







Biotic homogenisation and differentiation as directional change in beta diversity: synthesising driver–response relationships to develop conceptual models across ecosystems

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ABSTRACT

Biotic homogenisation is defined as decreasing dissimilarity among ecological assemblages sampled within a given spatial area over time. Biotic differentiation, in turn, is defined as increasing dissimilarity over time. Overall, changes in the spatial dissimilarities among assemblages (termed ‘beta diversity’) is an increasingly recognised feature of broader biodiversity change in the Anthropocene. Empirical evidence of biotic homogenisation and biotic differentiation remains scattered across different ecosystems. Most meta-analyses quantify the prevalence and direction of change in beta diversity, rather than attempting to identify underlying ecological drivers of such changes. By conceptualising the mechanisms that contribute to decreasing or increasing dissimilarity in the composition of ecological assemblages across space, environmental managers and conservation practitioners can make informed decisions about what interventions may be required to sustain biodiversity and can predict potential biodiversity outcomes of future disturbances. We systematically reviewed and synthesised published empirical evidence for ecological drivers of biotic homogenisation and differentiation across terrestrial, marine, and freshwater realms to derive conceptual models that explain changes in spatial beta diversity. We pursued five key themes in our review: (i) temporal environmental change; (ii) disturbance regime; (iii) connectivity alteration and species redistribution; (iv) habitat change; and (v) biotic and trophic interactions. Our first conceptual model highlights how biotic homogenisation and differentiation can occur as a function of changes in local (alpha) diversity or regional (gamma) diversity, independently of species invasions and losses due to changes in species occurrence among assemblages. Second, the direction and magnitude of change in beta diversity depends on the interaction between spatial variation (patchiness) and temporal variation (synchronicity) of disturbance events. Third, in the context of connectivity and species redistribution, divergent beta diversity outcomes occur as different species have different dispersal characteristics, and the magnitude of beta diversity change associated with species invasions also depends strongly on alpha and gamma diversity prior to species invasion. Fourth, beta diversity is positively linked with spatial environmental variability, such that biotic homogenisation and differentiation occur when environmental heterogeneity decreases or increases, respectively. Fifth, species interactions can influence beta diversity *via* habitat modification, disease, consumption (trophic dynamics), competition, and by altering ecosystem productivity. Our synthesis highlights the multitude of mechanisms that cause assemblages to be more or less spatially similar in composition (taxonomically, functionally, phylogenetically) through time. We consider that future studies should aim to enhance our collective understanding of ecological systems by clarifying the underlying

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mechanisms driving homogenisation or differentiation, rather than focusing only on reporting the prevalence and direction of change in beta diversity, *per se*.

Key words: biodiversity, beta diversity, biotic homogenisation, biotic differentiation, species assemblage, turnover.

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I. INTRODUCTION

Change in biodiversity across ecosystems and organism groups is a fundamental sign of the ‘Anthropocene’ (Albert *et al.*, 2021; McGill *et al.*, 2015; Ripple *et al.*, 2019). In turn, conservation policies and interventions seek to apply scientific

understanding and evidence to anticipate and address biodiversity change from local to global spatial extents (Heino *et al.*, 2020; Mazar *et al.*, 2018). Worldwide, substantial changes to spatial variation in the composition of ecological assemblages (termed ‘beta diversity’; Anderson *et al.*, 2011) over time have been reported in a variety of ecosystems

(Dornelas *et al.*, 2014; Hillebrand *et al.*, 2018; McGill *et al.*, 2015). Developing a conceptual framework highlighting the drivers of directional changes in beta diversity would strengthen our capacity to predict future biodiversity trends associated with anthropogenic impacts and conservation interventions across multiple spatial scales or ecological contexts (Chase *et al.*, 2020).

Directional change in beta diversity refers to the process of either decreasing or increasing dissimilarity among assemblages over time, referred to as ‘biotic homogenisation’ and ‘biotic differentiation’, respectively (e.g. Olden & Rooney, 2006). Interest in biotic homogenisation or differentiation increased rapidly following formalisation of these concepts by (McKinney & Lockwood, 1999). Previous studies of spatial changes in biodiversity have emphasised redistributions of species (e.g. *via* range expansions) or loss of species (e.g. *via* range contraction or local extinction) as drivers of either biotic homogenisation or differentiation in specific ecosystems and organism groups (e.g. Magurran *et al.*, 2015; Rahel, 2002). Changes in biodiversity from local to global extents have been recognised as a signal of anthropogenic impacts (e.g. Avolio *et al.*, 2021; McGill *et al.*, 2015). Furthermore, the relevance of beta diversity to informing management, conservation, and restoration across multi-scale systems, such as identifying appropriate conservation areas and delimiting the spatial arrangement of agriculture practices, is now well-recognised (e.g. Socolar *et al.*, 2016). However, despite burgeoning interest in reporting directional changes in spatial beta diversity (e.g. Olden, Comte & Giam, 2018), there is no unifying framework that systematically synthesises mechanisms driving such changes. Relevant evidence remains scattered across the ecological literature specific to particular environmental realms (i.e. marine, terrestrial, and fresh water; e.g. Petsch, 2016).

Our goal here is to synthesise empirical evidence of the drivers of change in spatial beta diversity in the context of biotic homogenisation and biotic differentiation across ecosystems. Changes in spatial beta diversity are routinely interpreted as being the outcome of a single ecological mechanism in isolated studies (e.g. the effects of adding non-native species into a regional species pool), which may lead to distorted perceptions regarding the broad range of genuine potential drivers (e.g. Cardinale *et al.*, 2018). Here, we integrate evidence sourced from a host of empirical studies to provide a systematic map of beta diversity change as studied in the context of five key themes – temporal environmental change, disturbance regime, connectivity alteration and species redistribution, habitat change, and biotic and trophic interactions. For each theme in research on biotic homogenisation–differentiation, we develop a conceptual model to explain mechanisms of spatial beta diversity responses. We conclude by illustrating how a conceptual framework of directional change in beta diversity can be applied to understand causes of biodiversity change across multiple spatial extents, thereby informing conservation actions.

II. DEFINING BIOTIC HOMOGENISATION AND DIFFERENTIATION AS DIRECTIONAL CHANGE IN BETA DIVERSITY

Beta diversity is broadly defined as the variation in the composition of assemblages among sample units within a given area (Anderson *et al.*, 2011; Table 1), following the original definition by Whittaker (1960, 1972). Quantifying beta diversity requires delineating at least two spatial scales (as grain and extent) within a standardised assessment protocol: a set of smaller-spatial units (e.g. quadrats of $50 \times 50 \text{ m}^2$) and a broader spatial unit (e.g. grid cells of $100 \times 100 \text{ km}^2$) that covers all smaller spatial units. Here, Whittaker’s (1960) diversity partitioning defines diversity for the broader spatial unit as ‘gamma’ (or regional) diversity (γ) and the average diversity at the smaller spatial unit as ‘alpha’ (or local) diversity ($\bar{\alpha}$). ‘Beta’ diversity (β) is then defined as the degree to which regional diversity exceeds local diversity (Fig. 1) and can be measured either multiplicatively ($\beta = \gamma / \bar{\alpha}$) or additively ($\beta = \gamma - \bar{\alpha}$) (Crist & Veech, 2006; Lande, 1996; Whittaker, 1960).

While the multiplicative definition of beta diversity is unit free (i.e. the ratio consists of two numbers each expressed as ‘numbers of species’ that cancel each other out), it remains clear that values for beta diversity will depend on the chosen extent of both regional and local sampling units. More species occur in sampling units spanning broader areas (Connor & McCoy, 1979). Gamma diversity can only exceed alpha diversity if and when the smaller sampling units contain different combinations of taxa (or composition) from one another. Therefore, the concept of beta diversity as differentiation in the identities of taxa among smaller sampling units within a larger spatial unit (Anderson, Ellingsen & McArdle, 2006) is effectively equivalent to Whittaker’s (1960) definition. The fundamental idea of differentiation in identities of taxa is captured by measures of dissimilarity in composition among small-scale sampling units. In turn, the concept of beta diversity has been broadened to include *variation in assemblage structure* more generally (Table 1; Anderson *et al.*, 2011, 2006; Jurasinski, Retzer & Beierkuhnlein, 2009; Legendre & De Cáceres, 2013) and can be quantified by any ecologically relevant dissimilarity measure [e.g. Jaccard or Sørensen index for presence/absence data, or percentage-difference (Bray–Curtis index of dissimilarity) for differences in relative abundances of species].

Variation in assemblage composition among sampling units at a given spatial scale based on a given measure of dissimilarity is quantified by dispersion in multivariate space (Jurasinski *et al.*, 2009; Legendre, Borcard & Peres-Neto, 2005; Legendre De Cáceres, 2013; Whittaker, 1960, 1972). Useful measures of dispersion (summarised in Anderson *et al.*, 2011) include: (i) average interpoint dissimilarities (Vellend *et al.*, 2007; Whittaker, 1960, 1972); and (ii) average distances-to-centroid (PERMDISP; Anderson, 2006; Anderson *et al.*, 2006) or components of variation from

Table 1. Definitions of key terms relevant to interpreting and conceptualising directional change in spatial beta diversity as adopted in this synthesis.

Term	Definition
Assemblage	A set of species (or a set of individuals belonging to a set of species) co-occurring at a given time within a defined spatial sampling unit or area.
Alpha richness	The number of species occurring within a small-scale (local) standardised sampling unit.
Alpha diversity	The mean number of species present, calculated from a set of small-scale (local) standardised sampling units taken from within a specified broad-scale (regional) area (see Whittaker, 1960).
Gamma diversity	The total number of species occurring (or listed to occur) within a broad-scale (regional) sampling unit or area (see Whittaker, 1960).
Beta diversity	The ratio (or difference) of gamma diversity to alpha diversity or the variation (or dissimilarity) in composition among assemblages within a defined spatial area (Whittaker, 1960; Anderson <i>et al.</i> , 2011).
Turnover	Change in composition of assemblages along a gradient (space, time, environmental) (see Anderson <i>et al.</i> , 2011). Also defined as a component of dissimilarity (see <i>Replacement dissimilarity</i>), as distinguished from nestedness (see Baselga, 2010).
Variation	The degree to which assemblages differ in composition among sample units (see Anderson <i>et al.</i> , 2011).
Replacement dissimilarity	The component of dissimilarity among assemblages that is due to the replacement of species or functional characteristics among assemblages (see Legendre, 2014).
Richness difference dissimilarity	The component of dissimilarity in assemblage composition due to assemblages having different numbers of species or functional characteristics (see Legendre, 2014).
Temporal change in spatial beta diversity	Change in the magnitude of dissimilarity among assemblages occurring in a set of spatial sampling units over time. (Note that this is distinct from ‘temporal beta diversity’, which is the change in assemblage composition through time for a given ecosystem or spatial area; see Legendre, 2019; Magurran <i>et al.</i> , 2019).
Biotic homogenisation	Increasing similarity (decreasing dissimilarity) among assemblages occurring in a set of spatial sampling units over time (Olden & Rooney, 2006). Measured as a decrease in the magnitude of beta diversity (as variation) among sample units.
Biotic differentiation	Opposite of biotic homogenisation; increasing dissimilarity (decreasing similarity) among assemblages occurring in a set of spatial sampling units over time (Olden & Rooney, 2006). Used synonymously with ‘biotic heterogenisation’ (Socolar <i>et al.</i> , 2016).
Ecosystem engineer	Organisms that modify the availability of abiotic or biotic resources other than themselves to other species (Jones <i>et al.</i> , 1994).
Spatial hierarchy	A nested hierarchy of spatial scales (e.g., quadrats, sites, regions, continents). Within each scale, changes through time in the magnitude of beta diversity can be measured and considered (Wiens, 1989; Pavoine <i>et al.</i> , 2016).

a dissimilarity-based partitioning (PERMANOVA; see Anderson, 2001; Legendre & Anderson, 1999; McArdle & Anderson, 2001). The latter is most easily extended to obtain independent measures of assemblage variation (beta diversity) for a hierarchy of spatial scales (e.g. Anderson *et al.*, 2005).

Temporal change in alpha diversity has been the predominant focus of research quantifying biodiversity change (e.g. Cardinale *et al.*, 2018; Hillebrand *et al.*, 2018; Vellend *et al.*, 2013). Yet measures of either alpha or gamma diversity alone do not reflect changes in species’ identities (Hillebrand *et al.*, 2018; Magurran & Henderson, 2010) and are inadequate for quantifying biotic homogenisation or differentiation (Olden & Rooney, 2006). Here, we focus on *directional change in spatial beta diversity*. Note that this is conceptually quite distinct from the notion of temporal beta diversity, *per se* [being simply the change in assemblage composition for a given spatial unit over time (e.g. Dornelas *et al.*, 2014; Legendre, 2019; McGill *et al.*, 2015)]. We define directional change in spatial beta diversity as either increasing dissimilarity in composition among sampling units (‘biotic differentiation’) or decreasing dissimilarity (i.e. increasing similarity)

in composition among sampling units over time (‘biotic homogenisation’) (McKinney & Lockwood, 1999; Olden, 2006; Olden & Rooney, 2006; Socolar *et al.*, 2016). There are naturally three possible ways beta diversity may vary over time within a specific time period: (i) no marked directional change, with assemblages having non-significant (and inconsistent) fluctuations in composition; (ii) divergence in assemblage composition (biotic differentiation); or (iii) convergence in assemblage composition (biotic homogenisation).

