

Linking human impacts to community processes in terrestrial and freshwater ecosystems

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Abstract

Human impacts such as habitat loss, climate change and biological invasions are radically altering biodiversity, with even greater effects projected into the future. Evidence suggests human impacts may differ substantially between terrestrial and freshwater ecosystems, but the reasons for these differences are poorly understood. We propose an integrative approach to explain these differences by linking impacts to the fundamental processes that structure communities: dispersal, speciation, ecological selection and ecological drift. Our goal is to provide process-based insights into why human impacts, and the responses to these impacts, may differ across ecosystem types within a mechanistic, eco-evolutionary comparative framework. To enable these insights, we review and synthesize i) how the four processes can influence diversity and dynamics in terrestrial and freshwater communities, focusing on whether their relative importance may or may not differ among ecosystems, and ii) how human impacts can alter terrestrial and freshwater biodiversity in different ways due to differences in process strength among ecosystems. Finally, we highlight research gaps and next steps, and discuss how this approach can provide new insights for conservation. By focusing on the processes that shape diversity in communities, we aim to mechanistically link human impacts to ongoing and future changes in ecosystems.

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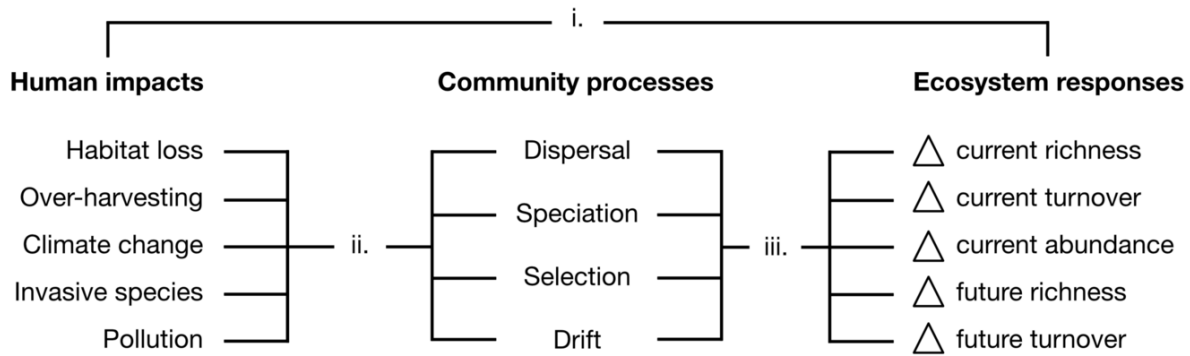
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0.1 Introduction

It is well-known that humans are fundamentally altering the biodiversity and functioning of ecosystems through impacts such as habitat loss, climate change and biological invasions (Ruckelshaus *et al.* 2020; Pörtner *et al.* 2021). However, recent studies suggest that global change drivers may cause divergent biodiversity responses in terrestrial and aquatic ecosystems (Blowes *et al.* 2019; van Klink *et al.* 2020), making it difficult to forecast future biodiversity changes. Indeed, that differences exist in human impacts across ecosystems was a key finding of the recent IPBES Global Assessment (Díaz *et al.* 2018; Ruckelshaus *et al.* 2020), which emphasized the importance of better understanding these differences. One potential reason the relative importance of human impacts may vary across ecosystems, beyond differing strength of impact, is that differences exist in the relative importance of core processes that govern biodiversity dynamics in these systems. Identifying differences in the strength and type of processes most important in a given ecosystem may allow for the development of comparative frameworks to understand and mitigate human impacts in both terrestrial and aquatic communities.

While studies have compared differences in processes and properties for terrestrial and marine habitats (May *et al.* 1994; Grosberget *et al.* 2012; Webb 2012), comparisons are lacking for terrestrial and freshwater ecosystems, which are highly threatened (Carpenter *et al.* 2011; Belletti *et al.* 2020). Here, we aim to build a more complete understanding of how and why human impacts vary among terrestrial and freshwater ecosystems by identifying differences and similarities in the fundamental processes shaping communities (Figure 1). To do this, we build on theory that distinguishes four fundamental processes (Box 1) that comprehensively describe how species are gained and lost from communities (Vellend 2010, 2016): dispersal, speciation, ecological selection (hereafter selection) and ecological drift (hereafter drift). These processes capture the mechanisms by which community attributes such as species richness, species-abundance relationships and species turnover emerge, and are general enough to allow for comparisons across many ecosystem types. Importantly, the relative importance of these processes is likely modulated by ecosystem-specific physical and spatial attributes, for example the properties of media (e.g., air vs water), or geometric constraints of habitat (e.g., open vs dendritic, Table 1). Thus, our goal is to develop mechanistic bridges between global change drivers and their impacts by explicitly considering both the fundamental processes and properties shaping ecosystems (Figure 1, Table 1).



i. Traditional approach in human impact studies

ii. Knowledge gap 1: How do humans impact community processes across blue-green ecosystems?

iii. Knowledge gap 2: How do community processes shape ecosystem responses to human impacts?

Fig. 1 | Impact, process and response-based approach to understand ecosystem change. Focusing on community processes can enable mechanistic inferences into how humans alter ecosystem dynamics in terrestrial and freshwater systems via effects on community structure and dynamics. Traditional approaches (i) identify various patterns of ecosystem responses and attribute them to specific human impacts, but often do not explicitly consider the community processes which shape these responses, in particular across ecosystems. By considering these processes we can better fill the twin knowledge gaps of (ii) how humans change the relative importance of processes operating in communities, and (ii) how these processes then create the observed ecosystem responses.

Box 1 | Glossary and contextualization of community processes used in the approach

Dispersal: The movement of organisms among sites (Stevens *et al.* 2014) and the process by which species can be added to a local site from a regional species pool via immigration, or removed from a local site via emigration. Along with speciation, dispersal is one of the two processes that can add species to communities (MacArthur & Wilson 1967; Vellend 2016).

Speciation: The process describing species splitting into two more or less reproductively isolated populations, either due to geographic barriers (allopatry) or in situ divergence (sympatry, Coyne & Orr 2004; Hernández-Hernández *et al.* 2021). Speciation has not traditionally been a focus in community ecology. However, this process is now recognized as an important mechanism influencing the size of regional species pools and the assembly of communities from them (Ricklefs 1987; Mittelbach & Schemske 2015). Speciation is one of two processes that can add species to a local community, along with immigration via dispersal. Allopatric speciation of geographically isolated populations in particular may increase the size of the regional species pool, and thus the number of species arriving at local sites.

Ecological selection: Species differ in their population growth rates. These differences emerge from the sum of the absolute fitness of all individuals in a population. Such species-level differences can cause variation in their relative abundance over time, which defines a selection process operating at the level of species that shapes community structure (Vellend 2010, 2016). Ecological selection is the best-studied of the four fundamental processes (Cottenie 2005), and is the most diverse with respect to ecological mechanisms it encompasses. It includes i) the impact of

the environment in filtering and sorting species from the species pool (e.g. “constant” selection, Leibold *et al.* 2004; Vellend 2010; Soininen 2014), ii) density and frequency-dependent effects of interactions (e.g. competition, predation and mutualisms), and iii) impacts of environmental heterogeneity over space or time (variable selection).

Ecological drift: The change in relative abundances of species over time due to random variation in births and deaths of individuals (Hubbell 2001; Vellend 2010; Gilbert & Levine 2017), leading to stochasticity in species’ abundances over time. Drift can ultimately only erode local biodiversity due to random losses of species from communities because it does not generate or introduce new species (Vellend 2016). Drift is likely the least well-studied of the four community processes, despite the fact that it can play an important role in community assembly even when other more deterministic processes are operating and species are not ecologically equivalent (Gilbert & Levine 2017; Svensson *et al.* 2018). One signature of drift is that its influence is greater when population sizes are small, such as on islands, isolated lakes, and in small habitat patches (Hubbell 2001; Melbourne & Hastings 2008; Orrock & Watling 2010).

Note: Ecological selection and drift refer to community-level processes shaping diversity in mixed-species assemblages (see Vellend 2016), not changes in allele frequencies or abundances within populations of single species as in evolutionary biology and population genetics.

0.2 Linking human impacts to community processes

In our approach (Figure 1) we focus on how human impacts are mediated by the fundamental community processes of dispersal, speciation, selection and drift. These processes are not always considered in studies of ecosystem responses to impacts, yet it is these processes that generate the observed responses of ecosystems. Traditional approaches to studying human impacts have documented how one or several drivers such as warming or habitat loss have altered the diversity of ecosystems such as changes in richness, turnover and abundance. These include studies comparing terrestrial and marine ecosystems (Blowes *et al.* 2019) or less often terrestrial and freshwater systems (van Klink *et al.* 2020). While many of these studies speculate as to the ultimate causes of ecosystem outcomes, few explicitly consider the full set of processes shaping diversity in ecosystems. In our approach we fully incorporate these processes of dispersal, speciation, selection and drift to more mechanistically link ecosystem responses now and in the future with the myriad ways humans alter these systems.

To demonstrate the utility of our approach, we provide an example of how it could be used to interpret and explain a hypothetical scenario in which freshwater ecosystems are experiencing less warming-related turnover (also known as thermophilization) than terrestrial ecosystems (Figure 2). By examining each fundamental community process as a possible driver of this pattern, we can gain a better understanding of why differences may emerge across terrestrial and freshwater ecosystems and use this knowledge to make predictions about other systems and future impacts. In this hypothetical scenario, freshwater communities are buffered from some warming effects due to the heat capacity of water, which slows warming in this system. This buffering effect decreases the selection pressure on freshwater communities to thermophilize, and could drive the hypothesized pattern in which freshwater communities experience weaker warming impacts. However, it may also be that the dendritic nature of freshwater systems, in particular streams and rivers, may reduce the capacity for warm-adapted species to enter the community via dispersal, which would also reduce thermophilization. Finally, our approach increases the focus on the under-studied processes of drift and speciation as drivers of changes in current and future ecosystems. For example, in the longer term, freshwater communities may recover from warming-related species losses faster than terrestrial ecosystems through speciation. This is because the more isolated habitat structure and smaller population sizes of many freshwater taxa may promote in situ speciation in this ecosystem.

