



# Key questions for understanding drivers of biodiversity-ecosystem service relationships across spatial scales

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Received: 20 July 2023 / Accepted: 10 January 2024 / Published online: 14 February 2024  
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## Abstract

**Context** Biodiversity loss is predicted to have significant impacts on ecosystem services based on previous ecological work at small spatial and temporal scales. However, scaling up understanding of biodiversity-ecosystem service (BES) relationships to broader scales is difficult since ecosystem services emerge from complex interactions between ecosystems, people, and technology.

**Objectives** In order to inform and direct future BES research, identify and categorise the ecological

and social-ecological drivers operating at different spatial scales that could strengthen or weaken BES relationships.

**Methods** We developed a conceptual framework to understand the potential drivers across spatial scales that could affect BES relationships and then categorized these drivers to synthesize the current state of knowledge.

**Results** Our conceptual framework identifies ecological/supply-side and social-ecological/demand-side drivers, and cross-scale interactions that

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influence BES relationships at different scales. Different combinations of these drivers in different contexts will lead to a variety of strengths, shape, and directionality in BES relationships across spatial scales.

**Conclusions** We put forward four predictions about the spatial scales that the effects of biodiversity, ecosystem service management, ecosystem co-production, and abiotic linkages or effects will be most evident on BES relationships and use these to propose future directions to best advance BES research across scales.

**Keywords** Spatial scale · Species complementarity · Sampling effects · Ecosystem service demand · Cross-scale interactions · Ecosystem service co-production

## Introduction

Earth's ecosystems and species are currently undergoing a mass extinction event due to human activities (IPBES 2019), with many ecosystem services crucial for human well-being also being degraded or lost, often due to the same drivers (e.g., land-use change, overexploitation, climate change; (IPBES 2019)). While there is evidence that biodiversity loss can impact the provision of many ecosystem services (Balvanera et al. 2006; Cardinale et al. 2012; Bennett et al. 2015; IPBES 2019), it is not always the primary driver (Srivastava and Vellend 2005). This is because biodiversity-ecosystem service (BES) relationships depend on both *ecological* and *socioecological* processes that operate and interact across spatial and temporal scales (Scholes et al. 2013; Provost et al. 2023). Therefore, the scales at which biodiversity effects are the strongest or most evident for a specific ecosystem service may be different from the scales at which the effects of human activities on that same ecosystem service are strongest. Currently, it is unclear how the importance of these ecological and social drivers vary across scales and impact observed BES relationships. This is a key and urgent knowledge gap both fundamentally but also for conservation actions, especially since policies intended to simultaneously safeguard biodiversity and ecosystem services (e.g., UN Sustainable Development Goals; Kunming-Montreal Global Biodiversity Framework) are applied across multiple spatial scales and jurisdictional boundaries.

Foundational experimental and theoretical work on the mechanistic links between biodiversity and ecosystem functioning (BEF) has provided strong evidence that increasing diversity (usually species richness (Balvanera et al. 2014) but increasingly evenness, functional, or trait diversity (Díaz et al. 2007; Lavorel et al. 2013; Gross et al. 2017) – is required to provide increasing numbers or levels of ecosystem functions (Isbell et al. 2011; Tilman et al. 2014; O'Connor et al. 2017). Mechanistically, there are several biological processes (e.g., niche complementarity, selection effects/competition, facilitation, or mass ratio effects (Tilman et al. 2014)) that lead to a greater efficiency in the capture of resources, biomass production, and decomposition and recycling of nutrients as diversity increases (Loreau 2010). In turn, these increases in functions can presumably result in greater ecosystem service supply and multifunctionality (Soliveres et al. 2016; Hautier et al. 2018; Provost et al. 2023). However, most of this research has been conducted using small-scale experiments spatially (e.g., 1–100 m<sup>2</sup>) (Gonzalez et al. 2020; Qiu and Cardinale 2020). Additionally, over 30 years of research in landscape ecology have shown the critical importance of spatial scaling and the influences of spatial scale on fluxes of organisms, materials and energy across the landscape (Wiens and Milne 1989), on feedbacks and interactions across systems (Peters et al. 2004) and on hierarchies of scale in understanding dynamics of landscapes (O'Neill et al. 1989). Consequently, it is clear that spatial scale is likely to affect BEF relationships, which has led to increasing attention both conceptually and empirically.

Over the past two decades, a growing number of BEF studies have begun to investigate whether and how biodiversity effects vary (i.e., amplify, weaken, or remain relatively constant) in ecosystems across a range of spatial scales, and the extent to which knowledge from small-scale experiments can be extrapolated and scaled up to inform conservation at landscape scales (Isbell et al. 2017; Gonzalez et al. 2020). For example, new empirical studies and syntheses at broader spatial scales (e.g., ecosystems and landscapes) have explored how biodiversity affects ecosystem functioning, with a particular focus on biomass production in larger and more natural systems (e.g., forests, grasslands, marine) (Grace et al. 2007; Mora et al. 2011; Duffy et al. 2017; Felipe-Lucia et al. 2020; Provost et al. 2023). These studies have

revealed that after statistically controlling for confounding abiotic factors, biodiversity effects are common in nature and likely more pronounced in real landscapes than previously reported from controlled experiments (Duffy et al. 2017). Nevertheless, these studies thus far have mainly focused on how biodiversity affects biological control or how biomass impacts crop yield, carbon sequestration, and fodder yield (Cardinale et al. 2012) and generally fail to incorporate social-ecological dynamics, although this is starting to be addressed (e.g., Provost et al. 2023).