In addition to the concept of beta diversity as variation in community structure among sampling units, beta diversity is also considered a measure of turnover (change) in assemblage structure between sampling units that are ordered along a nominated gradient of interest (e.g. elevation, depth, temperature, moisture, etc.). This is commonly measured using distance–decay curves (see Millar, Anderson & Tolimieri, 2011; Nekola & White, 1999; Vellend, 2001; Whittaker, 1960). We do not pursue this idea further in this synthesis; rather, we focus on measures of beta diversity as ‘variation’ (*sensu* Anderson *et al.*, 2011; Fig. 1). Furthermore, we focus specifically on studies that measured biotic homogenisation or biotic differentiation in ecological systems over time,

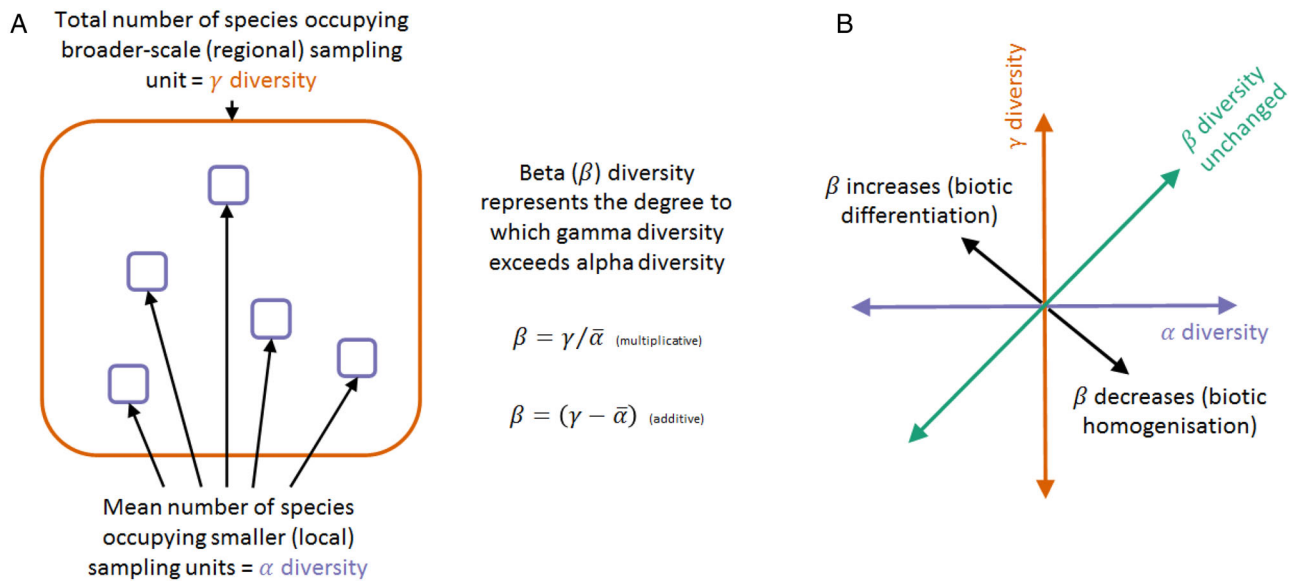


Fig. 1. (A) Schematic diagram illustrating the links between average alpha ($\bar{\alpha}$) diversity, gamma (γ) diversity, and beta (β) diversity. Beta diversity represents the degree to which gamma diversity exceeds alpha diversity, and therefore the degree to which assemblages (at the smaller scale) differ from one another in the identities of species they contain. (B) Directional change in beta diversity (i.e. decreasing and increasing beta diversity, termed ‘biotic homogenisation’ or ‘biotic differentiation’, respectively) occurs when there are changes in the numbers of species occupying local sampling units, broader regional units, or both. B also represents conceptual model 1.

rather than attempting to synthesise results from any study that quantified beta diversity.

Achieving a more detailed understanding of the mechanisms driving biotic homogenisation or differentiation can be gained by considering differences in richness and/or the replacement of taxa among sample units (Baselga, 2010; Legendre, 2014). Differences in the number of taxa (richness differences) occur when an assemblage has a larger number of taxa or functional traits compared to another assemblage (Carvalho, Cardoso & Gomes, 2012), whereas replacement refers to the fact that – even if richness remains constant – the species present in one unit may be absent in another, being replaced by a new species. A special form of richness difference is nestedness, whereby an assemblage in one sample unit is comprised of a subset of the taxa occupying another unit (Baselga, 2010). Importantly, pure nestedness directly implies differences in richness, whereas differences in richness may or may not be generated by nestedness (Legendre, 2014). Kraft *et al.* (2011) also noted the dependence of Jaccard dissimilarity on richness differences (specifically, on the size of the regional species pool); hence, they proposed the use of a probabilistic dissimilarity measure (Raup–Crick) to account for richness differences in beta diversity studies. However, most studies of biotic homogenisation or differentiation that we reviewed simply did not provide a formal partitioning of replacement or richness difference (*sensu* Legendre, 2014), nor was the Raup–Crick probabilistic measure commonly adopted. Therefore, our review draws conclusions regarding underlying drivers of biotic homogenisation or differentiation from all ancillary

information provided by the authors in the context of a given study.

The spatial scaling of patterns and processes is central to ecology (Allen & Starr, 1982; Wiens, 1989). Therefore, interpreting changes in beta diversity (as variation in community structure) can occur at any level within a hierarchy of scales spanning individual patches (e.g. quadrats within a forest) to the entire Earth (Barton *et al.*, 2013). In many studies, there are two spatial scales of interest (e.g. locations within regions), yet study designs involving multiple spatial scales (e.g. Fig. 2) are common and allow researchers to examine changes in beta diversity across different scales (e.g. Heino, Louhi & Muotka, 2004; Rolls *et al.*, 2019). Changes in beta diversity over time across different spatial scales may be inconsistent over time in both magnitude and direction, even in response to the same factor. Therefore, any study of beta diversity needs to specify the spatial scales relevant to the organisms of interest in any given environmental context, and interpreted accordingly (Pavoine, Marcon & Ricotta, 2016).

III. SYNTHESISING EVIDENCE OF DRIVERS OF CHANGE IN SPATIAL BETA DIVERSITY

We sourced all publications captured by *ISI Web of Science* using all possible combinations of terms ‘biotic OR biological’ AND ‘homogen* OR differentiat* OR heterogen*’ up until 21 January 2021 ($N = 1288$ articles). This search string was deliberately chosen to match the purpose of synthesising

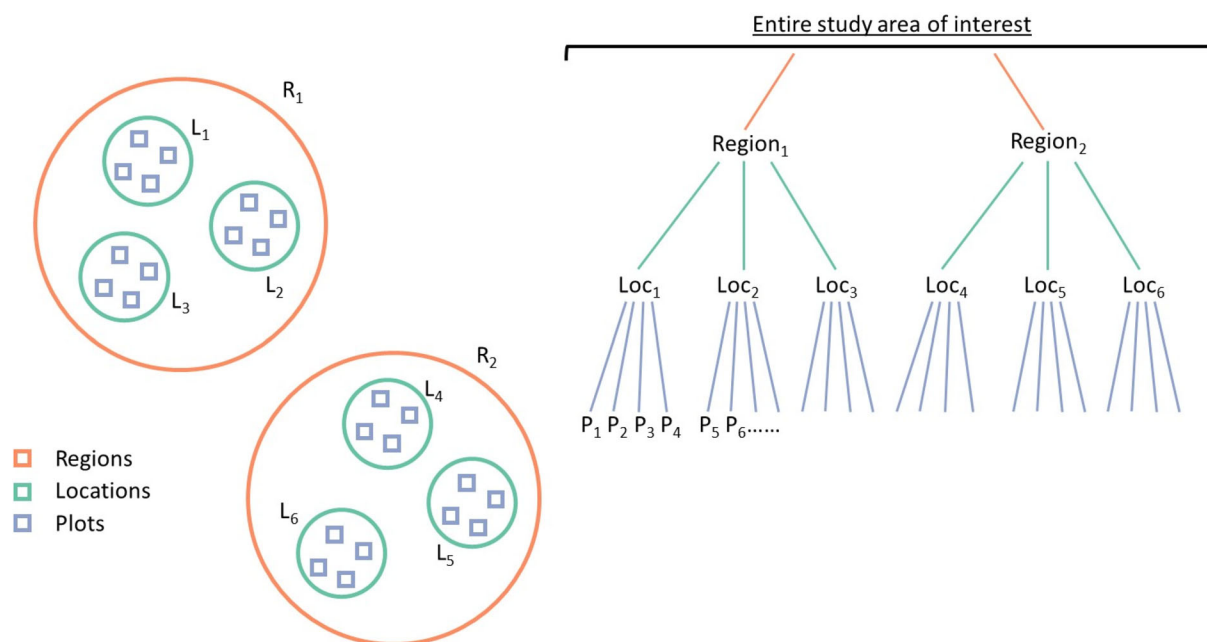


Fig. 2. Schematic diagram illustrating how beta diversity can be quantified and examined across multiple hierarchical spatial scales. For example, assemblages may be sampled across multiple region (R) units, multiple locations (L) within each region, and multiple plots (P) within each location. Analytically, beta diversity (and, therefore, temporal change in beta diversity) can be quantified at any spatial level within the sampling hierarchy.

evidence of biotic homogenisation and differentiation (i.e. studies of beta diversity with an applied or conservation emphasis). Publications were retained for full review if they sought to test hypotheses, identify drivers of biotic homogenisation or differentiation, or interpreted empirical analyses in the context of biotic homogenisation or differentiation *using raw data* ($N = 507$ publications) (see online Supporting Information, Fig. S1). We excluded the remaining 781 papers (deemed unsuitable for our synthesis) because they: (i) referred to directional change in beta diversity [e.g. citing McKinney & Lockwood (1999), Olden *et al.* (2004) or Olden & Rooney (2006)] without direct reference to primary data (e.g. speculating about the role of species' invasions as drivers of unstudied directional change in beta diversity, or review papers, etc.); (ii) cited papers that included at least one of the search terms in the title yet made no reference to the topic itself in the text; (iii) made predictions about future changes to spatial variation in composition (e.g. *via* simulation modelling); or (iv) incorrectly inferred conclusions about directional change in composition without reference to organisms' taxonomic, functional, or phylogenetic identities (e.g. used only community specialisation indices, species richness, etc.; Olden & Rooney, 2006). Importantly, directional change in beta diversity is a time-dependent process (Olden & Rooney, 2006). Our synthesis includes quantitative evidence obtained by studies assessing change in spatial beta diversity over time and also evidence drawn indirectly *via* space-for-time studies (Pickett, 1989).

All 507 empirical publications retained were fully reviewed and the following details compiled: (i) hypothesis

or context of interest; (ii) spatial extent of analysis (including countries or regions covered); (iii) temporal extent of analysis; (iv) measure of assemblage dissimilarity used; (v) analytical methods used to measure change in beta diversity; (vi) ecological realm (terrestrial, freshwater, marine); (vii) organism group (response variable, or variables); (viii) biodiversity facet for which change was being quantified (taxonomic, functional, phylogenetic); (ix) key relevant findings; and (x) inferred directional change (homogenisation, differentiation, neutral, or inconsistent/mixed). The resulting database (see Database S1) formed the basis for our synthesis.

We structured our synthesis around five key themes of biotic homogenisation–differentiation research identified during the review of literature (i.e. hypotheses being tested by authors of empirical publications; Table S1). The first theme was research examining temporal environmental change. Such studies typically analysed trends or variability in spatial beta diversity spanning time periods greater than 10 years, often in the context of change in abiotic conditions (e.g. climate), and are a useful starting point for identifying historical trends in spatial beta diversity. The second theme was effects of environmental disturbance regimes on spatial beta diversity patterns, such as fire, flooding, or heat waves. The third theme was the effects of connectivity alteration and species redistributions (e.g. invasions, human-facilitated translocations) on spatial beta diversity. This has been a major focus of research in the context of biotic homogenisation–differentiation. The fourth theme was habitat change (e.g. anthropogenic modification of landscapes),

and the fifth theme was biotic and trophic interactions (e.g. trophic interactions among species within assemblages). We accept inevitable overlap among these five themes of research, such as anthropogenic habitat change influencing connectivity among assemblages (themes 4 and 3) and connectivity facilitating species invasions and population size changes, which may in turn influence beta diversity through biotic interactions (themes 3 and 5).

For each of the five research themes on biotic homogenisation or differentiation, we summarised the hypothesised mechanism(s) driving reported changes or relationships. We recognise that there are many ways to measure beta diversity as variation in ecological assemblages. There are a host of methodological decisions made by the original researchers for every study, including: (i) whether to include relative abundances of organisms, or only to use presence/absence (identities of species); (ii) which dissimilarity measure to use (e.g. Jaccard, Sørensen, Bray–Curtis, Raup–Crick, Hellinger); (iii) which set of organisms to consider as potential members of the assemblage of interest (e.g. choice of sieve mesh size for sampling soft-sediment infauna, etc.); (iv) how to quantify relative abundance for various taxa (e.g. biomass, cover, counts, presence/absence); (v) which index of beta diversity to use (Anderson *et al.*, 2011; Tuomisto, 2010a); and, for any multi-scale studies, (vi) whether to use multiplicative or additive components in a beta diversity partitioning (Crist & Veech, 2006; Jost, 2007; Lande, 1996). All such decisions can affect outcomes. We assumed, in all cases, that the original authors made useful methodological choices for their study organisms and system of interest. Hence, we treated the results obtained by each study at face value, and the inferences drawn by the original authors were assimilated directly into our synthetic analysis (Table S2). The following sections synthesise the findings of these studies for hypothesised mechanisms across the three ecological realms.