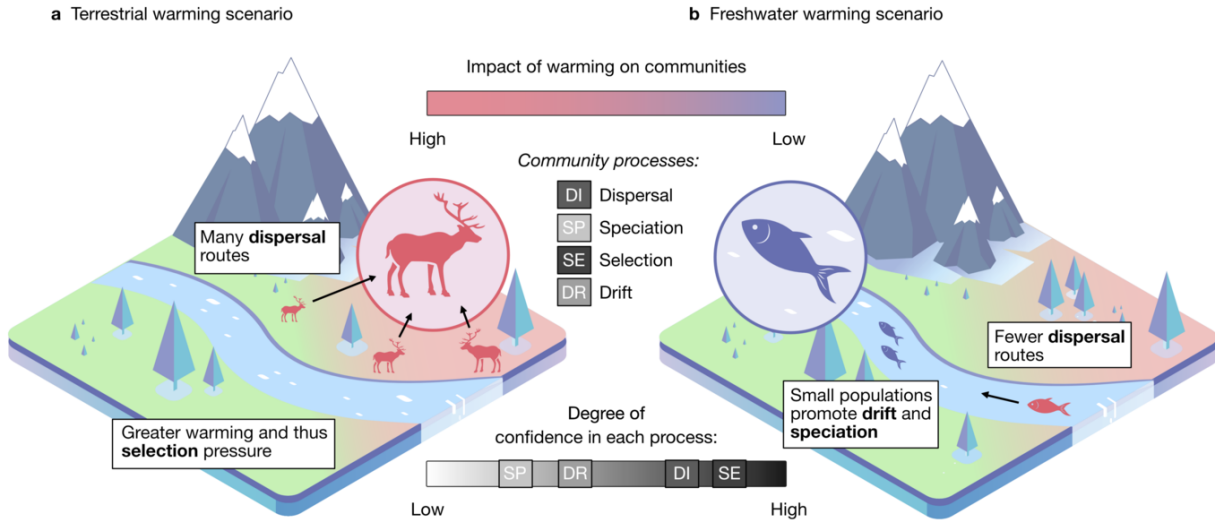


Fig. 2 | Demonstration of the impact, process & response approach for a warming scenario. In this hypothetical scenario terrestrial communities (red circle) are turning over towards more warm-adapted species (aka thermophilizing) faster than freshwater communities (blue circle). The four fundamental community processes are then used within the context of our approach (Figure 1) to explain this pattern as a function of potential differences in each process between ecosystem types (see main text and Table 1).

To implement the proposed approach, we synthesize the literature to find key differences and similarities in how the four major processes operate within each system. We then use the differences and similarities we identify to infer how terrestrial and freshwater biodiversity may respond to, and recover from, these impacts. For each process, we provide non-exhaustive but representative examples of some of the major ways humans impact terrestrial and freshwater ecosystems, paying particular attention to how the process might influence the magnitude of human impacts. We also identify the physical, habitat, chemical and community properties that likely underlie differences in the strength of processes among ecosystems (Table 1). Although we focus primarily on the understudied comparison between terrestrial and freshwater ecosystems, we also reference marine systems when information on oceanic environments and taxa can provide insights for comparisons.

0.2.1

0.2.2 Dispersal

Dispersal of organisms (Box 1) may be limited either by a lack of intrinsic adaptations for efficient movement or extrinsic barriers isolating species from suitable habitats. Here we first compare differences between terrestrial and freshwater systems in species intrinsic factors, i.e., attributes such as differences in physiology, behavior and life history (Stevens *et al.* 2014; Comte & Olden 2018). We then compare ecosystems in terms of extrinsic factors causing dispersal limitation, such as differences in habitat barriers, configuration and connectivity (Campbell Grant *et al.* 2007; Baguette *et al.* 2013). Overall, findings from the literature suggest that despite the often-strong intrinsic dispersal abilities of freshwater taxa, the limitations of extrinsic habitat structure ultimately lead to lower overall dispersal of taxa compared with terrestrial ecosystems.

Studies comparing dispersal distances for the same taxa, such as plants or invertebrates, in terrestrial and freshwater habitats suggest freshwater organisms have larger intrinsic dispersal abilities (Boedeltje *et al.* 2003; Kappes *et al.* 2014). A key factor that may lead to differences in dispersal abilities is the medium within which species move. Water is ~800x denser than air, and the high buoyancy this creates selects for passively-dispersed life stages and promotes long-distance dispersal by flows and currents (Bonte *et al.* 2012;

Cornell & Harrison 2013; Srivastava & Kratina 2013). These differences may be associated with life history and morphological traits in both aquatic and terrestrial organisms (but see Green *et al.* 2022 for a caution on using traits as proxies for dispersal distance). For example, small-bodied organisms generally require fewer adaptations and lower energetic costs to disperse longer distances in water, whereas traits designed to increase drag are required to overcome gravity in air (Dawson & Hamner 2008).

Despite the intrinsic potential for long-distance dispersal of many freshwater organisms, freshwater habitats may be effectively the most dispersal-limited of all major ecosystems. This is most likely due to the high degree of spatial isolation inherent in the structure of lakes, streams and rivers (Comte & Olden 2018) and the steep environmental gradients within them (e.g., of light, Stomp *et al.* 2007). Lakes are in many ways similar to oceanic islands, in that resident species are isolated by an uninhabitable terrestrial matrix (Kappes *et al.* 2014), though systems of ponds and lakes can be interconnected by a network of aquatic corridors (Baguette *et al.* 2013). Rivers experience isolation at two levels: first, because there is little exchange of organisms across drainage basins (Leuven *et al.* 2009) and second, because dispersal is constrained by the dendritic structure and directional flow of river networks (Hänfling & Weetman 2006; Campbell Grant *et al.* 2007; Carrara *et al.* 2012; Wubset *et al.* 2016). Therefore, many riverine organisms have relatively small ranges and high levels of differentiation across river branches. Due to the many spatial limitations just described, freshwater communities are often not saturated (Shurin *et al.* 2000; Irzet *et al.* 2004), suggesting species are limited in their ability to reach new sites via dispersal (Shurin & Smith 2006).

Human impacts can cause extrinsic limitations to dispersal by creating barriers, increasing heterogeneity or by reducing habitat connectivity (Figure 3). In highly fragmented landscapes, distances that must be traveled in order to grow and reproduce often increase, which may lower the fitness of dispersing organisms (Stamps *et al.* 2005). Although effects of habitat fragmentation are most often studied in terrestrial environments, they are thought to be more severe in freshwater systems (Fuller *et al.* 2015). Human-made obstacles such as river-crossings and dams can heavily alter species dispersal patterns, including aquatic invertebrates (Brooks *et al.* 2013; Sondermann *et al.* 2015), fish (Barbarossa *et al.* 2020; Duarte *et al.* 2021) and plants (Merritt & Wohl 2006). In addition, in comparison with terrestrial habitats, fragmentation in dendritic river networks creates habitat patches that are smaller and more varied in size (Fagan 2002; Fuller *et al.* 2015). Finally, as river networks influence dispersal between lakes, their fragmentation may also affect lake-dwelling species (Yi *et al.* 2010).

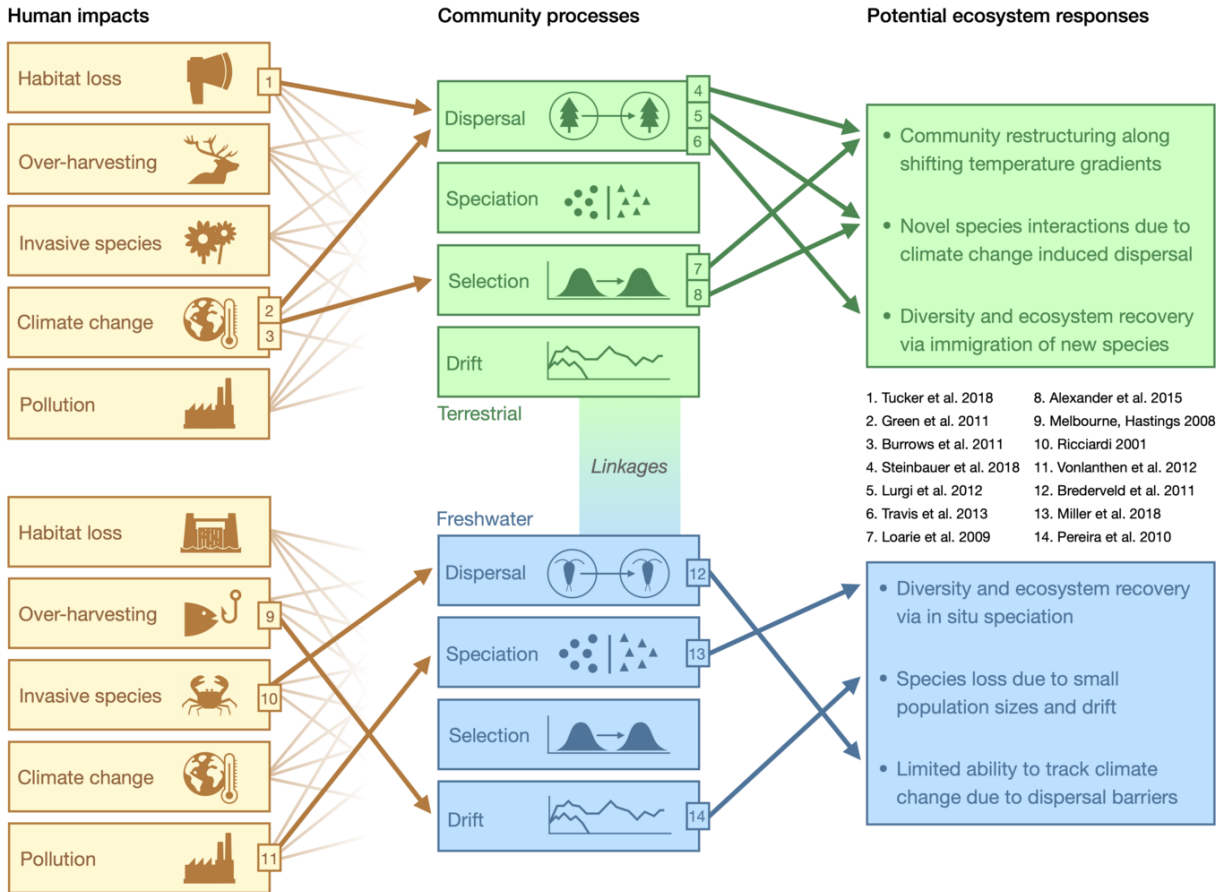


Fig. 3 | Links between impacts, processes and responses across ecosystems discussed here. An integrative approach to infer how human impacts may alter biodiversity in terrestrial and freshwater systems via their effects on the community processes of dispersal, speciation, selection and drift. Brown lines represent the effects of human impacts on community processes (note only a subset in bold are considered here), and green and blue lines the impacts of processes of varying intensity on biodiversity outcomes in ecosystems. Numbered boxes provide evidence for each highlighted link via the references listed on the right.

