

# ECOGRAPHY

## Research article

## Biodiversity dynamics in landscapes with fluctuating connectivity

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Biodiversity can increase in both high- and low-connected landscapes. However, we lack predictions related to biodiversity dynamics when accounting for the temporal heterogeneity in the connections among the habitats of a landscape. Here, we study the relationship between fluctuations in landscape connectivity and biodiversity dynamics at local and regional scales. We contrast predictions about species richness between landscapes with and without fluctuations in connectivity. Our results show that local ( $\alpha$ ) and regional ( $\gamma$ ) richness can increase together in dynamic landscapes characterized by periodic connectivity, clarifying empirical findings of high biodiversity in both low and high-connected landscapes. Our results also suggest that fluctuations in connectivity increase the overall number of species coexisting in dynamic landscapes when compared with static landscapes with no fluctuations in connectivity. Extending metacommunity theory, by including fluctuations in landscape connectivity, can thus provide new testable predictions about species diversity across broad spatiotemporal scales in rapidly changing landscapes.

Keywords: biodiversity, ecological drift, landscape genetics, metacommunity dynamics, speciation theory

### Introduction

Explaining the mechanisms driving spatiotemporal patterns of species diversity is a longstanding issue in ecology. Several models accounting for spatial structure have been proposed to describe species communities (MacArthur and Wilson 1967, Hanski and Gilpin 1997, Leibold and Chase 2018). Metacommunity theory provides several insights into the roles of dispersal and spatial heterogeneity for species coexistence (Fortuna and Bascompte 2001, Holyoak et al. 2005, Leibold and Chase 2018). Also, empirical studies taking into account heterogeneity and connections among available habitats have unfolded patterns of diversity across gradients of spatial connectivity



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(Kneitel and Chase 2004, Cadotte 2006, Watson et al. 2012). Some studies have shown that modularity, where species interact more frequently with species within their module than with species in other modules, increases population persistence and local species richness (Ellner et al. 2001, Davies et al. 2009, Fox et al. 2011, Gilarranz et al. 2017). Contrasting patterns, i.e. increasing richness with increasing connectivity, are also known (Shtilerman and Lewi 2015, Hock et al. 2017, Damschen et al. 2019). This last outcome is particularly relevant because metacommunity theory predicts that homogenization decreases species richness beyond a certain threshold of connectivity, due to more frequent migration events from the most abundant species (Leibold and Chase 2018). Overall, building theoretical frameworks accounting for the different temporal and spatial scales of landscape dynamics, which can differ by many orders of magnitude (Fig. 1), can be a challenging task. Since spatial connectivity plays a key role in determining species richness, the development of such frameworks is of paramount importance for understanding the maintenance of biodiversity in rapidly changing land- and seascapes.

Dynamic landscapes encompass a collection of phenomena at different temporal and spatial scales. We can decompose spatial dynamics into two main processes: patch and connectivity dynamics (Hanski 1999, Holyoak et al. 2005). A patch can be occupied or unoccupied by populations with species diversity limited by dispersal (Keymer et al. 2000, Leibold et al. 2004). Connectivity dynamics refers to all the dynamical changes affecting the topology of connected sites, i.e. changes in the configuration of the spatial network of sites (Watson et al. 2012, Ruiz et al. 2014, Shtilerman and Lewi 2015, Morel-Journel et al. 2016), reflecting the external fluctuation and temporal heterogeneity in the landscape. Patch and connectivity dynamics interact and affect populations and communities within the metacommunity at different spatiotemporal scales. At large spatiotemporal scales, transitions between habitat types at the continental scale occur, for example, during glacial–interglacial cycles (Werneck et al. 2011). As another example, the combination of fluctuations in tropical reef availability and plate tectonics driving habitat connectivity has played a major role in predicting the emergence and movement of biodiversity

