Pathways for cross-boundary effects of biodiversity on ecosystem functioning

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Review

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The biodiversity–ecosystem functioning concept asserts that processes in ecosystems are markedly influenced by species richness and other facets of biodiversity. However, biodiversity–ecosystem functioning studies have been largely restricted to single ecosystems, ignoring the importance of functional links – such as the exchange of matter, energy, and organisms – between coupled ecosystems. Here we present a basic concept and outline three pathways of cross-boundary biodiversity effects on ecosystem processes and propose an agenda to assess such effects, focusing on terrestrial–aquatic linkages to illustrate the case. This cross-boundary perspective of biodiversity–ecosystem functioning relationships presents a promising frontier for biodiversity and ecosystem science with repercussions for the conservation, restoration, and management of biodiversity and ecosystems from local to landscape scales.

Biodiversity and ecosystem functioning

Evidence of massive species loss at the global scale has prompted interest in quantifying how biodiversity relates to **ecosystem functioning** (see Glossary). This fundamental question has grown into one of the most vibrant areas of ecological research, with repercussions for both ecological theory and ecosystem management [1,2]. More than 25 years of effort has shown that biodiversity can be a key driver of ecosystem functioning. Diverse plant communities produce more biomass, do so less variably over time, use resources more efficiently, and exhibit greater resistance to invasive species [3]. Similar relationships exist in aquatic ecosystems between producer diversity and primary production, as well as resource-use efficiency [4], despite large differences in the life forms of the primary producers and other **ecosystem properties** [5]. Effects of biodiversity on plant decomposition are also well documented, although the importance and prevalence are less clear than for plant production [6–8].

Recent advances in this field cover five areas. First, emphasis has shifted from single processes to multifunctionality – the simultaneous influence of biodiversity on multiple **ecosystem processes** [9]. Second, efforts to identify diversity effects have moved towards unravelling the underlying mechanisms [10] (Box 1). Third, mechanistic studies of multitrophic interactions have been completed [11–13]. Fourth, genetic, phylogenetic, functional, or structural diversity, as well as patterns of community assembly, have been considered as biodiversity components in addition to species richness [14–16]. Fifth, studies on natural communities have shed light on biodiversity–ecosystem functioning relationships beyond theoretical and experimental investigations [17].

Despite these advances, the significance of biodiversity in an explicit spatial context remains poorly understood. Biodiversity effects on ecosystem functioning have been studied almost exclusively 'within' a given ecosystem type, but not 'across' ecosystem boundaries or among

Highlights
Theory and experiments have established the significance of biodiversity as a key driver of ecosystem functioning. Similarly, a rich theoretical framework and empirical evidence highlight the ecosystem-level importance of matter, energy, organism, and information fluxes across ecosystem boundaries.

However, tests of biodiversity–ecosystem functioning relationships have focused on effects within ecosystems, largely ignoring consequences across system boundaries.

Numerous well documented linkages between terrestrial and aquatic ecosystems provide an excellent starting point for systematic analyses of 'spill-over' effects of biodiversity on ecosystem functioning between 'donor' and 'recipient' ecosystems.

There are ample opportunities to develop new approaches and leverage existing research infrastructures to examine biodiversity–ecosystem functioning relationships in coupled ecosystems.

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Box 1. Mechanisms of biotic control on ecosystem functioning and its context dependency

Ecological processes are controlled by environmental variables and local biotic factors [65] (see Figure 2 in the main text). Biotic control can be driven by (i) species identity and dominance effects, or by (ii) effects of community composition and diversity:

(i) As a consequence of species trait differences, the presence of particular species can greatly affect rates of ecosystem processes. For example, tree species producing litter rich in calcium, compared with others, influence soil chemistry, fertility, and earthworm abundance and diversity [66]. This concords with the 'mass-ratio-hypothesis' stating that ecosystem processes should be controlled by the dominant primary producers [67].

(ii) The specific functional composition of communities arises from mixing species with different traits and abundances and modifies ecosystem functioning in important ways. In a first approximation, one would expect additive effects when mixing species, based on the effects they have when being present alone. However, changing diversity can also result in emergent properties that can be explained only by synergistic or antagonistic effects resulting from species interactions. **Complementarity** in resource use and **facilitation** are two important mechanisms underlying such interactive effects, as opposed to **selection effects**, which are related to identity and dominance of the species present [68]. Functional composition effects are usually stronger with larger trait differences among species.

The environmental context (i.e., configuration/values of environmental variables) strongly determines whether identity or diversity effects prevail, or whether they are suppressed by abiotic drivers. Woodward *et al.* [62] found that biotic effects associated with differences in community composition and body size of invertebrate consumers influence litter decomposition in streams at intermediate levels of nutrient loading – but they were not very influential at low nutrient levels (nutrient limitation for microbial consumers) nor at high nutrient levels (detrimental pollution, oxygen depletion). The magnitude and timing of resource fluctuations also determines effects of organisms on ecosystems, for example, invader plant performance can be promoted or suppressed, depending on those attributes of nutrient pulses [69]. At larger scales, the timing of resource fluxes can vary across biomes; in temperate regions aquatic and terrestrial prey production is temporally offset and results in reciprocal effects on forest bird and stream fish prey supply, whereas such effects are not observed in Mediterranean regions where offsets do not occur [70].

Thus, instead of assuming ubiquitous relationships between biodiversity and ecosystem functioning within or across ecosystems, a thorough quantification of the potential controlling variables and the partitioning of their relative importance is needed [58,71] (see Outstanding questions).

