in total annual catches (Rogers & Schindler, 2008; Schindler *et al.*, 2010). Similar benefits arise from diversification of harvesting across multiple species, including for revenue and income. When fishers participate in multiple fisheries, i.e. diversify their ‘catch portfolios’, high levels of diversification tend to reduce variability in revenues from fishing (Kasperski & Holland, 2013). Targeting a diverse set of species can also boost revenue from fishing (Sethi *et al.*, 2014) and reduce income variability (Anderson *et al.*, 2017) for individual fishers.

In line with the selection effect of biological insurance theory (Section III), diversification of fish stocks has also been shown to maintain high aggregate levels of fisheries catch and revenue against fluctuating and shifting conditions in both environment and market. For example, regime shifts in market and ocean conditions reduced fishing revenues by 85% in Alaska, but the fishing communities with the most diverse stocks experienced little change or even increase in revenue (Cline *et al.*, 2017). In this case, however, the underlying mechanism was not biological, but instead driven by human behaviour: fishing communities that targeted a greater number of fish species could alter the composition of their catch and adjust it to changing market or ocean conditions. Dee *et al.* (2016) found evidence for a performance-enhancing effect of diversity for global marine fisheries yields. Specifically, diversifying catch, in terms of the thermal traits of targeted species, buffered global aggregate fisheries yields against temperature variability, offsetting an average of 7% losses of global yields per year due to temperature variation. This result may be driven by a selection effect due to harvesting, where catching more species increases the chances of catching one that is thermally tolerant, or by a selection effect

due to environmental filtering, where different species or traits are favoured under different temperature regimes.

The evidence for benefits from diversification in fisheries, however, is not universal because of the trade-offs that may occur between the mean and stability of both ecological and economic properties of the social-ecological system. Just as in agriculture, higher revenues may also be associated with specialisation when specialisation comes with more efficient catch techniques or more efficient management (Holland *et al.*, 2017; Ward *et al.*, 2018). In a metapopulation context, harvesting a spatially structured population can also reduce stability at local scales *via* population collapse, while increasing stability at larger scales through adult migration (Okamoto *et al.*, 2020). Taken together, these results suggest that diversification often provides benefits to fisheries across several dimensions, but these benefits can also depend on the spatial scale and management context.

(3) Forestry

Forestry provides an interesting case study to explore the various aspects of biological insurance because the timescale of forest management – usually over several decades, if not centuries – and the hierarchical organisation of forest ecosystems – with management decisions taken from the level of a single tree up to entire landscapes – introduce multiple sources of uncertainty (Filotas *et al.*, 2014).

Several recent studies have shown that various components of forest diversity may buffer the inherent variability of tree productivity (Jucker *et al.*, 2014; Forrester & Bauhus, 2016; Aussenac *et al.*, 2017; del Rio *et al.*, 2017; Dolezal *et al.*, 2020). Some tree species are more affected by precipitation, and others by temperature. The resulting asynchronous variations in radial growth decrease variability in total stand productivity (Aussenac *et al.*, 2017). Perturbations are also pervasive in natural forests, sometimes reducing tree growth (e.g. insect outbreaks), sometimes destroying biomass (e.g. large fires). Complementarity in regrowth following perturbations owing to differences in maximal growth, seed production and dispersal tends to buffer the negative effects of perturbations (Morin *et al.*, 2014). Over longer timescales, climate changes, and forest composition adjusts accordingly. Diversity at the regional level ensures that selection of the most adapted species maintains productivity in response to warming, but other effects of tree diversity on the variability of forest productivity have also been documented. For instance, Pretzsch, Schütze & Uhl (2013) and Aussenac *et al.* (2019) observed that species-specific responses to climate fluctuations are reduced by species diversity, presumably because intraspecific competition increases water demand and thus magnifies the negative effects of drought. Species mixtures may also dilute the intensity, duration and extent of pest outbreaks (Jactel & Brockerhoff, 2007; Castagneyrol *et al.*, 2013).

A mixture of different tree species may be a good option for forest management for several reasons, which we illustrate with an application of the efficiency frontier approach to Québec's boreal forests under current and future climate scenarios

(Fig. 3). Balsam fir (*Abies balsamea*) and aspen (*Populus tremuloides*) are two dominant tree species in these forests. There is minimal overyielding between these species under current climatic conditions, and thus monocultures would be promoted if there were no interannual fluctuations in climate. The two species, however, respond differently to precipitation and temperature variations, such that total stand productivity is more stable in mixtures. Therefore, short-term forest management should balance risk and expected return, as evidenced by the current efficiency frontier (Fig. 3, bottom left). A management strategy based on average productivity alone would promote balsam fir monocultures, while a management strategy minimising risk would promote mixed stands. But the projected future climate scenario yields a different outcome. Balsam fir is better adapted to the projected warmer and wetter future climate, and transgressive overyielding occurs in mixture. The efficiency frontier changes accordingly, and a mixture is now the best option both to maximise yield and to minimise risk (Fig. 3, bottom right).

While a growing body of research is demonstrating the ecological importance of tree diversity, the economic implications of tree diversity have received relatively limited attention. Consequently, translating the concepts of biological insurance theory into operational and economically motivated forestry decisions remains challenging. Forestry has long focused on maximising short-term profits for landowners while maintaining long-term productivity. As such, forest management has a long history of favouring monocultures, which were thought to provide higher yields than do mixed stands. During the past 20 years, however, a number of studies applied portfolio theory to forest management and showed the advantages of diversification to promote economic returns on timber production and reduce risk (Knoke *et al.*, 2005; Knoke, 2008; Neuner, Beinhofer & Knoke, 2013; Dragicic, Lobianco & Leblois, 2016). Risk is typically calculated as the standard deviation of the economic return over the planning horizon and is associated with the volatility of timber prices or the unpredictable occurrence of severe natural disturbances. These studies used the efficiency frontier approach (Fig. 1) to determine the optimal forest composition that maximises economic return for different levels of risk. For an acceptable risk level, they determined the proportions of a forest landscape allocated to the production of different types of forest stands.

Ecological knowledge on the mechanisms that provide biological insurance has yet to be integrated into applications of biological insurance and portfolio theory to forest management. For example, García-Robredo (2018) recently demonstrated that reduced competition and facilitation between mixtures of two tree species can lead to overyielding, increased economic return and reduced financial risk. Most studies so far, however, have focused on demonstrating the positive effects of managing different types of stands (often monospecific) and have ignored complementarity effects within stands. Moreover, portfolio studies have not considered the variability in site conditions across the managed forest landscape and have disregarded spatial ecological

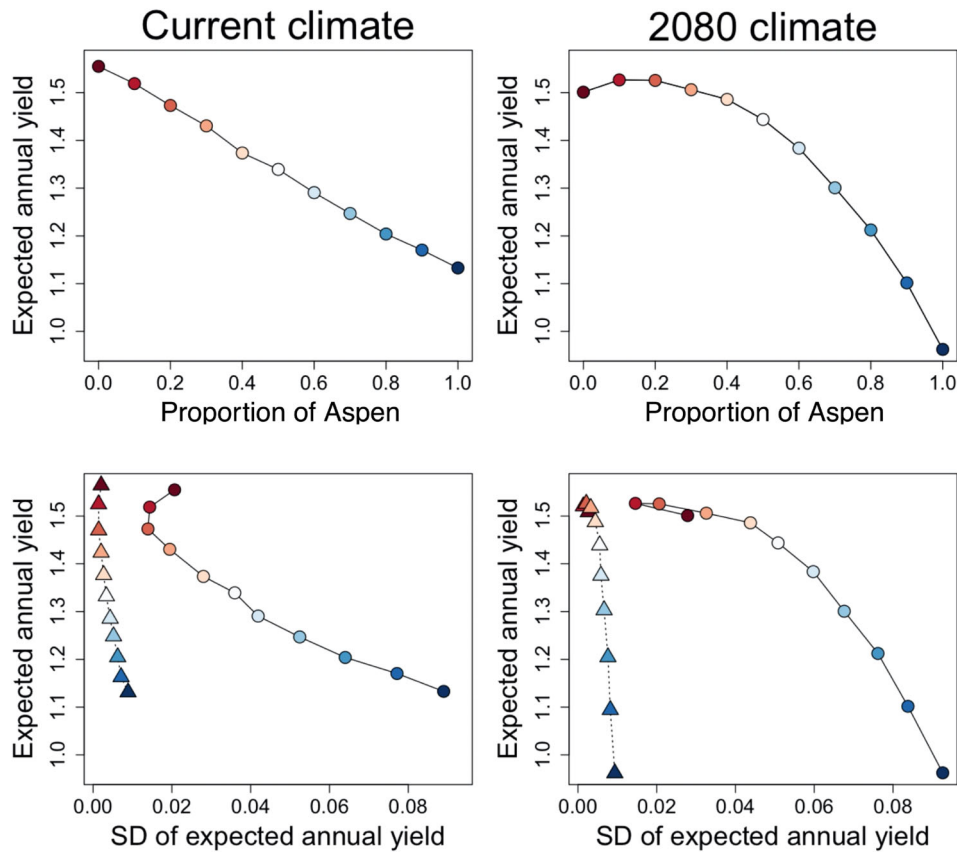


Fig 3. Efficiency frontiers of the productivity of boreal forests in Québec under current climate (left) and a future climate scenario (right). The colour gradient represents variations in the proportions of balsam fir (*Abies balsamea*) and aspen (*Populus tremuloides*), from pure balsam fir monocultures (dark red) to pure aspen monocultures (dark blue). Simulations were conducted with the observed/projected variation in annual temperature, total precipitation and drought code (solid lines). We also consider a scenario with reduced variation in climate, corresponding to 0.1 of the observed/projected standard deviation of climate parameters in order to approximate the intercept of the efficiency frontier (risk-free scenario, dotted lines). Methods: we investigated the effects of climate and competition on basal area increment using growth cores from individual trees sampled in natural forests through the permanent sampling plot survey of Québec’s Ministère des Forêts, de la Faune et des Parcs. We selected 455 sample plots where the two species were present along a gradient from pure stands to perfectly mixed stands. Individual basal area increment ($m^2/year$) was modelled using linear mixed models with fixed effects [annual average temperature, annual total precipitation, drought code, diameter at breast height (DBH), total competition, proportion of interspecific competition, drainage, soil texture] and random effects (individual, plot) (Aussenac, 2017). We then projected annual basal area increment (m^2/ha) for a hypothetical stand of 250 trees of 20 cm DBH under current and future climate conditions. We generated 1000 random draws of current and future climate conditions based on the observed average and standard deviation of historical climatic conditions and for climate projections under the RCP8.5 scenario (IPCC’s Representative Concentration Pathway corresponding to a radiative forcing of $8.5 W/m^2$ in the year 2100) for an average plot located in the centre of Québec’s boreal forest.

processes between stands, such as seed dispersal, which may lead to spatial insurance effects, especially over the long time-scales at which forests are typically managed (Pohjanmies, Eyvindson & Mönkkönen, 2019).