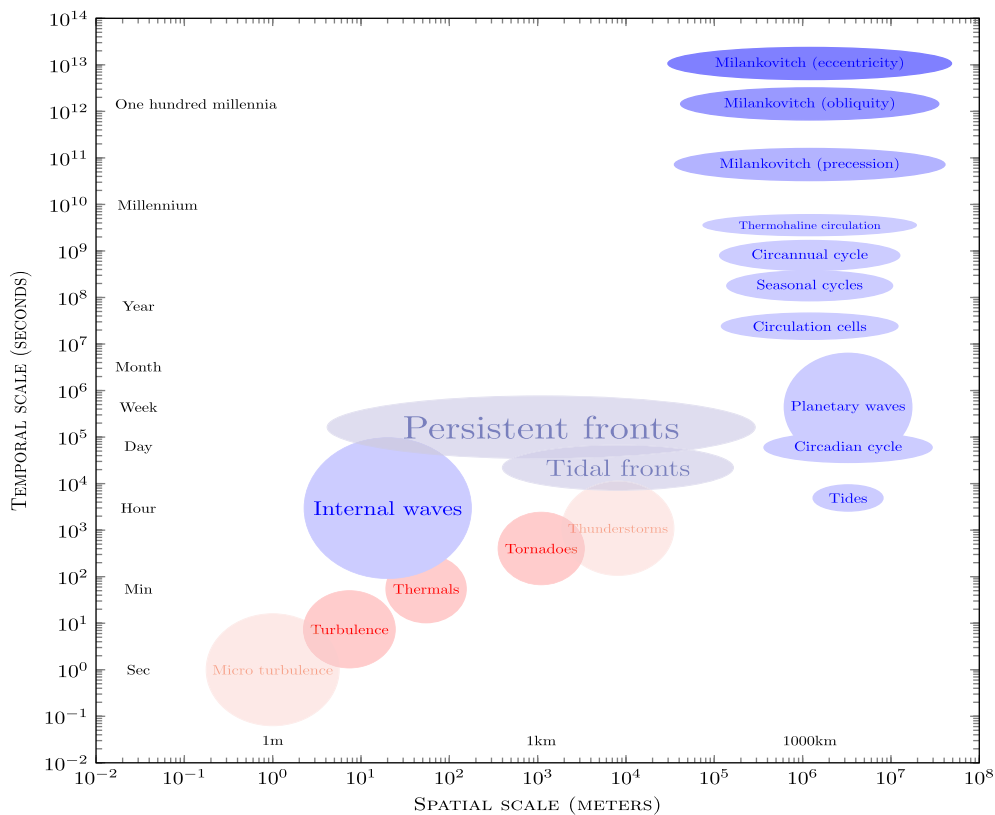


Figure 1. Spatiotemporal scales of the periodic (blue) and non-periodic (red) phenomena affecting land- and seascape connectivity dynamics. At large temporal scales, transitions between habitat types at the continental and ocean scale occur driven by periodic glacial–interglacial cycles and Milankovitch planetary factors (blue ellipses). There are also examples of periodic short-, medium- and large-scale land- and seascape dynamics over short time scales such as internal waves, persistent and tidal fronts, daily tides and seasonal changes of sea ice extent. Modeling one or multiple amplitudes and frequencies simultaneously – for example, connecting short- to medium-spatial- scale dynamics over short time scales – will strongly depend on the model system to study, i.e. lifespan and life history characteristics of each taxon or community. Here we simulate a range of values for the frequency and amplitude of landscape connectivity (Table 1), to understand their impact on biodiversity dynamics.

hot spots in coral reefs and fish-associated communities (Leprieur et al. 2016). Tides are the rise and fall of sea levels caused by the combined effects of the gravitational forces exerted by the Moon and the Sun, and the rotation of the Earth. In intertidal seascapes, such combined gravitational forces produce periodic dynamics with a given amplitude and frequency, conditioning the high and low tides. High tides drive large radii, for example with many small ponds closer to each other, facilitating migration among patches at local and regional scales (Fig. 1) (Roughgarden et al. 1991, McManus and Woodson 2012). Daily tides and seasonal changes of sea ice extent are examples of large-scale spatial dynamics over short time scales, as are phenomena acting at different temporal and spatial scales such as fire size distributions, characterized by very frequent small-scale fires and rare large-scale ones (Hantson et al. 2015) (Fig. 1). Fluctuations in connectivity might also impact the speed of establishment of invasive species (Morel-Journel et al. 2016), threatened populations (Loarie et al. 2009), affect population divergence and speciation (Aguilée et al. 2011), and shape phylogenetic trees (Gascuel et al. 2015).