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landscape patches ([18], but see [19]). This is surprising because concepts such as **resource subsidies**, **allochthony**, and **meta-ecosystem** dynamics provide a rich foundation for exploring cross-boundary relationships [20] (Box 2) which couple ecosystems at scales ranging from centimeters [21] to continents [22]. Closing this knowledge gap is key to evaluating consequences of biodiversity change in a landscape context.

Here, we assess the role of biodiversity in functionally coupled ecosystems, describe three pathways for transboundary biodiversity effects, and suggest an agenda for future research. To illustrate the concept, we primarily draw upon terrestrial–aquatic linkages, given the depth of knowledge on the exchange of organisms and resources and their ecosystem-level consequences across clearly demarcated boundaries [23,24] (Box 2). However, we expect the principles to apply similarly well to other coupled ecosystems (Box 3).

Biodiversity effects across ecosystem boundaries

Theory and empirical studies suggest that biodiversity change in one ecosystem can propagate across ecosystem boundaries to affect the functioning of other ecosystems, mediated by multiple connecting vectors (Figure 1A). These cross-boundary effects can arise through three main types of relationship connecting 'donor' and 'recipient' ecosystems, herein called 'pathways' (Figure 1B). In exploring these pathways, we follow the strict definition of biodiversity–ecosystem functioning relationships involving quantitative aspects of biodiversity that represent gradients of biological variability. This includes evenness, functional trait diversity, genotypic and phylogenetic diversity, structural diversity, and most commonly species richness. We also discuss how local abiotic and biotic conditions influence the pathways, to reveal the scope for potential biodiversity effects on ecosystem functioning in different settings (Box 1; see Outstanding questions).

Box 2. Subsidies, allochthony, and meta-ecosystems

Likens and Bormann [72] and Hynes [73] recognized the importance of organic matter from watersheds as key resources driving community structure, food web configuration, and matter fluxes in recipient aquatic ecosystems. Transport of matter and biologically available energy between ecosystems, including carbon, nutrients, and contaminants, results from run-off, precipitation, air flow, gravitation, animal movements, and other vectors (see Figure 1A in the main text) [22,24,74]. This recognition of cross-boundary exchange has given rise to the subsidy concept [23,75,76], which highlights the importance of active or passive transfer of materials or organisms for other ecosystems [37,77].

Examples include migratory animals that cross ecosystem boundaries and can have large effects on organic matter, nutrient and oxygen dynamics, with consequences for nutrient cycling, energy flow, productivity, and community structure [22,78]. Tree canopies shape stream food webs and biogeochemical processes by supplying allochthonous plant litter [79], giving rise to the notion that forests fuel fish growth [80]. Stream communities and biogeochemistry respond to disturbances such as logging, fire, pathogen-related plant mortality, or beaver dam construction, but also to nutrient leaching from tree canopies, soils, and groundwater into streams [81–85]. Moreover, arboreal invertebrates falling into streams – termed 'arthropod rain' – represent abundant high-quality food for aquatic consumers and contribute N and P to nutrient-poor waters [86] while also influencing food-web structure [40]. When inputs are large, or of high nutritional quality, subsidies become the dominant resource sustaining food webs in the 'recipient' ecosystem, a phenomenon referred to as allochthony [87].

Aquatic ecosystems are typically 'recipients' of resources and organisms, with terrestrial ecosystems serving as 'donors' [37,88]. However, flows can be also reversed and their magnitude can be similar [89,90]. Spectacular examples include marine nutrient inputs to islands from colony-breeding seabirds [91] or mass emergence of aquatic insects from rivers and lakes [34]. Salmon remains contribute significant amounts of nutrients to riparian forests, which can negatively affect plant diversity by shifting plant communities towards nutrient-rich species and influencing trophic relationships in food webs [92,93]. Such linkages are not limited to adjacent ecosystems but can also manifest through teleconnections, that is, links between distinct landscape elements or even geographically distant regions [94]. This includes the transfer of matter and organisms among patches in meta-ecosystems [95,96]. Despite the ubiquity of ecosystem connections, the subsidy and meta-ecosystem concepts have rarely been considered in analyses of biodiversity–ecosystem functioning relationships [11,18,19].

Pathway 1. 'Donor' system biodiversity directly affects 'recipient' ecosystem functioning
Rationale
Direct effects of 'donor' ecosystem biodiversity on the functioning of 'recipient' ecosystems are mediated either through the exchange of resources (e.g., organic matter, nutrients, prey, electron acceptors) or by modifying physical conditions such as light and water availability, temperature, or habitat structure (Figure 1B). Specifically, where diversity in 'donor' communities increases (or decreases) the flow of limiting resources to 'recipient' ecosystems, biomass production or other processes will be stimulated (or restrained). Likewise, favorable or unfavorable abiotic conditions attributable to high 'donor' system biodiversity will, respectively, increase or decrease process rates in the 'recipient' ecosystem.

Evidence
Plant litter is an important subsidy for both aquatic and terrestrial ecosystems (Boxes 2 and 3). Litter diversity can directly affect the functioning of 'recipient' ecosystems through at least two mechanisms that are independent of any effects mediated by the amounts of litter produced in 'donor' ecosystems and transported to the 'recipient'. First, variation among plant species in litterfall phenology prolongs seasonal cross-boundary litter supplies [25]. This mitigates resource limitation in the 'recipient' and thus promotes organic carbon turnover, nutrient cycling, and primary production, as well as microbial and detritivore secondary production [26]. Second, trait diversity of litter from the 'donor' affects rates of resource use in the 'recipient'. Litter traits important for decomposition include toughness, nutrient stoichiometry, and concentrations of inhibitory or essential compounds such as vitamins or fatty acids. Decomposition is stimulated when diversity in these traits facilitates the complementary use of diverse litter resources (elements or organic compounds) by decomposers but is slowed when effects of inhibitory litter constituents prevail [6].