IV. SYNTHESISING DRIVERS AND DIRECTIONS OF CHANGE IN SPATIAL BETA DIVERSITY ACROSS ENVIRONMENTAL REALMS

(1) Temporal environmental change

(a) Terrestrial ecosystems

Over decades to millennia, terrestrial beta diversity has had distinct periods of homogenisation and differentiation prior to major anthropogenic landscape change (Feurdean *et al.*, 2010). Beta diversity change in terrestrial systems is reportedly driven by three main processes: losses of species (extinctions) with narrow niches (i.e. ‘specialists’; e.g. Britton *et al.*, 2017), increases in the occurrence of species with broad ecological tolerances [i.e. ‘generalists’ (e.g. Flagmeier *et al.*, 2014; Johnson, Mudrak & Waller, 2014)], or both [i.e. true replacement (see e.g. Christian *et al.*, 2009; Heinrichs & Schmidt, 2017)]. Generalist species associated with biotic homogenisation originate either within or beyond the regional species pool (as native generalists or non-native invaders,

respectively) (Keith *et al.*, 2009; Le Viol *et al.*, 2012; Naaf & Wulf, 2010; Sullivan, Newson & Pearce-Higgins, 2016). Both homogenisation and differentiation of terrestrial assemblages have been associated with changes in climate spanning five decades (e.g. Flagmeier *et al.*, 2014; Ross *et al.*, 2012) or under specific environmental conditions such as increased nutrient availability (Reinecke, Klemm & Heinken, 2014). For example, beta diversity of terrestrial plants declined only among plots that were intact yet remained constant when compared among plots that were subjected to human impact in the UK (Diaz *et al.*, 2013), suggesting some element of context dependency regarding the direction of change in beta diversity across landscapes.

(b) Marine ecosystems

Changes in spatial beta diversity in marine ecosystems have been linked to changes in physical environmental variables. Fish assemblages in contrasting depth and salinity zones of a coastal bay became increasingly homogenised over an 18-year period in tropical Brazil, attributed to increasing temperature and decreasing water clarity (Araujo, De Azevedo & Guedes, 2016). In the Mediterranean, beta diversity of coral and algal assemblages declined, associated with species ranges expanding with increasing temperature (Bianchi *et al.*, 2019; Gatti *et al.*, 2015). Both contraction and expansion of species’ ranges were responsible for declining beta diversity of coastal mangrove plants over 28 years in Bangladesh (Sarker *et al.*, 2019). Despite homogenisation being frequently reported for change in taxonomic beta diversity, comparisons of functional and taxonomic beta diversity showed contrasting trajectories of temporal change. In North Sea fish assemblages, for example, functional beta diversity declined, whereas taxonomic beta diversity increased, over a 33-year period of changing climate (McLean *et al.*, 2019).

(c) Freshwater ecosystems

Change in spatial beta diversity over time is inconsistent in direction and magnitude in freshwater systems worldwide. Multiple facets of beta diversity of macrophytes, fish, macroinvertebrates, and phytoplankton assemblages remained stable across boreal, temperate, and tropical climates based on studies spanning up to 127 years (Angeler & Drakare, 2013; Gillette *et al.*, 2012; Lindholm *et al.*, 2020a,b; Parks, Quist & Pierce, 2014; Wojciechowski *et al.*, 2017). In other examples, trends of biotic homogenisation have occurred, often linked with changes in physico-chemical water quality and diminishing surface water availability and driven by increasing spatial similarity in population abundances and widespread loss of large, long-lived organisms (i.e. nestedness) (Ball-Damerow, M’Gonigle & Resh, 2014; dos Santos Bertoncin *et al.*, 2019; Cheng *et al.*, 2014; Lopes *et al.*, 2017; Miyazono, Patiño & Taylor, 2015). Trends of biotic homogenisation in freshwater systems are not consistent in time, space, nor facet of biodiversity (Gianuca *et al.*, 2018).

Taxonomic beta diversity of freshwater invertebrates increased among streams in the UK over 30 years, yet functional beta diversity showed no major change (Larsen *et al.*, 2018). Temporal patterns in homogenisation–differentiation of freshwater biodiversity were variable among river systems. In both France and the USA, for example, beta diversity of fish assemblages trended towards homogenisation within some streams and differentiation or no clear change in others over the same period (Kuczynski, Legendre & Grenouillet, 2018; Rogosch & Olden, 2019).

(d) *Conceptual model 1: temporal change in beta diversity through changes in species occurrence across spatial scales*

Does directional change in beta diversity occur in the absence of any obvious driving force (e.g. anthropogenic disturbance)? Considering change in spatial beta diversity over long time periods (100–10,000 years) is useful for assessing whether biotic homogenisation or differentiation are persistent, and if such events are ecologically significant against a backdrop of historical fluctuations in beta diversity. Across terrestrial, marine, and freshwater ecosystems, empirical studies highlight that spatial beta diversity can show distinct phases of stability (e.g. Benito *et al.*, 2020; Lindholm *et al.*, 2020a,b), punctuated by periods of biotic differentiation (e.g. Pinceloup *et al.*, 2020) or homogenisation (e.g. Britton *et al.*, 2009). Temporal trends in beta diversity did not appear to be associated with the duration or period of analysis. These findings suggest that directional change in beta diversity is not more or less evident when assessed over specific time periods (e.g. annual, decadal, etc.).

Olden & Poff (2003) have emphasised the role of combinations of species losses and species invasions (i.e. the spread of species beyond their natural range) in contributing to biotic homogenisation and differentiation. This idea emphasises that different beta diversity outcomes will occur, depending on (i) whether species losses or gains (i.e. colonisations) are consistent or inconsistent among pairs of assemblages, and (ii) the level of historical or ‘reference’ dissimilarity among assemblages. Here, decreased beta diversity occurs when assemblages consistently lose unique taxa and remaining taxa are shared among sampling units, or when species additions are ubiquitous among assemblages. Conversely, beta diversity among assemblages increases when the occurrence of taxa shifts from ubiquitous to patchy (i.e. patchy species losses), or as patchy taxa additions coincide with patchy losses (Olden & Poff, 2004).

We propose here that ecologists may conceptualise temporal change in beta diversity using Whittaker’s (1960) original measure: the ratio of richness in the regional species pool *versus* the mean richness in individual assemblages (i.e. gamma *versus* alpha diversity) (Fig. 1B). Beta diversity remains stable when there are either no substantial changes in the occurrence of taxa at both local or regional spatial scales, or when changes in both alpha and gamma diversity match each other proportionally (e.g. Angeler & Drakare, 2013). Species invasions (i.e. increases in gamma diversity) lead to beta

diversity decline only when those new species occur ubiquitously across most assemblages (thereby increasing mean alpha diversity). By contrast, when species invasions occur infrequently or patchily among assemblages, beta diversity increases as the increase in mean alpha diversity among assemblages will be minor relative to the change in gamma diversity. For example, biotic differentiation of plants occurred over 54 years as increases in gamma diversity (26%) were greater than increases in alpha diversity (12%) (Li & Waller, 2015). Furthermore, beta diversity fluctuations can occur in the absence of species invasions *via* changes in the occurrence of taxa across two sample units within the native species pool. For example, homogenisation of terrestrial plant assemblages occurred as the prevalence of native species spread across assemblages (McCune & Vellend, 2013). In this latter example, changes in alpha diversity (and not changes in gamma diversity) drove a decline in beta diversity.

This conceptual model of temporal change in beta diversity emphasises ‘broad-sense’ measures of dissimilarity among assemblages (*sensu* Koleff, Gaston & Lennon, 2003). It does, however, inadequately identify the relative contributions of replacement *versus* richness differences towards changing dissimilarity over time (*sensu* Legendre, 2014). However, understanding these contributions is useful in the context of biotic homogenisation or differentiation, because either outcome can occur *via* changes in the replacement of taxa among assemblages or *via* changes in richness (it is important to note here that richness differences correspond to the degree to which assemblages in different sampling units differ in their individual richness values. This is not the same as alpha diversity, which is the *average* richness for a set of sampling units). Biotic homogenisation can occur by way of either decreasing replacement of taxa among assemblages, or decreasing magnitudes in the degree to which assemblages differ in richness values. For example, homogenisation of woodland bird assemblages occurring with climate extremes was driven by declines in richness differences but not replacement (Haslem *et al.*, 2015). By contrast, homogenisation of freshwater invertebrates in New Zealand over 25 years was driven by declines in replacement among assemblages (Mouton *et al.*, 2020).

(2) Disturbance regime

(a) Terrestrial ecosystems

Individual disturbance *events* (e.g. fire, storms) and/or changes to disturbance regimes can trigger either homogenisation or differentiation for terrestrial assemblages. Both biotic homogenisation and biotic differentiation can occur with increases in fire frequency in different contexts, suggesting diverging outcomes for different landscape ecosystems (Da Silva *et al.*, 2018; Grau-Andres *et al.*, 2019; Li & Waller, 2015; Velle *et al.*, 2014). For example, increasing prevalence of later successional organisms across landscapes where fire disturbances have been reduced (‘mesophication’;

Nowacki & Abrams, 2008) is associated with decreased beta diversity (e.g. Li & Waller, 2015). Homogenisation also occurs through filtering of fire-intolerant species from the regional species pool by frequent disturbances (e.g. Da Silva *et al.*, 2018). By contrast, increased beta diversity can also be created by patchiness in disturbance histories (Grau-Andres *et al.*, 2019). Variable beta diversity outcomes occur in response to other disturbances, such as storms, with increases, decreases, or no significant changes in beta diversity having been detected in terrestrial plant assemblages before *vs* after storm events (e.g. Brewer *et al.*, 2012; Martinez-Ruiz & Renton, 2018; Savage *et al.*, 2018; Smart *et al.*, 2014). Such variable outcomes of terrestrial disturbance regimes are potentially explained by two main factors. First, individual studies differed in their temporal extent of monitoring, reporting outcomes at different points along the disturbance–response timeframe. Second, different studies are conducted at different spatial scales relative to the scale of disturbances. Third, there were differences in extent, frequency, severity (magnitude) and spatial variability of disturbance regimes across landscapes, indicating that the effects of different disturbance regimes on spatial beta diversity will vary with variation in historical disturbance context.

(b) *Marine ecosystems*

The single study testing the effects of disturbances on biotic homogenisation–differentiation in marine ecosystems revealed rapid change in beta diversity associated with extreme disturbance events. A heatwave in the northern Great Barrier Reef (Australia) caused mass coral bleaching, leading to both taxonomic and functional homogenisation of fish assemblages evident in less than 1 year (Richardson *et al.*, 2018). Here, neither taxonomic nor functional richness changed significantly over time, but biotic homogenisation occurred, with widespread and increasing dominance by algalivorous species occurring after the bleaching event (Richardson *et al.*, 2018). Additionally, high spatial variation in the composition of coral communities prior to bleaching was the primary predictor of decreasing beta diversity in fish assemblages, as opposed to the severity of overall coral loss (Richardson *et al.*, 2018).

(c) *Freshwater ecosystems*

Temporal variation in hydrology functions as a fundamental disturbance regime for freshwater ecosystems (Datry, Bonanda & Heino, 2016; Lepori & Hjerdt, 2006). Both temporal and spatial variation in hydrology can in some (but not all) cases cause significant changes in beta diversity over time (Crabot *et al.*, 2020). Almost all studies assessing homogenisation–differentiation outcomes associated with disturbance regimes in freshwater systems focused on assessing the effects of anthropogenic changes to hydrological disturbance regimes. In France, Brazil, and the USA, beta diversity of freshwater organisms in flow-regulated rivers was lower or declined over time compared to free-flowing

rivers where floods and low flows remained as hydrological disturbances and that contributed to spatial variation in assemblage (Braghin *et al.*, 2018; Bruno *et al.*, 2019; Lawson & Johnston, 2016). In some cases, differences in beta diversity among rivers with contrasting levels of anthropogenic alteration were either more, or solely, evident for functional rather than taxonomic beta diversity (Braghin *et al.*, 2018). However, beta diversity increased in hydrologically altered rivers due to patchy occupancy of non-native species (Gido, Dodds & Eberle, 2010). For wetlands, within-wetland beta diversity can vary over time with contrasting hydrological conditions. For example, nestedness on a gradient of decreasing inundation permanence (i.e. richness decline associated with systematic loss of species along the hydrological gradient) led to decreased beta diversity of amphibian assemblages (Ramalho, Machado & Vieira, 2018).