While the research described above has focused primarily on ecological processes, ecosystem service provision across scales can also be impacted by social drivers (e.g. demand/preferences), anthropogenic capitals (e.g., technologies, human and social capital), and more (e.g., management actions, investments). For example, food provision from croplands often depends on synthetic inputs and mechanisation at the farm scale that, in turn, can alter the relationships between food production and biodiversity at landscape scales (Provost et al. 2023). Similarly, recreation at the local scale often requires accessible infrastructure (trails, parking), or land use change that can in some cases lead to biodiversity loss at both local and regional scales (Miller et al. 2022; Virtanen et al. 2023). Thus, as the scale of observation varies, changes in the relative importance of ecosystem service supply and demand could produce more variable outcomes for observed BES relationships. One potential outcome is that the direct effects of biodiversity on ecosystem service provision might become less straightforward and more difficult to observe and quantify at broad spatial scales (Balvanera et al. 2014; Ricketts et al. 2016).

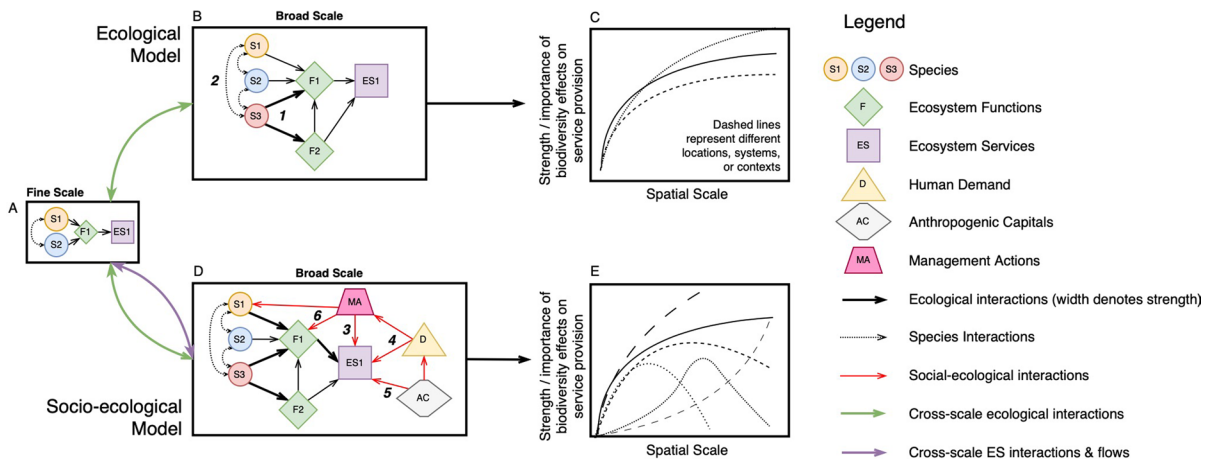
Consequently, different from BEF work, understanding BES relationships across scales is almost certainly complex because: (1) the different processes by which biodiversity affects different ecosystem services are likely service- (Balvanera et al. 2014) and scale-dependent (Gonzalez et al. 2020); and (2) other capitals (e.g., human and social capitals), in addition to natural capital, also play an important role in ecosystem service provision at different scales (Palomo et al. 2016; Barraclough et al. 2022) and can also influence the effects of biodiversity on specific services. Thus, across spatial scales it currently remains substantially challenging to predict which ecological, social, or socio-ecological processes are operating or

are most important for determining BES relationships for different ecosystem services.

Here, in this Perspective paper, we develop a conceptual framework to help identify and categorise the different ecological and social-ecological drivers operating at different spatial scales, or across scales, that might strengthen or weaken BES relationships. Changes in spatial scales involve both extent and resolution; here we include both but emphasise changes in spatial extent. Based on our framework, we then synthesize the literature to understand what the current state of knowledge is around drivers of BES relationships across scales in order to identify knowledge gaps. Our paper does not intend to provide an exhaustive list of drivers or a full and complete literature review of the field, nor is our framework capable of capturing all possibilities, given the social-ecological complexities as previously elaborated. Instead, we use the framework to help formulate hypotheses and identify research questions that we believe will help inform future research needs to improve understanding of BES relationships across scales.

### Conceptual framework of BES relationships across spatial scales

We present our heuristic conceptual framework in Fig. 1. Following the ecosystem service cascade model (Potschin and Haines-Young 2011), species ( $S_1$ ,  $S_2$ , etc.) that make up a community or ecosystem contribute to ecosystem functions ( $F_1$ ,  $F_2$ ) that produce an ecosystem service ( $ESI$ , Fig. 1 Box A). As spatial scale (e.g., the scale of observation) increases, observed environmental heterogeneity is assumed to increase, leading to more niche opportunities and increased species observed at broader scales (Fig. 1 Box B). Following an ecological model of service provision, these additional species contribute to greater ecosystem function ( $F_1$ ) and additional functions ( $F_2$ ), and thus increased ecosystem service provision becomes apparent (Fig. 1 Box B, Arrow 1). In our example, this broader scale is therefore more appropriate for evaluating this specific BES relationship since it encompasses the complete suite of species and functions that contribute to ecosystem service provision. As a result of these ecological dynamics, observed relationships between spatial scale and the strength or importance of biodiversity



**Fig. 1** Potential pathways and relationships between biodiversity and ecosystem service provision with increasing spatial scale, considering either a simple ecological (top row) or more complex socio-ecological view (bottom row) of ecosystem service provision (see “Conceptual Framework” section for full details). For simplicity we consider only two functions and one service while in reality numerous functions contribute to and interact to provide multiple services. We have also excluded

effects of abiotic variables on functions and services. We also focus on one potential driver (increasing extent of observation increases the number of niche opportunities and allows additional species to contribute to a function that leads to an ecosystem service) and do not include other potential drivers (e.g., changes in population sizes, reduced selection effects, changes in relative impacts of biodiversity versus abiotic drivers)

on ecosystem service provision will increase and saturate as spatial scale increases (Fig. 1 Box C), but will also vary in shape and strength across locations or contexts (different dashed lines) due to the level and scale of environmental heterogeneity in the system, the amount of functional redundancy between the species present, stochasticity in community assembly, as well as the strength and directions of species interactions, complementarity, or sampling effects (Fig. 1 Box B, Arrow 2).