Patch dynamics have been addressed by numerous theoretical and empirical studies of metapopulations (Hanski 1999, Keymer et al. 2000, Cornell and Ovaskainen 2008, Drechsler and Johst 2010, Reigada et al. 2015). There are

formulas for predicting patch occupancy of a single population in spatially explicit models characterized by temporal patch dynamics (Hanski 1999). The mean species lifetime in a network of dynamical patches can also be estimated (Drechsler and Johst 2010). Recent studies have shown that the rate of patch turnover is critical for metapopulation persistence. For example, increasing the rate of patch dynamics might decrease metapopulation persistence when dispersal is continuous, while persistence is facilitated by pulsed dispersal (Reigada et al. 2015). Evidence about the role of connectivity dynamics on species richness comes mostly from empirical studies of single-species metapopulations, where habitat connectivity is characterized by the landscape matrix (Eycott et al. 2012). For example, in amphibians, dispersal between ponds is strongly affected by the terrestrial habitat separating the ponds (Buskirk 2012, Cline and Hunter 2014) and by moisture conditions (Rittenhouse et al. 2009). Similarly, the dispersal of butterflies also depends on the landscape matrix (Kuefler et al. 2010) with dispersal kernels fluctuating over time (Schtickzelle et al. 2012). And in fish, interconnections between rivers that form during periods of heavy rain can connect otherwise disconnected habitats and allow for dispersal and gene flow among populations (Boizard et al. 2009).

The former studies suggest that changes in spatial connectivity play a pivotal role in metapopulation dynamics

