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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.

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Biodiversity as insurance: from concept to measurement and application

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Biodiversity as insurance: from concept to measurement and application

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Loreau and others: Biodiversity as insurance

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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 by 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 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 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

Loreau and others: Biodiversity as insurance

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4 55 approaches to partition biodiversity effects across scales, extending biological
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6 56 insurance theory to complex interaction networks, and developing new applications
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9 57 to biodiversity and ecosystem management.
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13 59 **Keywords:** Biodiversity, Ecosystems, Stability, Insurance, Portfolio, Theory,
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16 60 Management.
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62 **CONTENTS**

63		
64	I. INTRODUCTION	6
65	II. INSURANCE AND PORTFOLIO THEORIES IN ECONOMICS.....	9
66	(1) <i>Portfolios</i>	10
67	(2) <i>Options</i>	11
68	(3) <i>Insurance</i>	13
69	III. INSURANCE AND PORTFOLIO THEORIES IN ECOLOGY.....	14
70	(1) <i>Similarities and differences between insurance and portfolio theories in ecology</i>	14
71	(2) <i>Mechanisms of biological insurance</i>	16
72	(3) <i>Distinguishing between the effects of biodiversity on the mean and variability of ecosystem</i>	
73	<i>properties</i>	19
74	(4) <i>Spatial insurance</i>	21
75	IV. APPLICATIONS OF BIOLOGICAL INSURANCE IN ECOSYSTEM MANAGEMENT	25
76	(1) <i>Agriculture</i>	25
77	(2) <i>Fisheries</i>	28
78	(3) <i>Forestry</i>	30
79	V. SYNTHESIS.....	33
80	(1) <i>Shared features across disciplines</i>	33
81	(2) <i>Contrasts between ecological and economic concepts</i>	35
82	VI. FUTURE CHALLENGES	38
83	(1) <i>Linking the effects of biodiversity on ecosystem functioning and stability</i>	38
84	(2) <i>Incorporating multiple functions and feedbacks</i>	40
85	(3) <i>Developing new approaches to partition biodiversity effects across scales</i>	41
86	(4) <i>Extending biological insurance theory to complex interaction networks</i>	42
87	(5) <i>Developing new applications to biodiversity and ecosystem management</i>	45
88	VII. CONCLUSIONS	46
89	VIII. ACKNOWLEDGEMENTS	46
90	IX. REFERENCES.....	48

92 I. INTRODUCTION

93 The idea that biodiversity can buffer ecosystem functioning against the disruptive
94 effects of environmental fluctuations has been the focus of decades of research in
95 ecology (MacArthur, 1955; Patten, 1975; McNaughton, 1977). Yachi & Loreau
96 (1999) formalised this idea mathematically and introduced the insurance hypothesis,
97 which posits that, in a variable environment, aggregate ecosystem properties (e.g.
98 total biomass or production) will vary less in more diverse communities because
99 declines in the performance or abundance of some species or phenotypes will be
100 offset, at least partly, by smoother declines or increases by others. As a consequence,
101 biodiversity has been viewed as insuring against extreme lows in ecosystem
102 functioning.

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

113 Biodiversity can affect not only the temporal variability of ecosystem
114 properties, but also their temporal mean. That is why biological insurance theory
115 identified two ways in which biodiversity can enhance ecosystem functioning in

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4 116 fluctuating environments: (1) a “buffering effect”, i.e. an increased temporal stability
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6 117 or reduced variability of aggregate ecosystem properties that arises from species’
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8 118 differential responses to environmental variations (Yachi & Loreau, 1999; Loreau,
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10 119 2010; Loreau & de Mazancourt, 2013), and (2) a “performance-enhancing effect”,
11
12 120 i.e. an increase in the mean level of ecosystem properties, which occurs when the
13
14 121 best-performing species are favoured under each environmental condition (Table 1)
15
16 122 (Yachi & Loreau, 1999). Similarly, in economics, portfolio theory considers the dual
17
18 123 effects of asset diversification on the mean and variance (or risk) of portfolio returns
19
20 124 (Markowitz, 1952; Roy, 1952).

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25 125 Economic portfolio theory inspired other ecologists, who dubbed the buffering
26
27 126 effect of biodiversity on ecosystem properties the “portfolio effect” (Doak *et al.*,
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29 127 1998; Tilman, Lehman, & Bristow, 1998; Tilman, 1999). The buffering and portfolio
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31 128 effects of biodiversity are essentially identical since they describe the same
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33 129 ecological phenomenon. Unfortunately, the existence of two different terms to
34
35 130 denote the stabilising effect of biodiversity on ecosystem functioning and of two
36
37 131 different theoretical derivations of this effect has created confusion in the ecological
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39 132 literature as to the particular domain of phenomena each is referring to (Loreau,
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41 133 2010).

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45 134 Biological insurance and portfolio theories have been particularly influential
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47 135 in ecology during the past two decades. They have led to the development of a whole
48
49 136 body of new theoretical and empirical work that is changing our views of ecological
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51 137 stability and its relationships with biodiversity (Tilman, 1999; Loreau, 2010;
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53 138 Arnoldi, Loreau, & Haegeman, 2019). They have inspired a large number of
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55 139 empirical and experimental studies, which have largely confirmed the theoretical
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57 140 prediction that biodiversity can buffer ecosystem functioning against environmental
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4 141 variations (Tilman, Reich, & Knops, 2006; Jiang & Pu, 2009; Leary & Petchey,
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6 142 2009; Hector *et al.*, 2010; de Mazancourt *et al.*, 2013; Isbell *et al.*, 2015), although in
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8
9 143 most cases biodiversity stabilises ecosystem functioning through changes in both the
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11 144 mean and variability of ecosystem properties, making it often difficult to separate the
12
13 145 two effects. Further, biological insurance theory has been extended in several
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15 146 directions. In particular, it has been expanded to include the spatial dynamics of
16
17 147 biodiversity and ecosystem functioning and the role played by species dispersal in
18
19 148 maintaining the benefits of biodiversity at large spatial scales — this is known as
20
21 149 spatial insurance theory (Loreau, Mouquet, & Gonzalez, 2003a). It has also inspired
22
23 150 new methods to partition the buffering (Wang *et al.*, 2019a; Hammond *et al.*, 2020)
24
25 151 and performance-enhancing (Isbell *et al.*, 2018) effects of biodiversity across
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27 152 multiple scales in empirical data. Lastly, it has been applied in biodiversity and
28
29 153 ecosystem management, and has even fed back on economics through the
30
31 154 development of new approaches to quantify the insurance value of biodiversity
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33 155 (Baumgärtner, 2007).

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39 156 As biological insurance theory is reaching the stage of a mature theory that is
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41 157 both supported by experimental tests and branching into new basic and applied
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43 158 directions, we believe it is critical to revisit and clarify its conceptual foundations to
44
45 159 guide future developments, applications and measurements. In this paper, we do not
46
47 160 wish to duplicate previous reviews of the use of the insurance and portfolio concepts
48
49 161 in ecology (Loreau, 2010; Schindler, Armstrong, & Reed, 2015). Instead, we first
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51 162 seek to clarify the connections between these concepts and the economic concepts
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53 163 that inspired them. Doing so points to gaps and mismatches between ecology and
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55 164 economics that could be filled profitably by new theoretical developments and new
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57 165 management applications. Second, we discuss some fundamental issues in biological
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4 166 insurance theory that have gone unnoticed so far and that emerge from some of its
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6 167 recent applications. In particular, we draw a clear distinction between the two effects
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8 168 embedded in biological insurance theory, i.e., the buffering and performance-
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10 169 enhancing effects. We also discuss the potential for inherent trade-offs between the
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12 170 mean and stability of ecosystem processes and services. Lastly, we suggest new ways
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14 171 in which biological insurance theory could be extended to address new issues in
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16 172 ecology and ecosystem management.
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23 173 **II. INSURANCE AND PORTFOLIO THEORIES IN** 24 25 26 174 **ECONOMICS** 27 28 29

30 175 Both biological insurance and portfolio theories in ecology found inspiration from
31
32 176 several related but distinct concepts in economic theory: portfolios, options, and
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34 177 insurance (Table 1). Uses of these concepts in ecology, however, have been largely
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36 178 metaphorical, and there are significant differences in their uses between the two
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38 179 disciplines. In this section, we revisit the definition of these concepts in economics to
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40 180 help clarify the scope and limitations of their usage in ecology.
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44 181 Portfolios, options, and insurance are three approaches used in economics and
45
46 182 finance to manage risk arising from an uncertain future. In each case, an individual
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48 183 may pay to reduce variability in her income or wealth, giving up a higher mean in
49
50 184 exchange for a lower variance. In economics, individuals are assumed to decide
51
52 185 whether or not paying to reduce risk is worth it by maximizing their expected well-
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54 186 being or “utility” (von Neumann & Morgenstern, 1944). How risk factors into well-
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56 187 being (“risk preferences”) varies across individuals (Fig 1A): some dislike risk (“risk
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4 188 averse”), some enjoy it (“risk seeking”), and others are ambivalent (“risk neutral”).
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6 189 These preferences determine what level of certain wealth an individual would value
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8 190 the same as a risky gamble (“certainty equivalent”; Fig 1B), and, as a result, how
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10 191 much an individual is willing to give up to avoid risk entirely (“risk premium”).
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13 192 Portfolios, options, and insurance operationalize the trading off of mean and
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15 193 variance in slightly different ways. In portfolios, investors accept lower average
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17 194 returns (changes in value) from a group of assets (e.g., stocks) in exchange for lower
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19 195 variance in those returns. Options permit an investor to purchase the right to delay
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21 196 making a decision about whether to buy or sell an asset until more information
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23 197 becomes available. Finally, insurance allows a policy holder to pay an insurer to
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25 198 assume some or all of the risk stemming from an uncertain future (e.g. the possibility
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27 199 of a flood). In what follows, we provide more details on each approach.
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33 200 **(1) Portfolios**

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37 201 Economic portfolio theory deals with optimal financial investment in sets of assets
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39 202 (portfolios) with uncertain returns. A portfolio with lower risk can be constructed by
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41 203 choosing assets (e.g., stocks) that do not have highly positively correlated changes in
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43 204 price, thereby reducing the potential for all assets to plummet in value at the same
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45 205 time. However, reducing variance in returns is often assumed to come with the cost
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47 206 of lower average returns, yielding a risk-return or mean-variance trade-off. Basic
48
49 207 portfolio theory focuses on avoiding unnecessary mean-variance trade-offs,
50
51 208 identifying portfolios that maximise expected returns for a given level of risk (Fig
52
53 209 1C) (Markowitz, 1952, 2010). Those portfolios trace out an “efficiency frontier” of
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55 210 the best choices for each level of variance; which “efficient” portfolio an investor
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57 211 should select depends on how much that individual likes or dislikes risk. Even
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4 212 efficient portfolios cannot eliminate risk entirely; portfolios limit exposure to
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6 213 unsystematic or idiosyncratic risk, but systemic risks such as the recent Covid-19
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8 214 pandemic can negatively affect all assets at once (Fig 1D).