However, when a more socio-ecological model of ecosystem service provision is considered that incorporates human demand, management actions and anthropogenic capitals (Fig. 1 Box D), BES relationships across scales could vary even more substantially (Fig. 1 Box E). This arises because in addition to ecological effects across scales, changes in management actions (MA) to increase a focal service (Fig. 1 Box D, Arrow 3), changes in human demand (D) for specific ecosystem services (Fig. 1 Box D, Arrow 4), and changes in anthropogenic capitals (AC – human, social, physical, and financial capitals; Fig. 1 Box D, Arrow 5) that in turn influence human demand for services, management actions, and ultimately ecosystem service provision, can change. In particular, management actions can themselves impact species

(e.g., population sizes) or ecosystem functions (Fig. 1 Box D, Arrow 6), therefore influencing service provision. Given these more complex socio-ecological interactions across spatial scales, we predict that this will lead to more varied relationships between biodiversity and ecosystem services across spatial scales, including both stronger and weaker relationships, or ones where BES relationships approach zero, at broad spatial scales (Fig. 1 Box E).

In addition to ecological and socio-ecological interactions, cross-scale interactions (Fig. 1) are also likely to impact BES relationships. Cross-scale interactions are defined as synergistic and/or antagonistic interactions among multiple environmental drivers across multiple spatial scales (Darling and Côté 2008). Cross-scale interactions can be driven by: (1) effects of biophysical connections; (2) effects of dominant abiotic, land use, or management drivers; (3) combined effects of biophysical linkages and dominant drivers; and (4) artificial scale influences (Qiu et al. 2018). These cross-scale interactions can lead to positive or negative relationships between ecosystem services (Bennett et al. 2009), and likely a variety of context-dependent effects of management actions and biodiversity on ecosystem service provision across scales (Spake et al. 2019). For example, intensive

agriculture practices are a management action that leads to increased local or field-level food provision but negatively affects water quality at broader watershed scales downstream (Rodríguez et al. 2006). Similarly, competing land uses (e.g., agriculture versus working forests versus conservation areas) provide different suites of services at different scales (Felipe-Lucia et al. 2014; Dade et al. 2019). Further, the effect of common drivers of services may be context-specific due to cross-scale interactions, both in terms of identity and strength. For example, in some parts of England increasing forest cover by planting trees can increase risk of invasive species colonisation as new forests increase connectivity while in other locations this is not the case (Spake et al. 2019).

From our conceptual framework what arises is the existence of a wide variety of different and distinct pathways and drivers that could affect BES relationships across scales, especially when the full suite of socio-ecological drivers and dynamics are considered (Fig. 1 Boxes D & E). In the next section of the paper, we attempt to provide an overview of what is currently known about these pathways at single scales and across scales.

### Ecological or supply-side pathways

Current understanding of species-area relationships (SAR) predicts that the total number of species (species richness) encountered will increase as the extent or area of observation increases (Turner and Tjørve 2005). How might this impact BES relationships across spatial scales? In this section we identify several possible *ecological or ecosystem service supply-side pathways* that link biodiversity to service provision and which likely vary across spatial scales (Table 1).

#### Species complementarity

Species differ in their use of limiting resources, thereby reducing interspecific relative to intraspecific competition (Tilman 1999). As the observed spatial scale increases, environmental heterogeneity and niche variety also tend to increase, leading to increasing total numbers of species, higher overall ecosystem functioning (Cardinale et al. 2004; Tscharrntke et al. 2005; Reich et al. 2012; Thompson

et al. 2018) and potentially increased service provision underpinned by these functions. Species complementarity (Fig. 1 Box B) is predicted to be especially important for productivity-underpinned services and has been observed at single scales for forage, bioenergy, timber production (Gamfeldt et al. 2013; Isbell et al. 2018), and other services such as pest control (Dainese et al. 2017). While changes in the strength or importance of complementarity for services across scales have not been fully explored (Dimitrakopoulos and Schmid 2004; Qiu and Cardinale 2020), stronger effects at broader spatial scales (e.g. ecological community and regional scales) have been found for marine biomass (Bracken et al. 2017) and forest biomass production (Luo et al. 2019).

#### Sampling or species identity effects

Sampling or species identity effects refer to the fact that more diverse communities have a higher probability of including species with particularly effective functional traits that enable competitive dominance in the community (Cardinale et al. 2004), thus enhancing overall ecosystem functioning (Hector et al. 2002; Slade et al. 2019). Hence, as scale of observation increases and more species are encountered, there is an increased chance that the species disproportionately important for the ecosystem functions that underlie an ecosystem service will be present (Fig. 1 Box B Arrow 1). Empirical examples of the importance of specific species at single scales include pollination services (i.e., existence of particularly effective pollinators) (Albor et al. 2019), and recreational services (i.e., existence of iconic and/or rare species) (Dee et al. 2019; Lavorel et al. 2020). Across spatial scales, one example involves disease regulation (i.e., existence or loss of important host species (Ostfeld and LoGiudice 2003).