Habitat fragmentation and landscape modification are also severe threats to terrestrial biodiversity (Fischer & Lindenmayer 2007) and the linkages between terrestrial and freshwater ecosystems. For example, artificial constructions such as roads or fences have been shown to obstruct long-distance dispersal in mammals (Seidler *et al.* 2015; Tucker *et al.* 2018; Bartoń *et al.* 2019), plants (Dener *et al.* 2021) and even microbes (Le Provost *et al.* 2021), which were historically considered to be near-universally distributed. Interestingly, some freshwater species also utilize the terrestrial matrix for dispersal, which can help these taxa overcome effects of habitat fragmentation (Zuluaga *et al.* 2022). For example, freshwater invertebrates with adults dispersing actively over land through the air better track environmental variation and are less affected by barriers such as dams (Grönroos *et al.* 2013; Tonkin *et al.* 2018). Similarly, the ability of freshwater organisms to use other organisms (e.g., birds) as dispersal vectors may both mitigate effects of habitat fragmentation and facilitate the spread of invasive species (Incagnone *et al.* 2015; Coughlan *et al.* 2017).

0.2.3 Speciation

Speciation (Box 1) is the engine generating new biodiversity, and not only many species but the process of speciation itself is under threat from ongoing human activities (Barnosky *et al.* 2011). Studies have found that human impacts can both hinder and promote speciation, which has important implications for the long-term recovery of Earth’s biodiversity (Rosenzweig 2001). Both variation in speciation rate among lineages and the amount of time and area available for speciation to occur can influence the size of regional species pools (Rabosky 2020; Miller & Román-Palacios 2021) and community diversity assembled from it. This process can also add species to communities directly via in situ speciation (e.g., Gillespie 2004). However, despite an increasing focus on speciation as a driver of community diversity, less attention has been paid to how local and regional dynamics of speciation differ among terrestrial and freshwater habitats, and how these dynamics are altered by human impacts (Figure 3, Table 1). It should be noted that while the products of speciation can be quickly eradicated, recovering new species via this process occurs over longer timescales and is outside the scope of many traditional conservation approaches.

Though few direct comparisons of speciation rates have been made between terrestrial and freshwater habitats, the highest observed diversification rates per clade or lineage per unit time occur in freshwater ecosystems (Miller *et al.* 2018; Rabosky 2020; Miller 2021). This may be due in part to the greater isolation of freshwater habitats compared to terrestrial environments (Wiens 2015). However, a recent study found that on average, terrestrial taxa have higher diversification rates than freshwater taxa, though this could be due in part to older colonization events in freshwater (see below, Roman-Palacios *et al.* 2022). Future studies should compare speciation rates among terrestrial and freshwater ecosystems using matched pairs of clades with similar life histories and a range of dispersal abilities. Such studies would increase our mechanistic understanding of both the relative importance of speciation among terrestrial and freshwater ecosystems and how this process shapes the response of these systems to human impacts.

In addition to variation in speciation rates, the amount of time and area available for speciation to occur can also influence the size of regional species pools, the amount of in-situ speciation, and thus local community diversity. Terrestrial habitats tend to be older, larger and more stable over geologic timescales than freshwater habitats such as lakes and streams (Miller 2021). However, they also tend to be better connected than freshwater habitats, such that new species more quickly expand their ranges beyond their site of origin. Thus, it may be expected that freshwater systems will tend to have smaller regional species pools, but that in situ speciation plays a larger role than in terrestrial communities, in particular for organisms that cannot disperse through air or over land (Gillespie 2004; Miller *et al.* 2018). Indeed, the best-known cases of recent rapid in situ species radiations occur in lake-inhabiting fishes such as cichlids (McGee *et al.* 2020), salmoniformes (Hudson *et al.* 2011) and pupfish (Rabosky 2020; Miller 2021; Richards *et al.* 2021). These differences between ecosystems in area and time for speciation to occur have important implications for the recovery of diversity and ecological function after human impacts such as habitat and species loss. For example, immigration from the larger and more connected terrestrial matrix may allow terrestrial communities to recover more quickly over shorter timescales via dispersal. Whereas in freshwater communities due to isolation, the much slower process of speciation may be one of the primary ways these systems recover from species loss.

Perhaps the primary way human impacts can hinder or decrease speciation rates is through the destruction and fragmentation of habitat within which new species are formed (Figure 2, Rosenzweig 2001; Barnosky *et al.* 2011). This occurs primarily through deforestation (or any land-use conversion or intensification) on land, and damming, draining and eutrophication in freshwater systems (Butchart *et al.* 2010; Horvath *et al.* 2019; Ruckelshaus *et al.* 2020). Due to the relatively small existing area of freshwater habitats compared to terrestrial regions, future speciation in freshwaters may be more impacted by habitat loss as the small areas available for speciation to occur become smaller still. For example, pollution in freshwater systems can cause eutrophication and hypoxic conditions, which greatly reduce the available amount and diversity of habitats, and often create conditions where endemic species lose all habitat at once (Vonlanthen *et al.* 2012; Frei *et al.* 2022). Over time, pollution in freshwater systems can reduce and homogenize ecological niche space

previously partitioned by species, especially those formed via adaptive radiation, and lead to the sudden meltdown of species richness in a group, such as in whitefish (Vonlanthen *et al.* 2012). Overall, human impacts on local diversity may be greater in freshwater ecosystems, both in the short term due to habitat loss, over medium timescales as the recovery of diversity via immigration is limited by dispersal barriers, and over longer timescales as the opportunity for speciation becomes diminished due to anthropogenic activities. Thus, by incorporating speciation into our approach, we can make inference about future changes in richness and turnover in these systems (see Figure 1).

In addition to hindering speciation, human impacts may also promote speciation in terrestrial and freshwater habitats in at least two ways. First, it has been hypothesized that anthropogenic warming could cause once connected populations to move up in elevation to separate uplifted areas such as within a mountain range, isolating populations and potentially leading to allopatric speciation (Hua & Wiens 2013). However, there is no evidence that this process also occurs in freshwaters, as upward shifts in these habitats are also associated with strong changes in environmental conditions (e.g., water velocity) that cannot be easily adapted to (Timoner *et al.* 2020). Second, disturbances caused by habitat homogenization and human-mediated dispersal can bring new species into contact and thus promote hybrid speciation. For example, hybrid speciation at ecological time scales in response to human-mediated dispersal has been demonstrated in land plants (Abbott 1992) and freshwater fish (Marques *et al.* 2019). Once hybrids have formed, altered ecosystems created by humans may further facilitate their survival and spread (e.g., Hoban *et al.* 2012), but whether this process adds new species or removes them will depend on whether it is associated with the gain or loss of habitat and ecological opportunity. Overall, humans have and will continue to impact the diversity and dynamics of communities by reducing speciation potential, but may also in some cases promote speciation.

0.2.4

0.2.5 Ecological selection

Understanding biodiversity responses to human impacts will first require an understanding of how the strength of ecological selection, defined as deterministic differences in fitness among individuals of different species (Box 1, Vellend 2016), differs between ecosystems (Figure 3, Table 1). This is because human impacts such as land use, warming and invasive species alter the selection regime by modifying either abiotic gradients and heterogeneity (e.g., climate change velocity, Loarie *et al.* 2009) or biotic interactions such as competition, predation and mutualism (e.g., novel species interactions, Alberti 2015; Alexander *et al.* 2015). Below we compare abiotic and biotic aspects of selection across terrestrial and freshwater ecosystems, and how humans alter the selection regime through various global change drivers.

Selection caused by abiotic factors may vary across ecosystems due to variation in habitat properties (Table 1) and the strength of environmental gradients. For example, abiotic gradients can vary between different types of media (e.g., air vs water) due to differences in density, viscosity and heat capacities (Table 1). In addition, it has been suggested there is overall greater environmental structure on land than in freshwater systems (Herfindal *et al.* 2022). However, some gradients may be stronger in water than on land, such as for light, which can promote niche differentiation in freshwater habitats (Stomp *et al.* 2007). Possibly as a result of these differences, there is evidence that species sorting—when species tend to be found in local communities matching their environmental preferences (Heino *et al.* 2015; Govaert *et al.* 2021)—tends to be stronger on land. For example, species sorting appears to be weakest in lakes compared to riverine and terrestrial habitats (Soininen 2014), possibly due to their isolation (Heino *et al.* 2015). Finally, differences between ecosystems in environmental structure also have major implications for the evolution of thermal niches (Steele *et al.* 2018; Sunday *et al.* 2019) and suggest the ability of species to track thermal optima in response to climate change may differ across realms (Burrows *et al.* 2011).

In addition to abiotic effects, selection caused by biotic interactions may also vary between terrestrial and freshwater ecosystems (Gothe *et al.* 2013; Pringle *et al.* 2016; Garcia-Giron *et al.* 2020). Specifically, consumptive pressure via predation is thought to be stronger in aquatic systems (Cyr & Face 1993; Cebrian

& Lartigue 2004; Alofs & Jackson 2014). This may be because freshwater systems have a higher prevalence of generalist consumers, which cause strong top-down control (Cyr & Face 1993; Shurin & Smith 2006; Alofs & Jackson 2014). Alternatively, the generally higher nutritional quality of freshwater organisms (Twining *et al.* 2019; Shipley *et al.* 2022) may support larger consumer populations and thus increase predation pressure. However, the high consumptive pressure in freshwaters could also be due to greater heterogeneity in density of predators caused by dispersal limitation, which would lead to a higher naivete of prey populations compared to terrestrial habitats (Cox & Lima 2006; Anton *et al.* 2016, 2020). Finally, many studies highlight differences in selective pressures within freshwaters between lakes and streams, and suggest that biotic resistance is weaker in streams (Mitchell & Knouft 2009; Alofs & Jackson 2014).

As outlined above, human impacts are known to have multiple and severe effects on the selection process, to the point that they can overshadow effects of natural processes (Leprieur *et al.* 2008). For example, there is a large body of evidence demonstrating that climatic warming has different impacts in terrestrial vs marine habitats, however few studies have compared terrestrial and freshwater ecosystems. Freshwater habitats, being embedded in a terrestrial matrix, have thermal regimes that are closely tied to air and thus their temperatures tend to be similar to surrounding land areas (Grant *et al.* 2021). Among all major ecosystems, evidence suggests freshwater and terrestrial communities are less affected by warming than marine systems (Burrows *et al.* 2011). However, this apparent resilience may lead to accumulation of greater extinction debts compared to marine systems, which are experiencing the highest community turnover (Blowes *et al.* 2019).

A final way humans impact selection regimes is by facilitating biological invasions. For example, it has been argued that because freshwater habitats represent a more complex matrix of interacting abiotic and biotic components, invading freshwater species can more easily affect the properties and functions of their ecosystems than terrestrial taxa (Moorhouse & Macdonald 2015). Invasive species can also alter selection regimes in communities in a less direct way, by transmitting diseases or by altering abiotic conditions (via poisoning, bio-fouling or changing other ecosystem properties, Blackburn *et al.* 2014). These processes not only affect selection regimes, but can also facilitate further invasions (Ricciardi 2001; Green *et al.* 2011). Invasive species effects may also be transmitted between ecosystem in s through various linkages, such as when invasive plants alter nutrient flows between terrestrial and freshwater habitats (Stewart *et al.* 2019).