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11 215 Economic portfolio theory has many conceptual analogues in biological
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13 216 insurance and portfolio theories. Diverse portfolios in which each asset has a price
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15 217 that responds differentially to external conditions resemble biodiverse collections of
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17 218 species that may respond differently to environmental drivers. The use of efficiency
18
19 219 frontiers to evaluate trade-offs is widespread in multi-objective conservation
20
21 220 planning and ecosystem management (Armsworth & Roughgarden, 2003; Nelson *et*
22
23 221 *al.*, 2008; Polasky *et al.*, 2008; White, Halpern, & Kappel, 2012; Ando & Mallory,
24
25 222 2012; Lester *et al.*, 2013; Halpern *et al.*, 2013; Runting *et al.*, 2018), but that concept
26
27 223 has not yet been applied to evaluate potential mean-variance trade-offs in ecosystem
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29 224 functioning (Section III).

30 31 32 33 34 35 36 225 **(2) Options**

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39 226 Financial options grant an individual the right to wait (up to an expiration date)
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41 227 before making a decision about whether or not to buy or sell an asset at a given price.
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43 228 By waiting, the option owner can see if the asset price has risen above or fallen
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45 229 below the agreed-upon sale price (the “strike” or “exercise” price) before making a
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47 230 trade (“exercising the option”), reducing risk of a loss. The resulting “option value”
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49 231 of that delayed decision is reflected in the purchase price of that option (“option
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51 232 price”) (Black & Scholes, 1973). Because the option value arises from improved
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53 233 information, options are valuable to investors even if those investors are risk neutral.

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57 234 While the prices and contractual details of financial options do not have exact
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59 235 analogues in ecology, the concept of option value is used directly in applied ecology

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4 236 and conservation. In fact, prominent economic theory on option value was motivated
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6 237 by the decision about whether to preserve or develop natural landscapes when the
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8 238 benefits provided by an intact ecosystem are uncertain (Arrow & Fisher, 1974;
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10 239 Henry, 1974; Dixit & Pindyck, 1994). If economic development is irreversible,
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12 240 preserving a natural landscape maintains the option to benefit from that ecosystem in
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14 241 the future while permitting learning about potential benefits before revisiting the
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16 242 development decision (Traeger, 2014). Option value compares the benefits from
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18 243 preserving and learning to the benefits of development, and plays the role of the
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20 244 option price should one choose not to develop (Dixit & Pindyck, 1994).

25 245 Similar logic explains the option value in preserving biodiversity. We do not
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27 246 perfectly know the values of species or their future role in the provision of ecosystem
28
29 247 services, and maintaining biodiversity preserves the option to enjoy those future
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31 248 benefits (Polasky, Costello, & Solow, 2005; Leroux, Martin, & Goeschl, 2009;
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33 249 Traeger, 2014; Dee *et al.*, 2019). If the species needed to support ecosystem services
34
35 250 in the future were known to be lost irreversibly or persist with certainty, this option
36
37 251 value of biodiversity would vanish. Dee *et al.* (2017a) provided a general application
38
39 252 of this concept by showing that there is an added value of protecting more species
40
41 253 than presumed to be critical to ecosystem services today, because of uncertainty over
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43 254 which species are needed for ecosystem services and whether they will be the ones
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45 255 lost in the future (Isbell *et al.*, 2011; Reich *et al.*, 2018; Dee *et al.*, 2019).

50 256 There is also another way in which biodiversity may have option value. In an
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52 257 ecosystem, the loss or decrease in abundance of species ill-suited to environmental
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54 258 conditions may give rise to a performance-enhancing or selection effect (Section III).
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56 259 Similarly, in economics, an option owner can choose the best investment alternative
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58 260 (e.g., buy an asset or not) once future market conditions are known. The ability to
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4 261 invest in an asset only if it is performing well yields an increase in mean returns for
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6 262 the option owner akin to the performance-enhancing effect in ecology.
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11 263 **(3) Insurance**
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14 264 Insurance contracts offer the most direct way for individuals to reduce exposure to
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16 265 risk. Specifically, paying an insurance premium lowers mean wealth, but the
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18 266 coverage that premium buys lowers potential variance in wealth from accidents and
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20 267 disasters in the future. The insurance company assumes the associated risk but is
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22 268 compensated for doing so via the premium, and may pass along that risk through
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24 269 reinsurance markets (Borch, 1962). Insurance companies also manage risk by
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26 270 constructing portfolios of insurance policies across many customers, which act as
27
28 271 assets from the insurer's perspective. Individuals can also self-insure (e.g., through
29
30 272 the purchase of a fire sprinkler system), which may substitute for insurance
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32 273 purchased through the market (Ehrlich & Becker, 1972).
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37 274 Links between economic insurance and biological portfolio and insurance
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39 275 theories center primarily on the concepts of risk aversion rather than elements of the
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41 276 financial contract itself (e.g. insurance premiums). The preferences of ecosystem
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43 277 managers and conservation organisations may easily exhibit risk aversion (see e.g.
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45 278 Mouysset, Doyen, & Jiguet, 2013; Tulloch *et al.*, 2015; Xiao *et al.*, 2019). Yet most
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47 279 analyses of conservation decisions about biodiversity and/or ecosystem services
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49 280 under uncertainty consider risk-neutral managers and preferences (e.g., Wilson *et al.*,
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51 281 2006; Dee *et al.*, 2017a). Although these economic concepts have not been addressed
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53 282 explicitly by biological insurance theory, they are obviously relevant in applied
54
55 283 ecology and biodiversity and ecosystem management (Binder *et al.*, 2018).
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284 **III. INSURANCE AND PORTFOLIO THEORIES IN** 285 **ECOLOGY**

286 The insurance and portfolio concepts have been used in ecology as metaphors rather
287 than as strict applications of their economic counterparts. The shared conceptual
288 basis between the economic and ecological concepts is simple: much like a diverse
289 set of stocks or assets in a portfolio, an ecosystem process or property may, in
290 principle, be viewed as an aggregate of the contributions of the various species,
291 phenotypes or functional groups that make up the ecosystem to this process or
292 property. For instance, analogous to the summed value of a portfolio of assets, an
293 ecosystem's primary production is the sum of the productions of the various plant
294 species it contains. If different plant species have biomasses or mass-specific
295 productions that do not fluctuate in perfect synchrony, their contributions to primary
296 production will partly compensate for each other (Gonzalez & Loreau, 2009),
297 thereby decreasing fluctuations of total primary production. This is the shared
298 essence of the "buffering" and "portfolio" effects in ecology (Doak *et al.*, 1998;
299 Tilman *et al.*, 1998; Tilman, 1999; Yachi & Loreau, 1999).

300 **(1) Similarities and differences between insurance and portfolio theories in** 301 **ecology**

302 Despite their strong similarity, the insurance and portfolio metaphors have been used
303 in slightly different ways in ecology — and in ways that do not match their usage in
304 economics (Table 1). The term "portfolio effect" was used initially to specifically
305 define the stabilising effect of biodiversity on ecosystem properties that results from

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4 306 independent fluctuations (zero correlation) of species abundances through time,
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6 307 based on the assumption that independent fluctuations depict a statistical null
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8 308 hypothesis in the absence of biotic interactions (Doak *et al.*, 1998; Tilman, 1999),
9
10 309 although some authors adopted a broader view by allowing for non-zero correlations
11
12 310 between fluctuations of species abundances (Doak *et al.*, 1998; Thibaut, Connolly, &
13
14 311 Sweatman, 2012). Economic portfolio theory, however, does not require that
15
16 312 fluctuations of the various assets in a portfolio be statistically independent; it only
17
18 313 assumes that these fluctuations are determined by external factors and are
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20 314 sufficiently decoupled, i.e., assets do not fluctuate synchronously and do not interact
21
22 315 with each other (Section V). Absence of direct interactions between species does not
23
24 316 entail statistical independence as fluctuations in species abundances are often partly
25
26 317 driven by shared environmental factors that tend to generate positive correlations
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28 318 between them (Loreau & de Mazancourt, 2008).

319 Instead of focusing on a specific effect of biodiversity, biological insurance
320 theory has sought to identify a broader set of biological processes that generate the
321 stabilising effect of biodiversity on ecosystem functioning, and to explore its various
322 consequences (Yachi & Loreau, 1999). Following from this aim, this theory has
323 included additional features such as: (1) the effects of biodiversity on both the mean
324 (the “performance-enhancing effect”) and variability (the “buffering effect”) of
325 ecosystem properties; (2) positive, as well as zero or negative, correlations between
326 the fluctuations of species abundances through time; and (3) spatial variability
327 between patches or locations in heterogeneous landscapes (spatial insurance theory).
328 Biological insurance theory identified differential responses of species to
329 environmental variations through either time (Yachi & Loreau, 1999) or space
330 (Loreau *et al.*, 2003a) as the key underlying biological mechanism of the buffering

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4 331 effect. It also proposed metrics of synchrony or asynchrony to quantify these
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6 332 differential responses (Loreau & de Mazancourt, 2008).
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9 333 Although biological insurance theory has been more explicit about its
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11 334 mechanistic underpinning and implications than has biological portfolio theory, it is
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13 335 important to note that the two approaches share the same underpinning. In
14
15 336 economics, a portfolio helps to reduce variability in economic returns if and only if it
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17 337 contains assets that fluctuate asynchronously. If assets are subject to the same market
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19 338 forces and fluctuations (e.g. if they are exposed to systemic risk), increasing the
20
21 339 number of assets does little to reduce the fluctuations of the portfolio's value
22
23 340 (Section II). Similarly, in ecology, ecosystem functioning is stabilised if and only if
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25 341 the ecosystem contains species or phenotypes that fluctuate asynchronously, though
26
27 342 not necessarily independently. Thus, it is important to realise that the basic biological
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29 343 insurance and portfolio concepts and theories are fundamentally equivalent, and they
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31 344 are most closely related to portfolio theory in economics.
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345 **(2) Mechanisms of biological insurance**

42 346 While there is consensus on the fact that biological insurance or portfolio effects
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44 347 emerge from asynchronous fluctuations of system components, several hypotheses
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46 348 have been proposed to explain their origin. Biological insurance theory has
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48 349 consistently emphasised differential responses of system components to
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50 350 environmental variations as the key mechanism underlying the stabilising effect of
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52 351 biodiversity on ecosystem functioning (McNaughton, 1977; Yachi & Loreau, 1999;
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54 352 Loreau, 2010). This mechanism is deeply rooted in biology since differential
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56 353 responses to environmental variations are ultimately based on the universal presence
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58 354 of trade-offs in biological systems, which constrain species to evolve towards a
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4 355 species-specific balance between various biological functions, and thus to perform
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6 356 best under a species-specific set of environmental conditions (Chesson, Pacala, &
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9 357 Neuhauser, 2001). Differential environmental responses result in temporal
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11 358 complementarity between species at the community level (Loreau, 2000), which
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13 359 echoes the functional complementarity that underlies the effects of biodiversity on
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15 360 mean ecosystem functioning (Loreau & Hector, 2001; Cardinale *et al.*, 2007).
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18 361 Differential species responses to environmental variations were shown to explain the
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20 362 stabilising effect of species diversity on ecosystem functioning in several
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22 363 experiments (Leary & Petchey, 2009; Hector *et al.*, 2010; Allan *et al.*, 2011; Thibaut
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24 364 *et al.*, 2012; de Mazancourt *et al.*, 2013).