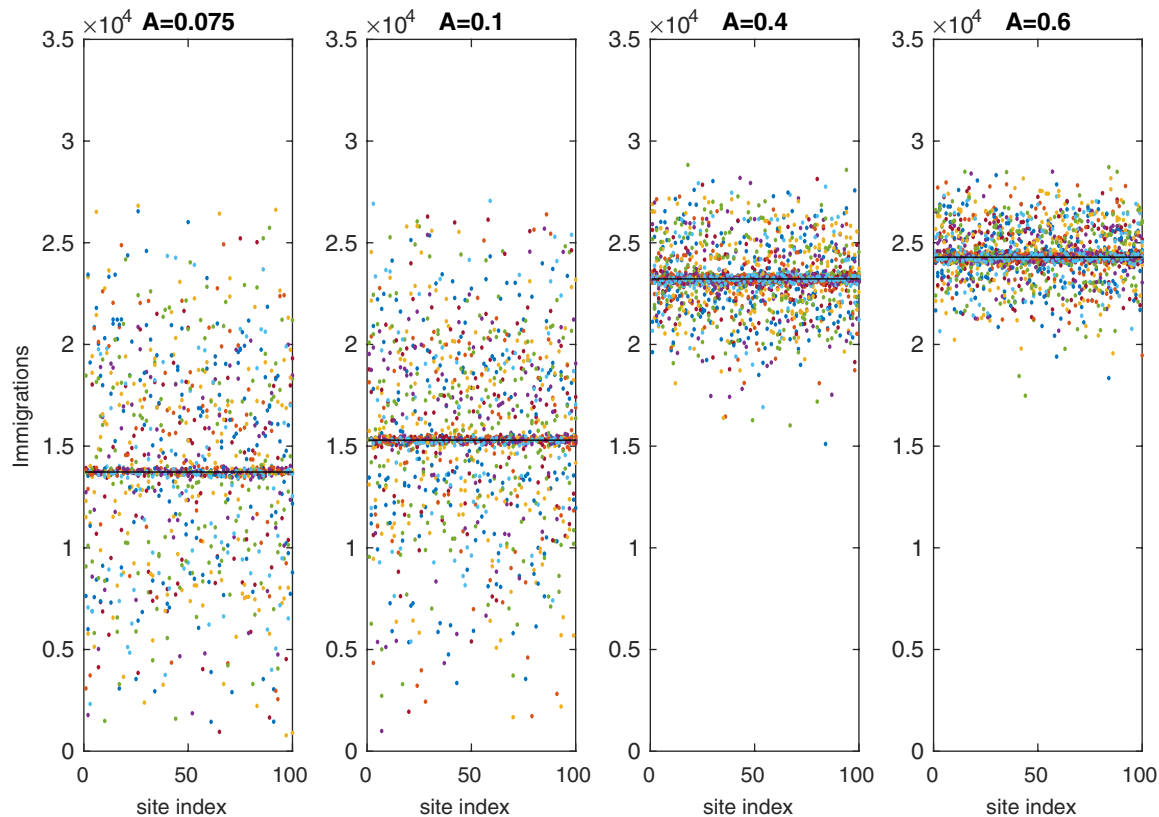


Figure 2. Number of immigration events per site (y-axis) for all the sites (indexed on the x-axis) for four different values of the amplitude of landscape connectivity (from left to right:  $A = 0.075, 0.1, 0.4, 0.6$ ;  $A = 0.075L, 0.1L, 0.4L, 0.6L$ ) Migration rate is  $\mu = 0.2 \text{ ind/gen}$  (Table 1 for other parameter values). Horizontal black line represents the mean taken for the simulations with the static landscapes.

(Hanski 1999). Despite the empirical evidence of the role of connectivity dynamics in metapopulations, there is a scarcity of theoretical predictions of how demographic processes and migration interfere with connectivity dynamics to integrate the empirical patterns of species richness across connectivity gradients at broad spatiotemporal scales. Only a few empirical studies have addressed factors affecting changes in connectivity at different spatiotemporal scales and their effects on biodiversity dynamics (Sprugel 1991, Stenseth et al. 2002, Ruiz et al. 2014, Helm et al. 2017). However, there is no previous systematic research on the effects of fluctuations in connectivity dynamics on species richness at different spatial scales, nor research on how to link connectivity dynamics to biodiversity gradients over ecological scales (Etienné et al. 2019, Gaboriau et al. 2019). Specifically, depending on the spatiotemporal scales at which patch and connectivity dynamics act, connectivity dynamics encompasses a variety of periodic and non-periodic cycles, ranging from seascapes and persistent and tidal fronts to daily tides, seasonality, and larger cycles (e.g. the Milankovitch cycles) (Fig. 1). Here, we propose to include the description of such phenomena in the metacommunity theory, by studying metacommunity dynamics on spatial networks with periodic connectivity over ecological scales, and assessing how the frequency and the amplitude of landscape connectivity affect local and regional richness with simulations from a dynamical model.

Our results suggest that periodic fluctuations in landscape connectivity increase local diversity in comparison to static landscapes with fixed connectivity (Fig. 2). Also, in such dynamic landscapes, sites that have higher connectivity sustain higher species richness than sites with lower connectivity (Fig. 3–6). Our predictions hold both for symmetric (i.e. individuals show strong philopatry, or a tendency to return to

a patch) and asymmetric (i.e. there is not a tendency to return to a patch, see Material and methods) migration rates. Overall, our results suggest that biodiversity dynamics with static connectivity strongly differ from the dynamics observed where fluctuations in connectivity occur. These contrasting differences between landscapes with static and fluctuating connectivity are obtained even in an extremely simplified model that is based on neutral interspecific competition in the absence of environmental heterogeneity. Our approach is theoretical and needs further scrutiny, e.g. by calibrating the demographic processes of the models to empirical ecological data.