0.2.6

0.2.7 Ecological drift

Ecological drift (Box 1) is generally the most understudied of the four community processes, and has primarily been considered in microbes and terrestrial plant communities (e.g., Hubbell 2001). However, it should be noted that the more general process of stochasticity is increasingly studied by ecologists (Shoemaker *et al.* 2020). For example, rather than being studied directly, the strength of drift has been inferred from random variation in species abundance distributions (Chase 2010) or quantified as unexplained variation in community dynamics models (Vellend *et al.* 2014). Because few studies directly quantify drift, in particular across several ecosystem types, we know very little about how humans impact this process in terrestrial and freshwater communities (Figure 3).

There are however a small number of studies quantifying drift in plant (e.g., Hubbell 2001; Gilbert & Lechowicz 2004; Gilbert & Levine 2017), bacterial (Vanwonterghem *et al.* 2014; Aguilar & Sommaruga 2020), and other microorganismal communities (Devercelli *et al.* 2016; Logares *et al.* 2018; Wu *et al.* 2018; Vass *et al.* 2020). And perhaps the best-documented studies of how drift shapes community structure come from damselfly (Odonata) communities, where species appear to closely approach ecological equivalence (Svensson *et al.* 2018; McPeck & Siepielski 2019). Despite this limited evidence, drift may be expected to be stronger in freshwater habitats than on land due to the much smaller total area these habitats occupy compared to their terrestrial counterparts (Wiens 2015), especially as these populations are reduced via ongoing impacts such as damming.

Despite the paucity of studies quantifying drift, it has been demonstrated that human impacts can increase

the overall importance of stochastic processes, which include drift, in both freshwater and terrestrial systems. For example, species losses, nutrient addition, and warming all increased the relative importance of stochastic processes in soil microbial communities (Zhang *et al.* 2016). Similarly, warming and nutrient addition increased the relative contribution of stochasticity—mainly caused by drift—among lake bacterioplankton communities (Ren *et al.* 2017). More generally and as mentioned above, we can expect that drift and drift-related extinctions will be greater in more isolated and smaller communities (Hubbell 2001; Vellend 2016). Thus, any anthropogenic changes which reduce community size and increase isolation (e.g., habitat fragmentation or land-use change) should tend to increase the contribution of drift to community dynamics (Melbourne & Hastings 2008). For example, biological invasions can cause decreased population sizes and thereby increase species vulnerability to stochastic extinctions (Gilbert & Levine 2013). Looking forward, a greater focus on the contribution of drift to community dynamics is warranted, as it is highly understudied but likely very important for shaping human impacts in both ecosystems.

0.3 Synthesis and future directions

Here we propose an integrative approach for comparing effects of human impacts on freshwater and terrestrial ecosystems using fundamental processes (Figures 1-3). We find several key differences in the strength and operation of these processes that suggest differing biodiversity responses in terrestrial and freshwater ecosystems (Figure 3, Table S1). For example, we find evidence suggesting that i) ecological selection due to abiotic gradients is stronger in terrestrial ecosystems than in freshwater, ii) that dispersal limitation may be greater in freshwater communities but by contrast that freshwaters have the highest potential for recovery via speciation, and iii) that the biggest data gap for cross-ecosystem comparisons is the relative influence of ecological drift among the two ecosystems. Overall, we found that quantitative comparisons across ecosystems are generally lacking, though data enabling such comparisons may be available for many organisms for the processes of dispersal and selection. In contrast, cross-ecosystem studies of speciation rates tend to focus on a few well-characterized organisms and such studies are largely missing for drift. Filling these gaps will be essential to fully link the processes of dispersal, speciation, selection and drift to the future dynamics and recovery of Earth's biodiversity.

In addition to filling data gaps, the mechanistic realism of our approach could be increased by considering interactions between community processes and between human impacts, as well as increased consideration of linkages and flows between ecosystems. For example, interactions between community processes can modify the effect of global change drivers, as has been found in experiments and models incorporating both competition and drift (Chesson 2000; Orrock & Watling 2010; Gilbert & Levine 2017), as well as experiments on the relative role of dispersal and selection (Ron *et al.* 2018). In addition, we focus primarily on the effects of single human impacts, though we recognize that these drivers interact in nature (Settele & Wiemers 2015). For example, invasive species are often positively affected by global change, such as increases in temperature or land use intensification (Occhipinti-Ambrogi 2007; Hellmann *et al.* 2008; Eisenhauer *et al.* 2012). Finally, many of the ecosystem processes depend to some extent on linkages between the systems, such as flows of nutrients and organisms between land, rivers and lakes (Soininen *et al.* 2015). For example, dispersal of many freshwater insects depends on adult forms that fly (Bilton *et al.* 2003). Furthermore, transport of nutrients and pollutants between freshwater and terrestrial systems is known to affect populations in both systems (Kraus 2019; Kraus *et al.* 2021). As linkages between systems may be affected by global change drivers (Kraus 2019; Johnson *et al.* 2021; Kraus *et al.* 2021), their role should be more fully addressed in future developments of the proposed approach.

Realizing the full predictive potential of our approach which links human impacts to community processes will require increased research efforts and dialog between aquatic and terrestrial ecologists, evolutionary biologists, conservationists and policymakers. Future research aimed at better forecasting human impacts across ecosystems should include targeted, quantitative studies of the strength and function of single or multiple processes in both terrestrial and freshwater ecosystems, especially for the understudied processes

of speciation and drift. Furthermore, our approach could be used to parametrize a mechanistic model of impacts, processes and biodiversity outcomes. Such a model would allow researchers to make more detailed, mechanistic predictions about how diversity may change in a given ecosystem. This work would build upon recent processes-based simulation studies used to infer the mechanisms shaping diversity through deep time, and across communities and spatial scales (Thompson *et al.* 2020; Hagen *et al.* 2021a, b). Mechanistic models, when combined with data, can provide more detailed estimates of the relative importance of processes shaping diversity across ecosystems and increase our understanding of how bio-physical properties influence the balance and strength of processes (Table 1).

In conclusion, to tackle the ongoing and accelerating impacts of humans on biodiversity, we must provide a mechanistic understanding of how these impacts cause changes in terrestrial and freshwater ecosystems. Our process-based approach developed here may be useful for mitigating many impacts of global change for several key reasons. First, focusing on the real-world processes which create the diversity and structure of communities creates a mechanistic bridge between a given human impact, such as climate warming, and the outcome of this process on assemblages, such as increased turnover or decreased diversity. Second, it provides a foundation for further research, especially quantitative comparisons and mechanistic models. Thus, in the same way that these processes are meant to open the 'black box' of community ecology to understand community patterns (Vellend 2010), our approach has the potential to do the same for understanding the mechanistic pathways by which humans impact Earth's biodiversity.

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0.5 References

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Table 1 | Key differences between freshwater and terrestrial ecosystems in physical, chemical, habitat and community properties and their hypothesized effect on community processes

Table S1 | Overview of studies comparing how human impacts may, or may not, differ in type or severity among terrestrial vs freshwater ecosystems, organized by the process which humans impact

Linking human impacts to community processes in terrestrial and freshwater ecosystems

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ABSTRACT

Human impacts such as habitat loss, climate change and biological invasions are radically altering biodiversity, with even greater effects projected into the future. Evidence suggests human impacts may differ substantially between terrestrial and freshwater ecosystems, but the reasons for these differences are poorly understood. We propose an integrative approach to explain these differences by linking impacts to the fundamental processes that structure communities: dispersal, speciation, ecological selection and ecological drift. Our goal is to provide process-based insights into why human impacts, and the responses to these impacts, may differ across ecosystem types within a mechanistic, eco-evolutionary comparative framework. To enable these insights, we review and synthesize i) how the four processes can influence diversity and dynamics in terrestrial and freshwater communities, focusing on whether their relative importance may or may not differ among ecosystems, and ii) how human impacts can alter terrestrial and freshwater biodiversity in different ways due to differences in process strength among ecosystems. Finally, we highlight research gaps and next steps, and discuss how this approach can provide new insights for conservation. By focusing on the processes that shape diversity in communities, we aim to mechanistically link human impacts to ongoing and future changes in ecosystems.

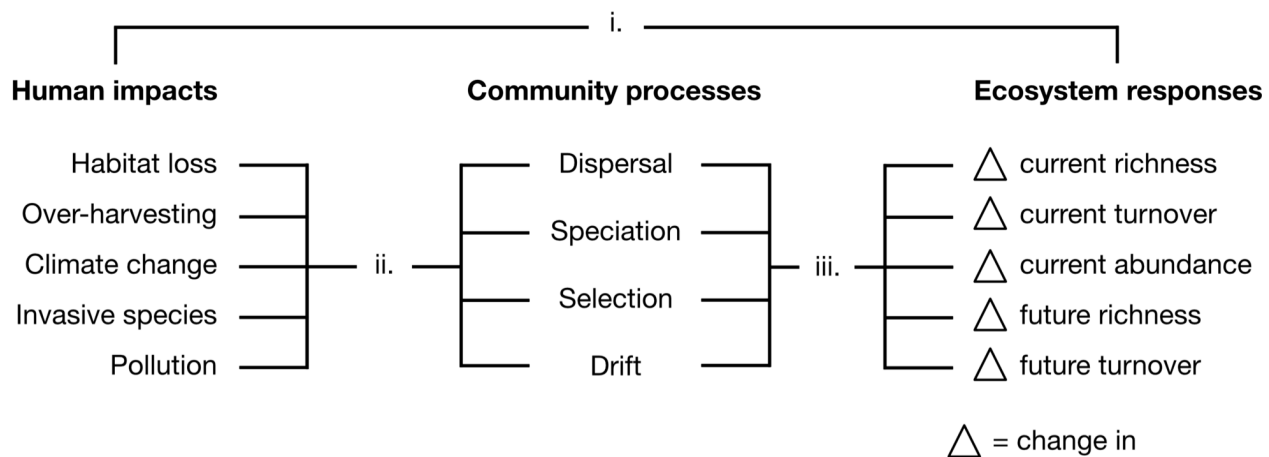
INTRODUCTION

It is well-known that humans are fundamentally altering the biodiversity and functioning of ecosystems through impacts such as habitat loss, climate change and biological invasions (Ruckelshaus *et al.* 2020; Pörtner *et al.* 2021). However, recent studies suggest that global change drivers may cause divergent biodiversity responses in terrestrial and aquatic ecosystems (Blowes *et al.* 2019; van Klink *et al.* 2020), making it difficult to forecast future biodiversity changes. Indeed, that differences exist in human impacts across ecosystems was a key finding of the recent IPBES Global Assessment (Díaz *et al.* 2018; Ruckelshaus *et al.* 2020), which emphasized the importance of better understanding these differences. One potential reason the relative importance of human impacts may vary across ecosystems, beyond differing strength of

impact, is that differences exist in the relative importance of core processes that govern biodiversity dynamics in these systems. Identifying differences in the strength and type of processes most important in a given ecosystem may allow for the development of comparative frameworks to understand and mitigate human impacts in both terrestrial and aquatic communities.