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26
27 365 In contrast, biological portfolio theory invoked statistical averaging as a purely
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29 366 statistical “mechanism” underlying the stabilising effect of biodiversity on ecosystem
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31 367 functioning (Doak *et al.*, 1998). Statistical averaging, however, cannot be regarded as
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33 368 a mechanism as it is the statistical outcome of large numbers of individual events that
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35 369 occur at smaller scales and that tend to average out at larger scales. When the scales
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37 370 considered differ greatly (such as between particle physics and thermodynamics),
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39 371 microscopic events appear as essentially independent, random events at the
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41 372 macroscopic scale. Thus, statistical averaging does not provide a mechanistic
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43 373 explanation for the stabilising effect of diversity at the ecosystem level; it merely
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45 374 describes this effect from a statistical viewpoint (Loreau, 2010). Differential
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47 375 responses of system components to environmental variations are often the basic
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49 376 ingredient that underpins statistical averaging and hence ecosystem stability.

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52 377 Some purely stochastic processes, such as demographic stochasticity and
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54 378 observation error, however, do contribute to statistical averaging and
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56 379 diversity–stability relationships (de Mazancourt *et al.*, 2013). Fluctuations in total
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4 380 biomass due to demographic stochasticity tend to decrease when species diversity
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6 381 increases because the latter often increases mean total abundance and biomass, which
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8 382 reduces the impact of demographic stochasticity at the community level. Observation
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11 383 error is typically independent in different species, and thus it contributes to increase
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13 384 asynchrony in the observed fluctuations of species abundances, thereby inflating the
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15 385 observed stabilising effect of biodiversity on ecosystem properties. An analysis of
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17 386 long-term grassland biodiversity experiments revealed, quite surprisingly, that much
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19 387 of the stabilising effect of biodiversity observed in these experiments was explained
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21 388 by the community-level effects of demographic stochasticity and observation error
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23 389 (de Mazancourt *et al.*, 2013), probably because of the relatively small size of the
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25 390 experimental plots and plant populations in these experiments.

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29 391 Other factors also come into play. In particular, interspecific competition tends
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31 392 to generate negative temporal covariances between species; accordingly, it has often
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33 393 been assumed to enhance community stability (Tilman, 1999; Klug *et al.*, 2000;
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35 394 Lehman & Tilman, 2000; Ernest & Brown, 2001; Houlahan *et al.*, 2007; Gross *et al.*,
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37 395 2014). Theory, however, predicts that interspecific competition should rarely
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39 396 stabilise aggregate community- or ecosystem-level properties (Ives, Gross, & Klug,
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41 397 1999; Loreau & de Mazancourt, 2013). The reason is that, while competition does
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43 398 contribute to increase the level of asynchrony of population fluctuations, which has a
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45 399 stabilising effect on ecosystem properties, it simultaneously increases the amplitude
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47 400 of population fluctuations, which has a destabilising effect. The net result of these
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49 401 countervailing effects is often a neutral or negative effect of competition on
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51 402 ecosystem stability, although exceptions are possible (Loreau & de Mazancourt,
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53 403 2013). Thus, generally speaking, one should expect reduction of competition, i.e.
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55 404 niche complementarity, not competition, to favour ecosystem stability. There is some
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4 405 experimental evidence that increased complementarity does lead to increased
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6 406 ecosystem stability (Isbell, Polley, & Wilsey, 2009).
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9 407 Differences in the speed at which different species or ecosystem components
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11 408 respond to perturbations are another mechanism that can generate asynchronous
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13 409 population dynamics and thereby promote ecosystem stability (Rooney *et al.*, 2006;
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15 410 Ranta *et al.*, 2008; Fowler, 2009; Rooney & McCann, 2012). This mechanism,
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17 411 however, operates under rather restrictive conditions (Loreau & de Mazancourt,
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19 412 2013) and has not been tested experimentally so far. More generally, the temporal
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21 413 scale of environmental fluctuations and their degree of autocorrelation play an
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23 414 important role in population and ecosystem stability (Gonzalez & Descamps-Julien,
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25 415 2004; Gonzalez & De Feo, 2007) as patterns of asynchrony between species depend
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27 416 upon the temporal grain and extent over which the community is measured
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29 417 (Gonzalez *et al.*, 2020).
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34 418 Lastly, species may differ in their population-level stability, and thus
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36 419 ecosystem stability may increase or decrease simply because communities are
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38 420 dominated by species that have a higher- or lower-than-average level of population
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40 421 stability. This is another variant of the selection effect, which was found in a number
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42 422 of experiments (Gonzalez & Descamps-Julien, 2004; Steiner *et al.*, 2006; Polley,
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44 423 Wilsey, & Derner, 2007; Grman *et al.*, 2010; Zhang *et al.*, 2016; Song *et al.*, 2019).
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50 424 **(3) Distinguishing between the effects of biodiversity on the mean and**
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52 425 **variability of ecosystem properties**
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55 426 By failing to clearly identify their connections and differences with economic
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57 427 theories, biological insurance and portfolio theories in ecology have missed some
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59 428 opportunities to develop to their full potential. In particular, economic portfolio
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4 429 theory does not simply describe the stabilising effect of diversification on a
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6 430 portfolio's return, it also considers the relationship between expected return and risk,
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8 431 which is then used to select the best portfolio for a given risk level (the efficiency
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10 432 frontier — Section II). Although some empirical ecological work investigated the
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12 433 relationship between the mean level and stability of ecosystem functioning
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14 434 (Cardinale *et al.*, 2013), biological insurance and portfolio theories have not so far
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16 435 considered communities that optimise ecosystem functioning for a given stability
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18 436 level, while some management applications have (Section IV). This is one obvious
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20 437 avenue for the further development of these theories (Section VI).

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25 438 This development, however, requires clarification of some the concepts used in
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27 439 biological insurance theory. While the breadth of biological insurance theory has
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29 440 been one of its greatest strengths — for it has allowed extensions in various
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31 441 directions —, it is also a weakness in other ways. In particular, merging the
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33 442 performance-enhancing and buffering effects under the joint term of “insurance
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35 443 effects” (Yachi & Loreau, 1999) was somewhat unfortunate as the two types of
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37 444 effects do not always go hand in hand. Economic portfolio theory is based precisely
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39 445 on the idea that there is often a trade-off between the average return of an investment
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41 446 and risk reduction, i.e. between its mean and stability, such that high-risk
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43 447 investments provide a higher return on average than do low-risk investments
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45 448 (Section II). Biological insurance theory has, until very recently, largely ignored the
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47 449 trade-offs that may exist between the mean and stability of ecosystem processes or
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49 450 services such as crop yield (Montoya *et al.*, 2019). It has also made an inconsistent
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51 451 usage of the insurance concept since an insurance typically has a cost (i.e. risk-averse
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53 452 people pay risk premiums — Section II), and thus it implies a reduction in mean
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4 453 performance that one is willing to accept to reduce the risk of a major loss at some
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6 454 unpredictable time in the future.

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9 455 The mechanism that underlies the performance-enhancing effect of
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11 456 biodiversity is clear: this effect arises when the best-performing species are selected
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13 457 for (i.e., increase in abundance, frequency or yield) in each environment (Yachi &
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15 458 Loreau, 1999). These conditions precisely define an ecological selection effect
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17 459 (Loreau, 2000). Therefore, for clarity's sake, we propose that the performance-
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19 460 enhancing effect be renamed a selection effect, which may operate in time, space, or
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21 461 both (Chesson *et al.*, 2001; Dee *et al.*, 2016; Isbell *et al.*, 2018; Gonzalez *et al.*,
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23 462 2020). It may be worth recalling here that the selection effect does not conflict with
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25 463 the positive effects of biodiversity. Not only does it require the maintenance of
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27 464 biodiversity at larger spatial and temporal scales (Loreau, 2000), it even turns into
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29 465 functional complementarity when considered at larger scales because selection of the
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31 466 best-performing species under each environmental condition tends to increase the
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33 467 average level of ecosystem properties across space or time (Chesson *et al.*, 2001;
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35 468 Dee *et al.*, 2016; Isbell *et al.*, 2018; Gonzalez *et al.*, 2020).

43 469 **(4) Spatial insurance**

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46 470 Scaling-up biological insurance theory is critical to guide policy and management,
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48 471 which typically deal with relatively large spatial scales (Gonzalez *et al.*, 2020). This
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50 472 is the goal of spatial insurance theory (Loreau *et al.*, 2003a), which extends
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52 473 biological insurance theory to metacommunities (Leibold *et al.*, 2004) or meta-
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54 474 ecosystems (Loreau, Mouquet, & Holt, 2003b), i.e. to ecological systems that are
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56 475 distributed patchily across space but that are connected by movements of organisms
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58 476 and/or materials. Spatial insurance theory alone has generated a large number of

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4 477 recent theoretical (Gonzalez, Mouquet, & Loreau, 2009; Thompson, Rayfield, &
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6 478 Gonzalez, 2014, 2017; Shanafelt *et al.*, 2015, 2018; Leibold, Chase, & Ernest, 2017)
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9 479 and experimental (France & Duffy, 2006; Matthiessen & Hillebrand, 2006; Staddon
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11 480 *et al.*, 2010; Bouvier *et al.*, 2012; Limberger *et al.*, 2019) and field (Brittain, Kremen,
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13 481 & Klein, 2013; Wilcox *et al.*, 2017; Winfree *et al.*, 2018; Lefcheck *et al.*, 2019;
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16 482 Catano *et al.*, 2020) studies.

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18 483 Spatial insurance implies considering variability in both time and space
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20 484 simultaneously, which adds new dimensions to biological insurance. The stability of
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22 485 aggregate ecosystem properties can be quantified for three types of variability: (1)
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24 486 local temporal variability, i.e. the degree to which local ecosystem properties vary
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26 487 through time, as is the focus of classic biological insurance theory; (2) spatial
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28 488 variability, i.e. the degree to which local ecosystem properties vary across space at
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30 489 any given time; and (3) regional temporal variability, i.e. the degree to which
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32 490 aggregate ecosystem properties at the landscape or regional scale varies through
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34 491 time. Spatial insurance theory shows how these three components of stability are
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36 492 interdependent, how different mechanisms contribute to stability in each case, and
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38 493 how biodiversity and dispersal affect these mechanisms.

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41 494 Local biodiversity decreases local temporal variability via the classic insurance
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43 495 mechanisms discussed in previous sections. Spatial insurance theory further shows
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45 496 how these local mechanisms can be maintained and enhanced by dispersal between
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47 497 local communities. In particular, dispersal can maintain alpha (local) diversity and
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49 498 ensure that species are present when they are favoured by the current environmental
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51 499 conditions (Loreau *et al.*, 2003a), thereby fostering local insurance effects.