Such effects of riparian plant diversity on litter decomposition have received considerable attention in streams and wetlands. They range from synergistic to neutral and antagonistic [6,8,27].

Glossary

Allochthony: the use of organic matter supplied from outside the boundaries of a 'recipient' ecosystem to support organismic growth in that system, resulting in the incorporation of organic matter into 'recipient' food webs. The concept has been mainly applied to the use of dissolved organic matter received by lakes from their catchments and channeled towards metazoan consumers.

Biodiversity experiment: experimental assembly of replicated communities, thereby creating a gradient of biological diversity (e.g., species richness, functional diversity, or genetic diversity). Extrinsic conditions (e.g., climate, soil, nutrient levels) are standardized across the diversity treatments to isolate effects of biodiversity on ecosystem functioning.

Comparative study design: assessment of biodiversity–ecosystem functioning relationships, along natural gradients of biodiversity, by relating rates of ecosystem processes to biodiversity in a similar number of selected plots or sites per realized diversity level, while attempting to maximize standardization of environmental conditions to minimize confounding effects.

Complementarity: differences between species, functional groups, or genotypes that may (but need not) enhance ecosystem functioning. It encompasses the combined effects of species interactions on mixture performance, including resource partitioning, abiotic facilitation, and biotic interactions. The complementarity effect is a statistical measure of performance of mixtures relative to the performance of the component monocultures.

Ecosystem functioning: the sum of all ecosystem processes.

Ecosystem processes: physical, chemical, and biological transformations of matter and energy involving organisms and their interactions with other organisms and the environment (e.g., primary production, organic matter decomposition, or nutrient transformations such as denitrification).

Ecosystem properties: characteristics of ecosystems such as the size of compartments (e.g., organic matter pools, nutrient stocks, plant or microbial biomass), stoichiometric ratios, the physical structure, the structure of populations and communities, as well as the spatial and

Box 3. Potential cross-boundary biodiversity effects on ecosystem processes in other ecosystems

Ecosystem coupling certainly exists in all biomes around the world. To date, efforts to quantify the functional consequences of biodiversity change across ecosystem boundaries have largely focused on terrestrial–freshwater linkages in biomes ranging from the boreal to the tropical zone (see Table S1 in the supplemental information online). However, examining studies of a variety of other ecosystems can yield insights, even when cross-boundary diversity effects on ecosystem functioning are not an explicit focus of the study.

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Terrestrial–terrestrial coupling

Spatial and functional coupling between managed and unmanaged ecosystems have emerged as a major theme in ecology [97]. On human-dominated land, mosaics of forest remnants and other non-cultivated landscape patches are often intermingled with crop fields, resulting in the exchange of organisms, matter, and energy between distinct ecosystems (Figure I). Biodiversity of these remnants may thus affect matter and nutrient fluxes (e.g., quantity and quality of litter fall, erosion, and sedimentation) or water relations (e.g., root competition, shading, interception). Other examples of potential cross-boundary biodiversity effects on important processes in such landscapes are pollination and insect pest regulation [36].

Marine–terrestrial coupling

Seabird foraging transfers nutrients from marine to terrestrial ecosystems. This has profound impacts on nutrient cycling and primary and secondary productivity on oceanic islands and other land where the birds rest and breed in colonies [22,91]. Seabird colonies across the globe exhibit considerable diversity (Figure II), but there has been little research on potential linkages between seabird species or functional diversity and seabird-related resource fluxes across ecosystem boundaries, influences on environmental conditions, and consequences for ecosystem functioning. Different feeding strategies, phenologies, and other traits provide considerable scope for the diversity of seabird communities to affect terrestrial biodiversity, productivity, and carbon and nutrient cycling. Conversely, intense predation of diverse seabird communities on marine food webs may have direct and indirect repercussions on ecosystem functioning in the ocean.

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Figure I. Biodiversity effects on terrestrial–terrestrial coupling. In many human-dominated landscapes, remnants of natural vegetation are embedded as islands within an often-homogenized agricultural matrix. Photograph: M. Scherer-Lorenzen, showing a forest-agricultural field ecotone in Picardie, France.

temporal variability of these characteristics at different scales.

Facilitation: increase of the performance of one species in response to an increase of another species. It can be driven by changes in the environment (e.g., microclimate, soil properties) which can enrich resource availability for co-occurring species or mediate physical stress.

Meta-ecosystem: a set of landscape elements or ecosystems connected by spatial flows of energy, materials, and organisms across ecosystem boundaries.

Monitoring/sample surveys: observation of biodiversity–ecosystem functioning relationships along natural biodiversity gradients by using a random or grid-based selection of study plots within a region. Environmental variables directly influencing diversity and/or ecosystem functioning can make it difficult to isolate diversity effects.

Removal experiment: manipulation of the diversity of naturally assembled communities by selectively removing various components (e.g., species, functional groups), thus creating a diversity gradient ranging from naturally rich to depauperate. Removal experiments can mimic the loss of species resulting from specific drivers of population decline and thus represent realistic nonrandom extinction scenarios. Such experiments need to include disturbance controls and to be run long enough to allow for potential system recovery.

Resource subsidies: supply of allochthonous resources such as biologically fixed energy, organic matter, including organisms, or nutrients by a 'donor' to a 'recipient' ecosystem.