(d) *Conceptual model 2: disturbance heterogeneity as a driver of beta diversity change*

The contribution of environmental disturbances to spatial patterns of biodiversity has been a persistent theme in ecology (e.g. Connell, 1978; Lepori & Hjerdt, 2006). Disturbance is defined as either predictable or unpredictable forces that cause a change in the environmental conditions of an ecosystem (Rykiel Jr, 1985). Disturbances (perturbations) are a feature of all ecosystems (Sousa, 1984), and disturbance regimes (temporal sequences of disturbance events) vary in their extent, frequency, severity, and duration. We can conceptualise a model of directional beta diversity change as a function of broad-scale variation in environmental disturbances (Fig. 3). The disturbance heterogeneity model of change in beta diversity emphasises the role of spatial variation (patchiness) and temporal variation (asynchrony) in environmental disturbances (i.e. ‘disturbance regimes’) in driving beta diversity. Ecological disturbances can be either predictable or unpredictable and they affect populations of species (typically *via* mortality) and their spatial distribution (Sousa, 1984). Some disturbance events may be considered as ‘extreme’ (e.g. drought, bleaching, earthquakes, etc.); their effects are superimposed on natural levels of temporal environmental variation. In other cases, stochastic disturbances (caused by floods, fires or waves) may be expected as part of the natural dynamics of a given ecosystem, landscape or region. Disturbance events influence the degree to which assemblages in different patches across and among regions are spatially synchronised (or desynchronised) in their relative positions along the natural successional progression of community assembly through time (Fig. 3). The ‘disturbance heterogeneity’ model is based on the idea that a single climax assemblage ‘type’ will eventually dominate a region unless the assemblage is ‘reset’ by disturbance. Spatial variation in the frequency, extent, and intensity of disturbance events generally increases beta diversity. Assemblages exposed to different disturbance histories will be at differing stages of succession within the overall spatial extent of interest.

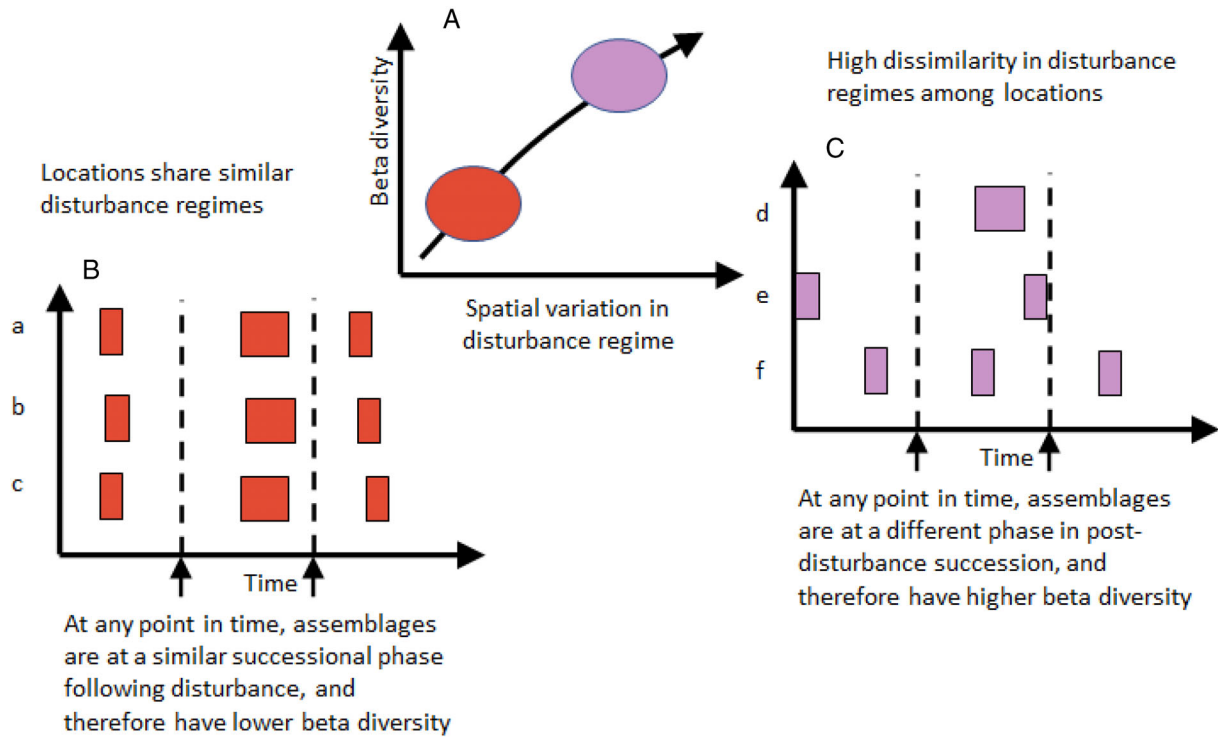


Fig. 3. Conceptual model 2 illustrating how beta diversity can be driven by spatio-temporal variation in disturbance regimes across scales. The overarching prediction is that beta diversity is positively associated with heterogeneity in disturbance regime (A). In B and C, letters a–c and d–f represent three study sites in two regions, and the red and purple boxes represent the timing and duration (or intensity) of disturbances. Dashed lines in B and C represent hypothetical points in time where assemblage composition at each study site is assessed (and therefore beta diversity quantified). In a region where disturbance heterogeneity is low (i.e. all sites are exposed to similar disturbance regimes in terms of frequency, timing, magnitude, B), beta diversity is predicted to be low because at any point in time, each assemblage is at a similar phase of post-disturbance recovery. By contrast, where variation in disturbance regimes among sites is high (C), assemblages will be in differing phases of post-disturbance recovery, and hence beta diversity will be higher. The model is applicable within any level of a spatial hierarchy (e.g. variation in disturbance regimes among locations within a region, or among regions).

Our disturbance heterogeneity model of beta diversity predicts that spatial variation in disturbance regimes among patches positively affects beta diversity (Fig. 3). This model is an adaptation of the heterogeneous disturbance hypothesis (Warren *et al.*, 2007), which emphasises the role of spatial variation in disturbances among patches within a region to maintain co-existence of species (gamma diversity). Spatial variation in temporal disturbance regimes drives beta diversity at corresponding spatial extents (‘asynchronous’ disturbances; Sousa, 1984). Beta diversity is hypothesised to be positively driven by spatial variation in temporal disturbance regimes. In regions where variation in disturbance (e.g. fire) is low, within-region beta diversity will be low, and beta diversity increases with increased spatial variation in disturbance. As disturbance heterogeneity increases, assemblages in different patches become temporally desynchronised in terms of their successional development towards a climax state. Fire, floods, and storm events are examples of disturbance forces in terrestrial, freshwater, and marine ecosystems, respectively. A prediction from terrestrial ecology is that high heterogeneity in fire regimes (pyrodiversity; patches with

contrasting histories of burning) support high levels of beta diversity (e.g. Kelly, Brotons & McCarthy, 2017). Empirical analyses provide moderate support for this hypothesis (e.g. Andersen *et al.*, 2014), for example, with bird assemblages in Spain having high levels of beta diversity with spatial variation in burning regimes (Clavero, Brotons & Herrando, 2011). In a freshwater context, increasing environmental heterogeneity can lead to a decrease in the occurrences of aquatic invertebrates that are active dispersers (with winged adults), increasing niche partitioning and hence beta diversity (Heino, 2013).

Useful tests of the disturbance heterogeneity–beta diversity hypothesis may be done where human activities and management interventions have altered the spatial variation of natural disturbance regimes (*sensu* Fukami & Wardle, 2005). For example, spatially consistent forest-management practices have reduced the beta diversity of plants in the Czech Republic (Prach & Kopeccky, 2018). Indigenous burning regimes (often patchy, low-intensity fires with varying frequency) have occurred historically across all inhabited continents (Trauernicht *et al.*, 2016). Across Australia,

Norway, and the USA, prescribed fire regimes and fire suppression (and concomitant loss of patchy, frequent, and low-intensity fires) have reduced spatial variation (hence decreased beta diversity) of plant assemblages (Li & Waller, 2015; Velle *et al.*, 2014). In freshwater ecosystems, management of water resources (such as dam construction and operation, and regulation and extraction of water) has altered the spatial variation in hydrological disturbance regimes both within and among river networks (McManamay, Orth & Dolloff, 2012; Poff *et al.*, 2007), leading to the hypothesis that reduced spatial heterogeneity in hydrology contributes to reduced beta diversity (Moyle & Mount, 2007). While empirical assessment of this overall hypothesis has received much more attention in terrestrial ecosystems (under the theme of ‘pyrodiversity’) than in freshwater systems (Rolls *et al.*, 2018), reduced frequency of hydrological disturbances along river channels due to flow regulation is also predicted to reduce beta diversity by causing all assemblages to be consistently in the same phase of succession (e.g. Johnson & Waller, 2013). In marine systems, human disturbances such as nutrient enrichment can lead to increases in biotic homogenisation (Chapman, Underwood & Skilleter, 1995; Séguin, Gravel & Archambault, 2014), as tolerant or opportunistic species can settle and dominate open space post-disturbance.

The disturbance heterogeneity–beta diversity model can be further developed with evidence of the effects of broad-scale environmental disturbance events on beta diversity. Disturbances that consistently affect large regions generally reduce beta diversity (within the disturbed region), yet the assemblage-level manifestations vary among studies (see also Huston, 1994). Recurrent fire disturbances reduced beta diversity of woody plant assemblages *via* both the removal of fire-sensitive species and the increasing prevalence of fire-tolerant taxa in Brazil (Da Silva *et al.*, 2018). In both marine and freshwater ecosystems, environmental disturbances that span entire groups of samples have led to increasing homogenisation (both taxonomically and functionally) (Chase, 2007; dos Santos Bertoncin *et al.*, 2019; Richardson *et al.*, 2018). Under broad-scale disturbances, the mechanism responsible for decreased within-region beta diversity is either elimination of taxa from the regional species pool (Chase, 2007), or alternatively, increased occurrence of taxa (increasing alpha diversity) across sites (dos Santos Bertoncin *et al.*, 2019).

(3) Connectivity alteration and species redistribution

(a) Terrestrial ecosystems

Both species invasion and extinction processes can drive either homogenisation and differentiation of terrestrial assemblages when assessed in terms of functional, taxonomic, or phylogenetic composition (Carvalho & Castro, 2017; Closset-Kopp, Hattab & Decocq, 2019; Howes *et al.*, 2014; Jackson *et al.*, 2015; Lambdon, Lloret & Hulme, 2008;

Winter *et al.*, 2010). Species invasion to regional species pools can occur *via* human-assisted dispersal across biogeographic boundaries, or removal or reduction of barriers to dispersal between regions. Depending on the context, either of these processes can lead to homogenisation, differentiation, or no change in beta diversity (e.g. Campagnaro *et al.*, 2018; Florencio *et al.*, 2015; McKinney, 2004), indicating that the effects of species invasions on beta diversity are not predictable. However, the effect of species invasions on beta diversity has been linked with the ratio of non-native to native species (McKinney, 2004), the distribution of invaders within the region of interest (Florencio *et al.*, 2015), and the history (i.e. duration) of invasion. Specifically, while invasions initially often have caused biotic differentiation, prolonged periods of invasion tend to lead increasingly to biotic homogenisation (Lososova *et al.*, 2016).

(b) Marine ecosystems

Alteration of habitat connectivity drives change in beta diversity of marine organisms by facilitating species invasions. Facilitated dispersal can occur either through the removal of barriers or by enhancing the ability of organisms to occupy formerly inhospitable locations. The invasion of 84 fish species from the Indo-Pacific region into the Mediterranean Sea occurred within 142 years since the construction of the Suez Canal, leading to homogenisation of assemblages across the two seas (Edelist *et al.*, 2013). Widespread invasion of *Caulerpa cernose* var. *cylindracea* in the north-western Mediterranean reduced beta diversity of seaweed assemblages compared to uninhabited regions (Piazzi & Balata, 2009). In both the Aegean Sea and North Atlantic Ocean, biotic homogenisation occurred over the scale of decades driven by a combination of changes in abundances or occurrence (redistribution) of indigenous species over time [Aegean Sea (Bianchi *et al.*, 2014); North Atlantic Ocean (Magurran *et al.*, 2015)]. However, patchy invasion of the marine algae *Sargassum muticum* in intertidal rockpools has increased beta diversity of sessile assemblages (i.e. biotic differentiation) compared to uninhabited areas (Vye *et al.*, 2018).

(c) Freshwater ecosystems

Facilitated dispersal, caused either by altering hydrological connectivity or by transporting organisms beyond their native ranges, is a major driver of change in freshwater beta diversity. Hydrological connectivity is a main determinant of the distribution and abundance of organisms in freshwater systems (Fullerton *et al.*, 2010) and anthropogenic alterations to hydrological connectivity (e.g. dams fragmenting river networks) significantly alter freshwater beta diversity (e.g. Crook *et al.*, 2015). Anthropogenic activities can also increase hydrological connectivity through the removal of natural or anthropogenic barriers (e.g. waterfalls or dams), or the creation of reservoirs, facilitating the dispersal of organisms between freshwater environments which, in turn, leads to reduced taxonomic and phylogenetic beta diversity of

fish and zooplankton (Munoz-Ramirez, Victoriano & Habit, 2015; Strecker & Brittain, 2017). In the Americas, the construction of large dams has increased hydrological connectivity between reaches formerly fragmented by natural dispersal barriers, reducing beta diversity (Vitule, Skóra & Abilhoa, 2012; Yamada *et al.*, 2017). In contrast to dam construction, dam removal has also reduced beta diversity of fish assemblages between formerly fragmented reaches, such as in the USA (Kornis *et al.*, 2015).