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54 500 Biodiversity decreases spatial variability when species compensate for each
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56 501 other in space because their growth is favoured under different environmental

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4 502 conditions (Fig. 2A) (Wang & Loreau, 2014, 2016; Isbell *et al.*, 2018), thereby
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6 503 generating a form of “spatial stability” of ecosystem functioning (Wang *et al.*,
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8 504 2019b). This aspect of spatial insurance is the direct spatial equivalent of the classic
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10 505 temporal insurance effect, but here it is spatial complementarity between species
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12 506 rather than local temporal complementarity that provides spatial insurance. Spatial
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14 507 complementarity arises from the local selection of species that are best adapted to the
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16 508 local environmental conditions, and this can occur through changes across space in
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18 509 species abundance, species composition, or both. Fig. 2A illustrates a simple
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20 510 example in which only species abundances change across space, but species
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22 511 composition also changes at large spatial scales, thereby generating beta (between-
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24 512 community) diversity. The importance of spatial complementarity between species in
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26 513 maintaining ecosystem functioning at the regional scale is nicely illustrated by a
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28 514 recent study which showed that the number of bee species needed to provide crop
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30 515 pollination was one order of magnitude higher in large-scale natural systems than in
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32 516 small-scale field experiments because of species turnover across space (Winfree *et*
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34 517 *al.*, 2018).

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40 518 Spatiotemporal stability of ecosystem functioning can also arise from the
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42 519 interactive effects of temporal and spatial variations in biodiversity such that
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44 520 different species show compensatory fluctuations across both space and time (Fig.
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46 521 2B). Spatial insurance theory has focused in particular on how dispersal can then
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48 522 maintain spatiotemporal complementarity between species by allowing them to shift
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50 523 their distributions to track conditions that support their growth (Loreau *et al.*, 2003a).
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52 524 Although not represented explicitly on Fig. 2B, beta diversity generally plays a key
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54 525 role in the spatiotemporal stability of ecosystem functioning by allowing the best-
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56 526 performing species to be present at the right place and time. A small-scale example

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4 527 of spatiotemporal complementarity between species that contributes to stabilising the
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6 528 provision of an ecosystem service is provided by honey bees and wild pollinators in
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9 529 California almond orchards as honey bees and wild pollinators preferentially visit
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11 530 different almond tree sections, and thus play complementary roles in pollination, but
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13 531 change their preferences depending on wind speed (Brittain *et al.*, 2013).

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16 532 Finally, at the regional scale, biodiversity contributes to reducing the temporal
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18 533 variability of ecosystem properties through any of the above-mentioned temporal,
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20 534 spatial or spatiotemporal insurance effects. Spatial asynchrony of environmental
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22 535 conditions that generates asynchronous fluctuations in ecosystem properties across
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24 536 space is an additional mechanism that may contribute to stabilising regional
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26 537 ecosystem functioning (Wang & Loreau, 2016). This can be seen from Fig. 2C,
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28 538 where summing the black curves that represent fluctuations in the total biomass or
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30 539 yield in the two sites would yield a constant regional-scale aggregate biomass or
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32 540 yield. Note that the same stabilising effect of spatial asynchrony occurs across
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34 541 populations of the same species within a metapopulation (Wang, Haegeman, &
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36 542 Loreau, 2015), thereby generating a spatial buffering or portfolio effect at the
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38 543 regional scale. A good example is provided by sockeye salmon subpopulations in
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40 544 Alaska, whose asynchronous fluctuations lead to reduced variability in sockeye
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42 545 salmon total annual catches (Rogers & Schindler, 2008; Schindler *et al.*, 2010).

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45 546 A growing body of theoretical and empirical work is seeking to disentangle
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47 547 the contributions of the various mechanisms underlying regional ecosystem stability.
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49 548 In particular, theory predicts that alpha diversity, beta diversity and spatial
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51 549 environmental asynchrony all contribute to providing insurance at large spatial scales
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53 550 (Wang & Loreau, 2016; Wang *et al.*, 2017; Delsol, Loreau, & Haegeman, 2018).
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55 551 Recent empirical studies have sought to assess the respective roles of these factors in
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4 552 regional ecosystem stability. For instance, Wilcox *et al.* (2017) found that regional
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6 553 ecosystem stability was driven by both local stability and spatial asynchrony in
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8 554 herbaceous plant communities across the world, but these responses could not be
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10 555 directly attributed to alpha and beta diversity. In contrast, Catano *et al.* (2020) found
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12 556 that spatial asynchrony explained three times more variation in the regional stability
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14 557 of total bird biomass across North America than did local stability, and that beta
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16 558 diversity played a key role in spatial asynchrony. Building new integrative
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18 559 approaches to partition biodiversity effects across scales is an active area of current
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20 560 research, which requires further development (Section VI).
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28 561 **IV. APPLICATIONS OF BIOLOGICAL INSURANCE IN** 29 30 31 562 **ECOSYSTEM MANAGEMENT**

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35 563 Although biological insurance and portfolio theories were developed initially to
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37 564 address issues in fundamental ecology, they are clearly relevant for managing
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39 565 ecosystem. In this section, we review how these theories have been applied in
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41 566 agriculture, fisheries, and forestry, and we suggest potential avenues by which the
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43 567 value of biological insurance could be further leveraged by both public and private
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45 568 natural resource managers.
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50 51 569 **(1) Agriculture**

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54 570 Most agricultural systems are far less diverse than the natural ecosystems they
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56 571 replaced (Newbold *et al.*, 2015) by design and due to inputs of fertilisers and
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58 572 pesticides. Strategies for diversifying agricultural systems are not new, but there is
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4 573 growing interest in leveraging biodiversity in a variety of ways to provide a partial to
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6 574 complete substitute for many costly agricultural inputs (Isbell *et al.*, 2017). Centuries
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8 575 ago, farmers discovered that combining grasses and legumes, either by sowing them
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10 576 together as an intercrop mixture or by sowing them consecutively in a crop rotation,
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12 577 can enhance crop yields (Trenbath, 1974; Harper, 1977; Vandermeer, 1989;
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14 578 Sanderson *et al.*, 2004). Intercropping and rotations can also help suppress weeds
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16 579 (Liebman & Dyck, 1993), in part because combining multiple crop species can
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18 580 enhance the exploitation of nutrients, water, and light (Liebman & Staver, 2001).
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20 581 Crop diversity enhances yield and weed suppression because of functional
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22 582 complementarity between species (Loreau, 2000; Loreau & Hector, 2001). As
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24 583 agricultural systems become increasingly diversified over time (e.g., rotations) and
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26 584 space (e.g., intercropping) at multiple spatial scales and multiple levels of biological
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28 585 organisation, local and spatial insurance effects may also arise. For example,
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30 586 increasing the number of crop genotypes can stabilise the production of livestock
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32 587 fodder (Prieto *et al.*, 2015), and planting forbs along field edges can help support
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34 588 crop pollination (Kremen *et al.*, 2007). Crop pollination at regional scales requires an
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36 589 order of magnitude more bees than are needed at very local scales, due to spatial
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38 590 turnover in which bees are providing pollination services at different places (Winfree
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40 591 *et al.*, 2018)..

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48 592 A private land manager may use biological insurance as a partial substitute for
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50 593 economic crop insurance (Quaas & Baumgärtner, 2008). For example, droughts are
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52 594 becoming increasingly frequent and intense in many parts of the world (Alexander *et*
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54 595 *al.*, 2013). Droughts are often difficult to predict, leading to unrecoverable up-front
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56 596 investments. Options to compensate for the undesirable impacts of droughts, such as
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58 597 irrigation, are often expensive, unfeasible, or unavailable. Consequently, droughts

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4 598 often reduce crop yields below profitable levels. Farmers in many parts of the world
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6 599 purchase crop insurance to recover unavoidable losses due to droughts and other
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9 600 similarly unpredictable and inescapable damages. In some agroecosystems,
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11 601 investments that enhance local biodiversity may provide biological insurance
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13 602 (Schläpfer, Tucker, & Seidl, 2002; Carnus *et al.*, 2014; Isbell *et al.*, 2017; Binder *et*
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15 603 *al.*, 2018), which could be viewed as a partial substitute for crop insurance. For
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17 604 example, grassland plant diversity enhances the resistance of productivity to extreme
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19 605 climate events, including droughts (Isbell *et al.*, 2015). Specifically, the productivity
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21 606 of low-diversity communities with one or two grassland plant species changes by
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23 607 about 50% during climate events, whereas that of high-diversity communities with
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25 608 16-32 species changes by only approximately 25%. In rangelands, pastures, and hay
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27 609 production systems, investing in diverse seed inputs may help reduce the frequency
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29 610 with which droughts, pest outbreaks, and other disturbances reduce profitability
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31 611 (Isbell *et al.*, 2017).

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36 612 Societies may also use biological insurance to stabilise food production at
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38 613 national, global, or other geopolitical scales. In addition to temporarily affecting
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40 614 yields on individual farms, climate extremes (both droughts and deluges) destabilise
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42 615 food production from one year to the next at larger spatial scales, including the
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44 616 national scale. This can create shortages and surpluses, both of which can result in
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46 617 economic inefficiencies. Spatial insurance may help dampen interannual fluctuations
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48 618 in total national harvest, especially if climate events affect yields in some, but not all,
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50 619 parts of a country. Indeed, countries with greater crop diversity also tend to have
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52 620 greater stability of total national harvest (Renard & Tilman, 2019). Thus, policies
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54 621 that encourage crop diversity, or limit current subsidies for small number of crops,
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56 622 may be economically efficient, if they reduce shortages and surpluses.
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(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; Cline, Schindler, & Hilborn, 2017; Anderson *et al.*, 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 (Holland *et al.*, 2017; Anderson *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

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4 647 reduced fishing revenues by 85% in Alaska, but the fishing communities with the
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6 648 most diverse stocks experienced little change or even increase in revenue (Cline *et*
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8 649 *al.*, 2017). In this case, however, the underlying mechanism was not biological, but
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10 650 instead driven by human behaviour: fishing communities that targeted a greater
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12 651 number of fish species could alter the composition of their catch and adjust it to
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14 652 changing market or ocean conditions. Dee *et al.* (2016) found evidence for a
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16 653 performance-enhancing effect of diversity for global marine fisheries yields.
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18 654 Specifically, diversifying catch, in terms of the thermal traits of targeted species,
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20 655 buffered global aggregate fisheries yields against temperature variability, offsetting
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22 656 an average of 7% losses of global yields per year due to temperature variation. This
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24 657 result may be driven by a selection effect due to harvesting, where catching more
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26 658 species increases the chances of catching one that is thermally tolerant, or by a
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28 659 selection effect due to environmental filtering, where different species or traits are
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30 660 favoured under different temperature regimes.
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36 661 The evidence for benefits from diversification in fisheries, however, is not
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38 662 universal because of the trade-offs that may occur between the mean and stability of
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40 663 both ecological and economic properties of the social-ecological system. Just as in
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42 664 agriculture, higher revenues may also be associated with specialisation when
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44 665 specialisation comes with more efficient catch techniques or more efficient
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46 666 management (Holland *et al.*, 2017; Ward *et al.*, 2018). In a metapopulation context,
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48 667 harvesting a spatially-structured population can also reduce stability at local scales
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50 668 via population collapse, while increasing stability at larger scales through adult
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52 669 migration (Okamoto *et al.*, 2020). Taken together, these results suggest that
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54 670 diversification often provides benefits to fisheries across several dimensions, but
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56 671 these benefits can also depend on the spatial scale and management context.
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672 **(3) Forestry**