Selection effect: greater probability that more diverse communities contain species that dominate the community and that have a strong positive or negative effect on ecosystem functioning.
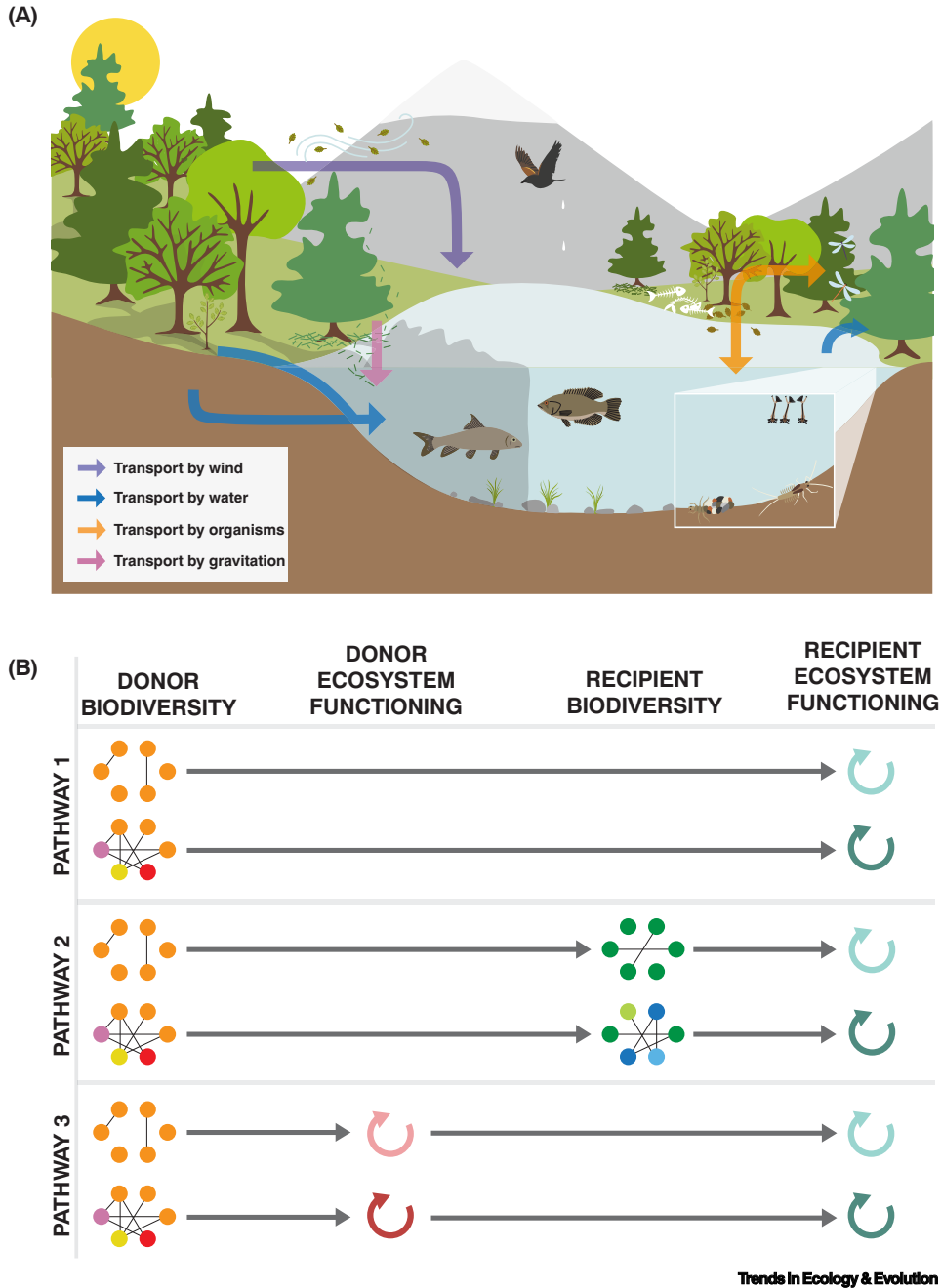
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Figure II. Biodiversity effects on marine–terrestrial coupling. Seabird colonies can transfer large amounts of nutrients (deposited as guano) from marine ecosystems to terrestrial islands or shorelines. Photograph: Alamy Stock Photo, showing seabirds nesting on Staple Island off the Northumberland Coast, UK. Included in the shot are kittiwakes (*Rissa tridactyla*), guillemots (*Uria aalge*), razorbills (*Alca torda*), and a shag (*Gulosus aristotelis*).

Generally, when effects are observed, they tend to be synergistic (see Table S1 in the supplemental information online), as is the case for active fungal nutrient transfer from one litter type to another [6]. Antagonistic litter diversity effects are less common but can occur when inhibitory compounds leaching from one type of litter affect another type nearby [6]. Interestingly, the direction of such diversity effects may depend on specific organismic groups. For example, rates of multiple ecosystem processes increased with litter diversity when stream detritivores were present, but decreased in their absence [28], underscoring the importance of community composition for biodiversity–ecosystem functioning relationships (Box 1). In some cases, elevated 'donor' system diversity decreases rather than increases resource flows to 'recipient' ecosystems or reduces resource availability through changes in environmental conditions. For example, tree diversity can increase canopy packing and space filling [15], changing the physical structure and properties of the ecosystem. This change limits light transmission, thus reducing solar radiation and water temperature in forest stream and curtails in-stream primary and consumer production [8,29].