V. SYNTHESIS

Previous sections show that biological insurance and portfolio theories have already had a significant impact on both basic and applied ecology. These theories, however, have

limitations, some of which are inherent in the corresponding economic theories, while others come from the way these concepts have been used in ecology (Table 1). In this section, we provide a synthetic conceptual framework that unifies the various approaches across disciplines, and we use this framework to identify the most salient limitations of existing theories.

(1) Shared features across disciplines

To understand better the connections and limitations of the various theories, it is useful to take a step back and examine

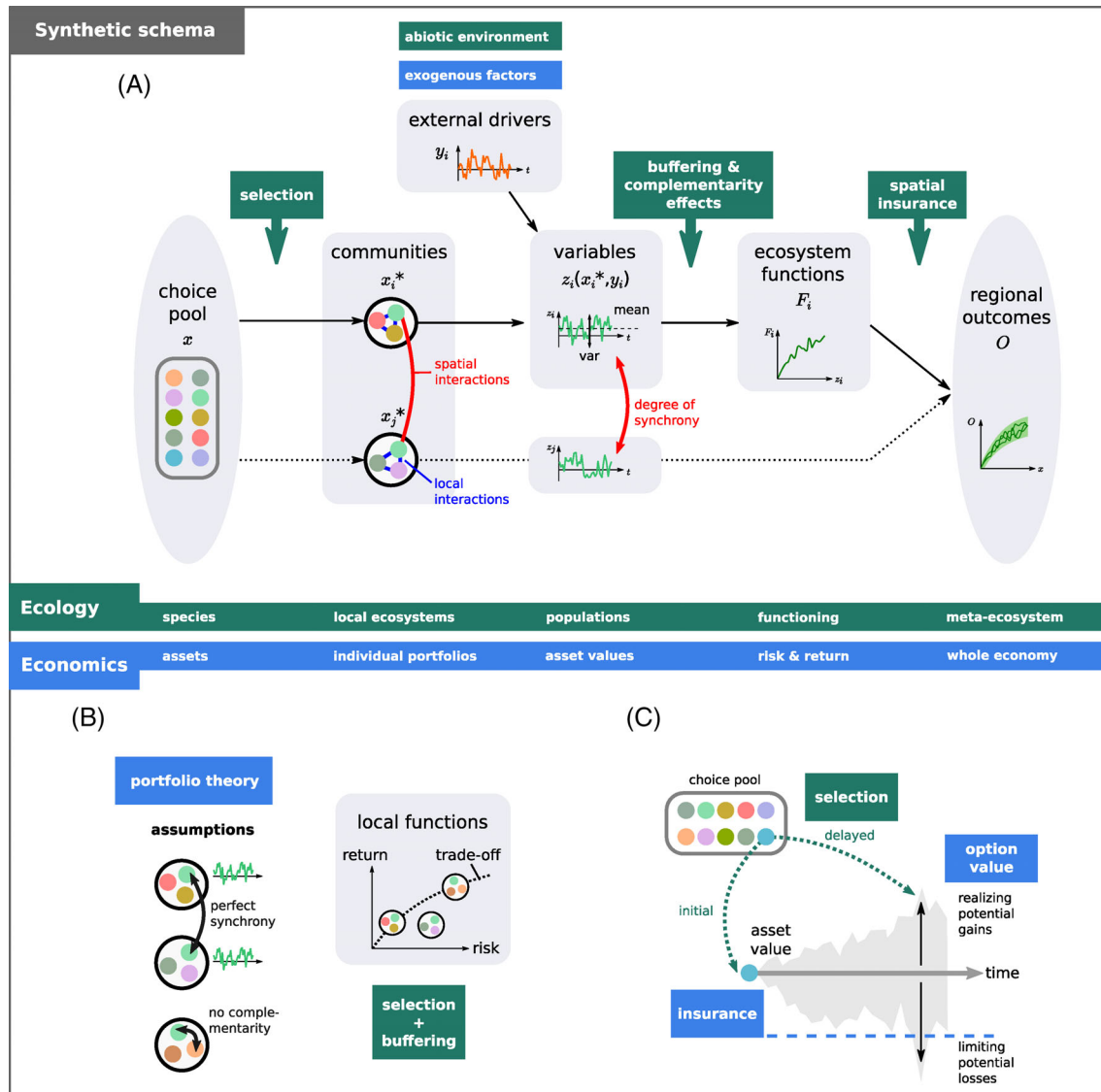


Fig 4. Synthesis of biological and economic insurance and portfolio theories. (A) Shared features across disciplines. The ecological functioning (or economic value) F_i of a community (or portfolio) i depends on its composition x_i^* , selected from a larger pool of species (or assets) x , whose individual properties fluctuate due to external factors y_i . Theories focus on the aggregated properties of a community (or portfolio) across time, as well as across space (across different communities or portfolios), which are summarized into regional outcomes O . (B) Classic economic portfolio theory encompasses both selection and buffering effects (Table 1), with two main assumptions. First, asset values are set by global market prices and are thus synchronised across portfolios. Second, initial investment is distributed among assets without any form of niche complementarity, which enhances species performance in ecological communities. These assumptions lead to a mean–variance trade-off, which is less common in ecology. (C) Economic insurance can be conceptualised as initial selection for lower-return but lower-variance assets. Options represent delayed selection, allowing future positive selection effects that exploit directional trends in asset value.

the basic features they share across disciplines, from economics and finance to fundamental and applied ecology (Fig. 4A).

Each theory first posits a set of choices, x , representing the general pool of possible species, assets or strategies that can enter into a local ecological community or economic portfolio (e.g. a regional species pool). Selection is the process through which, out of this pool of choices, only a subset x_i^* will be found in each community (or portfolio) i . This subset

is possibly weighted by species abundance, exploitation effort or initial investment. A higher pool diversity can allow the selection of better species in each community, and thereby have positive consequences on ecosystem functioning (or portfolio return). In a managed ecosystem, there may be two successive selection steps: managers may choose a subset of species to be introduced or preserved, and then ecological dynamics may cause part of this subset to go extinct.

Diversity after the first step thus acts like a pool diversity for the second step.

Within one community i , the set of species properties (e.g. biomasses, or asset values in economics) $z_i(t)$ follows a trajectory determined by the composition x_i^* of the community and by external drivers y_i , which are assumed to be unaffected by composition (e.g. abiotic environmental factors, stock prices on the global market). For simplicity, the variable $z_i(t)$ conflates two distinct sources of variation. In ecology, the performance of an individual is often fixed (by physiology), while the abundance of each species fluctuates. In economics, the weight of each asset in the portfolio (e.g. the number of stock shares) is often fixed (according to initial investment), while the unit value of each share fluctuates. The product of these two components determines the functional value of a species or asset.

Asynchronous fluctuations between the various species give rise to buffering effects, and thus reduce the variability of an aggregate ecosystem function or property F_i (e.g. total biomass or yield) in community i . In addition, local interactions between species may cause complementarity effects, such that the aggregate ecosystem function is larger than expected from the performance of its contributing species in isolation.

At the regional scale, the performance O of an entire meta-ecosystem (or regional economy) is an aggregate of its performances across the various local ecosystems. At this scale, there are no selection effects, except through possible regional extinctions. The performance of the meta-ecosystem, however, can be affected by selection effects at lower scales. These effects are described by the ecological concept of species sorting (Leibold *et al.*, 2004) and the equivalent economic concept of sorting (Tiebout, 1956): as local ecosystems offer different environmental conditions, species may be selected to occupy locations where they are most productive, leading to positive complementarity and/or buffering effects on aggregate meta-ecosystem performance. Likewise, complementarity can emerge for a regional economy in the form of economic diversification (Table 1).

Spatio-temporal insurance effects arise when fluctuations in the abundance (or value) of a species (or asset) are asynchronous between communities due to different external drivers or local interactions, thereby reducing the temporal variability of the aggregate performance O . Dispersal or migration between ecosystems can further affect spatial synchrony among populations (Section III). Similar concepts can be found in the social dynamics of stockholders, e.g. market contagion (Kaminsky, Reinhart & Vegh, 2003).

(2) Contrasts between ecological and economic concepts

Since the above synthesis draws more upon the language of biological insurance theory, it is worth discussing how the assumptions of economic theories tend to differ from this framework, and how these differences may illuminate ecological concepts.