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

678 Several recent studies have shown that various components of forest diversity
679 may buffer the inherent variability of tree productivity (Jucker *et al.*, 2014; Forrester
680 & Bauhus, 2016; Aussenac *et al.*, 2017; Rio *et al.*, 2017; Dolezal *et al.*, 2020). Some
681 tree species are more affected by precipitation, and others by temperature. The
682 resulting asynchronous variations in radial growth decrease variability in total stand
683 productivity (Aussenac *et al.*, 2017). Perturbations are also pervasive in natural
684 forests, sometimes reducing tree growth (e.g., insect outbreaks), sometimes
685 destroying biomass (e.g., large fires). Complementarity in regrowth following
686 perturbations owing to differences in maximal growth, seed production and dispersal
687 tends to buffer the negative effects of perturbations (Morin *et al.*, 2014). Over longer
688 timescales, climate changes, and forest composition adjusts accordingly. Diversity at
689 the regional level ensures that selection of the most adapted species maintains
690 productivity in response to warming, but other effects of tree diversity on the
691 variability of forest productivity have also been documented. For instance, Prestch *et*
692 *al.* (2013) and Aussenac *et al.* (2019) observed that species-specific responses to
693 climate fluctuations are reduced by species diversity, presumably because
694 intraspecific competition increases water demand and thus magnifies the negative

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4 695 effects of drought. Species mixtures may also dilute the intensity, duration and extent
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6 696 of pest outbreaks (Jactel & Brockerhoff, 2007; Castagneyrol *et al.*, 2013).

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9 697 A mixture of different tree species may be a good option for forest
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11 698 management for several reasons, which we illustrate with an application of the
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13 699 efficiency frontier approach to Québec's boreal forests under current and future
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15 700 climate scenarios (Fig. 3). Balsam fir and aspen are two dominant tree species in
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17 701 these forests. There is minimal overyielding among these species under current
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19 702 climatic conditions, and thus monocultures would be promoted if there were no
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21 703 interannual fluctuations in climate. The two species, however, respond differently to
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23 704 precipitation and temperature variations, such that total stand productivity is more
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25 705 stable in mixtures. Therefore, short-term forest management should balance risk and
26
27 706 expected return, as evidenced by the current efficiency frontier (Fig. 3, bottom left).
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29 707 A management strategy based on average productivity alone would promote balsam
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31 708 fir monocultures, while a management strategy minimising risk would promote
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33 709 mixed stands. But the projected future climate scenario yields a different outcome.
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35 710 Balsam fir is better adapted to the projected warmer and wetter future climate, and
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37 711 transgressive overyielding occurs in mixture. The efficiency frontier changes
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39 712 accordingly, and a mixture is now the best option both to maximise yield and to
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41 713 minimise risk (Fig. 3, bottom right).
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48 714 While a growing body of research is demonstrating the ecological importance
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50 715 of tree diversity, the economic implications of tree diversity have received relatively
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52 716 limited attention. Consequently, translating the concepts of biological insurance
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54 717 theory into operational and economically motivated forestry decisions remains
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56 718 challenging. Forestry has long focused on maximising short-term profits for
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58 719 landowners while maintaining long-term productivity. As such, forest management
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4 720 has a long history of favouring monocultures, which were thought to provide higher
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6 721 yields than do mixed stands. During the past 20 years, however, a number of studies
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8 722 applied portfolio theory to forest management and showed the advantages of
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10 723 diversification to promote economic returns on timber production and reduce risk
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12 724 (Knoke *et al.*, 2005; Knoke, 2008; Neuner, Beinhofer, & Knoke, 2013; Dragicevic,
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14 725 Lobianco, & Leblois, 2016). Risk is typically calculated as the standard deviation of
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16 726 the economic return over the planning horizon and is associated with the volatility of
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18 727 timber prices or the unpredictable occurrence of severe natural disturbances. These
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20 728 studies used the efficiency frontier approach (Fig. 1) to determine the optimal forest
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22 729 composition that maximises economic return for different levels of risk. For an
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24 730 acceptable risk level, they determined the proportions of a forest landscape allocated
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26 731 to the production of different types of forest stands.

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32 732 Ecological knowledge on the mechanisms that provide biological insurance
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34 733 have yet to be integrated into applications of biological insurance and portfolio
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36 734 theory to forest management. For example, Garcia-Robredo (2018) recently
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38 735 demonstrated that reduced competition and facilitation between mixtures of two
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40 736 species (beech and Scots pine) can lead to overyielding, increased economic return
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42 737 and reduced financial risk. Most studies so far, however, have focused on
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44 738 demonstrating the positive effects of managing different types of stands (often
45
46 739 monospecific) and have ignored complementarity effects within stands. Moreover,
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48 740 portfolio studies have not considered the variability in site conditions across the
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50 741 managed forest landscape and have disregarded spatial ecological processes between
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52 742 stands, such as seed dispersal, which may lead to spatial insurance effects, especially
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54 743 over the long timescales at which forests are typically managed (Pohjanmies,
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56 744 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 better understand the connections and limitations of the various theories, it is useful to take a step back and examine 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

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4 767 or preserved, and then ecological dynamics may cause part of this subset to go
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6 768 extinct. Diversity after the first step thus acts like a pool diversity for the second step.

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9 769 Within one community i , the set of species properties (e.g., biomasses, or asset
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11 770 values in economics) $z_i(\mathbf{t})$ follows a trajectory determined by the composition \mathbf{x}_i^* of
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13 771 the community and by external drivers \mathbf{y}_i , which are assumed to be unaffected by
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15 772 composition (e.g., abiotic environmental factors, stock prices on the global market).
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18 773 For simplicity, the variable $z_i(\mathbf{t})$ conflates two distinct sources of variation. In
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20 774 ecology, the performance of an individual is often fixed (by physiology), while the
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22 775 abundance of each species fluctuates. In economics, the weight of each asset in the
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24 776 portfolio (e.g. the number of stock shares) is often fixed (according to initial
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26 777 investment), while the unit value of each share fluctuates. The product of these two
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28 778 components determines the functional value of a species or asset.

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31 779 Asynchronous fluctuations between the various species give rise to buffering
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33 780 effects, and thus reduce the variability of an aggregate ecosystem function or
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35 781 property F_i (e.g., total biomass or yield) in community i . In addition, local
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37 782 interactions between species may cause complementarity effects, such that the
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39 783 aggregate ecosystem function is larger than expected from the performance of its
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41 784 contributing species in isolation.

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44 785 At the regional scale, the performance \mathbf{O} of an entire meta-ecosystem (or
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46 786 regional economy) is an aggregate of its performances across the various local
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48 787 ecosystems. At this scale, there are no selection effects, except through possible
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50 788 regional extinctions. The performance of the meta-ecosystem, however, can be
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52 789 affected by selection effects at lower scales. These effects are described by the
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54 790 ecological concept of species sorting (Leibold *et al.*, 2004) and the equivalent
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56 791 economic concept of sorting (Tiebout, 1956): as local ecosystems offer different

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4 792 environmental conditions, species may be selected to occupy locations where they
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6 793 are most productive, leading to positive complementarity and/or buffering effects on
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9 794 aggregate meta-ecosystem performance. Likewise, complementarity can emerge for
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11 795 a regional economy in the form of economic diversification (Table 1).
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13 796 Spatio-temporal insurance effects arise when fluctuations in the abundance (or
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15 797 value) of a species (or asset) are asynchronous between communities due to different
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17 798 external drivers or local interactions, thereby reducing the temporal variability of the
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19 799 aggregate performance *O*. Dispersal or migration between ecosystems can further
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21 800 affect spatial synchrony among populations (Section III). Similar concepts can be
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23 801 found in the social dynamics of stockholders, e.g. market contagion (Kaminsky,
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25 802 Reinhart, & Vegh, 2003).
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31 803 **(2) Contrasts between ecological and economic concepts**

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34 804 Since the above synthesis draws more upon the language of biological insurance
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36 805 theory, it is worth discussing how the assumptions of economic theories tend to
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38 806 differ from this framework, and how these differences may illuminate ecological
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40 807 concepts.
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44 808 Economic portfolio theory (Fig 4B) implicitly encompasses both what
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46 809 biological insurance theory would call selection and buffering (or portfolio) effects,
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48 810 i.e., benefits from selecting the best individual assets and from assembling assets
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50 811 with asynchronous fluctuations. Since the value of an asset is generally set by global
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52 812 market prices, it is perfectly synchronous between all portfolios, and thus there is no
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54 813 counterpart to spatial insurance effects for a single asset (except when including
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56 814 multiple regional markets). In ecology, synchronising the abundance of a given
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58 815 species across all locations would require strong spatial fluxes; these fluxes,
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4 816 however, would also homogenise species composition and prevent possibly
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6 817 beneficial selection effects, unless some species were actively removed locally by
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8 818 management actions.
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11 819 There are usually no local interactions between assets in an economic portfolio,
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13 820 except through initial investment decisions. In ecology, this would amount to a static
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15 821 community in which initial species abundances do not change through time. In this
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17 822 case, biodiversity may still induce stability-enhancing buffering effects, but in the
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19 823 absence of complementarity effects due to niche differentiation between species,
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21 824 mixtures cannot outperform the best species. Thus, a mean-stability trade-off
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23 825 emerges naturally in an economic context, whereas ecological interactions may allow
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25 826 both the mean and stability of ecosystem functioning to increase simultaneously with
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27 827 diversity (Wang *et al.*, 2021).
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32 828 Various types of interactions that commonly appear in ecological settings
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34 829 could thus inspire new developments in biological insurance theory (Section VI). In
35
36 830 particular, the expected performance or fluctuations of a species generally depends
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38 831 on its own density in the local community. A classic example is Taylor's (1961) law,
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40 832 which relates the variance and the mean of population abundance.
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43 833 Economic insurance and options (Fig 4C) can be conceptualised as types of
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45 834 selection effects in which preference is not given to those assets that have the highest
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47 835 current value, but to assets that may reach higher values, or avoid falling to low
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49 836 values, in the future. Insurance requires an upfront cost (or equivalently, the initial
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51 837 selection of a lower-value asset), whereas options delay selection until later times.
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53 838 Insurance parallels the biological concept of bet hedging, in which organisms
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55 839 decrease their short-term fitness under typical conditions in order to increase their
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57 840 probability to survive in unpredictably varying environments (Den Boer, 1968;
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4 841 Starrfelt & Kokko, 2012). The ecological counterparts of the economic concepts of
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6 842 option and insurance would be delayed selection effects and catastrophe avoidance,
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8 843 respectively (Table 1). In both cases, the maintenance of biodiversity implies
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10 844 reduced ecosystem performance because communities include species that are less
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12 845 productive under current conditions. But this short-term cost comes with long-term
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14 846 benefits, either by allowing selection of best-performing species under future
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16 847 conditions (delayed selection effect) or by preventing catastrophic declines in
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18 848 ecosystem functioning through the maintenance of species that resist major
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20 849 disturbances such as fires or biological invasions (catastrophe avoidance).
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25 850 These concepts could be applied to agricultural management. Most current
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27 851 applications of ecological theory consider what happens to the mean and variability
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29 852 of yields if different types of crops are planted together at the start of the season,
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31 853 which is the scope of portfolio theory in economics. The equivalent of an economic
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33 854 option would consist in growing seedlings of different crop types in a nursery, and
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35 855 then planting one later in the season once weather forecasts are refined. The
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37 856 equivalent of an economic insurance would consist in selecting a single crop that
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39 857 would have lower mean yield, but yield that is less variable across different
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41 858 environmental conditions.
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45 859 While the classic economic approach to portfolios deals with uncertain
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47 860 fluctuations of asset values around a stationary mean, options rely on an economic
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49 861 agent's ability to respond to directional fluctuations and exploit upward or downward
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51 862 trends. Situations where better knowledge about these trends can be accrued over
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53 863 time exhibit an exploration–exploitation trade-off, which is considered, for instance,
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55 864 in multi-armed bandit and foraging theories (Berger-Tal *et al.*, 2014). These various
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57 865 concepts may thus be relevant on timescales that are either shorter or longer than
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4 866 those considered by classic portfolio theory. This suggests that a new frontier for
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6 867 biological insurance theory would be to import these concepts in ecology to address
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8 868 transient ecological dynamics.
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14 869 **VI. FUTURE CHALLENGES**