Cross-system diversity effects on ecosystem functioning can be reciprocal. In riparian areas, emerging aquatic insects are valuable food for birds, bats, spiders, and ground beetles (Box 2). Therefore, an increase in the richness of aquatic insect species with distinct life histories leads to variation in emergence periods, which implies enhanced prey supply to terrestrial predators that promotes productivity of the terrestrial consumer community. Moreover, given stoichiometric differences among species, in terms of C:N:P ratios or contents of vitamins or fatty acids, prey diversity would support greater biomass production of terrestrial consumers even when the total prey biomass is unchanged ('balanced diet hypothesis') [30]. Spawning salmon are a well

Figure 1. Conceptual model of functional coupling between terrestrial and aquatic ecosystems, and pathways for the expression of biodiversity change on ecosystem functioning in coupled ecosystems. (A) Coupling is ensured by four main vectors – water, wind, gravitation, organisms – that transfer matter and energy across ecosystem boundaries. Transport by water can occur as run-off, subsurface flow, or flooding. (B) Pathways for biodiversity effects in coupled ecosystems with contrasted low- and high-diversity systems shown for each pathway. Pathway 1. 'Donor' system biodiversity directly affects 'recipient' ecosystem functioning. Pathway 2. 'Donor' ecosystem biodiversity indirectly affects 'recipient' ecosystem functioning by influencing biodiversity of the 'recipient' ecosystem. Pathway 3. 'Donor' ecosystem biodiversity affects 'recipient' ecosystem functioning mediated by 'donor' ecosystem functioning. These pathways need not be mutually exclusive – transitions exist, and some may even operate

documented example of aquatic–terrestrial coupling. Species and genotypic diversity lengthen the total time when salmon is present in headwaters [31,32], where bears catch large numbers of fish and scatter the carcasses on the floodplain. This temporally extended food supply for bears, resulting directly from 'donor' diversity, enhances resource availability on land and increases terrestrial plant and potentially also arthropod and songbird biomass production (Box 2).

Pathway 2. 'Donor' ecosystem biodiversity indirectly affects 'recipient' ecosystem functioning by influencing biodiversity of the 'recipient' ecosystem

Rationale

Biodiversity of 'donor' communities affects the functioning of 'recipient' ecosystems indirectly via changes in the diversity of the 'recipient' communities (Figure 1B). This pathway represents a cross-boundary case of 'diversity begets diversity' [33], which relates to the notion that diversity at one trophic level (or in one ecosystem) promotes diversity at another level (or in another ecosystem). This could occur when species move across ecosystem boundaries to enrich 'recipient' communities, or as a result of species interactions (e.g., grazing, predation, habitat provision). Depending on context, these diversity changes can increase or decrease process rates in the 'recipient', where within-ecosystem biodiversity–ecosystem functioning mechanisms can take effect.

Evidence

Species often 'spill over' from 'donor' to 'recipient' ecosystems due to ontogenetic shifts, especially when they have complex life cycles, or by periodic movement at seasonal, diel, or other time scales. Prime examples are amphibians that move between streams or ponds (tadpoles) and forests (adults), the emergence of aquatic insects from streams and lakes [34], or migratory insects, fish, birds, and mammals [22,35]. Foraging requirements also cause species periodically to cross ecosystem boundaries to access resources. Examples include predatory insects moving from agricultural to natural habitats [36], or water birds that feed in aquatic ecosystems and rest on land, or vice versa.

Another possibility is when species interactions occur across boundaries [37], particularly trophic interactions reflecting diversity across trophic levels (termed 'vertical diversity' [38]) within food webs. These have positive effects when ecological niche space is enlarged and diversity is increased in the 'recipient', for instance by increasing food quantity and variability, or habitat heterogeneity. Consider architectural complexity in diverse riparian tree communities which provides habitat for various canopy arthropod species [39]. This results in diverse prey available to aquatic predators [40], thus supporting stream food webs. Conversely, negative interactions such as competition, predation, or parasitism can decrease diversity in the 'recipient' (e.g., invasive species assuming dominance in the 'donor'). For instance, invasion of riparian zones by Japanese knotweed (*Fallopia japonica*) can alter the structure and dynamics of stream food webs with negative effects on the richness of aquatic macroinvertebrates colonizing leaf litter, although the response of fungal richness has been found to be inconsistent [41].

Given the abundant evidence of biodiversity effects on processes within ecosystems [3], these possibilities for cross-boundary 'diversity begets diversity' linkages suggest that changes in 'donor' diversity can cascade to cause changes in 'recipient' ecosystem functioning. However, to our knowledge, direct tests of this pathway are limited. The relevance of this kind of

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simultaneously at the same location. For simplicity, paths are shown from 'donor' to 'recipient' only, but note that bidirectional exchanges – in which 'donor' becomes 'recipient', and vice versa – are likely. We also note the potential for within-system biodiversity effects across trophic levels that then influence exchanges.

transboundary biodiversity effect is therefore difficult to assess. Nevertheless, there are hints from published studies that it can play a role. In particular, mixed terrestrial leaf litter, as opposed to single-species litter, can reduce the diversity (evenness) of aquatic fungal communities on decomposing leaves, whereas the decomposition by litter-consuming detritivores is enhanced [42]. In addition, there is evidence that forestry-related changes in 'donor' plant diversity influence the diversity of arthropod communities in water-filled tree holes [21,43]. A change in the diversity of these communities may affect multiple ecosystem processes, including litter decomposition, nitrate removal, and algal and fungal production, as shown in several manipulative experiments in other aquatic ecosystems (Table S1) [13,44].