While studies have compared differences in processes and properties for terrestrial and marine habitats (May *et al.* 1994; Grosberg *et al.* 2012; Webb 2012), comparisons are lacking for terrestrial and freshwater ecosystems, which are highly threatened (Carpenter *et al.* 2011; Belletti *et al.* 2020). Here, we aim to build a more complete understanding of how and why human impacts vary among terrestrial and freshwater ecosystems by identifying differences and similarities in the fundamental processes shaping communities (Figure 1). To do this, we build on theory that distinguishes four fundamental processes (Box 1) that comprehensively describe how species are gained and lost from communities (Vellend 2010, 2016): dispersal, speciation, ecological selection (hereafter selection) and ecological drift (hereafter drift). These processes capture the mechanisms by which community attributes such as species richness, species-abundance relationships and species turnover emerge, and are general enough to allow for comparisons across many ecosystem types. Importantly, the relative importance of these processes is likely modulated by ecosystem-specific physical and spatial attributes, for example the properties of media (e.g., air vs water), or geometric constraints of habitat (e.g., open vs dendritic, Table 1). Thus, our goal is to develop mechanistic bridges between global change drivers and their impacts by explicitly considering both the fundamental processes and properties shaping ecosystems (Figure 1, Table 1).

Our approach goes beyond other recent frameworks which argue for studying human impacts via the ecological scales at which they occur (Simmons *et al.* 2021) or the meta-community processes with which they interact (Chase *et al.* 2020) by explicitly considering all major ecological and evolutionary processes that shape communities. The increased evolutionary focus in particular via the addition of the



- i. Traditional approach in human impact studies
- ii. Knowledge gap 1: How do humans impact community processes across blue-green ecosystems?
- iii. Knowledge gap 2: How do community processes shape ecosystem responses to human impacts?

Figure 1 | Impact, process and response-based approach to understand ecosystem change. Focusing on community processes can enable mechanistic inferences into how humans alter ecosystem dynamics in terrestrial and freshwater systems via effects on community structure and dynamics. Traditional approaches (i) identify various patterns of ecosystem responses and attribute them to specific human impacts, but often do not explicitly consider the community processes which shape these responses, in particular across ecosystems. By considering these processes we can better fill the twin knowledge gaps of (ii) how humans change the relative importance of processes operating in communities, and (ii) how these processes then create the observed ecosystem responses.

Box 1 | Glossary and contextualization of community processes used in the approach

Dispersal: The movement of organisms among sites (Stevens *et al.* 2014) and the process by which species can be added to a local site from a regional species pool via immigration, or removed from a local site via emigration. Along with speciation, dispersal is one of the two processes that can add species to communities (MacArthur & Wilson 1967; Vellend 2016).

Speciation: The process describing species splitting into two more or less reproductively isolated populations, either due to geographic barriers (allopatry) or in situ divergence (sympatry, Coyne & Orr

2004; Hernández-Hernández *et al.* 2021). Speciation has not traditionally been a focus in community ecology. However, this process is now recognized as an important mechanism influencing the size of regional species pools and the assembly of communities from them (Ricklefs 1987; Mittelbach & Schemske 2015). Speciation is one of two processes that can add species to a local community, along with immigration via dispersal. Allopatric speciation of geographically isolated populations in particular may increase the size of the regional species pool, and thus the number of species arriving at local sites.

Ecological selection: Species differ in their population growth rates. These differences emerge from the sum of the absolute fitness of all individuals in a population. Such species-level differences can cause variation in their relative abundance over time, which defines a selection process operating at the level of species that shapes community structure (Vellend 2010, 2016). Ecological selection is the best-studied of the four fundamental processes (Cottenie 2005), and is the most diverse with respect to ecological mechanisms it encompasses. It includes i) the impact of the environment in filtering and sorting species from the species pool (e.g. “constant” selection, Leibold *et al.* 2004; Vellend 2010; Soininen 2014), ii) density and frequency-dependent effects of interactions (e.g. competition, predation and mutualisms), and iii) impacts of environmental heterogeneity over space or time (variable selection).

Ecological drift: The change in relative abundances of species over time due to random variation in births and deaths of individuals (Hubbell 2001; Vellend 2010; Gilbert & Levine 2017), leading to stochasticity in species’ abundances over time. Drift can ultimately only erode local biodiversity due to random losses of species from communities because it does not generate or introduce new species (Vellend 2016). Drift is likely the least well-studied of the four community processes, despite the fact that it can play an important role in community assembly even when other more deterministic processes are operating and species are not ecologically equivalent (Gilbert & Levine 2017; Svensson *et al.* 2018). One signature of drift is that its influence is greater when population sizes are small, such as on islands, isolated lakes, and in small habitat patches (Hubbell 2001; Melbourne & Hastings 2008; Orrock & Watling 2010).

Note: Ecological selection and drift refer to community-level processes shaping diversity in mixed-species assemblages (see Vellend 2016), not changes in allele frequencies or abundances within populations of single species as in evolutionary biology and population genetics.

process of speciation greatly broadens the timescales being considered when conserving ecosystems in the face of global change. This focus on speciation allows for the recovery time or extinction debt of a community to be considered in the long term when attempting to understand how a given ecosystem will respond to human impacts. This integrative approach is important because human activities can impact all of these fundamental processes, which in turn generate observed biodiversity responses such as species loss and community turnover. Making cross-ecosystem and process-based comparisons using our approach (Figure 1) will therefore help to develop a more mechanistic understanding of how humans impact biodiversity and ecosystem dynamics (Soininen *et al.* 2015; Twining *et al.* 2019). For example, knowing if fundamental differences exist in the strength of dispersal limitation between ecosystem types may help to understand how species track changing thermal environments during warming, or how invasive species spread across the two ecosystems. Further, identifying differences, as well as similarities, in how processes operate will facilitate collaboration between terrestrial and freshwater scientists who share the goal of reducing negative impacts on diversity (Menge *et al.* 2009; Mokany *et al.* 2010).

LINKING HUMAN IMPACTS TO COMMUNITY PROCESSES

In our approach (Figure 1) we focus on how human impacts are mediated by the fundamental community processes of dispersal, speciation, selection and drift. These processes are not always considered in studies of ecosystem responses to impacts, yet it is these processes that generate the observed responses of ecosystems. Traditional approaches to studying human impacts have documented how one or several drivers such as warming or habitat loss have altered the diversity of ecosystems such as changes in richness, turnover and abundance. These include studies comparing terrestrial and marine ecosystems (Blowes *et al.* 2019) or less often terrestrial and freshwater systems (van Klink *et al.* 2020). While many of these studies speculate as to the ultimate causes of ecosystem outcomes, few explicitly consider the full set of processes shaping diversity in ecosystems. In our approach we fully incorporate these processes of

dispersal, speciation, selection and drift to more mechanistically link ecosystem responses now and in the future with the myriad ways humans alter these systems.

To demonstrate the utility of our approach, we provide an example of how it could be used to interpret and explain a hypothetical scenario in which freshwater ecosystems are experiencing less warming-related turnover (also known as thermophilization) than terrestrial ecosystems (Figure 2). By examining each fundamental community process as a possible driver of this pattern, we can gain a better understanding of why differences may emerge across terrestrial and freshwater ecosystems and use this knowledge to make predictions about other systems and future impacts. In this hypothetical scenario, freshwater communities are buffered from some warming effects due to the heat capacity of water, which slows warming in this system. This buffering effect decreases the selection pressure on freshwater communities to thermophilize, and could drive the hypothesized pattern in which freshwater communities experience weaker warming impacts. However, it may also be that the dendritic nature of freshwater systems, in particular streams and rivers, may reduce the capacity for warm-adapted species to enter the community via dispersal, which would also reduce thermophilization. Finally, our approach increases the focus on the under-studied processes of drift and speciation as drivers of changes in current and future ecosystems. For example, in the longer term, freshwater communities may recover from warming-related species losses faster than terrestrial ecosystems through speciation. This is because the more isolated habitat structure and smaller population sizes of many freshwater taxa may promote in situ speciation in this ecosystem.

To implement the proposed approach, we synthesize the literature to find key differences and similarities in how the four major processes operate within each system. We then use the differences and similarities we identify to infer how terrestrial and freshwater biodiversity may respond to, and recover from, these impacts. For each process, we provide non-exhaustive but representative examples of some of the major ways humans impact terrestrial and freshwater ecosystems, paying particular attention to how the process

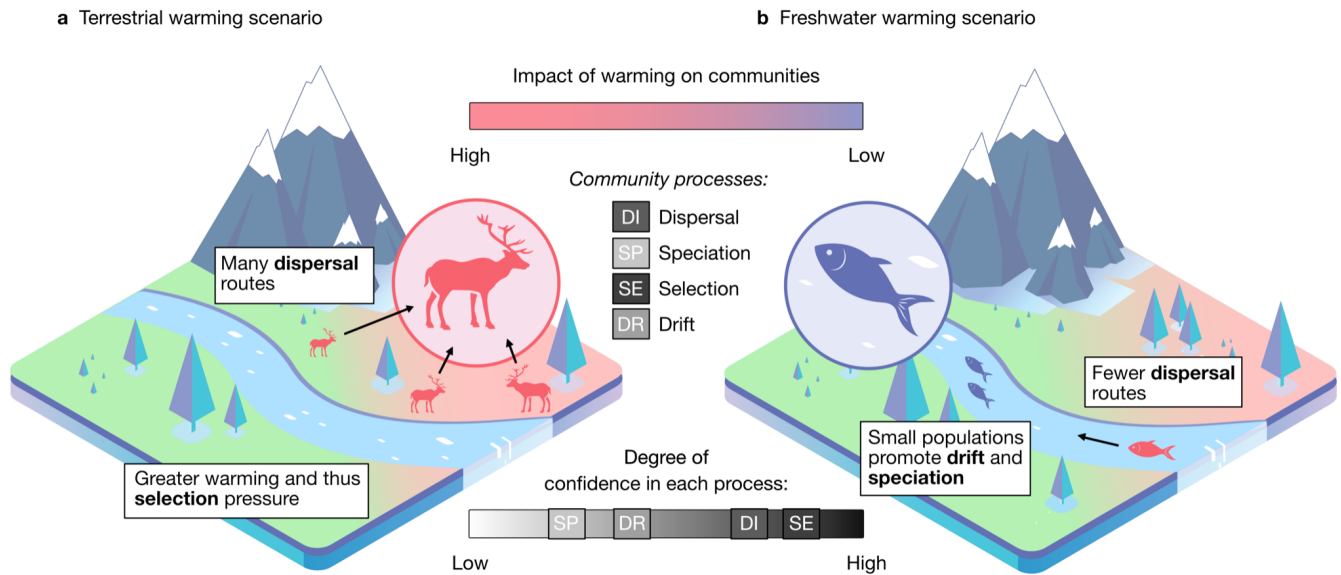


Figure 2 | Demonstration of the impact, process, response approach for a warming scenario. In this hypothetical scenario terrestrial communities (red circle) are turning over towards more warm-adapted species (aka thermophilizing) faster than freshwater communities (blue circle). The four fundamental community processes are then used within the context of our approach (Figure 1) to explain this pattern as a function of potential differences in each process between ecosystem types (see main text and Table 1).

might influence the magnitude of human impacts. We also identify the physical, habitat, chemical and community properties that likely underlie differences in the strength of processes among ecosystems (Table 1). Although we focus primarily on the understudied comparison between terrestrial and freshwater ecosystems, we also reference marine systems when information on oceanic environments and taxa can provide insights for comparisons.