Human-assisted translocation of freshwater biota has had variable outcomes for beta diversity. Establishment of non-native species (e.g. fish, macrophytes) can decrease beta diversity by increasing the proportion of shared species among river basins, ecoregions, or continents (e.g. Castano-Sanchez *et al.*, 2018; Hoagstrom *et al.*, 2007; Liu *et al.*, 2017; Marr *et al.*, 2010). However, spatial scaling and origin of the invasive species can strongly influence the size and direction of these effects. For example, the effect of non-native species was associated with contrasting directions of change in beta diversity over time when assessed at catchment (watershed), ecoregional, and continental spatial scales (e.g. Daga *et al.*, 2015; Taylor, 2010; Vargas, Arismendi & Gomez-Uchida, 2015). Furthermore, translocation of species within their natural range had a stronger impact on changes in beta diversity than the introduction of species from beyond the regional species pool (e.g. Leprieur *et al.*, 2008).

(d) *Conceptual model 3: dispersal and connectivity drive directional change in beta diversity, but responses are modulated by spatial extent and grain*

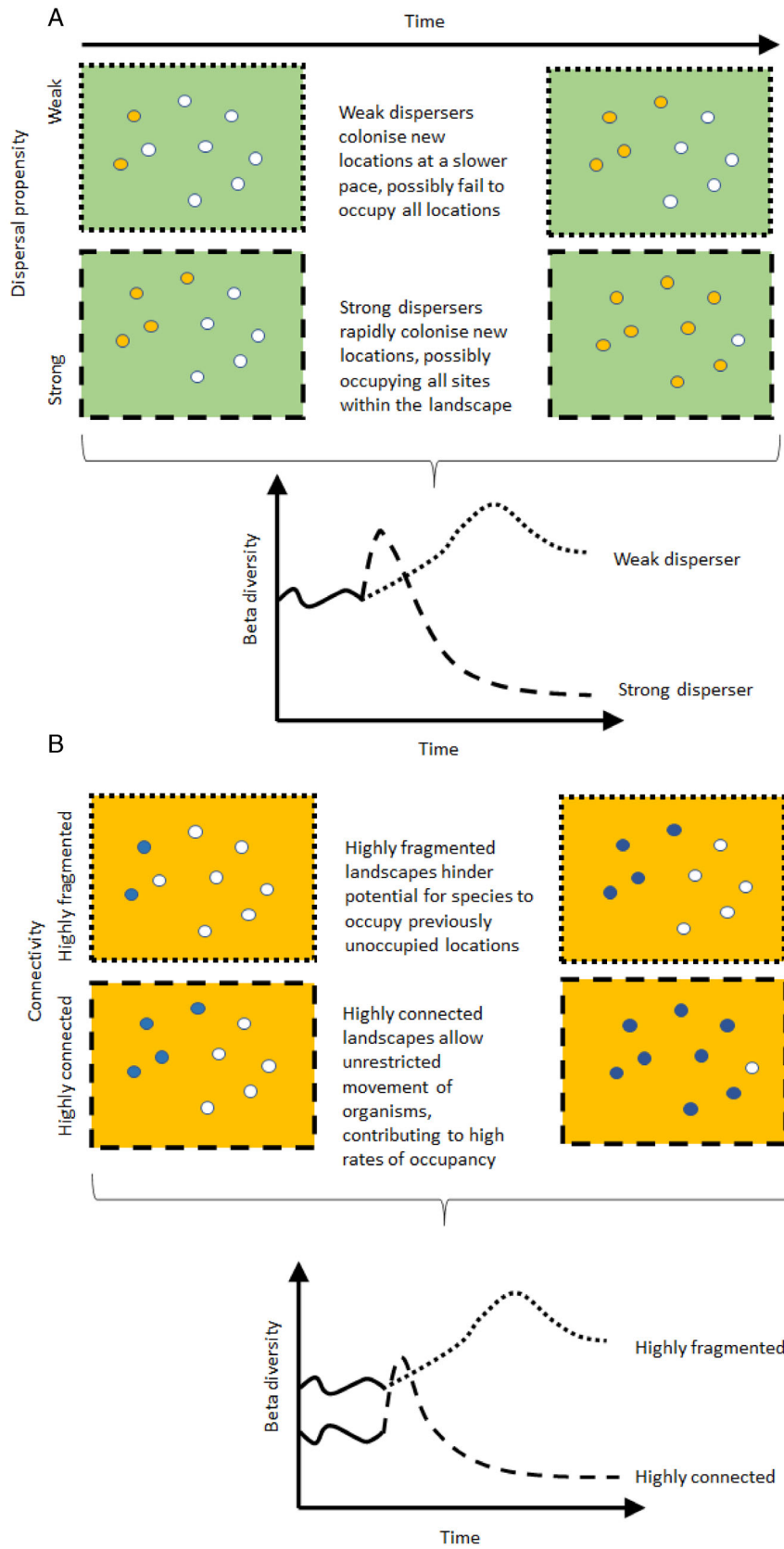
Connectivity and dispersal characteristics of species are key determinants of variation in the species composition among assemblages across multiple spatial scales (Krebs, 2001). Therefore, directional changes in beta diversity can be conceptualised as being driven by the dispersal characteristics of organisms and spatial connectivity among assemblages (Fig. 4). This conceptual model provides the simplest explanation as to why species invasions do not produce consistent results [in terms of homogenisation *versus* differentiation among empirical studies (Table S2)]. Invading species with strong dispersal capabilities (i.e. that can rapidly colonise regions) contribute towards a shorter period of biotic differentiation among assemblages compared to weak or slow dispersers as they become increasingly ubiquitous across a region (Harris, Smith & Hanly, 2011; Mouquet & Loreau, 2003). By contrast, poor dispersers are predicted to drive biotic differentiation either for a longer duration (until they occupy most assemblages), or permanently if they simply fail to establish in many of the potential locations across an invaded region, perhaps due to unsuitable environmental conditions (Thompson *et al.*, 2020).

Within-region connectivity (as a conduit for dispersal) is a significant factor explaining how species occupancy patterns influence temporal trends in beta diversity. This is specifically relevant in the context of species invasions, where broad-scale establishment is determined by the ability of an

invading species to spread within a region. Beta diversity of assemblages is negatively associated with the dispersal abilities of constituent species (e.g. Qian, 2009); therefore, the effect of species invasions on within-region beta diversity is hypothesised to be determined by among-patch connectivity and spatial extent (Cadotte & Fukami, 2005). Specifically, this third conceptual model predicts that invading species will contribute to more pronounced biotic homogenisation when their occupancy rates among patches are high due to the combined effects of dispersal ability and among-patch connectivity. By contrast, biotic differentiation is predicted when among-patch connectivity is hindered and the proportion of patches occupied remains low (*sensu* Harris *et al.*, 2011). While effects of landscape fragmentation on beta diversity are often considered in the context of invasive non-native species, changes to the occupancy and abundance of native species due to fragmentation also determine temporal variation in spatial beta diversity across landscapes (Tatsumi, Iritani & Cadotte, 2021). Specifically, increasing fragmentation hinders immigration of individuals to recolonise or support populations that are unable to persist in isolation (loss of rescue effects), causing extinction of species across landscapes, leading to biotic homogenisation (e.g. Jamoneau *et al.*, 2012; Si *et al.*, 2016).

Connectivity and dispersal are especially useful for interpreting and predicting the consequences of species invasions on beta diversity. There are three key characteristics that influence the direction and magnitude of change in beta diversity caused by species invasion. First, the magnitude of the effect of species invasions on beta diversity becomes less pronounced with increasing species richness of a region (gamma diversity) (Harris *et al.*, 2011). Second, the interaction between beta diversity (prior to invasion) and among-site occupancy of non-native species is relevant; regions with low 'pre-invasion' beta diversity are more likely to show biotic differentiation following invasion, especially during the initial phases of invasion (when within-region occupancy of non-native species is patchy). By contrast, biotic homogenisation is more likely to occur when pre-invasion beta diversity is high, particularly if non-native species already occupy a high proportion of sites. Third, the number of non-native species comprising both gamma and alpha diversity prior to invasion will determine the degree of homogenisation *versus* differentiation caused by non-native invaders (McKinney, 2004). Generally, beta diversity decreases when non-native species swamp the pre-invasion gamma diversity; differentiation is more likely to occur when there are fewer non-native species invading relative to the previously established species pool (McKinney, 2004).

Overall, conceptual model 3 assumes that dispersal and connectivity are the primary drivers of assemblage composition and, hence, beta diversity, and that abiotic conditions, disturbance, and/or other biotic interactions have relatively little effect on species occupancy and abundance. Because heterogeneity in abiotic conditions within landscapes is frequently associated with variation in composition among assemblages (e.g. Veech & Crist, 2007), the relevance of this



(Figure 4 legend continues on next page.)

conceptual model acting singularly to produce observed outcomes is likely to be limited to contexts where environmental heterogeneity within the region of interest is low.

Beta diversity values depend on the spatial scale (spatial grain and extent) at which they are quantified (e.g. Barton *et al.*, 2013; Bini *et al.*, 2014; Mac Nally *et al.*, 2004; Vellend *et al.*, 2021). The relevance of grain size is particularly pertinent in understanding the role of the species occupancy and invasion patterns on trends of biotic homogenisation and differentiation. Higher beta diversity is expected with decreasing sampling unit size due to declining probability of detecting organisms in each sample (Chase *et al.*, 2011). As sampling grain size increases, the probability of occupancy (and hence, detection) increases (e.g. McGeoch & Gaston, 2002; Tan *et al.*, 2017); therefore, declines in beta diversity are more likely to be detected with increasing grain size, while biotic differentiation is expected to be more apparent when assemblages are quantified at fine spatial extents (e.g. Taylor, 2004).

(4) Habitat change

(a) Terrestrial ecosystems

Anthropogenic habitat change remains the predominant context for examining biotic homogenisation or differentiation. Habitat conversion through urbanisation and agriculture drives change in beta diversity in contrasting and scale-dependent ways. Land-use change often increases beta diversity within landscapes by driving differences in composition between altered and unaltered locations (e.g. Endenburg *et al.*, 2019; Marconi & Armengot, 2020; Sattler *et al.*, 2011). By contrast, assemblages within altered habitat types are frequently found to become increasingly homogeneous compared to unaltered environments (e.g. Liang *et al.*, 2019; Rocha *et al.*, 2016; Steinitz, Robledo-Arnuncio & Nathan, 2012). Biotic homogenisation in altered habitats is primarily driven by reduced taxonomic, functional, or phylogenetic turnover among local assemblages (e.g. Dolan, Aronson & Hipp, 2017; Durak *et al.*, 2015; Staude *et al.*, 2018). Conversely, habitat alteration has resulted in increased beta diversity among altered locations in some cases (e.g. Newbold *et al.*, 2016; Noreika, Pajunen & Kotze, 2015) due to patchy redistribution of species among samples and widespread loss of generalist and wide-ranging taxa (e.g. Aronson *et al.*, 2015; Buhk *et al.*, 2017).

(b) Marine ecosystems

The role of habitat in influencing spatial beta diversity in marine ecosystems is typically studied in the context of understanding anthropogenic impacts, such as urbanisation, sedimentation, or pollution. Anthropogenic impacts on marine ecosystems typically cause loss of natural habitat and either the creation of entirely novel ecosystems or the alteration of spatial variation in benthic habitats. A series of experiments in the Mediterranean Sea revealed that increased sedimentation homogenised benthic infaunal assemblages by reducing habitat heterogeneity (Airoldi *et al.*, 2015; Balata, Piazzini & Benedetti-Cecchi, 2007a; Balata, Piazzini & Cinelli, 2007b; Bianchi *et al.*, 2018; Mayer-Pinto *et al.*, 2018; Oliveira *et al.*, 2014). Elsewhere, urbanised coastal marine environments supported lower beta diversity compared to undisturbed regions *via* creation of novel ecosystems occupied by only generalist, broad-niche species (e.g. Iacarella *et al.*, 2018; Tamburello *et al.*, 2012). By contrast, other studies have found that the creation of novel habitats for marine organisms (e.g. engineered marinas) caused biotic differentiation compared to unmodified habitats (Airoldi *et al.*, 2015; Bertocci *et al.*, 2017; Pastro *et al.*, 2017). In some cases, anthropogenically created novel marine habitats are occupied by non-native species, thereby increasing regional beta diversity among modified and reference habitats (Airoldi *et al.*, 2015).

(c) Freshwater ecosystems

Spatial variation in physical and chemical habitat characteristics significantly alters beta diversity of freshwater organisms. As with marine and terrestrial realms, most evidence of drivers of change in beta diversity in fresh waters by habitat-related mechanisms is in the context of assessing anthropogenic impacts. Furthermore, anthropogenic land-use change in the surrounding catchment is a major driver of change in freshwater beta diversity. However, synthesis of studies of land-use changes reveals that all possible outcomes for beta diversity are possible. Specifically, beta diversity among urban ponds was higher than ponds in non-urban landscapes due to the development of novel assemblages (e.g. Hill *et al.*, 2017; Skultety & Matthews, 2018). By contrast, homogenisation of assemblages in streams draining modified landscapes was driven by (i) increasing similarity of abundance-based assemblage composition or (ii) increased occurrence of generalist species and/or the loss of species with narrow environmental niches (Hermoso, Clavero & Kennard, 2012; Mykrä &

(Figure legend continued from previous page.)