Economic portfolio theory (Fig. 4B) implicitly encompasses both what biological insurance theory would call selection and buffering (or portfolio) effects, i.e. benefits from selecting the best individual assets and from assembling assets with asynchronous fluctuations. Since the value of an asset is generally set by global market prices, it is perfectly synchronous between all portfolios, and thus there is no counterpart to spatial insurance effects for a single asset (except when including multiple regional markets). In ecology, synchronising the abundance of a given species across all locations would require strong spatial fluxes; these fluxes, however, would also homogenise species composition and prevent possibly beneficial selection effects, unless some species were actively removed locally by management actions.

There are usually no local interactions between assets in an economic portfolio, except through initial investment decisions. In ecology, this would amount to a static community in which initial species abundances do not change through time. In this case, biodiversity may still induce stability-enhancing buffering effects, but in the absence of complementarity effects due to niche differentiation between species, mixtures cannot outperform the best species. Thus, a mean–stability trade-off emerges naturally in an economic context, whereas ecological interactions may allow both the mean and stability of ecosystem functioning to increase simultaneously with diversity (Wang *et al.*, 2021).

Various types of interactions that commonly appear in ecological settings could thus inspire new developments in biological insurance theory (Section VI). In particular, the expected performance or fluctuations of a species generally depends on its own density in the local community. A classic example is Taylor's (1961) law, which relates the variance and the mean of population abundance.

Economic insurance and options (Fig. 4C) can be conceptualised as types of selection effects in which preference is not given to those assets that have the highest current value, but to assets that may reach higher values, or avoid falling to low values, in the future. Insurance requires an upfront cost (or equivalently, the initial selection of a lower-value asset), whereas options delay selection until later times. Insurance parallels the biological concept of bet hedging, in which organisms decrease their short-term fitness under typical conditions in order to increase their probability of surviving in unpredictably varying environments (Den Boer, 1968; Starrfelt & Kokko, 2012). The ecological counterparts of the economic concepts of option and insurance would be delayed selection effects and catastrophe avoidance, respectively (Table 1). In both cases, the maintenance of biodiversity implies reduced ecosystem performance because communities include species that are less productive under current conditions. But this short-term cost comes with long-term benefits, either by allowing selection of best-performing species under future conditions (delayed selection effect) or by preventing catastrophic declines in ecosystem functioning through the maintenance of species that resist major disturbances such as fires or biological invasions (catastrophe avoidance).

These concepts could be applied to agricultural management. Most current applications of ecological theory consider what happens to the mean and variability of yields if different types of crops are planted together at the start of the season, which is the scope of portfolio theory in economics. The equivalent of an economic option would consist in growing seedlings of different crop types in a nursery, and then planting one later in the season once weather forecasts are refined. The equivalent of an economic insurance would consist in selecting a single crop that would have lower mean yield, but yield that is less variable across different environmental conditions.

While the classic economic approach to portfolios deals with uncertain fluctuations of asset values around a stationary mean, options rely on an economic agent's ability to respond to directional fluctuations and exploit upward or downward trends. Situations where better knowledge about these trends can be accrued over time exhibit an exploration-exploitation trade-off, which is considered, for instance, in multi-armed bandit and foraging theories (Berger-Tal *et al.*, 2014). These various concepts may thus be relevant on timescales that are either shorter or longer than those considered by classic portfolio theory. This suggests that a new frontier for biological insurance theory would be to import these concepts into ecology to address transient ecological dynamics.

VI. FUTURE CHALLENGES

Previous sections have identified a number of limitations that restrict the scope and domain of application of biological insurance theory. Here we propose new directions in which this theory could be profitably developed to address new issues in both basic and applied ecology.

(1) Linking the effects of biodiversity on ecosystem functioning and stability

As already noted earlier (Section III), most ecological studies have explored the effect of biodiversity on either ecosystem functioning or ecosystem stability separately. Few studies have attempted to clarify how ecosystem functioning and stability are interrelated, and when trade-offs may emerge between them (Montoya *et al.*, 2019), while the relationship between expected return and risk is at the core of economic portfolio theory (Section II). Biodiversity-ecosystem functioning research has showed that species diversity enhances both ecosystem functioning and ecosystem stability (Loreau *et al.*, 2001; Hooper *et al.*, 2005; Cardinale *et al.*, 2012; Tilman, Isbell & Cowles, 2014), which suggests a synergy between ecosystem functioning and stability along a gradient of species diversity. But synergy need not be the norm along other gradients. For instance, a recent meta-analysis found that biodiversity effects on ecosystem functioning and stability were often independent of each other (Cardinale

et al., 2013). Thus, new theory is required to understand covariations between ecosystem functioning and stability.

Using a Lotka-Volterra competition model, a recent study showed that complementarity and selection – the two main classes of biodiversity effects on ecosystem functioning (Loreau & Hector, 2001) – both promote average ecosystem functions but have contrasting effects on their stability (Wang *et al.*, 2021). In particular, selection of species with a high mean productivity enhances ecosystem productivity in the short term, but it decreases species diversity and its insurance effect on the stability of ecosystem productivity in the long term. Therefore, depending on which factor drives species interactions, ecosystem functioning and stability can exhibit either a synergy (along a gradient of complementarity) or a trade-off (along a gradient of selection). In the latter case, ecosystems achieving a higher biomass in constant environments tend to be more fragile in the face of large perturbations that are likely to occur in the long run. Consistent with these theoretical predictions, one biodiversity experiment found that strong selection effects led to declines in biodiversity over time, and that ecosystem stability was enhanced in mixtures with high levels of complementarity effects and low levels of selection effects (Isbell *et al.*, 2009).

Such a trade-off between ecosystem functioning and stability could be studied using the efficiency frontier concept used in economics and management (Sections II and IV). Since species interactions play an important role in community dynamics, however, the traditional assumption of economic portfolio theory that assets do not interact with each other in a portfolio (Section V) does not hold any more. Therefore, studying the relationship between ecosystem functioning and stability requires a dynamical approach, which could be combined with an efficiency frontier.

(2) Incorporating multiple functions and feedbacks

Economic portfolio and biological insurance theories have generally considered two objectives, i.e. total expected return and risk in economics and mean and variability of aggregate ecosystem properties in ecology. These two properties are enough when all the benefits from the various assets can be substituted for each other, but such perfect substitutability is rarely found in ecology. Future developments of biological insurance theory may require a clearer formulation and justification of the assumed objective function. Doing so may involve objectives imposed by human agents in the form of ecosystem services, preferences, implementation costs and benefits, but also objectives that emerge from other bodies of ecological theory.

For instance, the outcomes of portfolio choices can feed back on existing options, through either irreversible loss (global or regional species extinction, business closure) or eco-evolutionary dynamics that transform the set of options. They can also feed back on drivers since phenomena such as climate, fire prevalence and global markets, which are generally assumed to be exogenous drivers, can be affected by the aggregate effects of local and spatial dynamics. Due to such

feedbacks, empirical tests of biological insurance theory may require some care, as causality often goes both ways. But they can also reveal ecological properties that are intrinsically important for the maintenance of ecosystems, regardless of human preferences. Thus, while extending biological insurance theory to multiple ecosystem functions may increase its relevance (Gamfeldt, Hillebrand & Jonsson, 2008), there is a need for biologically grounded arguments for which functions matter most, and how to balance them against each other in an objective function (Kremen, 2005).

(3) Developing new approaches to partition biodiversity effects across scales

Biodiversity contributes to ecosystem stability through insurance effects at multiple organisational levels and spatial scales (Section III). Two integrative mathematical frameworks have been developed recently to link ecosystem stability and asynchrony across organisational levels and spatial scales (Wang *et al.*, 2019a; Hammond *et al.*, 2020). These frameworks have been used to quantify the relative importance of local and spatial insurance effects in several empirical data sets. Local insurance due to species diversity was shown to provide stronger stabilising effects on regional ecosystem functioning than did spatial insurance in a desert grassland ecosystem in New Mexico (Wang *et al.*, 2019a) and in a Californian kelp forest (Lamy *et al.*, 2019). Other studies, however, found that spatial insurance contributed more than did local insurance to the stability of benthic marine fish communities (Thorson *et al.*, 2018) and rock-pool invertebrate metacommunities in Jamaica (Hammond *et al.*, 2020). More empirical work is required to quantify insurance effects from different sources and across scales and organisational levels and clarify how their relative importance changes with abiotic and biotic factors.

A recent study also developed a new framework to quantify biodiversity effects on ecosystem functioning in space and time (Isbell *et al.*, 2018). This framework was built upon Loreau & Hector's (2001) classic additive partitioning of the net biodiversity effect on local ecosystem functioning into complementarity and selection effects. Isbell *et al.* (2018) extended this partitioning to split the selection effect into multiple additive terms that capture the contributions of spatial, temporal and spatiotemporal selection processes. In this new partition, temporal or spatial selection effects are positive when species dominate mixtures at the times or places where they are most productive in monoculture. For example, significant temporal selection effects were observed in a long-term experiment over a period of 18 years (Isbell *et al.*, 2018), suggesting substantial temporal turnover in which species are most productive (Allan *et al.*, 2011; Isbell *et al.*, 2011).

These new frameworks provide new opportunities to understand ecosystem functioning and stability across space and time. Future theoretical work should clarify how the various components of these frameworks are related, e.g. how the various selection effects are related to insurance effects

across scales, develop broader integrative frameworks that merge the effects of biodiversity on ecosystem functioning and stability across scales, and test them with experimental or observational data.