Contrastingly, some ecosystem services in specific contexts are related to individual species, often those that are most abundant or that are the most functionally important for a specific ecosystem service. For example, the abundance of common and dominant pollinator species, rather than pollinator richness overall, can be most important for pollination delivery (Winfree et al. 2015); monocultures of specific tree species can maximise individual services (Himes et al. 2020), although not multiple services at the same time (Gamfeldt et al. 2013); and for many

**Table 1** Examples of ecological and socio-ecological drivers and their potential effects on BES relationships across spatial scales. These drivers can either strengthen or weaken BES relationships as spatial scale increases. Examples of both types of effect are provided where applicable

Driver type	Predicted effect on BES relationships across spatial scales	Potential driver details	Selected single scale examples of driver	Selected multiscale examples of changing BES relationships
<i>Ecological or Supply-side drivers</i>				
Complementarity	Strengthen	Species diversity increases at broader scales, more environmental niches are occupied, resource use and production are maximized, leading to increased ES provision.	Species diversity drives pest regulation (Wilby and Thomas 2002; Dainese et al. 2017), forest ES (Gamfeldt et al. 2013), and various ES (Luck et al. 2009)	Marine production from site to regional scales (Bracken et al. 2017), forest production from neighbourhood to community scales (Luo et al. 2019)
Sampling or species identity effects	Strengthen	Communities with increased species diversity at broader spatial scales will have a higher probability of including those species that are key to ES provision.	Dominant/unique species drive grassland production (Hector et al. 2002); recreation (Dee et al. 2019); and biological control (Tschamtké et al. 2005)	Pollination from plot to community scales (Albor et al. 2019)
	Weaken	Species diversity increases at broader spatial scales, but at the same time, the relative species abundance of key ES provider species decreases.	Relative decrease in key species for pollination (Winfree et al. 2015), forest ES (Himes et al. 2020), and cultural ES (Bastian 2013)	Cultural services of rare species from local to global scales (Dee et al. 2019)
Species interactions	Strengthen (Facilitation)	Positive interactions between species at broader scales as environmental conditions vary (Mulder et al. 2001) increases resource-use efficiency, ecosystem functioning, and ES provision.	Positive interactions important for theoretical ES (Slade et al. 2019), and seed dispersal (García and Martínez 2012)	Food production/wave attenuation from site to reef scales (Reeves et al. 2020)
	Weaken (Competition)	Competition between species at broader scales leads to reduced abundances of key service providing species and trade-offs between provision of individual services and multifunctionality (Slade et al. 2019)	Competitive interactions lead to monocultures having increased functioning for dung beetles (Slade et al. 2017) and trees (Hertzog et al. 2019)	None found.



**Table 1** (continued)

Driver type	Predicted effect on BES relationships across spatial scales	Potential driver details	Selected single scale examples of driver	Selected multiscale examples of changing BES relationships
Abiotic conditions	<p>Weaken</p> <p>Strengthen</p>	<p>Greater abiotic variation with increasing spatial scale affects ES provision more strongly than changes in biodiversity.</p> <p>Strong influence of abiotic factors at local scales for ES weaken BES relationships, but these abiotic effects weaken at broader scales relative to diversity effects.</p>	<p>Abiotic conditions impact multiple ES (Crouzat et al. 2015), experimental design to test for (Redlich et al. 2022)</p> <p>Abiotic flows key to the provision of a range of ES (Meulen et al. 2016)</p>	<p>None found.</p> <p>Stronger functional trait effects on tropical carbon stocks across 160 m<sup>2</sup> to 640 m<sup>2</sup> plots (Bu et al. 2019), weaker environmental effects on tree growth from 400 m<sup>2</sup> to 3600 m<sup>2</sup> plots (Hao et al. 2018)</p>
<i>Socio-ecological or Demand-side drivers</i>				
Ecosystem service demand	Weaken	Ecosystem service demand varies across scales due to changes in predominant land use or other social-ecological dynamics which results in shifts in BES relationships across spatial scales.	Community and social values impact ES demand and provision (Raymond et al. 2009; Ripper and Kyle 2014)	Variation in relevant stakeholders and ES demand from local to national scales (Geizendorffer and Roche 2014), variation in institutional scales from municipal to international (Hein et al. 2006)
Ecosystem service co-production & management actions	Strengthen	Biodiversity at broader spatial scales (e.g., landscape diversity) drives demand and the provision of services that are also realised at these broader scales.	Landscape-level processes can impact ecosystem service demand (Metzger et al. 2021)	Nature-based recreation hotspots more consistent at national than regional scales (Scholte et al. 2018), landscape aesthetics from local to landscape scales (Tribot et al. 2018)
Ecosystem service co-production & management actions	Weaken	Changes in the management actions and the contribution of anthropogenic capital to ES provision across spatial scales can alter the relative contribution of biodiversity and natural capital to service provision.	Fisheries (Deutsch et al. 2007; Stuart-Smith et al. 2013), multiple ES in EU biosphere reserves (Palliwoda et al. 2021)	ES managed differently across local to regional scales could lead to ES supply-management scale mismatches (Raudsepp-Hearne and Peterson 2016).