Fig. 4. Conceptual model 3 depicting how dispersal propensity and landscape connectivity drive directional change in beta diversity over time. Situations where invading species have weak dispersal capability will result in higher levels of beta diversity for a more prolonged period compared to situations where invading species have strong dispersal capability (A). During initial phases of invasion, strong dispersers are predicted to drive a short period of increased beta diversity (as few locations are occupied), before rapidly causing beta diversity to decline as most (or all) locations become occupied. A similar pattern of beta diversity change is predicted to occur along a gradient of connectivity within a region (B). Invaders colonising regions with highly fragmented habitats are predicted to cause prolonged increases in beta diversity (as dispersal across fragments within a region is restricted), whereas beta diversity is expected to decline in regions with highly connected habitats where dispersal is not restricted.

Heino, 2017; Pavel *et al.*, 2016; Segovia *et al.*, 2016; Siqueira, Lacerda & Saito, 2015). Urbanisation had no effect on spatial beta diversity among cities in the UK due to high prevalence of assemblage turnover among ponds (Hill *et al.*, 2018). Furthermore, impacts of agricultural land-use change on beta diversity in temperate and boreal lakes varied among organism groups (increased for fish and invertebrates; no change for macrophytes and diatoms) (Johnson & Angeler, 2014).

Conversion of flowing water habitats to lentic habitats (e.g. reservoirs) typically causes biotic homogenisation, particularly in river systems where natural lakes are not a major feature (Castano-Sanchez *et al.*, 2018; Clavero & Hermoso, 2011; Glowacki & Penczak, 2013; Li *et al.*, 2013; Santos *et al.*, 2017; Zeng *et al.*, 2017). However, the origin of species driving reduced beta diversity in converted habitats is inconsistent among studies – in some cases it is driven by the invasion of non-native species (e.g. Castano-Sanchez *et al.*, 2018; Zeng *et al.*, 2017), while in others, increased occupancy of native species occurred (Glowacki & Penczak, 2013).

(d) *Conceptual model 4: environmental heterogeneity as a driver of directional change in beta diversity*

Spatial environmental heterogeneity is a feature of all major environmental realms (terrestrial, marine, fresh water),

underpinning community assembly and therefore beta diversity (e.g. Heino, Melo & Bini, 2015a). Our fourth conceptual model is based on the premise that beta diversity is positively affected by the breadth of environmental variation, and this concept is applicable across multiple spatial extents (Fig. 5). Under this model, directional change in beta diversity at a given spatial scale is predicted to mirror changes in the variation of environmental characteristics over time (such as habitat structure or abiotic conditions) that occur at that scale (Chase *et al.*, 2020). This conceptual model draws on relevant ideas developed in landscape ecology that emphasise the effects of spatial heterogeneity and the configuration of physical environmental conditions on biodiversity (e.g. Fahrig *et al.*, 2011; Forman, 1995; Palmer, 1992; Veech & Crist, 2007).

Our environmental heterogeneity model includes the effects of: (i) the heterogeneity and magnitude of variation among spatial units relative to that of the broader landscape and, (ii) the magnitude of variation in environmental conditions that historically occurred at a broad spatial scale. In metacommunity theory, our fourth conceptual model aligns with the species-sorting model of assemblage composition (Leibold *et al.*, 2004) and assumes that dispersal is not a constraint, so organisms are able to move to occupy locations within their optimal environmental niche space.

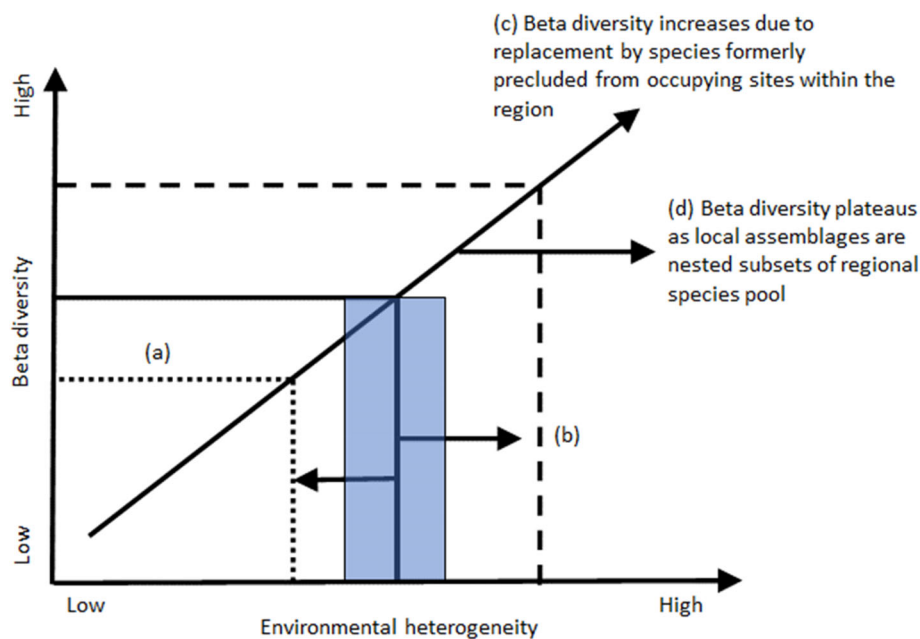


Fig. 5. Conceptual model 4 depicting the relationship between environmental heterogeneity and beta diversity. According to this model, beta diversity in a region is predicted to be positively associated with spatial variation in environmental characteristics (i.e. environmental heterogeneity). Lower (or decreased) environmental heterogeneity results in lower (or decreased) beta diversity (a, dotted line), predominantly generated by nestedness. Increasing environmental heterogeneity is predicted to increase beta diversity (b, dashed line). However, contrasting patterns can occur if increased environmental heterogeneity spans historical environmental conditions (solid diagonal line) or expands to encompass novel environmental conditions. For example, increased environmental heterogeneity spanning novel conditions is likely to increase beta diversity if novel conditions allow new species to add to the regional species pool (c). Alternatively, if increased environmental heterogeneity spans novel environmental conditions and new species are precluded from colonising the regional species pool, then beta diversity is predicted to reach an asymptote due to increased prevalence of nestedness (d).

Our environmental heterogeneity model predicts that beta diversity will be positively driven by *variation* in environmental conditions at a corresponding spatial extent (Anderson *et al.*, 2006; Heino *et al.*, 2015a). Changes in environmental heterogeneity across scales (*sensu* Stein & Kreft, 2015) are expected to cause change in the degree to which assemblages differ in composition (e.g. Keller *et al.*, 2009). Therefore, scenarios of biotic homogenisation are predicted when environmental heterogeneity declines (i.e. as environmental conditions become more stable or consistent), thereby facilitating the development of similar assemblages across space (Thompson *et al.*, 2020). Conversely, biotic differentiation is expected to occur as environmental heterogeneity increases by fostering the development of increasingly distinctive assemblages (either comprised of nested subsets of the regional species pool, or by supporting assemblages dominated by species with narrow environmental niches).

The environmental heterogeneity model explains the inconsistent or ‘mixed’ outcomes of beta diversity associated with habitat change across multiple spatial scales across terrestrial, marine, and freshwater realms. Comparisons between ‘control’ and ‘impact’ landscapes (e.g. unmodified *versus* urbanised or harvested ecosystems) frequently reveal biotic differentiation (e.g. Filloy *et al.*, 2010; de Avila *et al.*, 2015) as environmental conditions or habitats for organisms become increasingly different. By contrast, reduced beta diversity frequently occurs among assemblages occupying anthropogenically modified environments (e.g. Chakraborty *et al.*, 2019; Dopheide *et al.*, 2020) where environmental conditions become more consistent. These contrasting and scale-dependent responses of beta diversity to changing environmental conditions have been reported across all realms (Table S2), highlighting how the spatial scale at which environmental variation is altered contributes to the specific direction and magnitude of change in beta diversity.

A key feature of this model is that the effect of environmental heterogeneity on changes in beta diversity depends on the degree to which environmental conditions span or extend beyond those that historically occurred in the region of interest. Increasing environmental heterogeneity does not necessarily cause biotic differentiation. Rather, the direction of change in beta diversity depends on the environmental niches of species that either historically occurred within the region of interest (‘native species’) or those that were precluded from occupying the region due to earlier environmental conditions being beyond their envelope of tolerance. In the absence of species invasion, the effect of increased environmental heterogeneity on beta diversity is hypothesised to drive increased nestedness along environmental gradients, as broad-niche (more tolerant or generalist) species occupy (and narrow-niche species are precluded from occupying) novel environments within the region (Carscadden *et al.*, 2020). Beta diversity is therefore predicted to show a hump-shaped response to environmental heterogeneity, as, initially, more variable environments will

support a greater variety of assemblages, yet eventually habitat characteristics become increasingly novel compared to historical conditions, so unique combinations of maladapted species decline across space. By contrast, if habitat modification allows the invasion of species from beyond the historical regional species pool, beta diversity is predicted to increase (due to species-sorting mechanisms). This mechanism has some support in the beta diversity literature. For example, patchy occurrence of non-native plants contributed to higher beta diversity in increasingly modified ecosystems (Airoldi *et al.*, 2015; Aronson *et al.*, 2015; Skultety & Matthews, 2018). In contrast to the idea that increased beta diversity is driven by nestedness (as described above), biotic differentiation in modified habitats can support the increasing prevalence of species replacement among assemblages (Paquin *et al.*, 2021).

(5) Biotic and trophic interactions

(a) Terrestrial ecosystems

Biotic interactions within terrestrial communities affect the magnitude of temporal change in spatial beta diversity *via* dispersal, habitat modification, trophic and disease mechanisms. Dispersal of seeds by birds and bats as vectors among fragmented urban and forested habitats caused homogenisation of plant assemblages among fragments (Czarnecka *et al.*, 2013; Wandrag *et al.*, 2017). Expansion of ecosystem engineers (Jones *et al.*, 1994; Table 1) can lead to biotic homogenisation by reducing environmental heterogeneity, such as the effect of invasive plants modifying habitats for invertebrates (Hansen, Ortega & Six, 2009). In terms of trophic mechanisms, patch-specific grazing by herbivores increases beta diversity among grazed *versus* non-grazed environments (Nagaike, 2012). Top-down trophic cascades have variable consequences for beta diversity among patches exposed to similar grazing pressure, although most studies have been completed at relatively small extents (10–100 km²; Database S1). Across temperate regions in the Northern Hemisphere, increased grazing by deer and sheep was associated with biotic homogenisation of plants within grazed areas (Courchesne *et al.*, 2018; Holmes & Webster, 2011; Ohashi & Hoshino, 2014; Perea, Girardello & San Miguel, 2014; Rooney, 2009; Salgado-Luarte *et al.*, 2019). However, in contrast to increased grazing pressure, experimental removal of grazers (i.e. reduced grazing pressure) had either no effect on beta diversity or was associated with further homogenisation of plant assemblages (Abella *et al.*, 2019; Milligan, Rose & Marrs, 2016; Speed, Austrheim & Myserud, 2013; Watts, Griffith & MacKinlay, 2019).

(b) Marine ecosystems

Species interactions within ecosystems are also an important mechanism responsible for changes in marine beta diversity. These effects are mediated by the role of species in habitat modification (i.e. ecosystem engineers) or occur as top-down

effects of consumers on prey assemblages. Increased abundance or higher concentrations of consumers typically yield greater homogenisation on prey assemblages, particularly at small spatial extents (10–1000 km²). For example, biotic homogenisation of macroalgal assemblages was associated with the presence of high densities of herbivorous sea urchins compared to patches exposed to lower grazing pressure by urchins among neighbouring Atlantic Ocean islands (Sangil *et al.*, 2014). Elsewhere, invasion by oysters resulted in homogenisation of invertebrate and macroalgal assemblages in intertidal mudflats, due to the (structural) engineering effect of oysters on benthic habitat (Green & Crowe, 2014). Similar impacts of non-native species invasions have been reported, such as widespread dominance by macroalgae reducing beta diversity of invertebrate and fish assemblages (e.g. Navarro-Barranco *et al.*, 2018; Pacciardi, De Biasi & Piazzzi, 2011; Piazzzi & Balata, 2008, 2009). However, these ecosystem-engineering effects of invasive species such as marine algae vary among species. For example, seasonal persistence of the invasive marine algae *Womersleyella setacea* generated periodic biotic homogenisation of benthic invertebrates compared to invasion by *Lophocladia lallemandii*, which undergoes a prolonged seasonal period of no-growth that maintains spatial beta diversity of benthic invertebrates (Bedini *et al.*, 2015).

(c) Freshwater ecosystems

Eutrophication, disease, top-down predation, and ecosystem engineers are all biological drivers of change in beta diversity in freshwater systems (García-Girón *et al.*, 2020). Eutrophication generally decreases spatial beta diversity (both functional and taxonomic) within and among freshwater systems, as evidenced in invertebrates, zooplankton, bacteria, and plants. In Brazil and France, reservoir eutrophication was linked with biotic homogenisation of aquatic plants as assemblages became increasingly nested with increasing eutrophication, potentially driven by the loss of oligotrophic and mesotrophic specialist species (Leboucher *et al.*, 2019; Wengrat *et al.*, 2018). However, effects of eutrophication on freshwater beta diversity vary based on lake characteristics, with fish assemblages becoming more homogenous among shallow lakes and more differentiated among deeper lakes undergoing eutrophication (Menezes *et al.*, 2015). In terms of disease, selective removal of amphibian species by a fungal pathogen (*Batrachochytrium dendrobatidis*) caused rapid biotic homogenisation prior to complete assemblage extirpation in Panama (DiRenzo *et al.*, 2017). Ecosystem-level impacts (i.e. habitat modification) of species are also a reported driver of directional change in beta diversity, with non-native plants, algae, and mussels leading to reduced beta diversity of invertebrates and plants (Kilroy, Larned & Biggs, 2009; Sardina, Chaves & Marchese, 2011; Zhang *et al.*, 2019b), whereas tree encroachment in wetlands increased beta diversity of vascular plant and bryophyte assemblages (Favreau, Pellerin & Poulin, 2019).