Terrestrial ecosystem functioning may be similarly affected by aquatic diversity through the transboundary 'diversity begets diversity' Pathway 2. Increased diversity of aquatic macrophyte, invertebrate, or fish species differing in life histories, body sizes, or other traits conceivably enlarges the trophic niche space for water birds (e.g., ducks, dippers, shorebirds, seabirds), allowing the coexistence of a larger number of bird species in their respective habitat. Among the consequences for 'recipient' terrestrial ecosystems could be the fertilization of soils by guano deposition. This would promote nutrient cycling and increase the biomass production of plants on land and indirectly also the production of terrestrial herbivores and other animals. Thus, there is scope for aquatic biodiversity reverberating in food webs to boost the production of terrestrial consumers [38].

Pathway 3. 'Donor' ecosystem biodiversity affects 'recipient' ecosystem functioning mediated by 'donor' ecosystem functioning

Rationale
Biodiversity of 'donor' ecosystems affects 'recipient' ecosystem functioning indirectly through effects on 'donor' ecosystem processes that propagate across system boundaries (Figure 1B). The effects in the 'recipient' will generally be positive when the processes in the 'donor' entail increases in resource flows to the 'recipient' ecosystems and negative when resource flows are reduced. A second mechanism can be recognized when changes in environmental conditions in 'recipient' ecosystems are caused by the effects of 'donor' ecosystem processes, which can be either positive or negative, depending on context. This is in contrast to Pathway 1, where 'donor' diversity directly affects 'recipient' ecosystem functioning through cross-boundary resource flows or changes in environmental conditions.

Evidence
Plant productivity within ecosystems is often enhanced by diversity, the underlying mechanisms being facilitation, complementary resource use, selection effects, or trophic interactions [3,45]. Enhanced plant production leads to greater amounts of litter that can be transferred across ecosystem boundaries (Figure 1A), attenuating resource limitation in the 'recipient' [26]. Other ecosystem processes involved in carbon and nutrient cycling can also lead to resources being 'spilled over' from one ecosystem to another. When plant diversity favors nutrient retention in soils, due to complementary nutrient uptake strategies, leaching of these solutes to ground and surface waters will be reduced [46] and aquatic processes reliant on nutrient supplies will be limited [47]. Denitrification is an excellent example illustrating this mechanism, where nitrate removed by denitrifiers in soils or groundwater will be unavailable in streams, both for denitrification [48] and other processes relying on nutrient supply. This case shows that biodiversity effects in coupled ecosystems will often be opposite when the processes in the two ecosystems depend on the same resource.

Changes in plant biodiversity can also have cross-boundary repercussions on ecosystem processes when geomorphology is affected. In particular, where 'donor' diversity increases the

density of structures (e.g., shoots, roots) that interact with physical forces (e.g., wind, water flow), ecosystem processes related to geomorphic stability will be promoted. For example, observational and experimental work indicate a positive effect of riparian plant diversity on root production, with the resulting increase in root biomass stabilizing streambanks [49]. A reduction in suspended solids due to decreased riparian erosion, in concert with changes in stream channel morphology, enhances light availability and alters physical habitat configuration and stability in streams, both of which are important controlling factors of primary production and other ecosystem processes in running waters. Even long-distance effects involving soil or sediment fluxes are conceivable, whether in stream networks or other ecosystems. A case in point is the management-induced loss of plant diversity in semiarid shrubland where wind erosion can increase because of reduced plant cover [50], leading to long-range nutrient transport. Consequences could include increases in soil fertility and primary production thousands of kilometers away, as the nutrient transport from the Saharan desert to the eastern Mediterranean or Amazonia implies [51].

Plant biodiversity can influence community water balance through changes in water uptake and transpiration, precipitation interception, stemflow, and seepage [52], while below-ground biodiversity affects soil porosity and aggregate stability with consequences for water-flow paths in soils [53]. Such hydrological changes in 'donor' ecosystems can propagate to connected aquatic ecosystems where they affect ecosystem processes depending on water flows. For example, tree species richness that increases canopy packing and total leaf area [15] increases the ecosystem processes of transpiration and interception at the stand level [52], thereby reducing soil infiltration and water flows to adjacent aquatic ecosystems at the catchment level. Here, in contrast to the canopy packing example in Pathway 1, 'donor' ecosystem processes are involved in mediating the 'donor' diversity effect on 'recipient' ecosystem functioning.

Alternatively, tree diversity can enhance soil moisture levels through hydraulic redistribution and soil water partitioning due to differential rooting strategies [52], which potentially enhances transboundary water flow. These changes in transboundary water flows can influence flow volumes and thus also water temperatures, with repercussions for aquatic ecosystem processes like biomass production, litter decomposition, or nutrient transformations in streams.

Terrestrial ecosystem functioning can be affected by aquatic ecosystem functioning, driven by the diversity of 'donor' aquatic communities. For example, aquatic macrophyte diversity promotes aquatic plant production [45], and since part of the produced biomass is often deposited on land or consumed by terrestrial herbivores (e.g., moose, *Alces alces*), nutrient inputs (via microbial decomposition or herbivore feces), and hence plant productivity, are increased in the terrestrial environment [54]. Spawning salmon distinctly increase dissolved nutrient concentrations in headwaters and thereby foster benthic algal production [55], which benefits insects grazing on biofilms. Consequently, prolonged salmon residence in runs used by multiple species or genotypes [31,32] would promote aquatic insect emergence and food availability to terrestrial consumers. As a result, the productivity of terrestrial invertebrates and small vertebrates would be enhanced. Note that, in contrast to the salmon example under Pathway 1, where fish diversity directly influences terrestrial production through carcass deposition on land, here salmon diversity first influences a process in the aquatic 'donor' ecosystem which then induces a change in the functioning of 'recipient' terrestrial ecosystems, as illustrated in Pathway 3.