**Table 1** (continued)

Driver type	Predicted effect on BES relationships across spatial scales	Potential driver details	Selected single scale examples of driver	Selected multiscale examples of changing BES relationships
<i>Cross-scale interactions</i>				
Supply-side ecological interactions	Strengthen	Ecological processes at one spatial scale that are positively related to biodiversity influence and feedback on processes at another scale that determine ecosystem service provision.	Carbon and plant productivity (Chen et al. 2018), biodiversity and crop production (Daimeise et al. 2019), water quality and recreation (Doi et al. 2013), food production and regulating services (Tschamtkke et al. 2005)	Trophic cascades across station to bay scales impacts marine water quality (Donadi et al. 2017)
Ecosystem service flows & spatial lags	Weaken	Locations where ecosystem services are supplied where strong BES relationships exist may not be the same locations where ES are delivered or used. Thus, linking biodiversity with ES provision may depend on accurately determining ES “servicesheds.”	Not applicable.	Soil erosion control (García-Nieto et al. 2013), cultural services (Semmens et al. 2018), recreational services (Bagstad et al. 2019)

cultural or regulating services individual or small groups of species are key (Bastian 2013). Thus, as the spatial scale of observation increases and environmental heterogeneity and biodiversity increase (Stein et al. 2014), while rare species may be encountered driving increased species richness, these rare species may not contribute significantly to ecosystem service provision (Winfrey et al. 2015). Thus, BES relationships may not change significantly across spatial scales or may instead vary depending on the exact species-abundance variation that occurs across scales.

### Species interactions

Species interactions (i.e., competition or facilitation) can alter the efficiency by which ecological communities utilise resources and/or the total magnitude of resource use (Bruno et al. 2003). As broader scales contain greater numbers of species, this could lead to changes in the relative strength or direction of species interactions with both positive and negative impacts for service provision (Fig. 1 Box B *Arrow* 2). For example, increasing the scale of observation could lead to increased probability of encountering positive species interactions that enhance ecosystem functions and associated services, leading to stronger positive BES relationships. Examples of positive species interactions occurring at greater spatial scales include oyster reefs and associated aquaculture production and wave attenuation services (Reeves et al. 2020), plant-plant facilitation for coastal wetlands and their services (Zhang and Shao 2013), and positive interactions between frugivorous birds for seed dispersal (García and Martínez 2012). Conversely, relative abundances of species and the strength of competitive interactions between species will also vary across spatial scales, which can also influence service provision and potentially weaken BES relationships. For example, if combinations of species with strong interspecific competition are more likely to be encountered at broader scales, this could reduce the per capita contribution of each species to ecosystem functioning and ultimately the provision of individual services (Slade et al. 2019). Further, while increased diversity at broader scales could increase overall service multifunctionality, it could also lead to decreased provision of individual services (Fanin et al. 2018) and thus weaken individual BES relationships.



### Abiotic conditions

While biodiversity can contribute positively to the ecosystem functions that underlie ecosystem services, at the same time other environmental drivers also impact ecosystem services. For example, both abiotic drivers (e.g., rainfall and temperature) and biotic drivers (e.g., productivity) are known to impact soil organic carbon and climate regulation (Gaitán et al. 2019). A recent review of biodiversity impacts on ecosystem functioning (Plas 2019) found that abiotic drivers were more important than biodiversity effects for 66% of the cases examined, although this depended on the function or service in question and requires additional empirical evidence. Yet, in other cases biodiversity has been shown to be equal to or stronger than other abiotic variables (Paquette and Messier 2011; Hooper et al. 2012). In those cases where abiotic conditions vary more than levels of biodiversity at broader spatial scales and these abiotic conditions also strongly impact service provision, this could weaken BES relationships at larger spatial scales. At the same time, abiotic conditions and species diversity are often highly correlated (Stein et al. 2014), and therefore separating abiotic effects from other ecological effects is likely difficult. Therefore, strong BES relationships may not always indicate that species diversity is the strongest driver of service provision.

### Cross-scale ecological interactions

Some of the ecological processes relevant to one ecosystem service that are positively influenced by species diversity can themselves have impacts on additional ecosystem functions at different spatial scales that underlie other services (Fig. 1 Cross-scale ecological interaction arrows). Thus, as processes such as species complementarity or sampling effects become stronger at broader spatial scales, cross-scale ecological feedbacks could strengthen BES relationships and lead to synergies (e.g., positive relationships) between different ecosystem services. For example, increased species diversity can increase primary production by vegetation (see *Species Complementarity* above) and subsequently soil organic carbon and climate regulation. In turn, higher soil organic carbon, by increasing soil fertility and soil water-holding capacity, can create a positive feedback loop with species richness and

productivity, especially at broader regional or biome spatial scales (Chen et al. 2018). Another example relates to landscape structure and the presence of interspersed or connected patches of habitat more capable of supporting populations of mobile organisms and the ecosystem services they provide (Kremen et al. 2007; Riva and Fahrig 2023). Thus, at fine scales there may be negative relationships between food production and other services provided by natural habitats (pollination, pest control, recreation), but these may shift to positive relationships at landscape or regional scales as natural habitats provide connectivity and resilience to the ecological processes that underlie food production (Tschardt et al. 2005; Dainese et al. 2019).

### Socio-ecological or demand-side pathways

Ecosystem services emerge from complex interactions between people and nature, involving numerous pathways and inputs, both natural and anthropogenic, that can impact final service provision. This complexity and diversity in ecosystem service pathways, which occur across spatial scales, can result in varied BES relationships, and in many cases (but not all) decouple ecosystem service provision from biodiversity change at broader spatial scales. However, for many of the examples below there is, as of yet, little existing empirical work to support the dynamics we propose.