(d) Conceptual model 5: biotic interactions as drivers of change in beta diversity

By influencing the occurrence and abundance of organisms, trophic and non-consumptive biotic interactions (e.g. predation, competition, disease, or habitat modification) are potential drivers of change in spatial beta diversity over time. However, the ecological roles of species as drivers of changes in beta diversity have been less well developed conceptually compared to the potential drivers of dispersal, environmental filtering, or disturbance regimes [conceptual models 2–4 (Brustolin *et al.*, 2021; Chase *et al.*, 2020)]. Our fifth conceptual model centres on the role of biotic interactions and the multiple effects of species, including productivity on biotic homogenisation and differentiation (Fig. 6). This biotic interactions model emphasises the specific ecological roles of individual species within ecosystems on the presence (or absence) of other species (habitat modification, dispersal vectors, top-down trophic interactions) and how resource supply and use (bottom-up or top-down trophic interactions, competitive exclusion, etc.) affect beta diversity.

(i) *Habitat modification by organisms.* Both plants and animals have multiple ecological roles within ecosystems and the ecological effects of species can be consistent or context dependent. Plants in both terrestrial and aquatic ecosystems affect assemblages of other organisms by influencing habitat structure and local environmental conditions (e.g. sunlight). In freshwater and marine ecosystems, macrophytes provide habitat, refugia and feeding sites for different organism groups, such as fish, thereby affecting spatial variation in assemblage composition (Quirino *et al.*, 2021). Evidence from marine ecosystems also highlights that widespread dominance of single plant species or plant assemblage types can cause biotic homogenisation of benthic organisms (e.g. macroinvertebrates) by reducing habitat heterogeneity (e.g. Green & Crowe, 2014; Navarro-Barranco *et al.*, 2018; Pacciardi *et al.*, 2011; Piazzzi & Balata, 2009). The effect of a species on habitat heterogeneity across space and subsequent outcomes for beta diversity links to our fourth conceptual model (Section IV.4.d); the environmental heterogeneity experienced by a given assemblage may be influenced by the effects of an engineering or habitat-forming species. For example, the effect of two species of molluscs on macroinvertebrate beta diversity in New Zealand intertidal sandflats was attributed to their differential roles in influencing seagrass density (Brustolin *et al.*, 2021). Mangrove crabs function as ecosystem engineers by altering the functional diversity of microbial systems through burrowing and feeding activities that lead to biogeochemical heterogeneity (e.g. Kristensen, 2008). The density, diversity and distribution of habitat-forming species, such as macroalgae (Goodsell & Connell, 2008) or coral (Acosta-González *et al.*, 2013) in marine systems, can also have important effects on the beta diversity of organisms relying on them. Overall, change in the spatial variation of habitat characteristics is the hypothesised driver by which ecosystem engineers and habitat-forming species drive biotic homogenisation and differentiation across ecosystems.

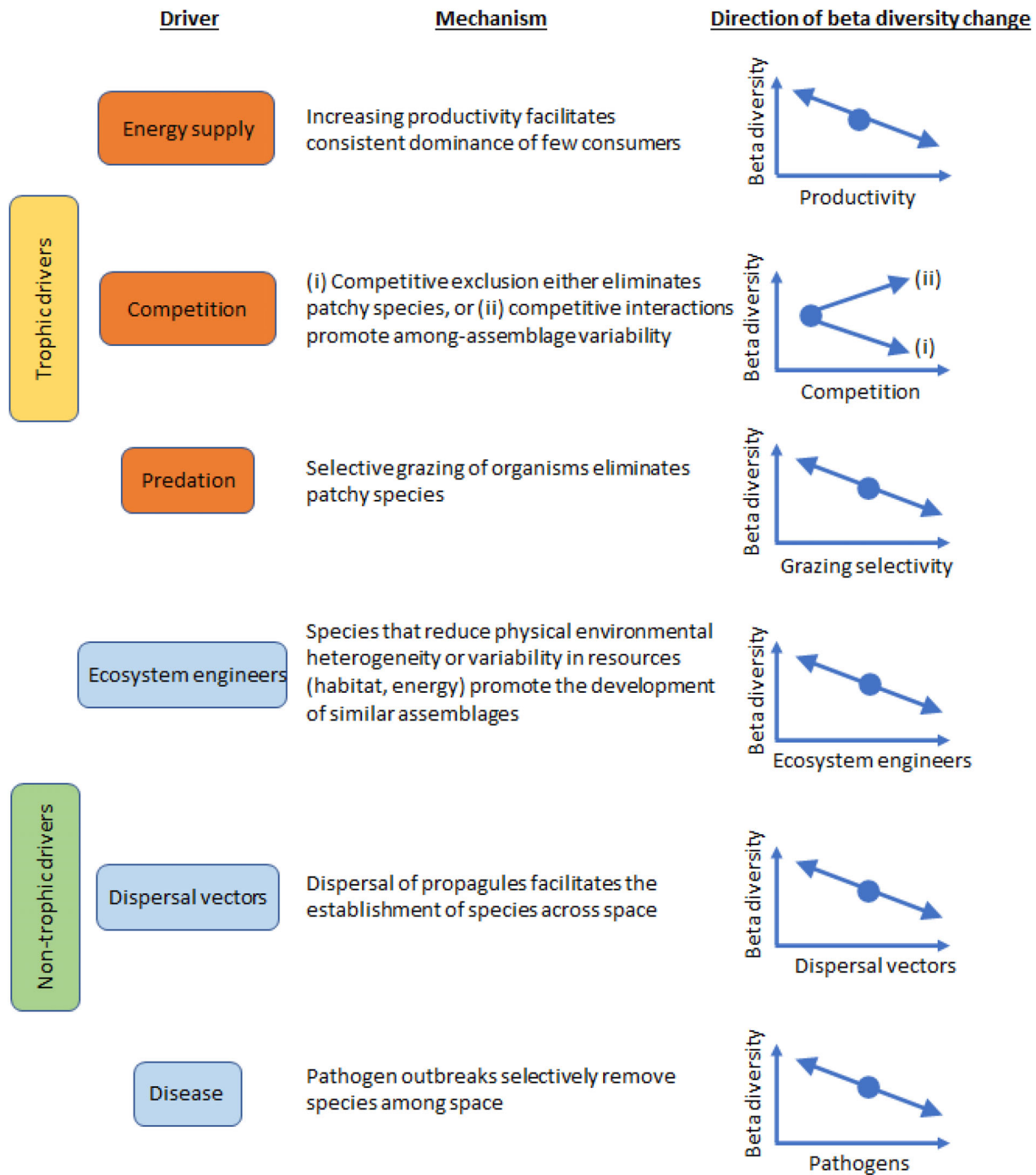


Fig. 6. Conceptual model 5 illustrating how biotic interactions can drive change in beta diversity across ecosystems. The description of each mechanism focuses on increases in their strength; reductions, in each case, will generate a change in beta diversity in the opposite direction.

(ii) *Vectors of disease and dispersal.* Dispersal of organisms by other organisms (e.g. ‘zoochory’) and pathogen transmission are two mechanisms leading to biotic homogenisation and differentiation. Pathogen outbreaks explain biotic homogenisation by species-specific losses among assemblages, manifesting as increasing nestedness among assemblages over

time, as has been reported for amphibians (DiRenzo *et al.*, 2017; Smith, Lips & Chase, 2009). Conversely, species additions through range expansions caused by organism-mediated dispersal (e.g. Reynolds, Miranda & Cumming, 2015) are hypothesised to result in biotic homogenisation. Birds and bats, for example, reduce terrestrial plant

assemblage turnover *via* seed transfer (e.g. Czarnecka *et al.*, 2013; Wandrag *et al.*, 2017). However, beta diversity outcomes are predicted to depend on the extent of organism-mediated dispersal, with patchy (or widespread) dispersal expected to increase (or decrease) beta diversity, respectively (see conceptual model 1 in Section IV.1.d; Harris *et al.*, 2011).

(iii) *Top-down trophic interactions.* Predation and grazing by consumers influence beta diversity by selective or patchy removal of species within prey assemblages. The magnitude and direction of change in beta diversity appear to depend on prey selectivity and spatial variation in predation pressure (Ryberg, Smith & Chase, 2012). For example, herbivory is associated with biotic homogenisation of plants in terrestrial and marine ecosystems *via* selective removal of organisms (e.g. Birtel & Matthews, 2016; Holmes & Webster, 2011; Ohashi & Hoshino, 2014; Perea *et al.*, 2014; Rooney, 2009). However, these responses were not consistent among studies; removal (as opposed to introductions) of herbivores can also reduce beta diversity (e.g. Milligan *et al.*, 2016), and in some cases alteration of herbivore densities had no effect on plant beta diversity (Speed *et al.*, 2013).

In marine ecosystems, classic ecological theory predicts that the maintenance of high beta diversity occurs in response to keystone species (e.g. Krebs, 2001). Keystone predators (Paine, 1969), such as the seastar *Pisaster ochraceus*, shift their diet to consume dominant prey species that are the most prevalent or abundant at any given time or place, thereby maintaining patchy multi-species prey communities with high overall (gamma) diversity, and hence, high beta diversity. By contrast, increased abundance of a generalist predator (the Atlantic cod, *Gadus morhua*) in the Barents Sea had a homogenising effect on benthic fish assemblages (Ellingsen *et al.*, 2015, 2020). Overall, these contrasting responses suggest that while predators can have a significant effect on beta diversity of prey assemblages, impacts are inconsistent across spatial extents and depend on spatial variation in predation pressure, predator richness, and prey selectivity (e.g. Antiquera *et al.*, 2018).

(iv) *Competitive interactions among species.* Competitive exclusion is the process where species either prevent the establishment of other species within a community or remove species from a community by functioning as superior competitors for habitat resources or energy (Cutler, 1998; Putman, 1994). Yet the role of competitive exclusion as a mechanism driving spatial beta diversity remains poorly studied (Segre *et al.*, 2014). Competitive exclusion is a fundamental aspect of community assembly–disassembly phenomena (Krebs, 2001), therefore likely influencing beta diversity in different environmental realms. Competitive interactions potentially explain the widely reported role of non-native species invasions in altering beta diversity (see Database S1). Competitive interactions are a frequently emphasised component of the impact of non-native species on invaded assemblages (e.g. Cucherousset & Olden, 2011; Simon & Townsend, 2003).

Competitive interactions (particularly competitive exclusion) likely have marked outcomes for change in beta diversity over time and studies of non-native species invasions serve as a useful context to frame predictions. Two key factors are predicted to interact and determine how competitive exclusion drives the direction and magnitude of change in beta diversity: pre-invasion beta diversity and the spatial extent of competitive exclusion. In a region with high pre-invasion beta diversity, competitive exclusion is hypothesised either to: (i) cause biotic homogenisation if an invading species excludes (or removes) native species from the entire region; (ii) cause little change on beta diversity if competitive exclusion applies to few patches within the region; or (iii) cause biotic differentiation by reducing the proportion of shared taxa among assemblages. By contrast, where pre-invasion beta diversity is low, competitive exclusion is predicted to cause beta diversity either to increase (if exclusion applies inconsistently to patches within the invaded region, or if exclusion applies inconsistently among native species), or change little (where an invading species excludes a native species from the entire region).

(v) *Bottom-up food web effects.* In addition to top-down trophic mechanisms, bottom-up ecosystem processes are also potentially important mechanisms influencing beta diversity. Tests of beta diversity patterns along gradients of productivity (i.e. from oligotrophic to eutrophic conditions) suggest either a negative or unimodal response. Increasingly eutrophic conditions have been associated with biotic homogenisation in terrestrial, marine, and freshwater ecosystems (e.g. Bianchi *et al.*, 2018; Bini *et al.*, 2014; de Sassi, Lewis & Tyljanakis, 2012; Donohue *et al.*, 2009; Zhang *et al.*, 2019a). Eutrophication affected beta diversity by creating conditions where a few tolerant species dominate and subsequently eliminate other species *via* competitive exclusion (Wengrat *et al.*, 2018) or where specialist (intolerant) species were removed (Leboucher *et al.*, 2019). Eutrophication leading to reduced beta diversity likely is to be somewhat context dependent. For example, increasing eutrophication was associated with homogenisation of lake fish assemblages in shallow lakes (0.5–2.9 m deep), but with differentiation in deep lakes (3.1–16.5 m depth), speculated to be driven by there being higher geomorphological variability on the lake bottom (Menezes *et al.*, 2015).