## Material and methods

We extend spatially explicit neutral models of biodiversity (Vallade and Houchmandzadeh 2003, Vanpeteghem and Haegeman 2010, Alzate et al. 2019) accounting for connectivity dynamics. Community dynamics follows a zero-sum game in a landscape composed of  $S$  sites whose connectivity changes over time. To isolate the role of the connectivity dynamics, our model considers all sites of the same size and habitat type and therefore the same carrying capacity (Rybicki and Hanski 2013). This allows us to explore the combined role of connectivity dynamics and demography on local and regional richness. Every site is saturated with  $J_S$  individuals and every dead individual is rapidly replaced by a new individual of the same or another species. Every time an individual dies in a given site  $i$ , it is replaced with an individual coming from either the same patch, another site  $j$ , or the regional pool of new species. Individuals coming from the same site as the dead individual are offspring, while individuals coming from other sites are migrants, which are themselves replaced by an offspring in

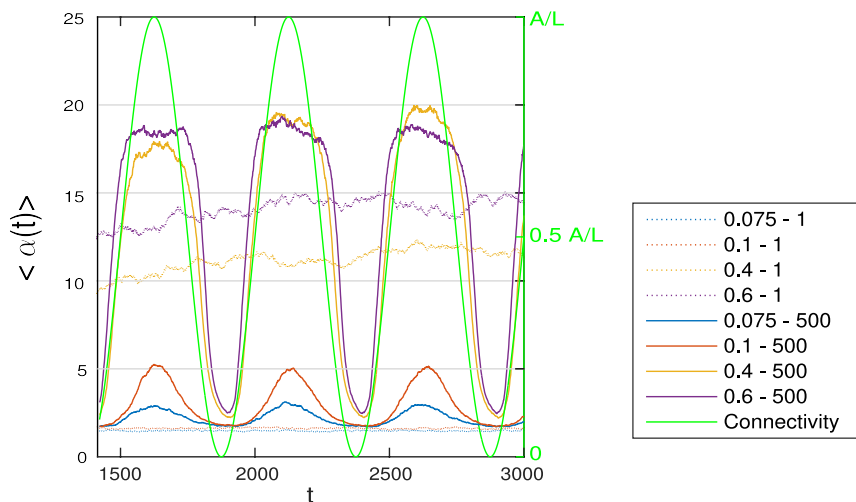


Figure 3. Mean local species richness,  $\langle \alpha(t) \rangle$  (y-axis) for the last 1500 generations (time  $t$  on the x-axis). Fluctuations in landscape connectivity are represented by  $r(t)/\mathcal{L}$  (the line with the greatest amplitude, green line), where  $\mathcal{A}$  is the amplitude of landscape connectivity and  $\mathcal{L}$  is the length of the landscape edge. Landscape connectivity goes from  $r(t) = 0$ , i.e. all sites are disconnected, to  $r(t) = \mathcal{A}/\mathcal{L}$ , a fully connected network. Values of  $\mathcal{A}$  below the percolation threshold are given by 0.075 and 0.1 (blue and red lines, respectively), while values of  $\mathcal{A}$  above the percolation threshold are 0.4 and 0.6 (yellow and purple lines, respectively). For each value of the amplitude of landscape connectivity, we compare predictions for a static landscape ( $\omega = 1GPT$ , dotted lines) and a dynamic landscape ( $\omega = 500GPT$ , continuous lines).