(4) Extending biological insurance theory to complex interaction networks

Biological insurance theory has so far been developed and tested for sets of similar species occupying a single trophic level. Real ecosystems, however, are characterised by complex networks that may involve multiple interactions, interaction types, and functional groups. Developing new theory for biological insurance in complex interaction networks is critical as predictions and results for a single trophic level might no longer apply. In particular, complex interaction networks raise at least three major difficulties: (i) the mean and variance of the performance of a mixture of species cannot be simply extrapolated from the mean and variance of its component species or of similar mixtures (Jaillard *et al.*, 2018); (ii) managing part of the network can impact other parts; and (iii) an arbitrary species composition cannot generally be imposed and maintained to achieve ecosystem-level objectives.

In economic portfolio theory, the fluctuations of an asset are assumed to respond to global market dynamics, independently of which other assets are selected in the portfolio (Section V). Some applications of biological insurance theory have also assumed that the success of a species at one location and time reflects local abiotic conditions, independently of which other species are present. Species fluctuations may be correlated, but these correlations are taken as exogenous and do not depend on community composition. This assumption is not overly restrictive in competitive communities because the strength of competitive interactions has little effect on the stability of aggregate ecosystem properties unless these interactions are strongly asymmetric (Ives *et al.*, 1999; Loreau & de Mazancourt, 2013). This simplifying assumption, however, must be relaxed when considering other ecological interactions. In particular, complex food webs demonstrate the practical importance of species interactions in approaches related to biological insurance. When managing or harvesting species in food webs, e.g. in fisheries, portfolios of target species that ignore interactions can face disastrous or unanticipated consequences (Van Leeuwen, De Roos & Persson, 2008). This has led to the emergence of the 'ecosystem-based management approach', which addresses these issues in many specific instances with complex simulation models, but little general theory exists to set expectations across ecosystems.

A theory of biological insurance for complex interaction networks must also acknowledge that species interactions can have a wide range of effects on the synchrony, strength and autocorrelation of fluctuations in species abundances. For instance, competitive interactions tend to create asynchrony (Section III), while mutualism tends to create synchrony, and predator-prey or other asymmetric

interactions tend to induce oscillations with phase lags between species. Sometimes, these complex dynamics display stabilising effects: species interactions can dampen environment-driven fluctuations (Tikhonov & Monasson, 2017), and, conversely, external perturbations can also stabilise interacting populations (Fox *et al.*, 2017). Most often, however, these effects are destabilising, i.e. species interactions are expected to create and amplify dynamical fluctuations at the population level (May, 1972). Finally, a species' interactions with other, possibly unobserved variables can be modelled as fluctuations with memory (i.e. temporal autocorrelation), such that acting on others implies delayed feedback on oneself. For instance, a predator that depletes its present prey inhibits its own growth in the future. In all these scenarios, biological insurance theory remains applicable, but it requires a careful treatment accounting for how species interactions alter the mean and variance of ecosystem properties for each species composition.

Complex interaction networks also challenge a basic tenet of the biological insurance concept, i.e. biodiversity or species composition may be viewed as a control variable that can be manipulated to achieve some target ecosystem properties. A common outcome of ecological interactions, however, is extinction, i.e. the loss of a species from the local community, or even from the regional pool. Even when biodiversity is stabilising at the ecosystem level, it tends to induce instability at the population level (Tilman *et al.*, 2006), which can make a diverse community more difficult to maintain. On the other hand, non-equilibrium coexistence theory suggests that fluctuations can also enhance the coexistence of interacting species (Barabás, D'Andrea & Stump, 2018). Thus, while May (1972) envisioned the instability of complex communities as a limitation, Roy *et al.* (2020) recently showed that the self-sustaining fluctuations of such communities can also enable more species to coexist. With arguments paralleling biological insurance theory, they identified conditions under which population responses become asynchronous and differentiated, leading to more species persisting in a chaotic state than at equilibrium. Higher levels of biodiversity, biomass and productivity may be attained at the cost of stronger fluctuations, thus creating an emergent trade-off between ecosystem functioning and stability.

(5) Developing new applications to biodiversity and ecosystem management

Our review identified some gaps between the concepts and terminology used in economics and biology with respect to insurance. These gaps also offer new research opportunities and directions. For instance, biological insurance theory currently lacks an analogy of utility functions and insurance or risk premiums, but recent theory development is starting to build these bridges, providing links between biodiversity as insurance with economic theory and management applications. In particular, Baumgärtner (2007) used utility theory

to define the insurance value of biodiversity formally as the reduction in the insurance premium that an ecosystem manager would be willing to pay to avoid the risk of an insufficient provision of ecosystem services. Applying and extending this theory would offer new research opportunities to quantify biological insurance in economic or ecosystem service terms. Further, as shown in Section IV, there is an opportunity to explore the economic and ecosystem consequences of biodiversity under future environmental conditions, e.g. under climate change scenarios as in Fig. 3. Similarly, the concepts of option value and economic insurance could offer new management and research opportunities for applied ecology and management.

VII. CONCLUSIONS

- (1) Biological insurance theory is reaching the stage of a mature theory that is supported by experimental tests and field studies and that is leading to a number of new basic and applied directions. This success, however, should not mask the need for a critical re-evaluation of its conceptual foundations, leading to new opportunities for synthesis and extensions in new directions.
- (2) In particular, we have argued that the buffering insurance effects of biodiversity should be distinguished more clearly from selection effects, and that trade-offs between the effects of biodiversity on the mean and on the variability of ecosystem properties should be acknowledged and studied more systematically in both basic and applied contexts.
- (3) Understanding the foundations and frontiers of biological insurance theory is also important to seize the new opportunities that this body of theory has to offer. We have shown that biological theory could be profitably expanded in several new directions to address exciting new issues in both fundamental ecology and ecosystem management.

VIII. ACKNOWLEDGEMENTS

M.L., M.B. and J.M.M. were supported by the TULIP Laboratory of Excellence (ANR-10-LABX-41). M.L. and M.B. were also supported by the BIOTASES Advanced Grant and J.M.M. by the FRAGCLIM Consolidator Grant, both of which were funded by the European Research Council under the European Union's Horizon 2020 research and innovation programme (grant agreements No 666971 and 726176). A.G. was supported by the Liber Ero Chair in Biodiversity Conservation. This paper arose from a joint working group supported by the Quebec Centre for Biodiversity Science (working group #12) and the Centre for Biodiversity Theory and Modelling (Moulis, France).