V. SYNTHESISING MECHANISMS UNDERPINNING CHANGE IN BETA DIVERSITY ACROSS ECOSYSTEM REALMS

Biotic homogenisation and differentiation are key concepts to consider in the context of multi-scale biodiversity change (e.g. McGill *et al.*, 2015). Beta diversity is a core theme of metacommunity ecology, combining ecological mechanisms operating at multiple spatial scales to explain why assemblages vary in composition across space and time (Chase *et al.*, 2020; Leibold *et al.*, 2004). Metacommunity ecology

provides a holistic framework to integrate environmental (abiotic) and ecological mechanisms (e.g. dispersal, environmental filtering, biotic interactions) that affect local community composition and therefore beta diversity (Chase *et al.*, 2020; Heino *et al.*, 2015b). By contrast, a persistent theme in the evolving theory of biotic homogenisation is the emphasis on species invasions and concurrent extinctions of native species (Cardinale *et al.*, 2018; McGill *et al.*, 2015; Olden *et al.*, 2018; Petsch *et al.*, 2022). The emphasis on species invasions and extinctions in reports of directional change in beta diversity is possibly due to the framing of biotic homogenisation as being driven by ‘winner’ and ‘loser’ species (Dornelas *et al.*, 2019; McKinney & Lockwood, 1999). Consequently, the fundamental *versus* conservation aspects of beta diversity theory have remained separated, yet both aspects would benefit from a greater integration of existing evidence (*sensu* Fukami & Wardle, 2005) to understand the mechanisms and contexts whereby beta diversity either increases or decreases over time.

Incorporating beta diversity into understanding multi-scaled changes in biodiversity is directly relevant for management efforts and conservation planning (Socolar *et al.*, 2016). Efforts to address the conservation realities of biotic homogenisation and differentiation can benefit greatly when they are placed within a broader conceptual understanding of the fundamental ecological mechanisms that affect change in beta diversity over time. Ecologists are more openly highlighting the need to move beyond analyses of non-native species invasions in the context of biotic homogenisation and differentiation to consider the potential role of environmental and ecological mechanisms driving beta diversity change (e.g. Brice, Pellerin & Poulin, 2017). Although species invasions and extinctions *are* a relevant component of change in beta diversity (Olden & Poff, 2003), variation in the occurrence and abundance of species across a given region is determined by a combination of biological, chemical and physical mechanisms (Chase *et al.*, 2020; Krebs, 2001). There are numerous relevant ideas and evidence in the broader field of metacommunity ecology that contribute to a more robust conceptualisation of the mechanisms that contribute to or explain directional change in beta diversity over time (Chase *et al.*, 2020). Our five conceptual models (Table 2; Figs 1B, 3–6) identify, broadly, the primary ecological mechanisms and contexts leading to biotic homogenisation or differentiation. These broad conceptual models each emphasise a specific control on community assembly, drawing on existing theories applicable to beta diversity. We develop these conceptual models in the context of mechanisms driving directional change in beta diversity along a gradient of biotic homogenisation and differentiation. We consider that these concepts are not mutually exclusive – one or more mechanisms, arising from one or more of these conceptual models, may indeed occur simultaneously (perhaps additively, synergistically, or interactively) to produce emergent observed patterns of change in beta diversity over time for a given ecological assemblage under study.

Table 2. Summary of mechanistic conceptual models driving change in spatial beta diversity (biotic homogenisation and biotic differentiation) across ecosystems.

Conceptual model	Key premise
(1) Temporal change in beta diversity through changes in species occurrence at different scales	Beta diversity changes are driven by changes in the occurrence of species at local and regional spatial scales.
(2) Disturbance heterogeneity as a driver of beta diversity change	Spatial heterogeneity in disturbance regimes across scales positively influences beta diversity. Assemblages that are exposed to similar disturbance regimes will be at a similar phase of community succession at any point in time, whereas variation in disturbance across scales means that assemblages are at differing phases of succession.
(3) Dispersal and connectivity drive directional change in beta diversity, but responses are modulated by spatial extent and grain	The contribution of species to beta diversity change is determined by their dispersal characteristics and connectivity of habitats. Weak dispersers drive increases in beta diversity, whereas strong dispersers decrease beta diversity.
(4) Environmental heterogeneity as a driver of directional change in beta diversity	Beta diversity is positively driven by environmental heterogeneity by facilitating variation in the distribution, abundance, and dominance of different species among assemblages.
(5) Biotic and trophic interactions as drivers of beta diversity	The ecological roles (competition, predation, herbivory, consumption, disease, dispersal) of individual species within ecosystems strongly affect variation in assemblage composition across multiple spatial scales.

VI. INTEGRATING CONCEPTUAL UNDERSTANDING OF DRIVERS OF CHANGE IN SPATIAL BETA DIVERSITY

Beta diversity has been an increasingly frequent topic of ecological research (Anderson *et al.*, 2011). Debate about definitions and methods to analyse beta diversity have been useful for encouraging researchers to be clear about interpreting outcomes of hypotheses (e.g. Anderson *et al.*, 2011; Barwell, Isaac & Kunin, 2015; Baselga, 2010; Legendre, 2014; Legendre & De Cáceres, 2013; Tuomisto, 2010a,b), including how it can be measured and analysed across multiple spatial scales

(e.g. Crist & Veech, 2006; Jost, 2007). As empirical research has become available, syntheses and meta-analyses have focussed heavily on quantifying the prevalence of the direction of change in spatial beta diversity (e.g. Li *et al.*, 2020; Olden *et al.*, 2018).

Change in spatial beta diversity over time is disproportionately framed around the role of species invasions as these relate to homogenisation (McKinney, 2008; McKinney & Lockwood, 1999; Petsch *et al.*, 2022; Wilkinson, 2004), and indeed studies finding homogenisation dominate the literature. However, as local assemblages are shaped by multiple factors operating simultaneously (Lindholm *et al.*, 2020a; Mori, Isbell & Seidl, 2018), testing single hypotheses about the drivers of change in beta diversity risks leading to distorted perceptions about the outcomes and causes of biotic homogenisation or differentiation when findings are not considered in the context of other possible mechanisms. In an applied context, the use of such evidence in conservation interventions therefore has a high risk of failing to meet biodiversity management goals if other (possibly multiple) factors that have a relevant role in driving beta diversity are not considered throughout the process of incorporating scientific evidence into decision making. Synthesis of the empirical evidence examining change in beta diversity reveals that community- or ecosystem-level effects of specific species within assemblages can underpin temporal change in spatial beta diversity and that the direction of change varies across spatial scales. For example, in the northern Atlantic Ocean, homogenisation of fish assemblages occurred in the Barents Sea, whereas biotic differentiation was identified on the Scotian Shelf, driven by increasing or declining population size, respectively, of the apex predator Atlantic cod (Ellingsen *et al.*, 2015, 2020).

Species invasion and/or extinctions are not necessarily a defining characteristic of biotic homogenisation or differentiation. There are scenarios where changes in either the occurrence or spatial variation in the abundance of native species manifests as either biotic homogenisation or differentiation over time (Tabarelli, Peres & Melo, 2012). In terrestrial ecosystems, for example, anthropogenic rearrangement of landscapes by urbanisation reduced spatial variation among local habitat characteristics, fostering the increasing prevalence of generalist, broad-niche taxa among assemblages (Durak, 2010; Hodges & McKinney, 2018; Knop, 2016). Framing change in beta diversity by reference to 'winner' and 'loser' species [typically corresponding to non-native and rare native species, respectively, *sensu* McKinney & Lockwood (1999) and Olden & Poff (2003)] disregards the fact that both native and non-native species may jointly occupy a region where the environmental and biotic conditions support their respective ecological niches, given their traits and tolerances (Cassini, 2020; Tabarelli *et al.*, 2012).

One of the most challenging aspects of change in beta diversity through time is the scale dependence of variation in assemblage composition (Barton *et al.*, 2013; Pavoine *et al.*, 2016). Temporal change in the composition among local assemblages is a pronounced feature of global

biodiversity (Dornelas *et al.*, 2014; Hillebrand *et al.*, 2018). However, in isolation, such analyses of temporal change in assemblage composition, *per se*, do not reveal changes in the magnitude of beta diversity across spatial scales but rather straightforwardly quantify the degree to which local assemblages have changed over time. Such studies, while naturally extremely useful for contributing to evidence of the pace (in time) and consistency (among locations) of biodiversity change (e.g. McGill *et al.*, 2015) do not yield information regarding potential changes in spatial beta diversity (i.e. the spatial variability among assemblages within a given time point) through time.

Most empirical studies that identified inconsistent or variable beta diversity responses to environmental factors (e.g. habitat change, species redistribution) found that the direction of change in beta diversity was dependent on a specific spatial scale (Database S1). Inconsistent beta diversity responses across spatial scales to ecological drivers have been recognised throughout the history of research into beta diversity and biotic homogenisation (e.g. Rooney *et al.*, 2007). However, conceptual models can be applied to predict the direction of change in beta diversity across multiple spatial scales. For example, conceptual model 4 can be used to explain and predict why changes in land use (yielding a variety of land-use 'types') frequently causes beta diversity to be maintained or increased at a regional scale, yet within a given habitat or land-use type, biotic homogenisation occurs due a reduction in environmental variation (e.g. Filloy *et al.*, 2010; Holting, Bovolo & Ernst, 2016). Because beta diversity is a multi-scaled concept, it is necessary for change in beta diversity to be communicated in terms of (i) the spatial scale(s) from which conclusions are drawn (Heino *et al.*, 2015a,b) and to which inferences apply (Chase *et al.*, 2018) and (ii) the temporal scale (extent) over which change has occurred (Lindholm *et al.*, 2020a).

The direction, magnitude, and pace of change in beta diversity is highly variable across the globe and can be linked with different environmental variables (Blowes *et al.*, 2019; Su *et al.*, 2021), even within the same organism group (e.g. freshwater fish; Su *et al.*, 2021). This suggests, overall, a high degree of context dependency in the spatial and temporal characteristics of change in beta diversity (e.g. for floodplain biota; Lansac-Tôha *et al.*, 2021), posing challenges for deriving generalisations or predictions. However, understanding the ecological mechanisms underpinning why change in beta diversity is more pronounced in some areas and less so (or absent) in others provides opportunities for ecologists and managers to identify specific spatial units that may serve as priorities for monitoring or to prioritise regions that require spatially targeted research foci or conservation interventions (see Socolar *et al.*, 2016). Our conceptual framework provides an integrated platform from which future meta-analyses and quantitative assessments of changes in beta diversity, along with their associated underlying ecological mechanisms, can be articulated and developed further, to enhance our collective understanding and stewardship of dynamic ecosystems.

VII. CONCLUSIONS

(1) The degree to which ecological assemblages differ in composition from each other across space (termed 'beta diversity') provides a tractable method to assess, understand, and communicate biodiversity change. Biotic homogenisation and biotic differentiation represent a gradient of decreasing and increasing beta diversity, respectively. Despite substantial empirical research and meta-analyses reporting the prevalence of biotic homogenisation, the lack of a conceptual synthesis regarding underlying mechanisms hinders scientists and conservation managers from identifying the true drivers of change in beta diversity across ecosystems.

(2) Five distinct themes of biotic homogenisation–differentiation research were identified in our evidence synthesis. Beta diversity of marine, terrestrial, and freshwater organisms is rarely static in time, and often fluctuates between periods of increasing dissimilarity (biotic differentiation) and similarity (biotic homogenisation), even in the absence of anthropogenic impact or species invasions.

(3) We developed five conceptual models that mechanistically identify the ecological drivers of biotic homogenisation and differentiation as directional change in spatial beta diversity. Our first conceptual model identifies effects of changes in local and/or regional diversity (i.e. alpha and/or gamma diversity, respectively). This conceptual model clarifies how biotic homogenisation or differentiation can occur independently of species invasions or losses *via* changes in the spatial patterning of species occurrences among assemblages. Our second conceptual model centres on the effects of disturbance intensity and disturbance heterogeneity as a driver of beta diversity change. In this model, the direction and magnitude of change in beta diversity depend on the interaction between spatial variation (patchiness) and temporal variation (asynchronicity) of disturbance. The third conceptual model highlights the role of connectivity and species dispersal among assemblages and regions in driving biotic homogenisation and differentiation. Divergent beta diversity outcomes in response to connectivity and dispersal limitation occur because different species have different dispersal characteristics (e.g. ability, propensity), and the magnitude of beta diversity change associated with species invasion also depends strongly on both gamma and beta diversity prior to invasion. The fourth conceptual model emphasises how changes to habitat and environmental heterogeneity drive variable biotic homogenisation and biotic differentiation outcomes across spatial scales. This model predicts that beta diversity is positively linked to spatial environmental variability, such that biotic homogenisation or differentiation occur when environmental heterogeneity decreases or increases, respectively. Our fifth conceptual model is focussed on how the varying roles of species and trophic interactions influence beta diversity by way of habitat modification, disease and transfer of organisms, consumption, competition, and alteration of productivity.

(4) Conclusions regarding biotic homogenisation or differentiation depend on the spatial and temporal extent of a given study along with the combined effects of broad-scale environmental characteristics and the biological traits of the organisms being examined. Ongoing studies of change in beta diversity would be greatly strengthened by examining (and emphasising) the underlying biological and ecological mechanisms ultimately responsible for detected patterns, rather than simply reporting of change in beta diversity, *per se*, in the absence of ecological context.

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X. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Database S1. Database of evidence extracted from empirical studies examining biotic homogenisation or biotic differentiation sourced from Web of Science Core Collection to January 2021.

Fig. S1. Flow chart of the process used to synthesis empirical evidence of drivers and responses of beta diversity change across ecosystems.

Table S1. Research themes identified in a synthesis of empirical evidence of biotic homogenisation and biotic differentiation, and scope of research questions on hypotheses covered by each theme.

Table S2. Summary of the 507 unique empirical studies assessing directional change in beta diversity spanning terrestrial, freshwater, and marine realms associated with the five major research themes and their key beta diversity outcomes.

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