#### Ecosystem service demand

Ecosystem service provision not only depends on the capacity of ecosystems to supply a service, but also on the level of demand for that service by people (Villamagna et al. 2013; Mitchell et al. 2015). At what scale demand is generated for different services can vary because the scale at which the relevant socio-ecological interaction or stakeholder/organisation/institution operates and initiates management actions also vary (Hein et al. 2006; Geijzendorffer and Roche 2014; Lindborg et al. 2017). For example, demand for pollination is generated at the scale of agricultural fields or landscapes, for wild medicinal plants at the level of individuals or institutions, whereas demand for outdoor recreation often occurs at regional scales (Geijzendorffer and Roche 2014). Thus, incorporating

demand into the quantification of ecosystem services across scales has the potential to significantly alter BES relationships (Fig. 1. Box D Arrow 4). In particular, if the biodiversity or species most related to the provision of a particular ecosystem service increase across spatial scales whereas relative demand for that service decreases, this could lead to negative BES relationships at broader landscape spatial scales (Watson et al. 2019). For example, demand at the field or farm scale for agriculturally-relevant services like pollination or pest control might be high, leading to positive BES relationships (Schulp et al. 2014). However, as spatial scale increases, a shift from agricultural- to forest-dominated land cover could occur, leading to lower overall demand and provision for these two services at landscape scales despite potentially increased pollinator diversity at this scale.

#### Ecosystem service co-production

Similar but distinct to changes in ecosystem service demand across scales, the nature of the co-production of services across scales can also shift and change (Fig. 1 Box D Arrow 5). Ecosystem services depend on a number of capitals, including natural, human, social, physical/manufactured, and economic capitals (Palomo et al. 2016). For example, agricultural production depends on soil fertility and primary production (natural capitals), as well as farming infrastructure and technology (manufactured capital), farming knowledge (human capital), and the institutions that support and govern agriculture (social capital). However, the contribution of these different capitals can shift across scales, for example moving from service provision being determined predominantly by natural capital and biodiversity, to being influenced to a greater degree by human or manufactured capitals (Kachler et al. 2023). For example, at local scales communities can depend on local fisheries as their food source, whose abundance is influenced by the diversity of fish (Stuart-Smith et al. 2013) and local knowledge of fishing techniques and stewardship, whereas at larger scales (e.g., metropolitan or continental scales), people may shift towards dependence on supplies from more remote aquaculture or fish farm infrastructures (Deutsch et al. 2007) as trade networks facilitate access to more distant ecosystems. Thus, shifts away from natural capital contributions

across these zones could weaken the link between biodiversity and ecosystem service provision.

#### Cross-scale ecosystem service flows

Ecosystem services are not always produced in situ, but instead can be supplied in one location and then deliver benefits in another via complex ecosystem service flows (Fig. 1 Cross-scale ES interactions & flows) between areas of service supply and use (Costanza 2008; Mitchell et al. 2021). For example, regulation of freshwater amounts and quality often occur in upstream watersheds or ecosystems while the benefits are delivered to downstream beneficiaries (Brauman et al. 2007; Bagstad et al. 2014). Because of this, the biodiversity present in the location where a particular ecosystem service is being used or delivered to beneficiaries may not be directly influencing service provision due to such flows, in which case strong BES relationships may not be detected at fine scales. In other cases, as the spatial scale of the study increases (e.g., to the scale of watersheds or 'service-sheds'), these BES relationships will become apparent. For example, relationships exist between prairie potholes, waterfowl populations, and the recreational services of bird watching and hunting at broad scales but not fine scales (Bagstad et al. 2019). Further, different spatial flows and ecosystem services dynamics can be evident across spatial scales (Andersson et al. 2015). For example, the cultural benefits of monarch butterflies in the USA and Canada are provided at a broad scale by overwintering habitat in Mexico, but also at finer scales between rural areas and urban residents (Semmens et al. 2018). Unfortunately, consistent methods to quantify these flows (Koellner et al. 2019; Chalkiadakis et al. 2022) as well as specific studies investigating the scale of ecosystem service flow and BES relationships are rare.