IX. REFERENCES

- ALEXANDER, L. V., ALLEN, S. K., BINDOFF, N. L., BREON, F.-M., CHURCH, J. A., CUBASCH, U., EMORI, S., FORSTER, P., FRIEDLINGSTEIN, P., GILLETT, N., GREGORY, J. M., HARTMANN, D. L., JANSEN, E., KIRTMAN, B., KNUTTI, R., et al. (2013). Summary for policymakers. In *Climate Change 2013: The Physical Science Basis* (eds T. F. STOCKER, D. QIN, G.-K. PLATTNER, M. M. B. TIGNOR, S. K. ALLEN, J. BOSCHUNG, A. NAUELS, Y. XIA, V. BEX and P. M. MIDDLE), pp. 3–30. Cambridge University Press, Cambridge.
- ALLAN, E., WEISSER, W., WEIGELT, A., ROSCHER, C., FISCHER, M. & HILLEBRAND, H. (2011). More diverse plant communities have higher functioning over time due to turnover in complementary dominant species. *Proceedings of the National Academy of Sciences of the United States of America* **108**, 17034–17039.
- ANDERSON, S. C., WARD, E. J., SHELTON, A. O., ADKISON, M. D., BEAUDREAU, A. H., BRENNER, R. E., HAYNIE, A. C., SHRIVER, J. C., WATSON, J. T. & WILLIAMS, B. C. (2017). Benefits and risks of diversification for individual fishers. *Proceedings of the National Academy of Sciences of the United States of America* **114**, 10797–10802.
- ANDO, A. W. & MALLORY, M. L. (2012). Optimal portfolio design to reduce climate-related conservation uncertainty in the prairie pothole region. *Proceedings of the National Academy of Sciences of the United States of America* **109**, 6484–6489.
- ARMSWORTH, P. R. & ROUGHGARDEN, J. E. (2003). The economic value of ecological stability. *Proceedings of the National Academy of Sciences of the United States of America* **100**, 7147–7151.
- ARNOLDI, J.-F., LOREAU, M. & HAEGEMAN, B. (2019). The inherent multidimensionality of temporal variability: how common and rare species shape stability patterns. *Ecology Letters* **22**, 1557–1567.
- ARROW, K. & FISHER, A. C. (1974). Environmental preservation, uncertainty, and irreversibility. *The Quarterly Journal of Economics* **88**, 312–319.
- ASHBY, W. R. (1958). Requisite variety and its implications for the control of complex systems. *Cybernetica* **1**, 83–99.
- AUSSENAC, R. (2017). *La relation diversité-stabilité dans les écosystèmes forestiers: mécanismes et implications face aux changements climatiques*. PhD Thesis, Université du Québec en Abitibi-Témiscamingue, Canada.
- AUSSENAC, R., BERGERON, Y., GRAVEL, D. & DROBYSHEV, I. (2019). Interactions among trees: a key element in the stabilising effect of species diversity on forest growth. *Functional Ecology* **33**, 360–367.
- AUSSENAC, R., BERGERON, Y., MEKONTCHOU, C. G., GRAVEL, D., PILCH, K. & DROBYSHEV, I. (2017). Intraspecific variability in growth response to environmental fluctuations modulates the stabilizing effect of species diversity on forest growth. *Journal of Ecology* **105**, 1010–1020.
- BARABÁS, G., D'ANDREA, R. & STUMP, S. M. (2018). Chesson's coexistence theory. *Ecological Monographs* **88**, 277–303.
- BAUMGÄRTNER, S. (2007). The insurance value of biodiversity in the provision of ecosystem services. *Natural Resource Modeling* **20**, 87–127.
- BERGER-TAL, O., NATHAN, J., MERON, E. & SALTZ, D. (2014). The exploration-exploitation dilemma: a multidisciplinary framework. *PLoS One* **9**, e95693.
- BINDER, S., ISBELL, F., POLASKY, S., CATFORD, J. A. & TILMAN, D. (2018). Grassland biodiversity can pay. *Proceedings of the National Academy of Sciences of the United States of America* **115**, 3876–3881.
- BLACK, F. & SCHOLES, M. (1973). The pricing of options and corporate liabilities. *Journal of Political Economy* **81**, 637–654.
- BORCH, K. (1962). Equilibrium in a reinsurance market. *Econometrica* **30**, 424–444.
- BOUVIER, T., VENAIL, P., POMMIER, T., BOUVIER, C., BARBERA, C. & MOUQUET, N. (2012). Contrasted effects of diversity and immigration on ecological insurance in marine bacterioplankton communities. *PLoS One* **7**, e37620.
- BRITTAİN, C., KREMEN, C. & KLEIN, A.-M. (2013). Biodiversity buffers pollination from changes in environmental conditions. *Global Change Biology* **19**, 540–547.
- CARDINALE, B. J., DUFFY, J. E., GONZALEZ, A., HOOPER, D. U., PERRINGS, C., VENAIL, P., NARWANI, A., MACE, G. M., TILMAN, D., WARDLE, D. A., KINZIG, A. P., DAILY, G. C., LOREAU, M., GRACE, J. B., LARIGAUDERIE, A., et al. (2012). Biodiversity loss and its impact on humanity. *Nature* **486**, 59–67.
- CARDINALE, B. J., GROSS, K., FRITSCHIE, K., FLOMBAUM, P., FOX, J. W., RIXEN, C., VAN RUIJVEN, J., REICH, P. B., SCHERER-LORENZEN, M. & WILSEY, B. J. (2013). Biodiversity simultaneously enhances the production and stability of community biomass, but the effects are independent. *Ecology* **94**, 1697–1707.
- CARDINALE, B. J., WRIGHT, J. P., CADOTTE, M. W., CARROLL, I. T., HECTOR, A., SRIVASTAVA, D. S., LOREAU, M. & WEIS, J. J. (2007). Impacts of plant diversity on biomass production increase through time because of species complementarity. *Proceedings of the National Academy of Sciences of the United States of America* **104**, 18123–18128.
- CARNUS, T., FINN, J. A., KIRWAN, L. & CONNOLLY, J. (2014). Assessing the relationship between biodiversity and stability of ecosystem function—is the coefficient of variation always the best metric? *Ideas in Ecology and Evolution* **7**, 89–96.
- CASTAGNEYROL, B., GIFFARD, B., PÉRÉ, C. & JACTEL, H. (2013). Plant apparency, an overlooked driver of associational resistance to insect herbivory. *Journal of Ecology* **101**, 418–429.
- CATANO, C. P., FRISTOE, T. S., LAMANNA, J. A. & MYERS, J. A. (2020). Local species diversity, β -diversity and climate influence the regional stability of bird biomass across North America. *Proceedings of the Royal Society B: Biological Sciences* **287**, 20192520.
- CHESSON, P., PACALA, S. & NEUHAUSER, C. (2001). Environmental niches and ecosystem functioning. In *The Functional Consequences of Biodiversity: Empirical Progress and Theoretical Extensions* (eds A. KINZIG, S. PACALA and D. TILMAN), pp. 213–262. Princeton University Press, Princeton.
- CLINE, T. J., SCHINDLER, D. E. & HILBORN, R. (2017). Fisheries portfolio diversification and turnover buffer Alaskan fishing communities from abrupt resource and market changes. *Nature Communications* **8**, 14042.
- DE MAZANCOURT, C., ISBELL, F., LAROCQUE, A., BERENDSE, F., DE LUCA, E., GRACE, J. B., HAEGEMAN, B., POLLEY, H. W., ROSCHER, C., SCHMID, B., TILMAN, D., VAN RUIJVEN, J., WEIGELT, A., WILSEY, B. J. & LOREAU, M. (2013). Predicting ecosystem stability from community composition and biodiversity. *Ecology Letters* **16**, 617–625.
- DEE, L. E., COWLES, J., ISBELL, F., PAU, S., GAINES, S. D. & REICH, P. B. (2019). When do ecosystem services depend on rare species? *Trends in Ecology & Evolution* **34**, 746–758.
- DEE, L. E., DE LARA, M., COSTELLO, C. & GAINES, S. D. (2017). To what extent can ecosystem services motivate protecting biodiversity? *Ecology Letters* **20**, 935–946.
- DEE, L. E., MILLER, S. J., PEAVEY, L. E., BRADLEY, D., GENTRY, R. R., STARTZ, R., GAINES, S. D. & LESTER, S. E. (2016). Functional diversity of catch mitigates negative effects of temperature variability on fisheries yields. *Proceedings of the Royal Society B: Biological Sciences* **283**, 20161435.
- DELSOL, R., LOREAU, M. & HAEGEMAN, B. (2018). The relationship between the spatial scaling of biodiversity and ecosystem stability. *Global Ecology and Biogeography* **27**, 439–449.
- DEN BOER, P. J. (1968). Spreading of risk and stabilization of animal numbers. *Biological Station* **136**, 165–194.
- DIXIT, R. K. & PINDYCK, R. S. (1994). *Investment Under Uncertainty*. Princeton University Press, Princeton.
- DOAK, D. F., BIGGER, D., HARDING, E. K., MARVIER, M. A., O'MALLEY, R. E. & THOMSON, D. (1998). The statistical inevitability of stability-diversity relationships in community ecology. *American Naturalist* **151**, 264–276.
- DOLEZAL, J., FIBICH, P., ALTMAN, J., LEFS, J., UEMURA, S., TAKAHASHI, K. & HARA, T. (2020). Determinants of ecosystem stability in a diverse temperate forest. *Oikos* **129**, 1692–1703.
- DRAGICEVIC, A., LOBIANCO, A. & LEBLOIS, A. (2016). Forest planning and productivity-risk trade-off through the Markowitz mean-variance model. *Forest Policy and Economics* **64**, 25–34.
- EHRlich, I. & BECKER, G. S. (1972). Market insurance, self-insurance, and self-protection. *Journal of Political Economy* **80**, 623–648.
- ERNEST, S. K. M. & BROWN, J. H. (2001). Homeostasis and compensation: the role of species and resources in ecosystem stability. *Ecology* **82**, 2118–2132.
- FILOTAS, E., PARROTT, L., BURTON, P. J., CHAZDON, R. L., COATES, K. D., COLL, L., HAEUSSLER, S., MARTIN, K., NOCENTINI, S., PUETTMANN, K. J., PUTZ, F. E., SIMARD, S. W. & MESSIER, C. (2014). Viewing forests through the lens of complex systems science. *Ecosphere* **5**, Article 1.
- FORRESTER, D. I. & BAUHU, J. (2016). A review of processes behind diversity—productivity relationships in forests. *Current Forestry Reports* **2**, 45–61.
- FOWLER, M. S. (2009). Increasing community size and connectance can increase stability in competitive communities. *Journal of Theoretical Biology* **258**, 179–188.
- FOX, J. W., VASSEUR, D., COTRONEO, M., GUAN, L. & SIMON, F. (2017). Population extinctions can increase metapopulation persistence. *Nature Ecology & Evolution* **1**, 1271–1278.
- FRANCE, K. E. & DUFFY, J. E. (2006). Diversity and dispersal interactively affect predictability of ecosystem function. *Nature* **441**, 1139–1143.
- GAMFELDT, L., HILLEBRAND, H. & JONSSON, P. R. (2008). Multiple functions increase the importance of biodiversity for overall ecosystem functioning. *Ecology* **89**, 1223–1231.
- GARCÍA-ROBREDO, F. (2018). Effect of species complementarity on financial return in mixed stands of European beech and Scots pine in northern Spain. *Forests* **9**, 559.
- GONZALEZ, A. & DE FEO, O. (2007). Environmental variability modulates the insurance effects of diversity in non-equilibrium communities. In *The Impact of Environmental Variability on Ecological Systems*, pp. 159–177. Springer, New York.
- GONZALEZ, A. & DESCAMPS-JULIEN, B. (2004). Population and community variability in randomly fluctuating environments. *Oikos* **106**, 105–116.
- GONZALEZ, A., GERMAIN, R. M., SRIVASTAVA, D. S., FILOTAS, E., DEE, L. E., GRAVEL, D., THOMPSON, P. L., ISBELL, F., WANG, S., KÉFI, S., MONTOYA, J., ZELNIK, Y. R. & LOREAU, M. (2020). Scaling-up biodiversity-ecosystem functioning research. *Ecology Letters* **23**, 757–776.