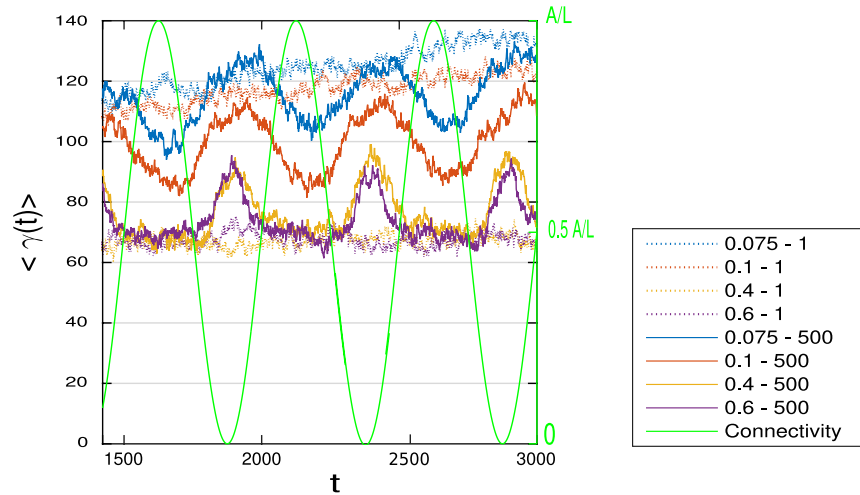


Figure 4. Mean regional species richness,  $\gamma$  (y-axis) for the last 1500 generations (time  $t$  on the x-axis). Fluctuations in landscape connectivity are represented by  $r(t)/\mathcal{L}$  (the line with the greatest amplitude, green line), where  $\mathcal{A}$  is the amplitude of landscape connectivity and  $\mathcal{L}$  is the length of the landscape edge. Landscape connectivity goes from  $r(t) = 0$ , i.e. all sites are disconnected, to  $r(t) = \mathcal{A}/\mathcal{L}$ , a fully connected network. Values of  $\mathcal{A}$  below the percolation threshold are given by 0.075 and 0.1 (blue and red lines, respectively), while values of  $\mathcal{A}$  above the percolation threshold are 0.4 and 0.6 (yellow and purple lines, respectively). For each value of the amplitude of landscape connectivity, we compare predictions for a static landscape ( $\omega = 1GPT$ , dotted lines) and a dynamic landscape ( $\omega = 500GPT$ , continuous lines).

their original site. Immigration of individuals coming from the regional pool corresponds to regional immigration instead of speciation used in the context of metacommunity models (Vanpeteghem and Haegeman 2010).

We consider a diverse regional species pool containing a very large number of equally abundant species. Therefore, every immigration event from the regional species pool introduces a new species. Regional immigration arises homogeneously in the landscape. In sum, at every generation, there will be  $S_j$  death events followed by a replacement. At every death,

replacements are chosen from the migration rate (individuals per generation),  $\mu$ , from an outside site within the network, with rate  $\nu$  from the regional species pool, or with rate  $\lambda$  from the same site. Rates were constrained to sum 1 individual per generation, i.e.  $\lambda = 1 - \mu - \nu$ .  $\lambda$ ,  $\mu$ , and  $\nu$  are fixed parameters within each replicate from the outset to fulfill the constraint. Given this normalization, the characteristic time of the metacommunity  $\tau = (\lambda + \mu + \nu)^{-1}$  (Ontiveros et al. 2021) has been set to 1. In other words, we explore metacommunity dynamics without relating it to any specific system.