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18 870 Previous sections have identified a number of limitations that restrict the scope and
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20 871 domain of application of biological insurance theory. Here we propose new
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22 872 directions in which this theory could be profitably developed to address new issues
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24 873 in both basic and applied ecology.
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30 874 **(1) Linking the effects of biodiversity on ecosystem functioning and stability**

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33 875 As already noted earlier (Section III), most ecological studies have explored the
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35 876 effect of biodiversity on either ecosystem functioning or ecosystem stability
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37 877 separately. Few studies have attempted to clarify how ecosystem functioning and
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39 878 stability are interrelated, and when trade-offs may emerge between them (Montoya *et*
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41 879 *al.*, 2019), while the relationship between expected return and risk is at the core of
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43 880 economic portfolio theory (Section II). Biodiversity–ecosystem functioning research
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45 881 has showed that species diversity enhances both ecosystem functioning and
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47 882 ecosystem stability (Loreau *et al.*, 2001; Hooper *et al.*, 2005; Cardinale *et al.*, 2012;
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49 883 Tilman, Isbell, & Cowles, 2014), which suggests a synergy between ecosystem
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51 884 functioning and stability along a gradient of species diversity. But synergy need not
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53 885 be the norm along other gradients. For instance, a recent meta-analysis found that
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55 886 biodiversity effects on ecosystem functioning and stability were often independent of
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4 887 each other (Cardinale *et al.*, 2013). Thus, new theory is required to understand
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6 888 covariations between ecosystem functioning and stability.
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9 889 Using a Lotka–Volterra competition model, a recent study showed that
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11 890 complementarity and selection — the two main classes of biodiversity effects on
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13 891 ecosystem functioning (Loreau & Hector, 2001) — both promote average ecosystem
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15 892 functions but have contrasting effects on their stability (Wang *et al.*, 2021). In
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17 893 particular, selection of species with a high mean productivity enhances ecosystem
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19 894 productivity in the short term, but it decreases species diversity and its insurance
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21 895 effect on the stability of ecosystem productivity in the long term. Therefore,
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23 896 depending on which factor drives species interactions, ecosystem functioning and
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25 897 stability can exhibit either a synergy (along a gradient of complementarity) or a
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27 898 trade-off (along a gradient of selection). In the latter case, ecosystems achieving a
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29 899 higher biomass in constant environments tend to be more fragile in the face of large
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31 900 perturbations that are likely to occur in the long run. Consistent with these theoretical
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33 901 predictions, one biodiversity experiment found that strong selection effects led to
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35 902 declines in biodiversity over time, and that ecosystem stability was enhanced in
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37 903 mixtures with high levels of complementarity effects and low levels of selection
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39 904 effects (Isbell *et al.*, 2009).
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46 905 Such a trade-off between ecosystem functioning and stability could be studied
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48 906 using the efficiency frontier concept used in economics and management (Sections II
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50 907 and IV). Since species interactions play an important role in community dynamics,
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52 908 however, the traditional assumption of economic portfolio theory that assets do not
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54 909 interact with each other in a portfolio (Section V) does not hold any more. Therefore,
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56 910 studying the relationship between ecosystem functioning and stability requires a
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58 911 dynamical approach, which could be combined with an efficiency frontier.
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(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).

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

937 Biodiversity contributes to ecosystem stability through insurance effects at multiple
938 organisational levels and spatial scales (Section III). Two integrative mathematical
939 frameworks have been developed recently to link ecosystem stability and asynchrony
940 across organisational levels and spatial scales (Wang *et al.*, 2019a; Hammond *et al.*,
941 2020). These frameworks have been used to quantify the relative importance of local
942 and spatial insurance effects in several empirical datasets. Local insurance due to
943 species diversity was shown to provide stronger stabilising effects on regional
944 ecosystem functioning than did spatial insurance in a desert grassland ecosystem in
945 New Mexico (Wang *et al.*, 2019a) and in a Californian kelp forest (Lamy *et al.*,
946 2019). Other studies, however, found that spatial insurance contributed more than did
947 local insurance to the stability of benthic marine fish communities (Thorson *et al.*,
948 2018) and rock-pool invertebrate metacommunities in Jamaica (Hammond *et al.*,
949 2020). More empirical work is required to quantify insurance effects from different
950 sources and across scales and organisational levels and clarify how their relative
951 importance changes with abiotic and biotic factors.

952 A recent study also developed a new framework to quantify biodiversity effects
953 on ecosystem functioning in space and time (Isbell *et al.*, 2018). This framework was
954 built upon Loreau & Hector's (2001) classic additive partition of the net biodiversity
955 effect on local ecosystem functioning into complementarity and selection effects.
956 Isbell *et al.* (2018) extended this partition to split the selection effect into multiple
957 additive terms that capture the contributions of spatial, temporal and spatiotemporal
958 selection processes. In this new partition, temporal or spatial selection effects are
959 positive when species dominate mixtures at the times or places where they are most

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4 960 productive in monoculture. For example, significant temporal selection effects were
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6 961 observed in a long-term experiment over a period of 18 years (Isbell *et al.*, 2018),
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8 962 suggesting substantial temporal turnover in which species are most productive (Isbell
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11 963 *et al.*, 2011; Allan *et al.*, 2011).

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13 964 These new frameworks provide new opportunities to understand ecosystem
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15 965 functioning and stability across space and time. Future theoretical work should
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17 966 clarify how the various components of these frameworks are related, e.g., how the
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19 967 various selection effects are related to insurance effects across scales, develop
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21 968 broader integrative frameworks that merge the effects of biodiversity on ecosystem
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23 969 functioning and stability across scales, and test them with experimental or
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25 970 observational data.

31 971 **(4) Extending biological insurance theory to complex interaction networks**

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34 972 Biological insurance theory has so far been developed and tested for sets of similar
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36 973 species occupying a single trophic level. Real ecosystems, however, are
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38 974 characterised by complex networks that may involve multiple interactions,
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40 975 interaction types, and functional groups. Developing new theory for biological
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42 976 insurance in complex interaction networks is critical as predictions and results for a
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44 977 single trophic level might no longer apply. In particular, complex interaction
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46 978 networks raise at least three major difficulties: (i) the mean and variance of the
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48 979 performance of a mixture of species cannot be simply extrapolated from the mean
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50 980 and variance of its component species or of similar mixtures (Jaillard *et al.*, 2018);
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52 981 (ii) managing part of the network can impact other parts; and (iii) an arbitrary species
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54 982 composition cannot generally be imposed and maintained to achieve ecosystem-level
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56 983 objectives.
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4 984 In economic portfolio theory, the fluctuations of an asset are assumed to
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6 985 respond to global market dynamics, independently of which other assets are selected
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9 986 in the portfolio (Section V). Some applications of biological insurance theory have
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11 987 also assumed that the success of a species at one location and time reflects local
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13 988 abiotic conditions, independently of which other species are present. Species
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15 989 fluctuations may be correlated, but these correlations are taken as exogenous and do
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17 990 not depend on community composition. This assumption is not overly restrictive in
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19 991 competitive communities because the strength of competitive interactions has little
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21 992 effect on the stability of aggregate ecosystem properties unless these interactions are
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23 993 strongly asymmetric (Ives *et al.*, 1999; Loreau & de Mazancourt, 2013). This
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25 994 simplifying assumption, however, must be relaxed when considering other ecological
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27 995 interactions. In particular, complex food webs demonstrate the practical importance
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29 996 of species interactions in approaches related to biological insurance. When managing
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31 997 or harvesting species in food webs, e.g. in fisheries, portfolios of target species that
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33 998 ignore interactions can face disastrous or unanticipated consequences (Van Leeuwen,
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35 999 De Roos, & Persson, 2008). This has led to the emergence of the “ecosystem-based
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37 1000 management approach”, which addresses these issues in many specific instances
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39 1001 with complex simulation models, but little general theory exists to set expectations
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41 1002 across ecosystems.

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48 1003 A theory of biological insurance for complex interaction networks must also
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50 1004 acknowledge that species interactions can have a wide range of effects on the
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52 1005 synchrony, strength and autocorrelation of fluctuations in species abundances. For
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54 1006 instance, competitive interactions tend to create asynchrony (Section III), while
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56 1007 mutualism tends to create synchrony, and predator-prey or other asymmetric
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58 1008 interactions tend to induce oscillations with phase lags between species. Sometimes,
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4 1009 these complex dynamics display stabilising effects: species interactions can dampen
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6 1010 environment-driven fluctuations (Tikhonov & Monasson, 2017), and, conversely,
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8 1011 external perturbations can also stabilise interacting populations (Fox *et al.*, 2017).
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10 1012 Most often, however, these effects are destabilising, i.e. species interactions are
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12 1013 expected to create and amplify dynamical fluctuations at the population level (May,
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14 1014 1972). Finally, a species' interactions with other, possibly unobserved variables can
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16 1015 be modelled as fluctuations with memory (i.e., temporal autocorrelation), such that
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18 1016 acting on others implies delayed feedback on oneself. For instance, a predator that
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20 1017 depletes its present prey inhibits its own growth in the future. In all these scenarios,
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22 1018 biological insurance theory remains applicable, but it requires a careful treatment
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24 1019 accounting for how species interactions alter the mean and variance of ecosystem
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26 1020 properties for each species composition.