Dispersal

Dispersal of organisms (Box 1) may be limited either by a lack of intrinsic adaptations for efficient movement or extrinsic barriers isolating species from suitable habitats. Here we first compare differences

between terrestrial and freshwater systems in species intrinsic factors, i.e., attributes such as differences in physiology, behavior and life history (Stevens *et al.* 2014; Comte & Olden 2018). We then compare ecosystems in terms of extrinsic factors causing dispersal limitation, such as differences in habitat barriers, configuration and connectivity (Campbell Grant *et al.* 2007; Baguette *et al.* 2013). Overall, findings from the literature suggest that despite the often-strong intrinsic dispersal abilities of freshwater taxa, the limitations of extrinsic habitat structure ultimately lead to lower overall dispersal of taxa compared with terrestrial ecosystems.

Studies comparing dispersal distances for the same taxa, such as plants or invertebrates, in terrestrial and freshwater habitats suggest freshwater organisms have larger intrinsic dispersal abilities (Boedeltje *et al.* 2003; Kappes *et al.* 2014). A key factor that may lead to differences in dispersal abilities is the medium within which species move. Water is ~800x denser than air, and the high buoyancy this creates selects for passively-dispersed life stages and promotes long-distance dispersal by flows and currents (Bonte *et al.* 2012; Cornell & Harrison 2013; Srivastava & Kratina 2013). These differences may be associated with life history and morphological traits in both aquatic and terrestrial organisms (but see Green *et al.* 2022 for a caution on using traits as proxies for dispersal distance). For example, small-bodied organisms generally require fewer adaptations and lower energetic costs to disperse longer distances in water, whereas traits designed to increase drag are required to overcome gravity in air (Dawson & Hamner 2008).

Despite the intrinsic potential for long-distance dispersal of many freshwater organisms, freshwater habitats may be effectively the most dispersal-limited of all major ecosystems. This is most likely due to the high degree of spatial isolation inherent in the structure of lakes, streams and rivers (Comte & Olden 2018) and the steep environmental gradients within them (e.g., of light, Stomp *et al.* 2007). Lakes are in many ways similar to oceanic islands, in that resident species are isolated by an uninhabitable terrestrial matrix (Kappes *et al.* 2014), though systems of ponds and lakes can be interconnected by a network of aquatic

corridors (Baguette *et al.* 2013). Rivers experience isolation at two levels: first, because there is little exchange of organisms across drainage basins (Leuven *et al.* 2009) and second, because dispersal is constrained by the dendritic structure and directional flow of river networks (Hänfling & Weetman 2006; Campbell Grant *et al.* 2007; Carrara *et al.* 2012; Wubs *et al.* 2016). Therefore, many riverine organisms have relatively small ranges and high levels of differentiation across river branches. Due to the many spatial limitations just described, freshwater communities are often not saturated (Shurin *et al.* 2000; Irz *et al.* 2004), suggesting species are limited in their ability to reach new sites via dispersal (Shurin & Smith 2006).

Human impacts can cause extrinsic limitations to dispersal by creating barriers, increasing heterogeneity or by reducing habitat connectivity (Figure 3). In highly fragmented landscapes, distances that must be traveled in order to grow and reproduce often increase, which may lower the fitness of dispersing organisms (Stamps *et al.* 2005). Although effects of habitat fragmentation are most often studied in terrestrial environments, they are thought to be more severe in freshwater systems (Fuller *et al.* 2015). Human-made obstacles such as river-crossings and dams can heavily alter species dispersal patterns, including aquatic invertebrates (Brooks *et al.* 2013; Sondermann *et al.* 2015), fish (Barbarossa *et al.* 2020; Duarte *et al.* 2021) and plants (Merritt & Wohl 2006). In addition, in comparison with terrestrial habitats, fragmentation in dendritic river networks creates habitat patches that are smaller and more varied in size (Fagan 2002; Fuller *et al.* 2015). Finally, as river networks influence dispersal between lakes, their fragmentation may also affect lake-dwelling species (Yi *et al.* 2010).

Habitat fragmentation and landscape modification are also severe threats to terrestrial biodiversity (Fischer & Lindenmayer 2007) and the linkages between terrestrial and freshwater ecosystems. For example, artificial constructions such as roads or fences have been shown to obstruct long-distance dispersal in mammals (Seidler *et al.* 2015; Tucker *et al.* 2018; Bartoń *et al.* 2019), plants (Dener *et al.* 2021) and even microbes (Le Provost *et al.* 2021), which were historically considered to be near-universally

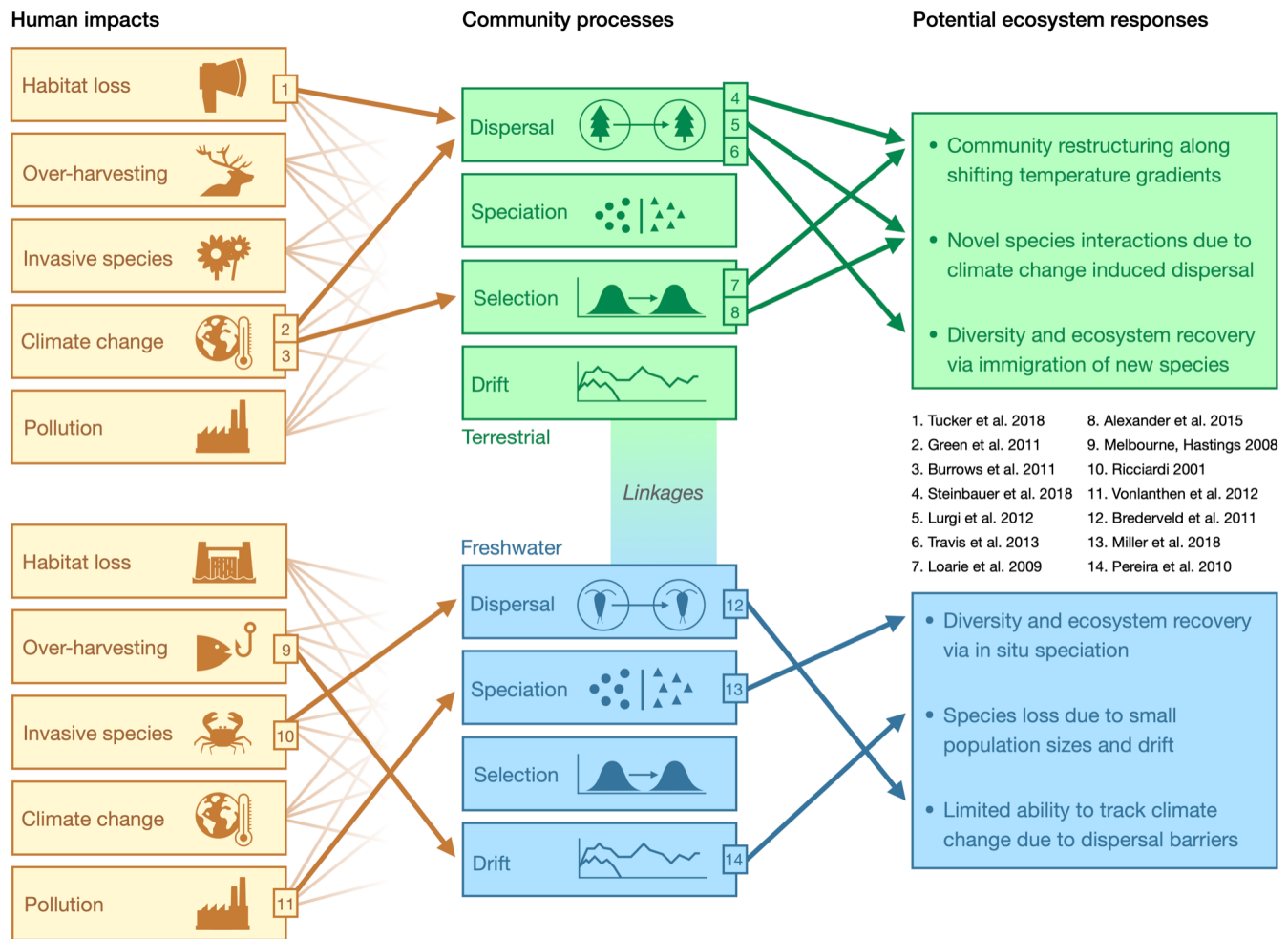


Figure 3 | Links between impacts, processes and responses across ecosystems discussed here. An integrative approach to infer how human impacts may alter biodiversity in terrestrial and freshwater systems via their effects on the community processes of dispersal, speciation, selection and drift. Brown lines represent the effects of human impacts on community processes (note only a subset in bold are considered here), and green and blue lines the impacts of processes of varying intensity on biodiversity outcomes in ecosystems. Numbered boxes provide evidence for each highlighted link via the references listed on the right.

distributed. Interestingly, some freshwater species also utilize the terrestrial matrix for dispersal, which can help these taxa overcome effects of habitat fragmentation (Zuluaga *et al.* 2022). For example, freshwater invertebrates with adults dispersing actively over land through the air better track environmental variation and are less affected by barriers such as dams (Grönroos *et al.* 2013; Tonkin *et al.* 2018). Similarly, the ability of freshwater organisms to use other organisms (e.g., birds) as dispersal vectors may both mitigate effects of habitat fragmentation and facilitate the spread of invasive species (Incagnone *et al.* 2015; Coughlan *et al.* 2017).