Conclusion

Overall, evidence for relationships between biodiversity and processes within ecosystems, combined with knowledge of ecosystem linkages, suggests that biodiversity has important effects on

ecosystem functioning beyond ecosystem boundaries. Such effects can be both positive and negative. Furthermore, because multiple mechanisms can operate simultaneously, the direction and strength of cross-boundary diversity effects will vary, depending on the relative contribution of different pathways and mechanisms. Therefore, we call for research to unravel the mechanisms, quantify their importance, and assess the context-dependency of observed effects (see Outstanding questions).

Testing for biodiversity–ecosystem functioning relationships in coupled ecosystems: a research agenda

Capitalizing on biodiversity–ecosystem functioning infrastructure by adding contrasting microcosms and mesocosms

Existing infrastructure ranges from facilities for **biodiversity experiments** at multiple scales to locations equipped for long-term observations of natural communities and ecosystems. Novel experimental units can be readily installed along gradients of 'donor' biodiversity to quantify effects on biodiversity and functioning of 'recipient' ecosystems. More specifically, aquatic microcosms or mesocosms (as 'recipient') can be used to quantify terrestrial plant diversity effects on water chemistry, biological communities (e.g., succession by aquatic microbes or invertebrates), and rates of ecosystem processes (e.g., litter decomposition) [56]. Experimental units may range in size from a few centimeters (e.g., water-filled tree holes), to tens of meters (artificial ponds) [57], and could be filled with water free from organisms, or from natural water bodies to incorporate potential founder effects (see Outstanding questions). Terrestrial mesocosms could be deployed in existing aquatic biodiversity–ecosystem functioning experiments to determine effects of aquatic diversity on adjacent terrestrial ecosystems. Such mesocosms could consist of floating plant mats, artificial islands, or adjacent shore habitats, and facilitate the quantification of the effect of aquatic invertebrate diversity on nutrient fluxes to land.

Well-designed, replicated biodiversity experiments further allow the separation of species richness effects from functional composition effects, and from context dependence effects, if the diversity treatments are crossed with an environmental manipulation, such as drought or fertilization [58].

Biodiversity experiments explicitly addressing aquatic–terrestrial coupling

New biodiversity experiments can be developed that focus on cross-ecosystem biodiversity effects, ideally leveraging coordinated networks to span compositional and environmental variation [59]. For example, artificial mini-catchments or ponds could be created within experimental plots differing in 'donor' community diversity, which is most easily varied as plant species richness. Moreover, factorial terrestrial–aquatic biodiversity experiments can be envisaged in which terrestrial and/or aquatic biodiversity is manipulated in the 'donor' system to assess effects in an adjoining 'recipient' system. A third option is **removal experiments,** in which genotypes, species, or functional groups are selectively eliminated from ecosystems [60]. However, fully factorial designs of biodiversity experiments usually involve many treatment combinations, even within a single focal system, and hence become easily unmanageable if not restricted on the basis of field observations or forecasts of future conditions.

Observational studies

Observational studies relate variation in diversity across the landscape to rates of ecosystem processes and reflect natural conditions with respect to, for example, species composition, age structure, and biogeochemical cycles.

Inventories, whether from long-term **monitoring** programs or individual **surveys**, exemplify this approach. Existing large-scale inventories of forest and aquatic ecosystems could be combined

to explore transboundary relationships between biodiversity and ecosystem functioning. These relationships are modulated by environmental and catchment properties, as well as functional traits of the dominant species. For example, climatic variables, such as mean air temperature, may outweigh the importance of local environmental variables in driving algal species distributions in streams [61], and body size of decomposers can strongly affect aquatic litter decomposition [62], highlighting the importance of considering both environmental and biotic drivers of ecosystem functioning (Box 1 and Figure 2).