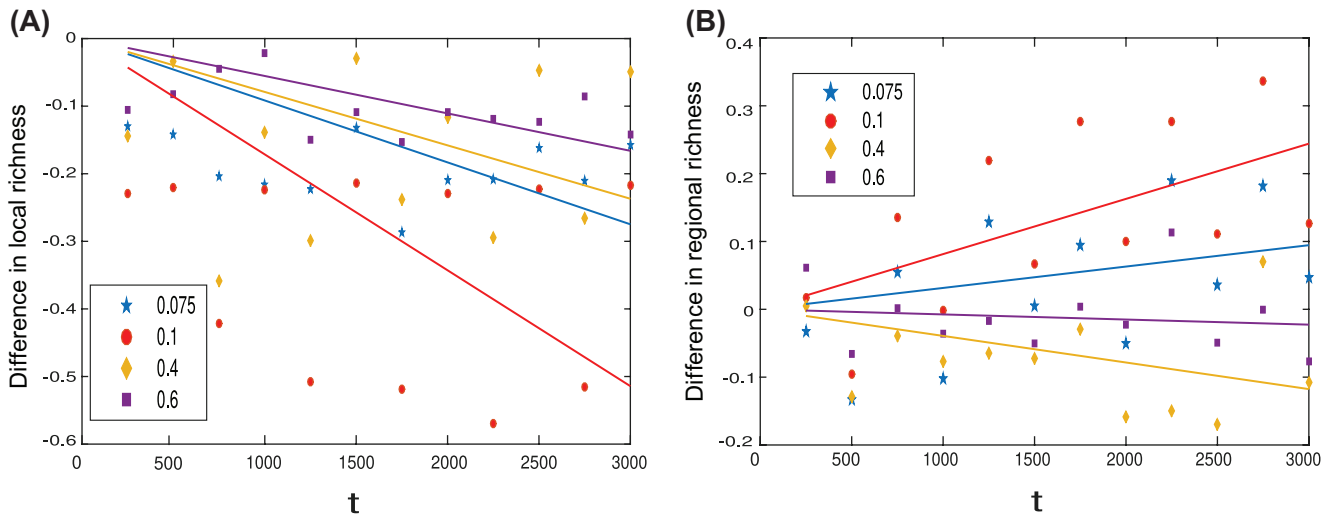


Figure 5. (A) Difference in local (A, y-axis) and regional (B, y-axis) richness between static and dynamic landscapes as a function of time (x-axis). The difference for the local species richness was calculated as  $\frac{[\langle \alpha_{stat}(t) \rangle - \langle \alpha_{dyn}(t) \rangle]}{\min(\langle \alpha_{stat} \rangle, \langle \alpha_{dyn} \rangle)}$  (y-axis), where  $\langle \alpha_{stat}(t) \rangle$ ,  $\langle \alpha_{dyn}(t) \rangle$  and  $\min(\langle \alpha_{stat} \rangle, \langle \alpha_{dyn} \rangle)$  are the mean local species richness for the static landscape ( $\omega = 1GPT$ ) and the dynamic landscape ( $\omega = 500GPT$ ), and the minimum value of the two, respectively. Regional species richness in (B, y-axis) was calculated as in (A).