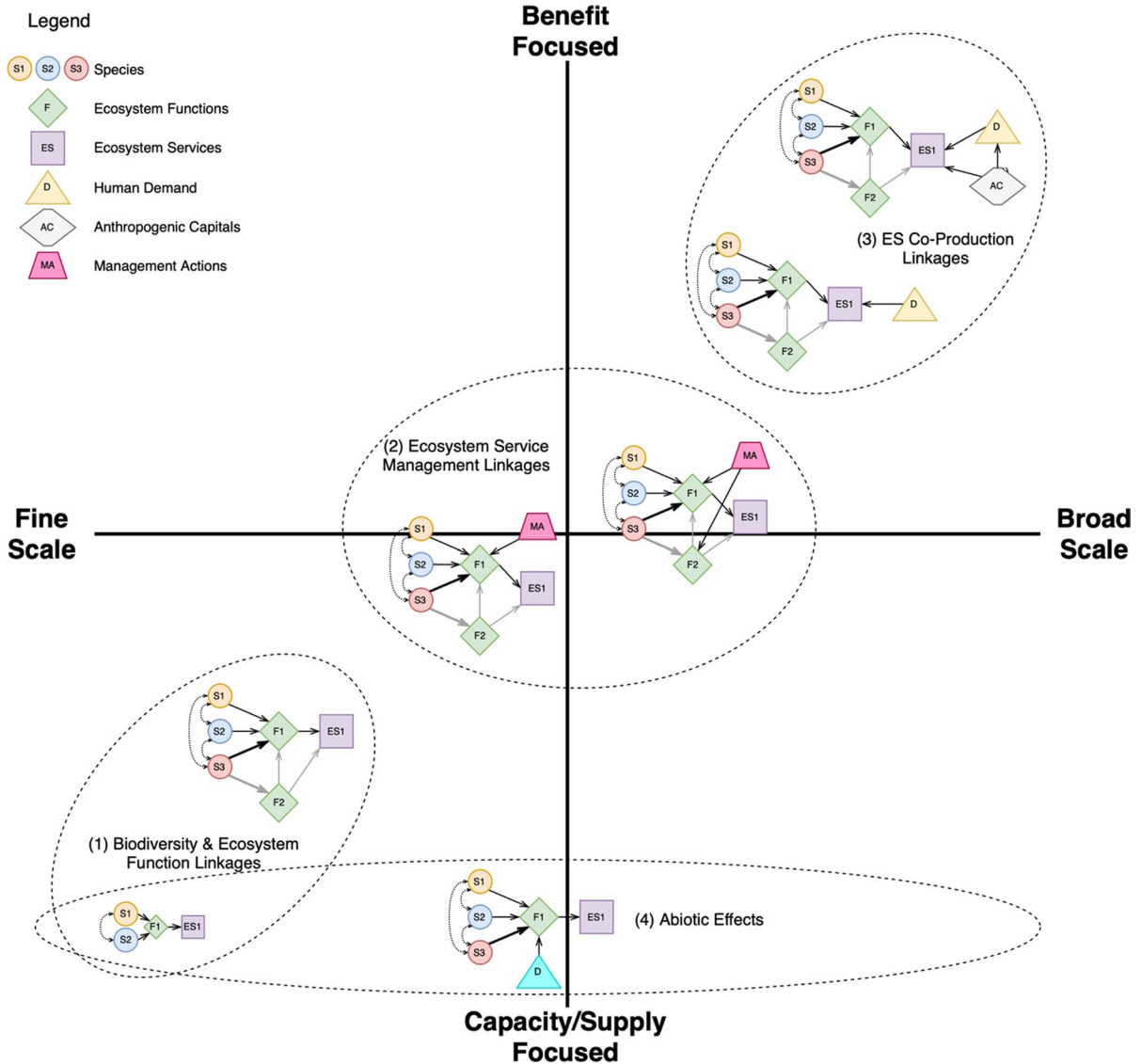
#### Four approaches to advance knowledge on BES relationships across spatial scales

From our review above, it is evident that a variety of ecological and socio-ecological drivers exist that could either strengthen or weaken BES relationships across scales. So how best to move forward and understand BES relationships? Here, we briefly introduce four propositions that could be used as a

starting point to better understand the scale-dependent dynamics of BES relationships and use these to formulate hypotheses, design empirical investigations, and develop predictions about the spatial and conceptual scales at which different processes will be most important for BES relationships (Fig. 2).

Proposition 1

*Ecological BES linkages or drivers will have the greatest importance on ecosystem service supply at fine spatial scales. It is at these fine scales where abiotic conditions and social-ecological contexts*



**Fig. 2** Predicted two-dimensional conceptual scales at which different ecosystem service dynamics will be most important for influencing BES relationships across scales. We expect that (1) ecological linkages involving species and ecosystem functions which generally strengthen BES relationships will be most important at fine spatial scales and when studies focus on service capacity or supply, (2) human management actions

will be most important at intermediate spatial and conceptual scales, and (3) that ecosystem service co-production and shifts in human demand (D) for specific services will be most important at broad scales and when studies focus on measuring actual ecosystem service benefits. We also expect abiotic effects (AB) to be most important at a variety of spatial scales but mainly when the focus is on the capacity/supply of services

are relatively uniform with less spatial heterogeneity across sample locations, allowing ecological processes to dominate and alter the supply of ecosystem services. Thus, we predict that ecological drivers including complementarity, sampling effects, and species interactions are more likely to be strongest at fine spatial scales (e.g., plots, fields, patches) and also when the nature of ES quantification is supply/capacity-focused (e.g., biomass, productivity, nutrient cycling). As spatial scale increases and other variables important to service provision such as human demand and human capitals vary, or when measures of service provision better incorporate actual or realised benefits, we expect overall weaker or more variable BES relationships.

#### Proposition 2

*Human management actions will have the greatest influence on BES relationships at intermediate spatial scales (e.g., ecosystem, landscape).* This expectation arises from the fact that many natural resource and land use decisions, as well as the consequences of human management actions, occur primarily at ecosystem, watershed, or landscape scales where changes to land cover and landscape structure become evident. Thus, at these intermediate spatial scales, changes to landscape structure—by altering species dispersal and biodiversity levels, as well as socio-ecological interactions and ecosystem service flows (Mitchell et al. 2015)—will alter ecosystem service provision and therefore the strength of BES relationships.

#### Proposition 3

*Ecosystem service co-production and demand will have their greatest influence on BES relationships at broad (regional, national, global) scales and when quantification of ES is more benefit-focused.* While differences in environmental values or technologies that drive ecosystem service demand do occur sometimes at the individual, farm/field, or property level, we expect that these processes are most likely to exert substantial influences on BES relationships at much broader scales. For example, when investigating BES relationships across biomes, regions, or countries where the environmental conditions, institutions, or cultural norms have resulted in fundamentally different social-ecological dynamics that contribute to

ecosystem service provision. In this case, the spatial scales at which these effects become most important may vary depending on how human systems of governance, economics, or institutions are organized (i.e., size of nation-states varies significantly).