Comparative studies represent a form of observational studies with greater control of potential confounding factors [63]. Accordingly, plots differing in plant diversity could be selected next to aquatic ecosystems, or vice versa, to test the described pathways. Minimizing climatic and other environmental covariation is essential to enable isolating biodiversity effects from abiotic influences on ecosystem processes. Consequently, such studies are best implemented within single regions or latitudes characterized by some variation in species composition. Opportunities
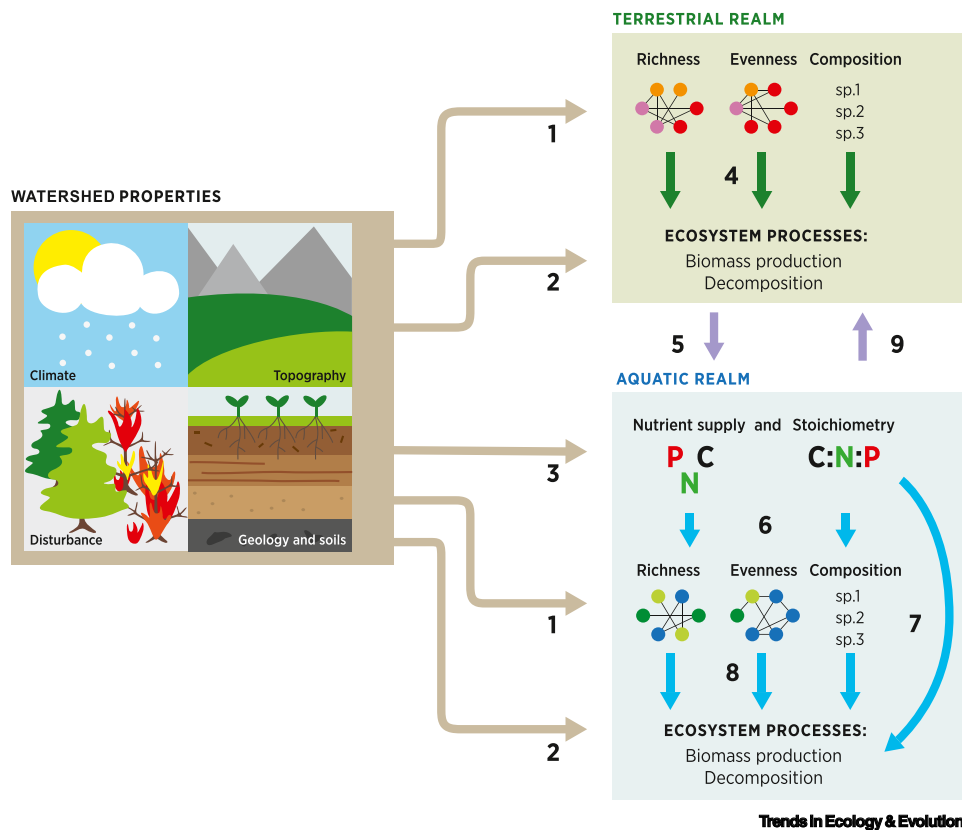
Figure 2. Environmental and biodiversity-related drivers of ecosystem functioning across ecosystem boundaries, illustrated with terrestrial–aquatic linkages. Watershed properties (e.g., disturbance regimes, geology, soil properties, topography, and climate) can directly affect biodiversity (species richness, evenness, etc.) (1) and ecosystem processes (2) (e.g., biomass production, decomposition, nutrient transformations) of the terrestrial and aquatic realm. For the aquatic realm, catchment characteristics directly affect carbon and nutrient supply (N, P) and stoichiometry (e.g., C:N:P ratios), with generally important repercussions for aquatic community composition and diversity (3). Terrestrial biodiversity affects ecosystem processes in the terrestrial system (4), which influences nutrient supply and stoichiometry in the connected aquatic system (5), which in turn affect aquatic biodiversity (6) and ecosystem processes (7); the latter are also driven by aquatic biodiversity (8). Conversely, changes in the aquatic realm can also affect ecosystem properties and processes in the terrestrial realm (9). Abbreviation: sp., species. Figure modified from [65], now including cross-boundary interactions.

for landscape-scale studies are also foreseeable. One example is to select replicate watersheds differing in landscape heterogeneity or diversity of communities and compare nutrient and carbon fluxes into water bodies, and their influences on biodiversity and ecosystem processes within the 'recipient' aquatic system [18]. A similar approach is to use other 'recipient' ecosystem 'islands' within landscapes, such as wetlands, meadows, agricultural fields, or mountain tops.

Concluding remarks

Theoretical arguments and emerging empirical evidence support the idea that changes in biodiversity within a given ecosystem can 'spill over' to affect ecosystem functioning in coupled ecosystems [19,20]. This recognition has implications for the scale dependence of biodiversity–ecosystem functioning relationships as the flow of organisms and resources in coupled ecosystems can drive local and regional biodiversity and rates of ecosystem processes [64]. Another corollary is that effects of biodiversity changes on ecosystem linkages likely vary with trophic levels [19,20]. Therefore, broadening the biodiversity–ecosystem functioning framework to the meta-ecosystem and landscape level has promise to improve our mechanistic understanding of ecosystem linkages and to add new dimensions and realism to assessments of the functional role of biodiversity.

Opportunities for research in coupled ecosystems are manifold, with great potential to extend insights from small-scale studies towards the broad spatial scales that are most relevant for managing ecosystems under environmental change (see Outstanding questions). Specifically, cross-ecosystem linkages other than terrestrial–aquatic, and processes other than litter decomposition, must be explored to evaluate the general significance of such biodiversity–ecosystem functioning teleconnections. Seizing these opportunities will advance understanding of whether important 'spill-over' effects are a pervasive feature in coupled ecosystems, how environmental drivers interact with biodiversity, and the degree to which specific characteristics of ecosystems are overriding biodiversity effects across ecosystem boundaries.

Declaration of interests

No interests are declared.

Supplemental information

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Outstanding questions

Are 'spill-over' effects scale-dependent, such that small ecosystems (e.g., tree cavities) are more strongly affected than large ones (e.g., lakes)?

Are cross-boundary biodiversity effects on ecosystem functioning stronger in similar (e.g., upland and floodplain forests) or dissimilar systems (e.g., mangroves and arid hinterland)?

Are 'spill-over' effects different among biomes, being more important in cold and resource-poor boreal compared with lush tropical ecosystems?

Do cross-system biodiversity effects diminish along food chains, meaning that effects driven by low trophic levels are stronger than those caused by higher trophic levels?

Are cross-system biodiversity effects typically driven by resource subsidies from bottom-up or are top-down effects also important?

How significant are founder effects in the context of cross-boundary biodiversity–ecosystem functioning relationships?

To what extent do water-borne diseases, such as malaria, where vectors cross ecosystem boundaries during their life cycle, affect the biodiversity and functioning of terrestrial ecosystems?

What is the importance of community evenness in 'donor' and 'recipient' ecosystems on the relative importance of species-identity versus richness effects on cross-boundary biodiversity–ecosystem functioning relationships?

Can ecosystem properties predict cross-boundary biodiversity–ecosystem functioning effects despite context dependencies? Is there a hump-shaped pattern of biodiversity–ecosystem functioning effect sizes along gradients of environmental stress (e.g., temperature, pH) or fertility (e.g., nutrients), with the largest effect sizes at intermediate levels?

Under which circumstances are cross-boundary diversity effects on ecosystem functioning influential, and when are they overridden by environmental controls or species identity effects?

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