Speciation

Speciation (Box 1) is the engine generating new biodiversity, and not only many species but the process of speciation itself is under threat from ongoing human activities (Barnosky *et al.* 2011). Studies have found that human impacts can both hinder and promote speciation, which has important implications for the long-term recovery of Earth's biodiversity (Rosenzweig 2001). Both variation in speciation rate among lineages and the amount of time and area available for speciation to occur can influence the size of regional species pools (Rabosky 2020; Miller & Román-Palacios 2021) and community diversity assembled from it. This process can also add species to communities directly via in situ speciation (e.g., Gillespie 2004). However, despite an increasing focus on speciation as a driver of community diversity, less attention has been paid to how local and regional dynamics of speciation differ among terrestrial and freshwater habitats, and how these dynamics are altered by human impacts (Figure 3, Table 1). It should be noted that while the products of speciation can be quickly eradicated, recovering new species via this process occurs over longer timescales and is outside the scope of many traditional conservation approaches.

Though few direct comparisons of speciation rates have been made between terrestrial and freshwater habitats, the highest observed diversification rates per clade or lineage per unit time occur in freshwater ecosystems (Miller *et al.* 2018; Rabosky 2020; Miller 2021). This may be due in part to the greater isolation

of freshwater habitats compared to terrestrial environments (Wiens 2015). However, a recent study found that on average, terrestrial taxa have higher diversification rates than freshwater taxa, though this could be due in part to older colonization events in freshwater (see below, Román-Palacios *et al.* 2022). Future studies should compare speciation rates among terrestrial and freshwater ecosystems using matched pairs of clades with similar life histories and a range of dispersal abilities. Such studies would increase our mechanistic understanding of both the relative importance of speciation among terrestrial and freshwater ecosystems and how this process shapes the response of these systems to human impacts.

In addition to variation in speciation rates, the amount of time and area available for speciation to occur can also influence the size of regional species pools, the amount of in-situ speciation, and thus local community diversity. Terrestrial habitats tend to be older, larger and more stable over geologic timescales than freshwater habitats such as lakes and streams (Miller 2021). However, they also tend to be better connected than freshwater habitats, such that new species more quickly expand their ranges beyond their site of origin. Thus, it may be expected that freshwater systems will tend to have smaller regional species pools, but that in situ speciation plays a larger role than in terrestrial communities, in particular for organisms that cannot disperse through air or over land (Gillespie 2004; Miller *et al.* 2018). Indeed, the best-known cases of recent rapid in situ species radiations occur in lake-inhabiting fishes such as cichlids (McGee *et al.* 2020), salmoniformes (Hudson *et al.* 2011) and pupfish (Rabosky 2020; Miller 2021; Richards *et al.* 2021). These differences between ecosystems in area and time for speciation to occur have important implications for the recovery of diversity and ecological function after human impacts such as habitat and species loss. For example, immigration from the larger and more connected terrestrial matrix may allow terrestrial communities to recover more quickly over shorter timescales via dispersal. Whereas in freshwater communities due to isolation, the much slower process of speciation may be one of the primary ways these systems recover from species loss.

Perhaps the primary way human impacts can hinder or decrease speciation rates is through the destruction and fragmentation of habitat within which new species are formed (Figure 2, Rosenzweig 2001; Barnosky *et al.* 2011). This occurs primarily through deforestation (or any land-use conversion or intensification) on land, and damming, draining and eutrophication in freshwater systems (Butchart *et al.* 2010; Horváth *et al.* 2019; Ruckelshaus *et al.* 2020). Due to the relatively small existing area of freshwater habitats compared to terrestrial regions, future speciation in freshwaters may be more impacted by habitat loss as the small areas available for speciation to occur become smaller still. For example, pollution in freshwater systems can cause eutrophication and hypoxic conditions, which greatly reduce the available amount and diversity of habitats, and often create conditions where endemic species lose all habitat at once (Vonlanthen *et al.* 2012; Frei *et al.* 2022). Over time, pollution in freshwater systems can reduce and homogenize ecological niche space previously partitioned by species, especially those formed via adaptive radiation, and lead to the sudden meltdown of species richness in a group, such as in whitefish (Vonlanthen *et al.* 2012). Overall, human impacts on local diversity may be greater in freshwater ecosystems, both in the short term due to habitat loss, over medium timescales as the recovery of diversity via immigration is limited by dispersal barriers, and over longer timescales as the opportunity for speciation becomes diminished due to anthropogenic activities. Thus, by incorporating speciation into our approach, we can make inference about future changes in richness and turnover in these systems (see Figure 1).

In addition to hindering speciation, human impacts may also promote speciation in terrestrial and freshwater habitats in at least two ways. First, it has been hypothesized that anthropogenic warming could cause once connected populations to move up in elevation to separate uplifted areas such as within a mountain range, isolating populations and potentially leading to allopatric speciation (Hua & Wiens 2013). However, there is no evidence that this process also occurs in freshwaters, as upward shifts in these habitats are also associated with strong changes in environmental conditions (e.g., water velocity) that cannot be easily adapted to (Timoner *et al.* 2020). Second, disturbances caused by habitat homogenization

and human-mediated dispersal can bring new species into contact and thus promote hybrid speciation. For example, hybrid speciation at ecological time scales in response to human-mediated dispersal has been demonstrated in land plants (Abbott 1992) and freshwater fish (Marques *et al.* 2019). Once hybrids have formed, altered ecosystems created by humans may further facilitate their survival and spread (e.g., Hoban *et al.* 2012), but whether this process adds new species or removes them will depend on whether it is associated with the gain or loss of habitat and ecological opportunity. Overall, humans have and will continue to impact the diversity and dynamics of communities by reducing speciation potential, but may also in some cases promote speciation.

Ecological selection

Understanding biodiversity responses to human impacts will first require an understanding of how the strength of ecological selection, defined as deterministic differences in fitness among individuals of different species (Box 1, Vellend 2016), differs between ecosystems (Figure 3, Table 1). This is because human impacts such as land use, warming and invasive species alter the selection regime by modifying either abiotic gradients and heterogeneity (e.g., climate change velocity, Loarie *et al.* 2009) or biotic interactions such as competition, predation and mutualism (e.g., novel species interactions, Alberti 2015; Alexander *et al.* 2015). Below we compare abiotic and biotic aspects of selection across terrestrial and freshwater ecosystems, and how humans alter the selection regime through various global change drivers.

Selection caused by abiotic factors may vary across ecosystems due to variation in habitat properties (Table 1) and the strength of environmental gradients. For example, abiotic gradients can vary between different types of media (e.g., air vs water) due to differences in density, viscosity and heat capacities (Table 1). In addition, it has been suggested there is overall greater environmental structure on land than in freshwater systems (Herfindal *et al.* 2022). However, some gradients may be stronger in water than on land, such as for light, which can promote niche differentiation in freshwater habitats (Stomp *et al.* 2007).

Possibly as a result of these differences, there is evidence that species sorting—when species tend to be found in local communities matching their environmental preferences (Heino *et al.* 2015; Govaert *et al.* 2021)—tends to be stronger on land. For example, species sorting appears to be weakest in lakes compared to riverine and terrestrial habitats (Soininen 2014), possibly due to their isolation (Heino *et al.* 2015). Finally, differences between ecosystems in environmental structure also have major implications for the evolution of thermal niches (Steele *et al.* 2018; Sunday *et al.* 2019) and suggest the ability of species to track thermal optima in response to climate change may differ across realms (Burrows *et al.* 2011).

In addition to abiotic effects, selection caused by biotic interactions may also vary between terrestrial and freshwater ecosystems (Göthe *et al.* 2013; Pringle *et al.* 2016; García-Girón *et al.* 2020). Specifically, consumptive pressure via predation is thought to be stronger in aquatic systems (Cyr & Face 1993; Cebrian & Lartigue 2004; Alofs & Jackson 2014). This may be because freshwater systems have a higher prevalence of generalist consumers, which cause strong top-down control (Cyr & Face 1993; Shurin & Smith 2006; Alofs & Jackson 2014). Alternatively, the generally higher nutritional quality of freshwater organisms (Twining *et al.* 2019; Shipley *et al.* 2022) may support larger consumer populations and thus increase predation pressure. However, the high consumptive pressure in freshwaters could also be due to greater heterogeneity in density of predators caused by dispersal limitation, which would lead to a higher naïveté of prey populations compared to terrestrial habitats (Cox & Lima 2006; Anton *et al.* 2016, 2020). Finally, many studies highlight differences in selective pressures within freshwaters between lakes and streams, and suggest that biotic resistance is weaker in streams (Mitchell & Knouft 2009; Alofs & Jackson 2014).

As outlined above, human impacts are known to have multiple and severe effects on the selection process, to the point that they can overshadow effects of natural processes (Leprieur *et al.* 2008). For example, there is a large body of evidence demonstrating that climatic warming has different impacts in terrestrial vs marine habitats, however few studies have compared terrestrial and freshwater ecosystems. Freshwater

habitats, being embedded in a terrestrial matrix, have thermal regimes that are closely tied to air and thus their temperatures tend to be similar to surrounding land areas (Grant *et al.* 2021). Among all major ecosystems, evidence suggests freshwater and terrestrial communities are less affected by warming than marine systems (Burrows *et al.* 2011). However, this apparent resilience may lead to accumulation of greater extinction debts compared to marine systems, which are experiencing the highest community turnover (Blowes *et al.* 2019).

A final way humans impact selection regimes is by facilitating biological invasions. For example, it has been argued that because freshwater habitats represent a more complex matrix of interacting abiotic and biotic components, invading freshwater species can more easily affect the properties and functions of their ecosystems than terrestrial taxa (Moorhouse & Macdonald 2015). Invasive species can also alter selection regimes in communities in a less direct way, by transmitting diseases or by altering abiotic conditions (via poisoning, bio-fouling or changing other ecosystem properties, Blackburn *et al.* 2014). These processes not only affect selection regimes, but can also facilitate further invasions (Ricciardi 2001; Green *et al.* 2011). Invasive species effects may also be transmitted between ecosystem in s through various linkages, such as when invasive plants alter nutrient flows between terrestrial and freshwater habitats (Stewart *et al.* 2019).

Ecological drift

Ecological drift (Box 1) is generally the most understudied of the four community processes, and has primarily been considered in microbes and terrestrial plant communities (e.g., Hubbell 2001). However, it should be noted that the more general process of stochasticity is increasingly studied by ecologists (Shoemaker *et al.* 2020). For example, rather than being studied directly, the strength of drift has been inferred from random variation in species abundance distributions (Chase 2010) or quantified as unexplained variation in community dynamics models (Vellend *et al.* 2014). Because few studies directly

quantify drift, in particular across several ecosystem types, we know very little about how humans impact this process in terrestrial and freshwater communities (Figure 3).