#### Proposition 4

*Effects of abiotic drivers on BES relationships will be evident at varied scales depending on the scale of abiotic variation and species turnover, and when studies focus on service capacity/supply.* Abiotic conditions change at a variety of scales, from the continental with gradients of temperature or precipitation to the local where soil conditions, topography, and land use can vary across short distances. Thus, effects of abiotic conditions on BES relationships will vary depending on the ecosystem service- and study system-specific context with respect to relevant species turnover with abiotic variables, the scales at which specific abiotic drivers operate, as well as how the scale of observation of the study compares to the scale of abiotic heterogeneity. In addition, since we expect that human demand and changes in anthropogenic capitals can help decouple service provision from abiotic variables, we expect that studies focused primarily on the supply-side of ecosystem services will observe abiotic effects on BES relationships.

#### Key future directions for understanding BES relationships across scales

In this section, we highlight several key future research directions that can advance BES research across scales. First, because the scale at which BES relationships will be strongest or most relevant likely changes depending on the ecosystem service(s) in question, considerable thought should be put into determining the most effective scales at which to measure services and biodiversity. This includes an understanding of the relevant scales at which a service is provided or contributes to human wellbeing, an awareness of the organizational hierarchies that are present across scales (e.g., communities, ecosystems, biomes or municipalities, states, and countries) that influence service provision, identification of emergent processes at broader scales that could influence BES relationships (e.g., connectivity, landscape

heterogeneity, disturbance regimes), as well as the specific spatial scales at which species or functional diversity varies and contributes to service provision for a given context. Second, given the social-ecological nature of ecosystem services, it is important to go beyond measuring ecosystem functions or biomass to quantify actual ecosystem service benefits, such as the amount of calories produced/consumed, quantity of clean water supplied, or quantity and quality of time spent in recreational opportunities. In particular, incorporating or reconciling measurements of ecosystem service supply with demand that are directly pertinent to human well-being, especially for regulating services, will be a fruitful avenue of future research to better understand how service demand, anthropogenic capital, and human values alter BES relationships. Such understanding could also provide more leverage for translating knowledge into management actions. Third, efforts are needed to quantify, measure, and map biodiversity, ecosystem functions, and services across scales. While some research initiatives and monitoring programs have increasingly recognized the importance of multi-scale studies (ResNet, Biodiversity Exploratories), most studies tend to be focused on individual scales. There is a great potential to explicitly build consistent, multi-scale measurements into existing research infrastructures, especially with the increasing adoption of Earth Observations into ecosystem service and biodiversity assessments (Ramirez-Reyes et al. 2019). Such multi-scale research can also be achieved through multi-researcher large-scale projects or research networks (e.g., ResNet, GeoBON). Fourth, research is needed to build multi-scale BES models using current knowledge and modelling frameworks. While there are a plethora of models or model ensembles (e.g., ARIES, InVEST, Co\$ting Nature, SWAT) for quantifying and assessing ecosystem services suitable for varied scales (e.g., local, regional watersheds, or continental assessments; (Vigerstol and Aukema 2011; Bagstad et al. 2013)), there are much fewer models that can characterise and predict the influences of biodiversity on ES across scales. One exception is mathematical or theoretical models for population or community dynamics. Hence, there is an important gap to bridge that: (1) integrates current knowledge of different drivers and underlying BES relationships into dynamic ES models; (2) integrates current ecosystem service assessment models with biodiversity

or community dynamics models; and (3) integrates ecological/biological models with social models, to incorporate the entire system of dynamics and feedbacks that determine service provision. Lastly, while we focused mainly on spatial scales, which is where most of the literature is currently grounded, we also expect that temporal scales could alter and moderate effects of biodiversity on ecosystem functions and therefore service provision (Reich et al. 2012; Isbell et al. 2017; Qiu and Cardinale 2020). In particular, increased species diversity and functional redundancy could influence ecosystem function and service provision stability, thus leading to more reliable ecosystem service provisioning (Biggs et al. 2020). However, there is very limited research thus far exploring the importance and processes through which biodiversity and ES relationships change over time. This limits our ability to understand influences of time lags or temporal scales in mediating BES relationships, as well as feedbacks between biodiversity, ES, management and other human actions.

## Conclusions

A large number of potential drivers can contribute to BES relationships observed across spatial scales. While understanding the spatial dynamics of biodiversity and ecosystem services is central to identifying actions that can conserve both species and the benefits upon which people depend, few studies have explicitly investigated these BES relationships across spatial scales from a social-ecological lens. Identifying key variables to measure across spatial scales, integrating broad-scale biodiversity and ecosystem service data through the use of new Earth observation and modelling tools, and explicitly incorporating different spatial, institutional, and temporal scales into ecosystem service research are all required to fill this gap. Improving understanding of BES relationships across scales is critical as global conservation efforts accelerate and the need to identify actions at multiple scales that can safeguard biodiversity and maintain or increase ecosystem services grows.

**Acknowledgements** The ideas that formed the foundation for this paper were conceived of in part at an organized symposium entitled “Understanding the relationships between biodiversity



and ecosystem service supply, demand, and provision” at the 2017 Ecological Society of America conference in Portland, Oregon, USA. We thank the conference organizers for facilitating this symposium.

**Author contributions** MGEM and JQ led the study conception and design with contributions from all other authors and wrote the first draft of the manuscript. All authors commented on previous versions of the manuscript and read and approved the final manuscript.

**Funding** This research was supported by an NSERC Postdoctoral Fellowship to MGEM.

**Data availability** The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

### Declarations

**Competing interests** The authors have no relevant financial or non-financial interests to disclose.

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