- GONZALEZ, A. & LOREAU, M. (2009). The causes and consequences of compensatory dynamics in ecological communities. *Annual Review of Ecology, Evolution, and Systematics* **40**, 393–414.
- GONZALEZ, A., MOUQUET, N. & LOREAU, M. (2009). Biodiversity as spatial insurance: the effects of habitat fragmentation and dispersal on ecosystem functioning. In *Biodiversity, Ecosystem Functioning, and Human Wellbeing: An Ecological and Economic Perspective* (eds S. NAEEM, D. BUNKER, A. HECTOR, M. LOREAU and C. PERRINGS), pp. 134–146. Oxford University Press, Oxford.
- GRMAN, E., LAU, J. A., SCHOOLMASTER, D. R. J. & GROSS, K. L. (2010). Mechanisms contributing to stability in ecosystem function depend on the environmental context. *Ecology Letters* **13**, 1400–1410.
- GROSS, K., CARDINALE, B. J., FOX, J. W., GONZALEZ, A., LOREAU, M., POLLEY, H. W., REICH, P. B. & VAN RUIJVEN, J. (2014). Species richness and the temporal stability of biomass production: a new analysis of recent biodiversity experiments. *American Naturalist* **183**, 1–12.
- HALPERN, B. S., KLEIN, C. J., BROWN, C. J., BEGER, M., GRANTHAM, H. S., MANGUBHAI, S., RUCKELSHAUS, M., TULLOCH, V. J., WATTS, M., WHITE, C. & POSSINGHAM, H. P. (2013). Achieving the triple bottom line in the face of inherent trade-offs among social equity, economic return, and conservation. *Proceedings of the National Academy of Sciences of the United States of America* **110**, 6229–6234.
- HAMMOND, M., LOREAU, M., DE MAZANCOURT, C. & KOLASA, J. (2020). Disentangling local, metapopulation and cross-community sources of stabilization and asynchrony in metacommunities. *Ecosphere* **11**, e03078.
- HARPER, J. L. (1977). *Plant Population Biology*. Academic Press, London.
- HECTOR, A., HAUTIER, Y., SANER, P., WACKER, L., BAGCHI, R., JOSHI, J., SCHERER-LORENZEN, M., SPEHN, E. M., BAZELEY-WHITE, E., WEILENMANN, M., CALDEIRA, M. C., DIMITRAKOPOULOS, P. G., FINN, J. A., HUSS-DANELL, K., JUMPPONEN, A., et al. (2010). General stabilizing effects of plant diversity on grassland productivity through population asynchrony and overyielding. *Ecology* **91**, 2213–2220.
- HENRY, C. (1974). Investment decisions under uncertainty: the 'irreversibility effect'. *American Economic Review* **64**, 1006–1012.
- HOLLAND, D. S., SPEIR, C., AGAR, J., CROSSON, S., DEPIPER, G., KASPERSKI, S., KITTS, A. W. & PERRUSO, L. (2017). Impact of catch shares on diversification of fishers' income and risk. *Proceedings of the National Academy of Sciences of the United States of America* **114**, 9302–9307.
- HOOPER, D. U., CHAPIN, F. S., EWEL, J. J., HECTOR, A., INCHAUSTI, P., LAVOREL, S., LAWTON, J. H., LODGE, D. M., LOREAU, M., NAEEM, S., SCHMID, B., SETÁLA, H., SYMSTAD, A. J., VANDERMEER, J. & WARDLE, D. A. (2005). Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* **75**, 3–35.
- HOULAHAN, J. E., CURRIE, D. J., COTTENIE, K., CUMMING, G. S., ERNEST, S. K. M., FINDLAY, C. S., FUHLENDORF, S. D., GAEDKE, U., LEGENDRE, P., MAGNUSON, J. J., MCARDLE, B. H., MULDAVIN, E. H., NOBLE, D., RUSSELL, R., STEVENS, R. D., et al. (2007). Compensatory dynamics are rare in natural ecological communities. *Proceedings of the National Academy of Sciences of the United States of America* **104**, 3273–3277.
- ISELL, F., ADLER, P. R., EISENHAUER, N., FORNARA, D., KIMMEL, K., KREMEN, C., LETOURNEAU, D. K., LIEBMAN, M., POLLEY, H. W., QUIJAS, S. & SCHERER-LORENZEN, M. (2017). Benefits of increasing plant diversity in sustainable agroecosystems. *Journal of Ecology* **105**, 871–879.
- ISELL, F., CALCAGNO, V., HECTOR, A., CONNOLLY, J., HARPOLE, W. S., REICH, P. B., SCHERER-LORENZEN, M., SCHMID, B., TILMAN, D., VAN RUIJVEN, J., WEIGELT, A., WILSEY, B. J., ZAVALA, E. S. & LOREAU, M. (2011). High plant diversity is needed to maintain ecosystem services. *Nature* **477**, 199–202.
- ISELL, F., COWLES, J., DEE, L. E., LOREAU, M., REICH, P. B., GONZALEZ, A., HECTOR, A. & SCHMID, B. (2018). Quantifying effects of biodiversity on ecosystem functioning across times and places. *Ecology Letters* **21**, 763–778.
- ISELL, F., CRAVEN, D., CONNOLLY, J., LOREAU, M., SCHMID, B., BEIERKUHNEIN, C., BEZEMER, T. M., BONIN, C., BRUELHEIDE, H., DE LUCA, E., EBELING, A., GRIFFIN, J. N., GUO, Q., HAUTIER, Y., HECTOR, A., et al. (2015). Biodiversity increases the resistance of ecosystem productivity to climate extremes. *Nature* **526**, 574–577.
- ISELL, F., POLLEY, H. W. & WILSEY, B. J. (2009). Biodiversity, productivity and the temporal stability of productivity: patterns and processes. *Ecology Letters* **12**, 443–451.
- IVES, A. R., GROSS, K. & KLUG, J. L. (1999). Stability and variability in competitive communities. *Science* **286**, 542–544.
- JACTEL, H. & BROCKERHOFF, E. G. (2007). Tree diversity reduces herbivory by forest insects. *Ecology Letters* **10**, 835–848.
- JAILLARD, B., RICHON, C., DELEPORTE, P., LOREAU, M. & VIOLLE, C. (2018). An a posteriori species clustering for quantifying the effects of species interactions on ecosystem functioning. *Methods in Ecology and Evolution* **9**, 704–715.
- JIANG, L. & PU, Z. (2009). Different effects of species diversity on temporal stability in single-trophic and multitrophic communities. *American Naturalist* **174**, 651–659.
- JUCKER, T., BOURIAUD, O., AVACARITEI, D. & COOMES, D. A. (2014). Stabilizing effects of diversity on aboveground wood production in forest ecosystems: linking patterns and processes. *Ecology Letters* **17**, 1560–1569.
- KAMINSKY, G. L., REINHART, C. M. & VEGH, C. A. (2003). The unholy trinity of financial contagion. *Journal of Economic Perspectives* **17**, 51–74.
- KASPERSKI, S. & HOLLAND, D. S. (2013). Income diversification and risk for fishermen. *Proceedings of the National Academy of Sciences of the United States of America* **110**, 2076–2081.
- KLUG, J. L., FISCHER, J. M., IVES, A. R. & DENNIS, B. (2000). Compensatory dynamics in planktonic community responses to pH perturbations. *Ecology* **81**, 387–398.
- KNOKE, T. (2008). Mixed forests and finance—methodological approaches. *Ecological Economics* **65**, 590–601.
- KNOKE, T., STIMM, B., AMMER, C. & MOOG, M. (2005). Mixed forests reconsidered: a forest economics contribution on an ecological concept. *Forest Ecology and Management* **213**, 102–116.
- KREMEN, C. (2005). Managing ecosystem services: what do we need to know about their ecology? *Ecology Letters* **8**, 468–479.
- KREMEN, C., WILLIAMS, N. M., AIZEN, M. A., GEMMILL-HERREN, B., LEBUHN, G., MINKLEY, R., PACKER, L., POTTS, S. G., ROULSTON, T., STEFFAN-DEWENTER, I., VÁZQUEZ, D. P., WINFREE, R., ADAMS, L., CRONE, E. E., GREENLEAF, S. S., et al. (2007). Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. *Ecology Letters* **10**, 299–314.
- LAMY, T., WANG, S., RENARD, D., LAFFERTY, K. D., REED, D. C. & MILLER, R. J. (2019). Species insurance trumps spatial insurance in stabilizing biomass of a marine macroalgal metacommunity. *Ecology* **100**, e02719.
- LEARY, D. J. & PETCHEY, O. L. (2009). Testing a biological mechanism of the insurance hypothesis in experimental aquatic communities. *Journal of Animal Ecology* **78**, 1143–1151.
- LEFCHUCK, J. S., INNES-GOLD, A. A., BRANDL, S. J., STENECK, R. S., TORRES, R. E. & RASHER, D. B. (2019). Tropical fish diversity enhances coral reef functioning across multiple scales. *Science Advances* **5**, eaav6420.
- LEHMAN, C. L. & TILMAN, D. (2000). Biodiversity, stability, and productivity in competitive communities. *American Naturalist* **156**, 534–552.
- LEIBOLD, M. A., CHASE, J. M. & ERNEST, S. K. M. (2017). Community assembly and the functioning of ecosystems: how metacommunity processes alter ecosystems attributes. *Ecology* **98**, 909–919.
- LEIBOLD, M. A., HOLYOAK, M., MOUQUET, N., AMARASEKARE, P., CHASE, J. M., HOOPES, M. F., HOLT, R. D., SHURIN, J. B., LAW, R., TILMAN, D., LOREAU, M. & GONZALEZ, A. (2004). The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters* **7**, 601–613.
- LEROUX, A. D., MARTIN, V. L. & GOESCHL, T. (2009). Optimal conservation, extinction debt, and the augmented quasi-option value. *Journal of Environmental Economics and Management* **58**, 43–57.
- LESTER, S. E., COSTELLO, C., HALPERN, B. S., GAINES, S. D., WHITE, C. & BARTH, J. (2013). Evaluating tradeoffs among ecosystem services to inform marine spatial planning. *Marine Policy* **38**, 80–89.
- LIEBMAN, M. & DYCK, E. (1993). Crop rotation and intercropping strategies for weed management. *Ecological Applications* **3**, 92–122.
- LIEBMAN, M. & STAYER, C. P. (2001). Crop diversification for weed management. In *Ecological Management of Agricultural Weeds*, pp. 322–374. Cambridge University Press, Cambridge.
- LIMBERGER, R., PITT, A., HAHN, M. W. & WICKHAM, S. A. (2019). Spatial insurance in multi-trophic metacommunities. *Ecology Letters* **22**, 1828–1837.
- LOREAU, M. (2000). Biodiversity and ecosystem functioning: recent theoretical advances. *Oikos* **91**, 3–17.
- LOREAU, M. (2010). *From Populations to Ecosystems: Theoretical Foundations for a New Ecological Synthesis*. Princeton University Press, Princeton.
- LOREAU, M. & DE MAZANCOURT, C. (2008). Species synchrony and its drivers: neutral and nonneutral community dynamics in fluctuating environments. *The American Naturalist* **172**, E48–E66.
- LOREAU, M. & DE MAZANCOURT, C. (2013). Biodiversity and ecosystem stability: a synthesis of underlying mechanisms. *Ecology Letters* **16**(S1), 106–115.
- LOREAU, M. & HECTOR, A. (2001). Partitioning selection and complementarity in biodiversity experiments. *Nature* **412**, 72–76.
- LOREAU, M., MOUQUET, N. & GONZALEZ, A. (2003a). Biodiversity as spatial insurance in heterogeneous landscapes. *Proceedings of the National Academy of Sciences of the United States of America* **100**, 12765–12770.
- LOREAU, M., MOUQUET, N. & HOLT, R. D. (2003b). Meta-ecosystems: a theoretical framework for a spatial ecosystem ecology. *Ecology Letters* **6**, 673–679.
- LOREAU, M., NAEEM, S., INCHAUSTI, P., BENTGTON, J., GRIME, J. P., HECTOR, A., HOOPER, D. U., HUSTON, M. A., RAFFAELLI, D., SCHMID, B., TILMAN, D. & WARDLE, D. A. (2001). Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science* **294**, 804–808.