There are however a small number of studies quantifying drift in plant (e.g., Hubbell 2001; Gilbert & Lechowicz 2004; Gilbert & Levine 2017), bacterial (Vanwonderghem *et al.* 2014; Aguilar & Sommaruga 2020), and other microorganismal communities (Devercelli *et al.* 2016; Logares *et al.* 2018; Wu *et al.* 2018; Vass *et al.* 2020). And perhaps the best-documented studies of how drift shapes community structure come from damselfly (Odonata) communities, where species appear to closely approach ecological equivalence (Svensson *et al.* 2018; McPeck & Siepielski 2019). Despite this limited evidence, drift may be expected to be stronger in freshwater habitats than on land due to the much smaller total area these habitats occupy compared to their terrestrial counterparts (Wiens 2015), especially as these populations are reduced via ongoing impacts such as damming.

Despite the paucity of studies quantifying drift, it has been demonstrated that human impacts can increase the overall importance of stochastic processes, which include drift, in both freshwater and terrestrial systems. For example, species losses, nutrient addition, and warming all increased the relative importance of stochastic processes in soil microbial communities (Zhang *et al.* 2016). Similarly, warming and nutrient addition increased the relative contribution of stochasticity—mainly caused by drift—among lake bacterioplankton communities (Ren *et al.* 2017). More generally and as mentioned above, we can expect that drift and drift-related extinctions will be greater in more isolated and smaller communities (Hubbell 2001; Vellend 2016). Thus, any anthropogenic changes which reduce community size and increase isolation (e.g., habitat fragmentation or land-use change) should tend to increase the contribution of drift to community dynamics (Melbourne & Hastings 2008). For example, biological invasions can cause decreased population sizes and thereby increase species vulnerability to stochastic extinctions (Gilbert & Levine

2013). Looking forward, a greater focus on the contribution of drift to community dynamics is warranted, as it is highly understudied but likely very important for shaping human impacts in both ecosystems.

SYNTHESIS AND FUTURE DIRECTIONS

Here we propose an integrative approach for comparing effects of human impacts on freshwater and terrestrial ecosystems using fundamental processes (Figures 1-3). We find several key differences in the strength and operation of these processes that suggest differing biodiversity responses in terrestrial and freshwater ecosystems (Figure 3, Table S1). For example, we find evidence suggesting that i) ecological selection due to abiotic gradients is stronger in terrestrial ecosystems than in freshwater, ii) that dispersal limitation may be greater in freshwater communities but by contrast that freshwaters have the highest potential for recovery via speciation, and iii) that the biggest data gap for cross-ecosystem comparisons is the relative influence of ecological drift among the two ecosystems. Overall, we found that quantitative comparisons across ecosystems are generally lacking, though data enabling such comparisons may be available for many organisms for the processes of dispersal and selection. In contrast, cross-ecosystem studies of speciation rates tend to focus on a few well-characterized organisms and such studies are largely missing for drift. Filling these gaps will be essential to fully link the processes of dispersal, speciation, selection and drift to the future dynamics and recovery of Earth's biodiversity.

In addition to filling data gaps, the mechanistic realism of our approach could be increased by considering interactions between community processes and between human impacts, as well as increased consideration of linkages and flows between ecosystems. For example, interactions between community processes can modify the effect of global change drivers, as has been found in experiments and models incorporating both competition and drift (Chesson 2000; Orrock & Watling 2010; Gilbert & Levine 2017), as well as experiments on the relative role of dispersal and selection (Ron *et al.* 2018). In addition, we focus primarily on the effects of single human impacts, though we recognize that these drivers interact in nature

(Settele & Wiemers 2015). For example, invasive species are often positively affected by global change, such as increases in temperature or land use intensification (Occhipinti-Ambrogi 2007; Hellmann *et al.* 2008; Eisenhauer *et al.* 2012). Finally, many of the ecosystem processes depend to some extent on linkages between the systems, such as flows of nutrients and organisms between land, rivers and lakes (Soininen *et al.* 2015). For example, dispersal of many freshwater insects depends on adult forms that fly (Bilton *et al.* 2003). Furthermore, transport of nutrients and pollutants between freshwater and terrestrial systems is known to affect populations in both systems (Kraus 2019; Kraus *et al.* 2021). As linkages between systems may be affected by global change drivers (Kraus 2019; Johnson *et al.* 2021; Kraus *et al.* 2021), their role should be more fully addressed in future developments of the proposed approach.

Realizing the full predictive potential of our approach which links human impacts to community processes will require increased research efforts and dialog between aquatic and terrestrial ecologists, evolutionary biologists, conservationists and policymakers. Future research aimed at better forecasting human impacts across ecosystems should include targeted, quantitative studies of the strength and function of single or multiple processes in both terrestrial and freshwater ecosystems, especially for the understudied processes of speciation and drift. Furthermore, our approach could be used to parametrize a mechanistic model of impacts, processes and biodiversity outcomes. Such a model would allow researchers to make more detailed, mechanistic predictions about how diversity may change in a given ecosystem. This work would build upon recent processes-based simulation studies used to infer the mechanisms shaping diversity through deep time, and across communities and spatial scales (Thompson *et al.* 2020; Hagen *et al.* 2021a, b). Mechanistic models, when combined with data, can provide more detailed estimates of the relative importance of processes shaping diversity across ecosystems and increase our understanding of how biophysical properties influence the balance and strength of processes (Table 1).

In conclusion, to tackle the ongoing and accelerating impacts of humans on biodiversity, we must provide a mechanistic understanding of how these impacts cause changes in terrestrial and freshwater ecosystems. Our process-based approach developed here may be useful for mitigating many impacts of global change for several key reasons. First, focusing on the real-world processes which create the diversity and structure of communities creates a mechanistic bridge between a given human impact, such as climate warming, and the outcome of this process on assemblages, such as increased turnover or decreased diversity. Second, it provides a foundation for further research, especially quantitative comparisons and mechanistic models. Thus, in the same way that these processes are meant to open the 'black box' of community ecology to understand community patterns (Vellend 2010), our approach has the potential to do the same for understanding the mechanistic pathways by which humans impact Earth's biodiversity.

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Icons and landscapes in Fig. 2 and human impact icons in Fig. 3 are modified from reshot.com.

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Table 1 | Key differences between freshwater and terrestrial ecosystems in physical, chemical, habitat and community properties and their hypothesized effect on community processes

Category	Property	Ecosystem comparison	Relevant process	Hypothesized effect on process	Reference
Physical	Buoyancy	Water > air	Dispersal	Intrinsic dispersal ability is greater in freshwater than on land	Bonte <i>et al.</i> 2012; Cornell & Harrison 2013; Srivastava & Kratina 2013
	Terminal velocity	Air > water	Dispersal	Intrinsic dispersal ability is greater in freshwater than on land	Denny 1990; Dawson & Hamner 2008
	Spatial structure of environmental variation	Terrestrial > marine > freshwater	Selection (abiotic)	Greater environmental structure on land could lead to stronger species sorting compared to freshwater	Herfindal <i>et al.</i> 2022
	Light attenuation	Water > air	Selection (abiotic)	Freshwater < terrestrial (greater niche differentiation)	Stomp <i>et al.</i> 2007
Habitat	Habitat structure	Rivers: dendritic Lakes: isolated Terrestrial: open (2D) Marine: open (3D)	Dispersal	Dispersal limitations (extrinsic) are greatest in freshwater habitats, and lowest in marine habitats	Baguette <i>et al.</i> 2013; Kappes <i>et al.</i> 2014; Wubs <i>et al.</i> 2016; Comte & Olden 2018
	Habitat stability	Terrestrial > freshwater	Speciation	In situ speciation plays larger role in dynamics of freshwater than terrestrial communities	Gillespie 2004; Miller <i>et al.</i> 2018
Chemical	Food quality	Freshwater > terrestrial	Selection (biotic)	May increase insect consumer populations and thus consumptive pressure in freshwater systems	Elser <i>et al.</i> 2000; Twining <i>et al.</i> 2021
Community	Species richness per area	Freshwater > terrestrial	Speciation	In freshwater habitats the diversification rates-per clade or lineage per unit time is highest	Miller <i>et al.</i> 2018; Rabosky 2020; Miller 2021
	Frequency of generalists	Freshwater > terrestrial	Selection (biotic)	Consumptive pressure expected to be stronger in aquatic compared to terrestrial habitats	Pringle <i>et al.</i> 2016; García-Girón <i>et al.</i> 2020
	Naïvete to predators	Freshwater > terrestrial	Selection (biotic)	Consumptive pressure expected to be stronger in aquatic compared to terrestrial habitats	Cox & Lima 2006; Anton <i>et al.</i> 2016, 2020
	Saturation of communities	Freshwater > terrestrial	Selection (biotic)	Competitive selection is weaker in freshwater habitats	Shurin <i>et al.</i> 2000; Shurin & Smith 2006; Alofs & Jackson 2014

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SUPPORTING INFORMATION

Table S1 | Overview of studies comparing how human impacts may, or may not, differ in type or severity among terrestrial vs freshwater ecosystems, organized by the process which humans impact

Process	Human impact	Effects in freshwater ecosystems	Effects in terrestrial ecosystems
<i>Dispersal</i>	Habitat fragmentation	Fragmentation in freshwater systems creates smaller and less uniform patches (Fagan 2002; Fuller <i>et al.</i> 2015)	Extrinsic features of terrestrial systems (e.g., more topological linkages) favor more dispersal (Srivastava & Kratina 2013; Fuller <i>et al.</i> 2015)
		Freshwater organisms have more intrinsic adaptations to disperse in fragmented habitats (Boedeltje <i>et al.</i> 2003)	
	Climate change		To track changing climates, species disperse and alter habitat structure and diversity (Lurgi <i>et al.</i> 2012; Travis <i>et al.</i> 2013; Steinbauer <i>et al.</i> 2018)
<i>Speciation</i>	Habitat loss	Because of the smaller existing area of freshwaters (Wiens 2015), effect of habitat destruction on speciation may be stronger	
	Eutrophication	Eutrophication in freshwaters can cause stronger changes (e.g., depletion of oxygen) and a greater reduction in speciation (Vonlanthen <i>et al.</i> 2012; Frei <i>et al.</i> 2022)	
	Climate change		Shifts in elevation could separate previously connected terrestrial populations, leading to increased speciation (Hua & Wiens 2013)
<i>Ecological selection</i>	Climate change	Due to buffering capacity of water, warming may be less severe in freshwater systems (Steele 1985; Vasseur & Yodzis 2004)	Selection regimes may be altered via novel competitors moving across elevation in response to climate change (Alexander <i>et al.</i> 2015)
			Increased species sorting (selection) along shifting terrestrial gradients (Loarie <i>et al.</i> 2009)
	Invasive species	Because of more complex freshwater interactions, invasions may have more complex effects on freshwater systems (Moorhouse & Macdonald 2015)	
		Higher naivete of prey populations to exotic predators in freshwater systems (Cox & Lima 2006; Anton <i>et al.</i> 2016, 2020)	
<i>Ecological drift</i>	Habitat loss	Decrease in population sizes (Pereira <i>et al.</i> 2010)	Decrease in population sizes (Pereira <i>et al.</i> 2010)