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31 1021 Complex interaction networks also challenge a basic tenet of the biological
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33 1022 insurance concept, i.e., biodiversity or species composition may be viewed as a
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35 1023 control variable that can be manipulated to achieve some target ecosystem properties.
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37 1024 A common outcome of ecological interactions, however, is extinction, i.e., the loss of
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39 1025 a species from the local community, or even from the regional pool. Even when
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41 1026 biodiversity is stabilising at the ecosystem level, it tends to induce instability at the
42
43 1027 population level (Tilman *et al.*, 2006), which can make a diverse community more
44
45 1028 difficult to maintain. On the other hand, nonequilibrium coexistence theory suggests
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47 1029 that fluctuations can also enhance the coexistence of interacting species (Barabás,
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49 1030 D'Andrea, & Stump, 2018). Thus, while May (1972) envisioned the instability of
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51 1031 complex communities as a limitation, Roy *et al.* (2020) recently showed that the self-
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53 1032 sustaining fluctuations of such communities can also enable more species to coexist.
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55 1033 With arguments paralleling biological insurance theory, they identified conditions
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4 1034 under which population responses become asynchronous and differentiated, leading
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6 1035 to more species persisting in a chaotic state than at equilibrium. Higher levels of
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8 1036 biodiversity, biomass and productivity may be attained at the cost of stronger
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10 1037 fluctuations, thus creating an emergent trade-off between ecosystem functioning and
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12 1038 stability.
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18 1039 **(5) Developing new applications to biodiversity and ecosystem management**
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21 1040 Our review identified some gaps between the concepts and terminology used in
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23 1041 economics and biology with respect to insurance. These gaps also offer new research
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25 1042 opportunities and directions. For instance, biological insurance theory currently lacks
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27 1043 an analogy of utility functions and insurance or risk premiums, but recent theory
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29 1044 development is starting to build these bridges, providing links between biodiversity
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31 1045 as insurance with economic theory and management applications. In particular,
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33 1046 Baumgärtner (2007) used utility theory to formally define the insurance value of
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35 1047 biodiversity as the reduction in the insurance premium that an ecosystem manager
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37 1048 would be willing to pay to avoid the risk of an insufficient provision of ecosystem
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39 1049 services. Applying and extending this theory would offer new research opportunities
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41 1050 to quantify biological insurance in economic or ecosystem service terms. Further, as
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43 1051 shown in Section IV, there is an opportunity to explore the economic and ecosystem
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45 1052 consequences of biodiversity under future environmental conditions, e.g., under
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47 1053 climate change scenarios as in Fig. 3. Similarly, the concepts of option value and
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49 1054 economic insurance could offer new management and research opportunities for
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51 1055 applied ecology and management.
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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.

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For Review Only

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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 ¹)	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 variation² 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>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>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>Biological insurance³: 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>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)⁴.</p> <p>Mean-variance trade-off: Occurs when reduced variance or risk comes at the cost of lower expected return.</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 though 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>Spatial insurance: Concept used to denote the fact that aggregate ecosystem properties vary less in more diverse</p>	<p>No economic equivalent of spatial insurance. The closest analogy is spatial equilibrium, whereby</p>	<p>Crop pollination in large-scale natural systems requires a much higher number of bee species than in small-scale</p>

<p>metacommunities because of compensatory changes between species or communities across space, or across both time and space.</p>	<p>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>experiments because of spatial complementarity between species.</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 best-performing species under future conditions.</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>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>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 catastrophic declines in ecosystem functioning in the long run through the maintenance of species that resist major disturbances (e.g. fires or biological invasions).</p> <p>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.</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 it generally applies to risk incurred by the purchaser, who often has some control over their own risk factors.</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> <p>Another potential application would be selecting a crop whose yield is lower on average but less variable across different environmental conditions.</p>
<p>Complementarity effect: Occurs when a mixture of species performs better than would be expected based on their performance in isolation because of niche differentiation between species.</p>	<p>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).</p>	<p>Intercropping and crop rotations often enhance crop yields and help suppress weeds because of complementarity in resource use between species.</p>

¹ The 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.

² The 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.

³ Follows the common-language usage of “insuring” as “guaranteeing safety”.

⁴ In ecological terms, economic portfolio theory thus encompasses both buffering and selection effects.

FIGURE LEGENDS

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 represent 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).

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

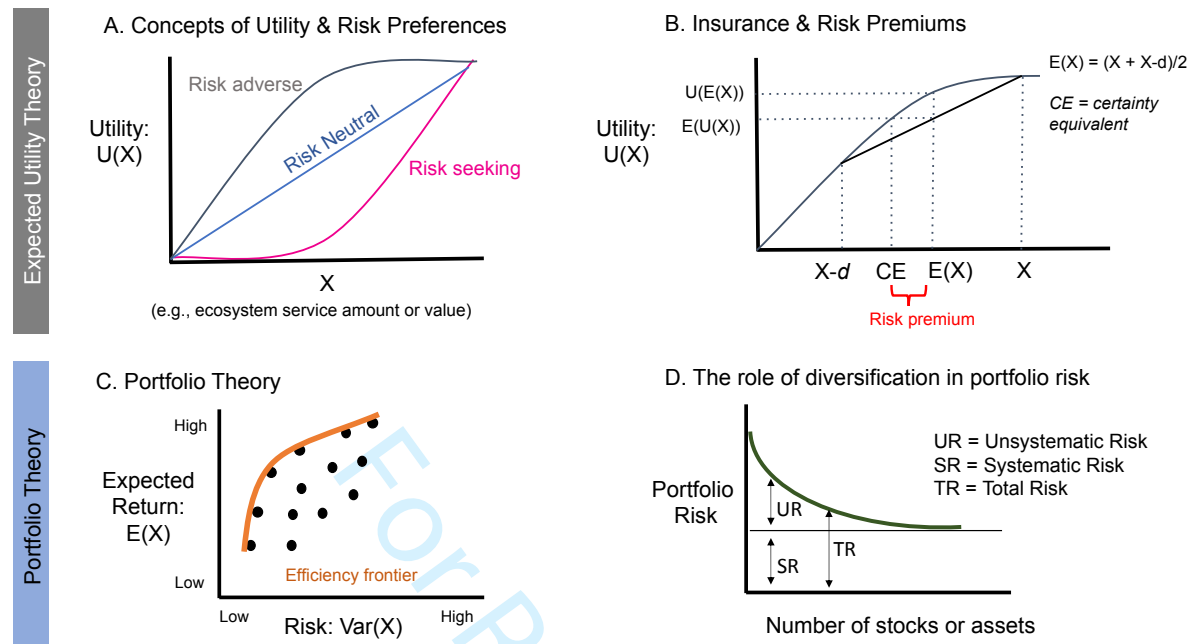
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3 fluctuations across both space and time **C**: Spatial asynchrony of environmental conditions
4 generates asynchronous fluctuations in ecosystem properties across space, thereby stabilising
5 total biomass or yield at the regional scale (as measured by the sum of the two black curves).
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7 Horizontal arrows represent dispersal, which helps maintain rare species in a site when
8 environment conditions are unfavourable. The same red and blue species are shown in the two
9 sites for simplicity, but changes in species composition are expected at large spatial scales.
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11 Local fluctuations in species contributions to ecosystem functioning are assumed to be periodic
12 for simplicity, but they could be also stochastic, with similar outcomes.
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24 **Fig. 3.** Efficiency frontiers of the productivity of boreal forests in Québec under current climate
25 (left) and a future climate scenario (right). The colour gradient represents variations in the
26 proportions of balsam fir and aspen, from pure balsam fir monocultures (dark red) to pure aspen
27 monocultures (dark blue). Simulations were conducted with the observed/projected variation in
28 annual temperature, total precipitation and drought code (solid lines). We also consider a
29 scenario with reduced variation in climate, corresponding to 0.1 of the observed/projected
30 standard deviation of climate parameters in order to approximate the intercept of the efficiency
31 frontier (risk-free scenario, dotted lines). Methods: We investigated the effects of climate and
32 competition on basal area increment using growth cores from individual trees sampled in
33 natural forests through the permanent sampling plot survey of Quebec's Ministère des Forêts,
34 de la Faune et des Parcs. We selected 455 sample plots where the two species were present
35 along a gradient from pure stands to perfectly mixed stands. Individual basal area increment
36 (m^2/yr) was modelled using linear mixed models with fixed effects (annual average
37 temperature, annual total precipitation, drought code, diameter at breast height, total
38 competition, proportion of interspecific competition, drainage, soil texture) and random effects
39 (individual, plot) (Aussenac, 2018). We then projected annual basal area increment (m^2/ha) for
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3 a hypothetical stand of 250 trees of 20 cm DBH under current and future climate conditions.
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5 We generated 1,000 random draws of current and future climate conditions based on the
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7 observed average and standard deviation of historical climatic conditions and for climate
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9 projections under RCP8.5 scenario for an average plot located in the centre of Quebec's boreal
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11 forest.
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17 **Fig. 4.** Synthesis of biological and economic insurance and portfolio theories. **A:** Shared
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19 features across disciplines. The ecological functioning (or economic value) of a community (or
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21 portfolio) depends on its composition, selected from a larger pool of species (or assets), whose
22
23 individual properties fluctuate due to external factors. Theories focus on the aggregated
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25 properties of a community (or portfolio) across time, as well as across space (across different
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27 communities or portfolios). **B:** Classic economic portfolio theory encompasses both selection
28
29 and buffering effects (Table 1), with two main assumptions. First, asset values are set by global
30
31 market prices and are thus synchronised across portfolios. Second, initial investment is
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33 distributed among assets without any form of niche complementarity, which enhances species
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35 performance in ecological communities. These assumptions lead to a mean–variance trade-off,
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37 which is less common in ecology. **C:** Economic insurance can be conceptualised as initial
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39 selection for lower-return but lower-variance assets. Options represent delayed selection,
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41 allowing future positive selection effects that exploit directional trends in asset value.
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Figure 1