- MACARTHUR, R. H. (1955). Fluctuations of animal populations and a measure of community stability. *Ecology* **36**, 533–535.
- MARKOWITZ, H. (1952). Portfolio selection. *Journal of Finance* **7**, 77–91.
- MARKOWITZ, H. M. (2010). Portfolio theory: as I still see it. *Annual Review of Financial Economics* **2**, 1–23.
- MATSUZAKI, S.-I. S., SHINOHARA, R., UCHIDA, K. & SASAKI, T. (2019). Catch diversification provides multiple benefits in inland fisheries. *Journal of Applied Ecology* **56**, 843–854.
- MATTHESEN, B. & HILLEBRAND, H. (2006). Dispersal frequency affects local biomass production by controlling local diversity. *Ecology Letters* **9**, 652–662.
- MAY, R. M. (1972). Will a large complex system be stable? *Nature* **238**, 413–414.
- MCCAUGHTON, S. J. (1977). Diversity and stability of ecological communities: a comment on the role of empiricism in ecology. *American Naturalist* **111**, 515–525.
- MONTOYA, D., HAEGEMAN, B., GABA, S., DE MAZANCOURT, C., BRETAGNOLLE, V. & LOREAU, M. (2019). Trade-offs in the provisioning and stability of ecosystem services in agroecosystems. *Ecological Applications* **29**, e01853.
- MORIN, X., FAHSE, L., DE MAZANCOURT, C., SCHERER-LORENZEN, M. & BUGMANN, H. (2014). Temporal stability in forest productivity increases with tree diversity due to asynchrony in species dynamics. *Ecology Letters* **17**, 1526–1535.
- MOUYSSET, L., DOYEN, L. & JIGUET, F. (2013). How does economic risk aversion affect biodiversity? *Ecological Applications* **23**, 96–109.
- NELSON, E., POLASKY, S., LEWIS, D. J., PLANTINGA, A. J., LONSDORF, E., WHITE, D., BAEL, D. & LAWLER, J. J. (2008). Efficiency of incentives to jointly increase carbon sequestration and species conservation on a landscape. *Proceedings of the National Academy of Sciences of the United States of America* **105**, 9471–9476.
- NEUNER, S., BEINHOFER, B. & KNOKE, T. (2013). The optimal tree species composition for a private forest enterprise – applying the theory of portfolio selection. *Scandinavian Journal of Forest Research* **28**, 38–48.
- NEUBOLD, T., HUDSON, L. N., HILL, S. L. L., CONTU, S., LYSSENKO, I., SENIOR, R. A., BOERGER, L., BENNETT, D. J., CHOIMES, A., COLLEN, B., DAY, J., DE PALMA, A., DIAZ, S., ECHEVERRIA-LONDONO, S., EDGAR, M. J., et al. (2015). Global effects of land use on local terrestrial biodiversity. *Nature* **520**, 45–50.
- OKAMOTO, D. K., HESSING-LEWIS, M., SAMHOURI, J. F., SHELTON, A. O., STIER, A., LEVIN, P. S. & SALOMON, A. K. (2020). Spatial variation in exploited metapopulations obscures risk of collapse. *Ecological Applications* **30**, e02051.
- PATTEN, B. C. (1975). Ecosystem linearization: an evolutionary design problem. *American Naturalist* **109**, 529–539.
- POHJANMIES, T., EYVINDSON, K. & MÖNKKÖNEN, M. (2019). Forest management optimization across spatial scales to reconcile economic and conservation objectives. *PLoS One* **14**, e0218213.
- POLASKY, S., COSTELLO, C. & SOLOW, A. (2005). The economics of biodiversity. In *Handbook of Environmental Economics: Economywide and International Environmental Issues* (eds K. G. MÄLER and J. R. VINCENT), pp. 1517–1560. Elsevier, Amsterdam.
- POLASKY, S., NELSON, E., CAMM, J., CSUTI, B., FACKLER, P., LONSDORF, E., MONTGOMERY, C., WHITE, D., ARTHUR, J., GARBER-YONTS, B., HAIGHT, R., KAGAN, J., STARFIELD, A. & TOBALSKE, C. (2008). Where to put things? Spatial land management to sustain biodiversity and economic returns. *Biological Conservation* **141**, 1505–1524.
- POLLEY, H. W., WILSEY, B. J. & DERNER, J. D. (2007). Dominant species constrain effects of species diversity on temporal variability in biomass production of tallgrass prairie. *Oikos* **116**, 2044–2052.
- PRETZSCH, H., SCHÜTZE, G. & UHL, E. (2013). Resistance of European tree species to drought stress in mixed versus pure forests: evidence of stress release by inter-specific facilitation. *Plant Biology (Stuttgart, Germany)* **15**, 483–495.
- PRIETO, I., VIOLLE, C., BARRE, P., DURAND, J.-L., GHESQUIERE, M. & LITRICO, I. (2015). Complementary effects of species and genetic diversity on productivity and stability of sown grasslands. *Nature Plants* **1**, 15033.
- QUAAS, M. F. & BAUMGÄRTNER, S. (2008). Natural vs. financial insurance in the management of public-good ecosystems. *Ecological Economics* **65**, 397–406.
- RANTA, E., KAITALA, V., FOWLER, M. S., LAAKSO, J., RUOKOLAINEN, L. & O'HARA, R. (2008). Detecting compensatory dynamics in competitive communities under environmental forcing. *Oikos* **117**, 1907–1911.
- REICH, P. B., HOBBS, S. E., LEE, T. D. & PASTORE, M. A. (2018). Unexpected reversal of C3 versus C4 grass response to elevated CO₂ during a 20-year field experiment. *Science* **360**, 317–320.
- RENARD, D. & TILMAN, D. (2019). National food production stabilized by crop diversity. *Nature* **571**, 257–260.
- DEL RIO, M., PRETZSCH, H., RUÍZ-PEINADO, R., AMPOORTER, E., ANNIGHÖFER, P., BARBEITO, I., BIELAK, K., BRAZAITIS, G., COLL, L., DRÖSSLER, L., FABRIKA, M., FORRESTER, D. I., HEYM, M., HURT, V., KURYLYAK, V., et al. (2017). Species interactions increase the temporal stability of community productivity in Pinus sylvestris–Fagus sylvatica mixtures across Europe. *Journal of Ecology* **105**, 1032–1043.
- ROGERS, L. A. & SCHINDLER, D. E. (2008). Asynchrony in population dynamics of sockeye salmon in Southwest Alaska. *Oikos* **117**, 1578–1586.
- ROONEY, N., MCCANN, K., GELLNER, G. & MOORE, J. C. (2006). Structural asymmetry and the stability of diverse food webs. *Nature* **442**, 265–269.
- ROONEY, N. & MCCANN, K. S. (2012). Integrating food web diversity, structure and stability. *Trends in Ecology and Evolution* **27**, 40–46.
- ROY, A. D. (1952). Safety first and the holding of assets. *Econometrica* **20**, 431–449.
- ROY, F., BARBIER, M., BIROLI, G. & BUNIN, G. (2020). Complex interactions can create persistent fluctuations in high-diversity ecosystems. *PLoS Computational Biology* **16**, e1007827.
- RUNTING, R. K., BEYER, H. L., DUJARDIN, Y., LOVELOCK, C. E., BRYAN, B. A. & RHODES, J. R. (2018). Reducing risk in reserve selection using modern portfolio theory: coastal planning under sea-level rise. *Journal of Applied Ecology* **55**, 2193–2203.
- SANDERSON, M. A., SKINNER, R. H., BARKER, D. J., EDWARDS, G. R., TRACY, B. F. & WEDIN, D. A. (2004). Plant species diversity and management of temperate forage and grazing land ecosystems. *Crop Science* **44**, 1132–1144.
- SCHINDLER, D. E., ARMSTRONG, J. B. & REED, T. E. (2015). The portfolio concept in ecology and evolution. *Frontiers in Ecology and the Environment* **13**, 257–263.
- SCHINDLER, D. E., HILBORN, R., CHASCO, B., BOATRIGHT, C. P., QUINN, T. P., ROGERS, L. A. & WEBSTER, M. S. (2010). Population diversity and the portfolio effect in an exploited species. *Nature* **465**, 609–612.
- SCHLÄPFER, F., TUCKER, M. & SEIDL, I. (2002). Returns from hay cultivation in fertilized low diversity and non-fertilized high diversity grassland. *Environmental and Resource Economics* **21**, 89–100.
- SETHI, S. A. (2010). Risk management for fisheries. *Fish and Fisheries* **11**, 341–365.
- SETHI, S. A., REIMER, M. & KNAPP, G. (2014). Alaskan fishing community revenues and the stabilizing role of fishing portfolios. *Marine Policy* **48**, 134–141.
- SHANAFELT, D. W., CLOBERT, J., FENICHEL, E. P., HOCHBERG, M. E., KINZIG, A., LOREAU, M., MARQUET, P. A. & PERRINGS, C. (2018). Species dispersal and biodiversity in human-dominated metacommunities. *Journal of Theoretical Biology* **457**, 199–210.
- SHANAFELT, D. W., DIECKMANN, U., JONAS, M., FRANKLIN, O., LOREAU, M. & PERRINGS, C. (2015). Biodiversity, productivity, and the spatial insurance hypothesis revisited. *Journal of Theoretical Biology* **380**, 426–435.
- SONG, M., ZONG, N., JIANG, J., SHI, P., ZHANG, X., GAO, J., ZHOU, H., LI, Y. & LOREAU, M. (2019). Nutrient-induced shifts of dominant species reduce ecosystem stability via increases in species synchrony and population variability. *Science of the Total Environment* **692**, 441–449.
- STADDON, P., ZOÏ, L., PETER, D. C., FRANCIS, G. & ANDREW, G. (2010). Connectivity, non-random extinction and ecosystem function in experimental metacommunities. *Ecology Letters* **13**, 543–552.
- STARRFELT, J. & KOKKO, H. (2012). Bet-hedging—a triple trade-off between means, variances and correlations. *Biological Reviews* **87**, 742–755.
- STEINER, C. F., LONG, Z. T., KRUMINS, J. A. & MORIN, P. J. (2006). Population and community resilience in multitrophic communities. *Ecology* **87**, 996–1007.
- TAYLOR, L. R. (1961). Aggregation, variance and the mean. *Nature* **189**, 732–735.
- THIBAUT, L. M., CONNOLLY, S. R. & SWEATMAN, H. P. A. (2012). Diversity and stability of herbivorous fishes on coral reefs. *Ecology* **93**, 891–901.
- THOMPSON, P. L., RAYFIELD, B. & GONZALEZ, A. (2014). Robustness of the spatial insurance effects of biodiversity to habitat loss. *Evolutionary Ecology Research* **16**, 445–460.
- THOMPSON, P. L., RAYFIELD, B. & GONZALEZ, A. (2017). Loss of habitat and connectivity erodes species diversity, ecosystem functioning, and stability in metacommunity networks. *Ecography* **40**, 98–108.
- THORSON, J. T., SCHEUERELL, M. D., OLDEN, J. D. & SCHINDLER, D. E. (2018). Spatial heterogeneity contributes more to portfolio effects than species variability in bottom-associated marine fishes. *Proceedings of the Royal Society B: Biological Sciences* **285**, 20180915.
- TIEBOUT, C. M. (1956). A pure theory of local expenditures. *Journal of Political Economy* **64**, 416–424.
- TIKHONOV, M. & MONASSON, R. (2017). Collective phase in resource competition in a highly diverse ecosystem. *Physical Review Letters* **118**, 048103.
- TILMAN, D. (1999). The ecological consequences of changes in biodiversity: a search for general principles. *Ecology* **80**, 1455–1474.
- TILMAN, D., ISBELL, F. & COWLES, J. M. (2014). Biodiversity and ecosystem functioning. *Annual Review of Ecology, Evolution, and Systematics* **45**, 471–493.
- TILMAN, D., LEHMAN, C. L. & BRISTOW, C. E. (1998). Diversity-stability relationships: statistical inevitability or ecological consequence? *American Naturalist* **151**, 277–282.
- TILMAN, D., REICH, P. B. & KNOPS, J. M. H. (2006). Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature* **441**, 629–632.
- TRAEGER, C. P. (2014). On option values in environmental and resource economics. *Resource and Energy Economics* **37**, 242–252.
- TRENBATH, B. R. (1974). Biomass productivity of mixtures. *Advances in Agronomy* **26**, 177–210.
- TULLOCH, A. I. T., MALONEY, R. F., JOSEPH, L. N., BENNETT, J. R., DI FONZO, M. M. I., PROBERT, W. J. M., O'CONNOR, S. M., DENSEM, J. P. &

- POSSINGHAM, H. P. (2015). Effect of risk aversion on prioritizing conservation projects. *Conservation Biology* **29**, 513–524.
- VAN LEEUWEN, A., DE ROOS, A. M. & PERSSON, L. (2008). How cod shapes its world. *Journal of Sea Research* **60**, 89–104.
- VANDERMEER, J. (1989). *The Ecology of Intercropping*. Cambridge University Press, Cambridge.
- VON NEUMANN, J. & MORGENSTERN, O. (1944). *Theory of Games and Economic Behavior*. Princeton University Press, Princeton.
- WANG, S., HAEGEMAN, B. & LOREAU, M. (2015). Dispersal and metapopulation stability. *PeerJ* **3**, e1295.
- WANG, S., ISBELL, F., DENG, W., HONG, P., DEE, L. E., THOMPSON, P. L. & LOREAU, M. (2021). How complementarity and selection affect the relationship between ecosystem functioning and stability. *Ecology*, e03347.
- WANG, S., LAMY, T., HALLETT, L. M. & LOREAU, M. (2019a). Stability and synchrony across ecological hierarchies in heterogeneous metacommunities: linking theory to data. *Ecography* **42**, 1200–1211.
- WANG, S. & LOREAU, M. (2014). Ecosystem stability in space: alpha, beta and gamma variability. *Ecology Letters* **17**, 891–901.
- WANG, S. & LOREAU, M. (2016). Biodiversity and ecosystem stability across scales in metacommunities. *Ecology Letters* **19**, 510–518.
- WANG, S., LOREAU, M., ARNOLDI, J.-F., FANG, J., RAHMAN, K. A., TAO, S. & DE MAZANCOURT, C. (2017). An invariability-area relationship sheds new light on the spatial scaling of ecological stability. *Nature Communications* **8**, 15211.
- WANG, Y., CADOTTE, M. W., CHEN, Y., FRASER, L. H., ZHANG, Y., HUANG, F., LUO, S., SHI, N. & LOREAU, M. (2019b). Global evidence of positive biodiversity effects on spatial ecosystem stability in natural grasslands. *Nature Communications* **10**, 3207.
- WARD, E. J., ANDERSON, S. C., SHELTON, A. O., BRENNER, R. E., ADKISON, M. D., BEAUDREAU, A. H., WATSON, J. T., SHRIVER, J. C., HAYNIE, A. C. & WILLIAMS, B. C. (2018). Effects of increased specialization on revenue of Alaskan salmon fishers over four decades. *Journal of Applied Ecology* **55**, 1082–1091.
- WHITE, C., HALPERN, B. S. & KAPPEL, C. V. (2012). Ecosystem service tradeoff analysis reveals the value of marine spatial planning for multiple ocean uses. *Proceedings of the National Academy of Sciences of the United States of America* **109**, 4696–4701.
- WILCOX, K. R., TREDENICK, A. T., KOERNER, S. E., GRMAN, E., HALLETT, L. M., AVOLIO, M. L., PIERRE, K. J. L., HOUSEMAN, G. R., ISBELL, F., JOHNSON, D. S., ALATALO, J. M., BALDWIN, A. H., BORK, E. W., BOUGHTON, E. H., BOWMAN, W. D., et al. (2017). Asynchrony among local communities stabilises ecosystem function of metacommunities. *Ecology Letters* **20**, 1534–1545.
- WILSON, K., MCBRIDE, M. F., BODE, M. & POSSINGHAM, H. P. (2006). Prioritizing global conservation efforts. *Nature* **440**, 337–340.
- WINFREE, R., REILLY, J. R., BARTOMEUS, I., CARIVEAU, D. P., WILLIAMS, N. M. & GIBBS, J. (2018). Species turnover promotes the importance of bee diversity for crop pollination at regional scales. *Science* **359**, 791–793.
- XIAO, H., McDONALD-MADDEN, E., SABBADIN, R., PEYRARD, N., DEE, L. E. & CHADES, L. (2019). The value of understanding feedbacks from ecosystem functions to species for managing ecosystems. *Nature Communications* **10**, 3901.
- YACHI, S. & LOREAU, M. (1999). Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *Proceedings of the National Academy of Sciences of the United States of America* **96**, 1463–1468.
- ZHANG, Y., LOREAU, M., LÜ, X., HE, N., ZHANG, G. & HAN, X. (2016). Nitrogen enrichment weakens ecosystem stability through decreased species asynchrony and population stability in a temperate grassland. *Global Change Biology* **22**, 1445–1455.

(Received 21 September 2020; revised 25 May 2021; accepted 26 May 2021; published online 2 June 2021)