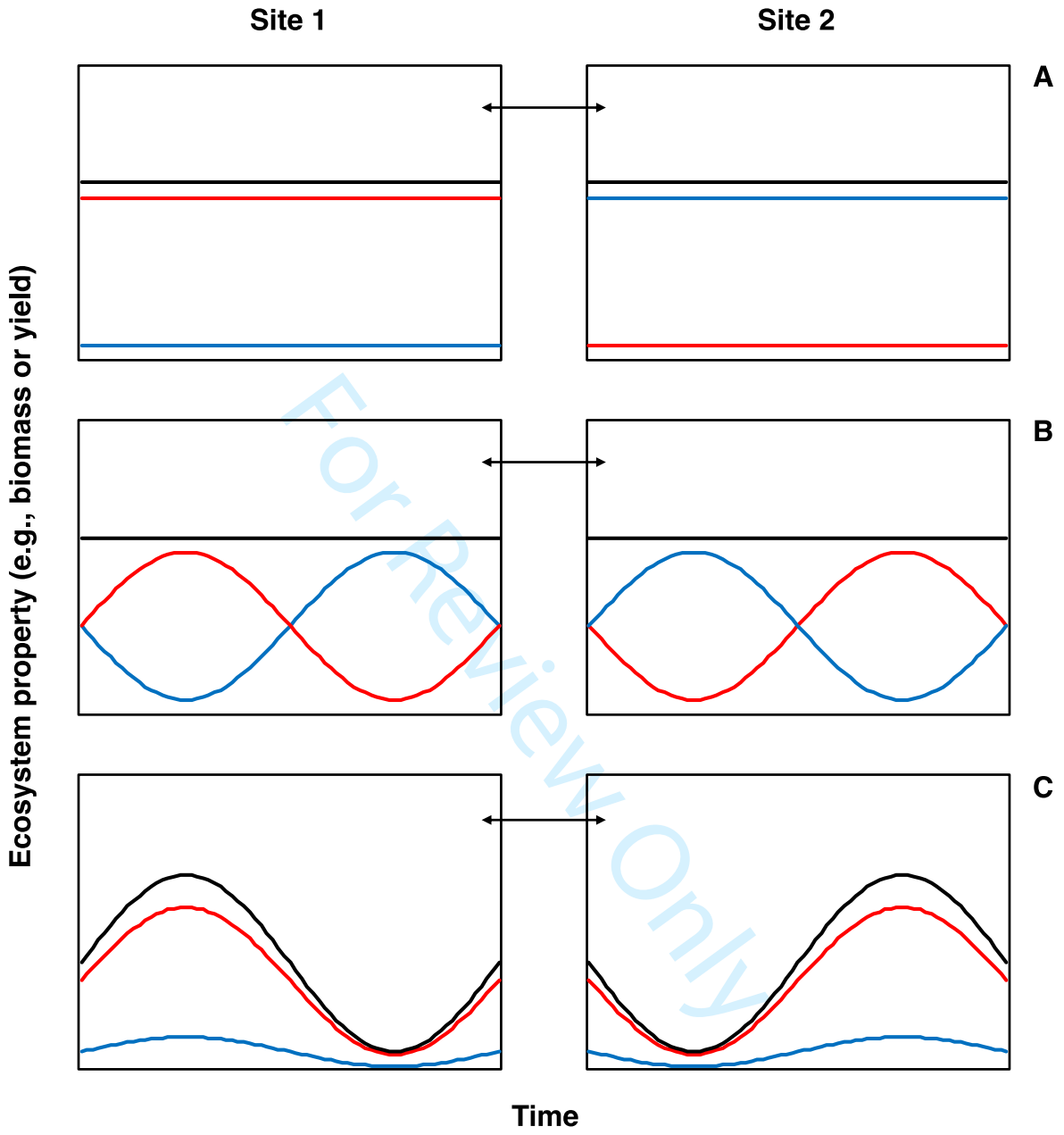
Expected Utility Theory

Portfolio Theory

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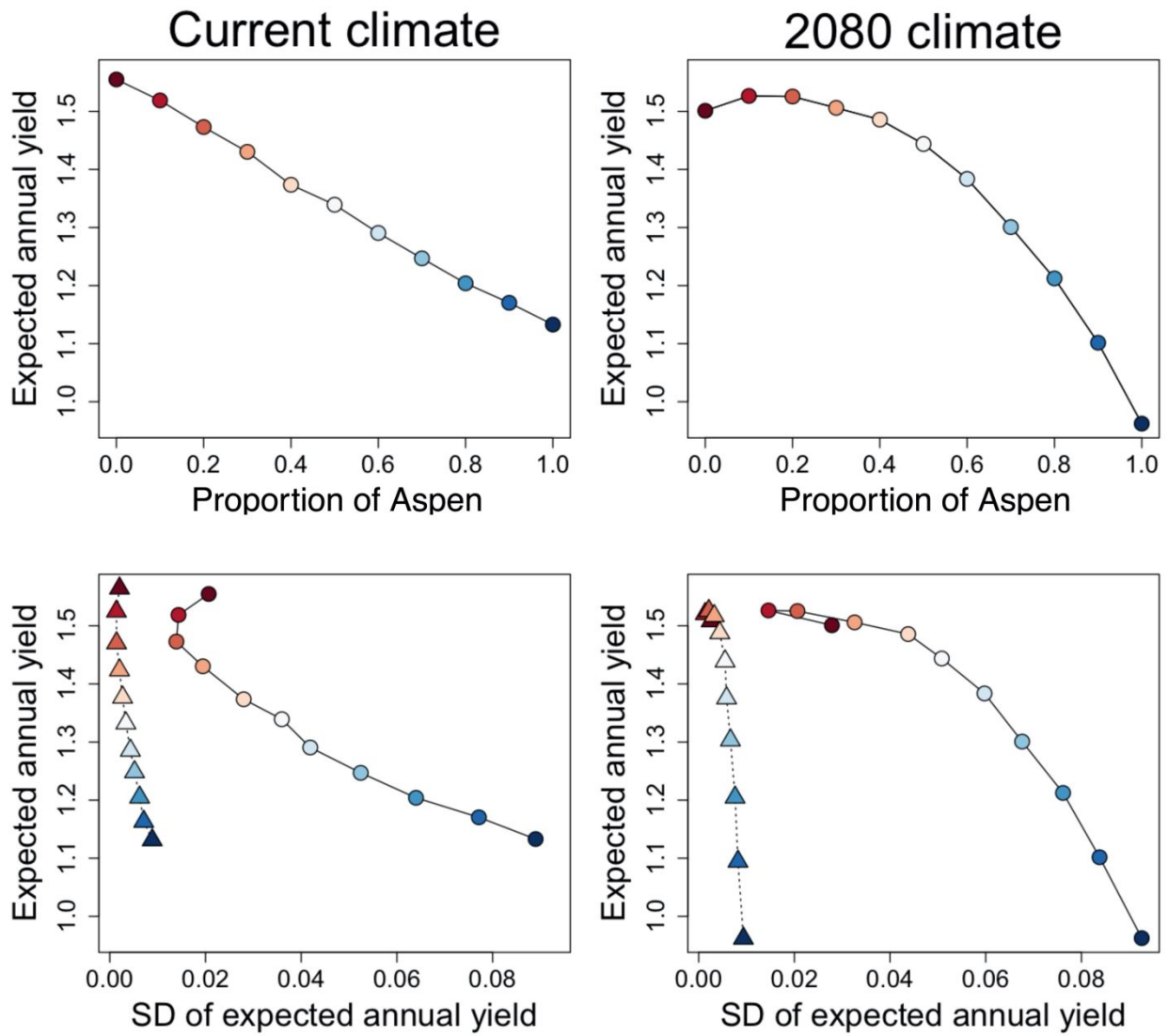
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Figure 2



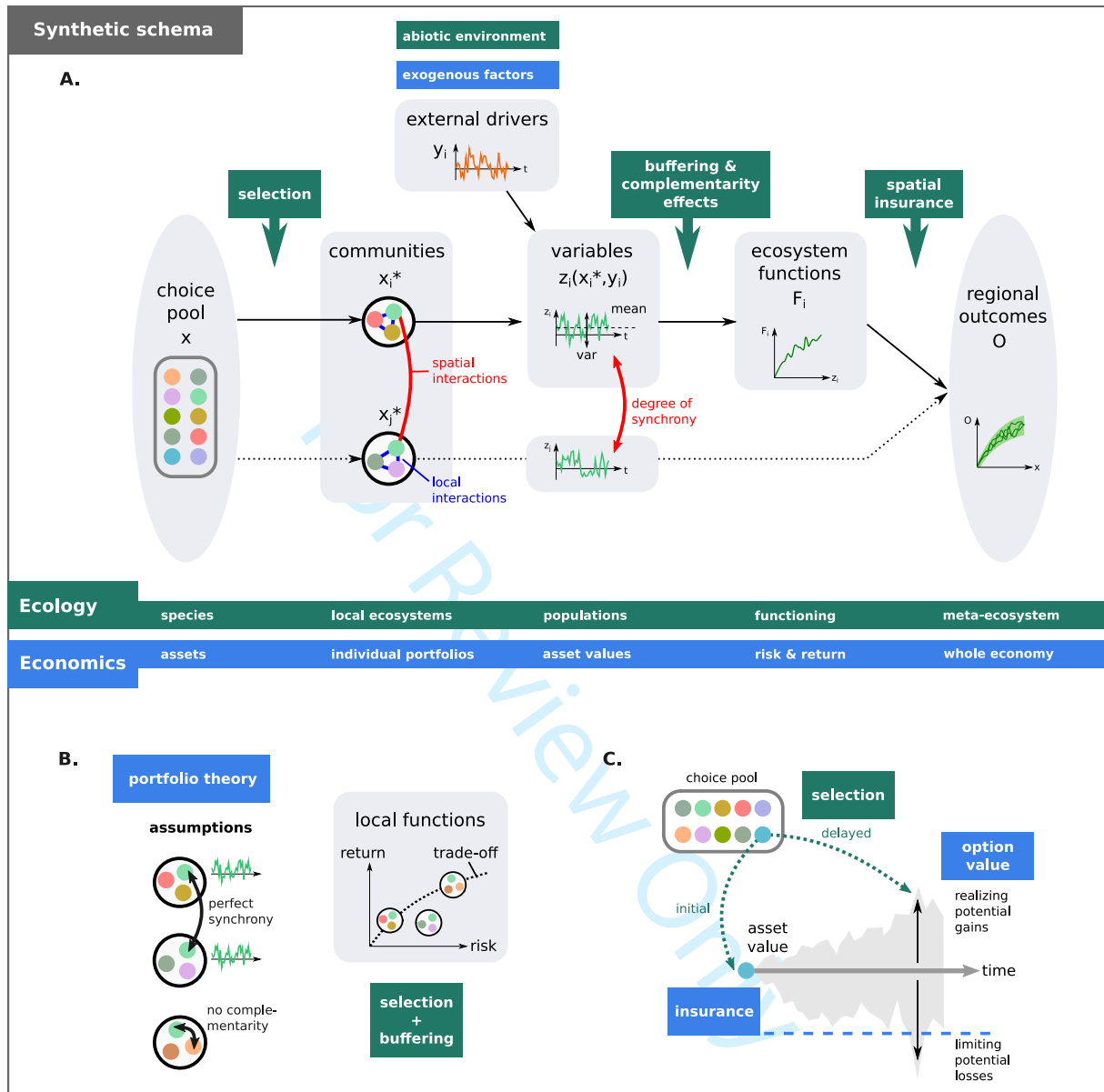
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Figure 3



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Figure 4



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