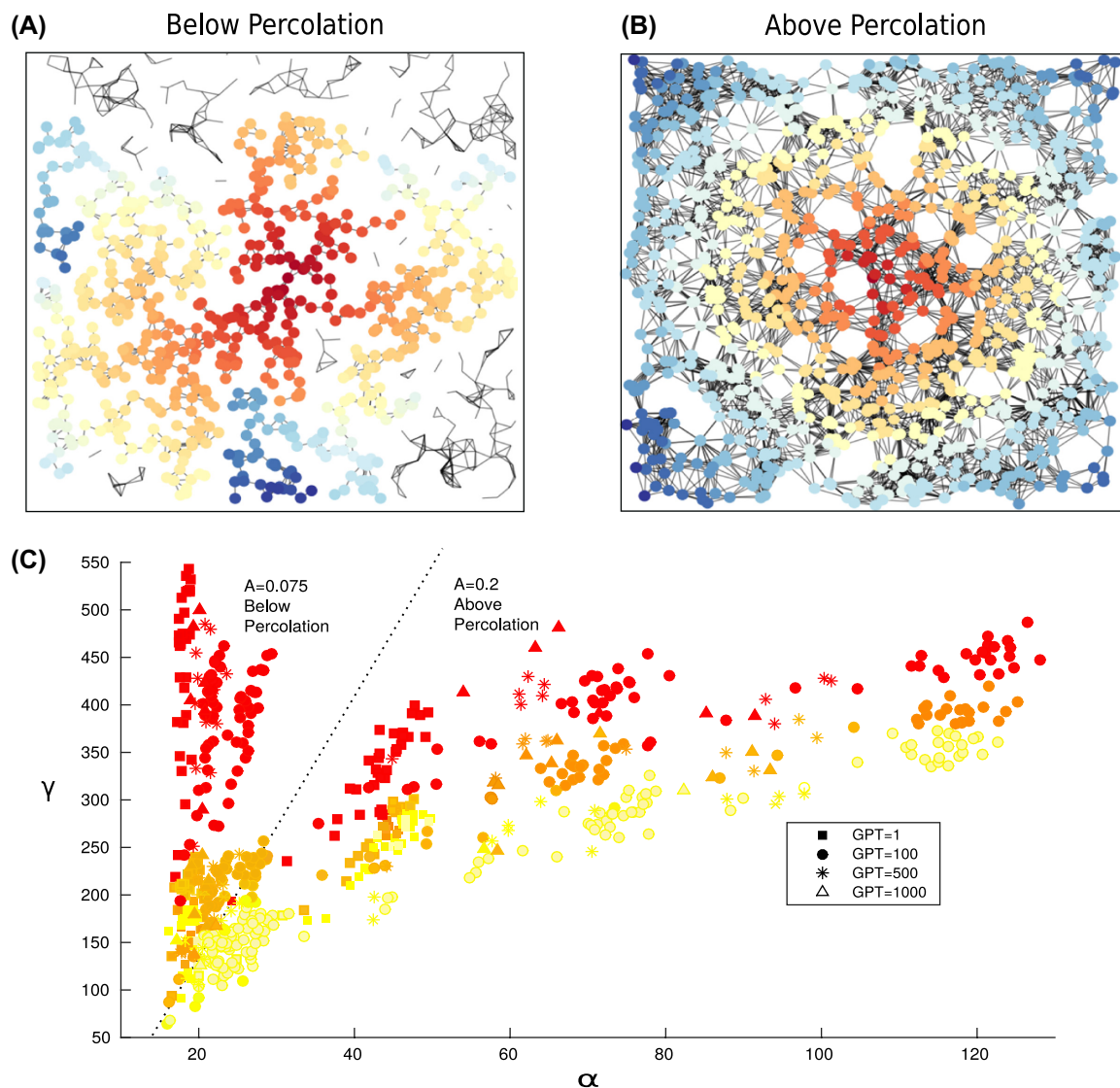


Figure 6. General patterns of local and regional species richness for dynamic landscapes with periodic connectivity. Panels (A) and (B) show landscape configurations at the maximum of connectivity both below the percolation threshold ( $\mathcal{A} = 0.075$  in panel A), and above the percolation threshold, ( $\mathcal{A} = 0.2$  in panel B). Circles in (A) and (B) represent sites, and links are connections between sites. Colors of the circles refer to their distance to the center of the network, from center to periphery: red (center) refers to the radii of the rings between  $[0, 0.125] L$ , orange refers to  $[0.125, 0.375] L$ , yellow to  $[0.375, 0.6] L$  and blue (periphery) to the outermost region. Colors are also assigned to have the same number of sites inside each concentric ring. Panel (C) shows local ( $\alpha$ ) versus regional ( $\gamma$ ) richness, where each point represents the metacommunity in the different concentric rings (shown in panels A and B for two examples), for four values of the frequency of landscape connectivity (static landscapes,  $\omega = 1GPT$ , squares;  $\omega = 100GPT$ , circles;  $\omega = 500GPT$ , asterisks; and  $\omega = 1000GPT$ , triangles) replicated 10 times. The dotted line represents the prediction at the percolation threshold.  $\langle \alpha \rangle$  and  $\gamma$  in the rings are calculated for landscapes with fluctuating connectivity ( $\omega > 1GPT$ ) when their connectivity is comparable to the static one, i.e. at half the period.

The landscape matrix is defined through connections among habitat sites. We used a center-periphery structure for the landscapes instead of periodic boundary conditions, which would be needed to describe landscape configurations of planetary distributions. An important property in empirical landscapes is the existence of thresholds, i.e. shifts in connectivity and in the size of the largest area, with implications for population persistence (de Filho and Metzger 2006). We explore landscapes with thresholds by defining sites as the nodes of a bi-dimensional

random geometric graph (RGG) in a square landscape of size  $\mathcal{L}$  (Penrose et al. 2003). The two coordinates of each site are drawn from a uniform distribution in the interval  $[0, \mathcal{L}]$  and two sites are connected if their geometric distance is smaller or equal to a given distance  $[0, \mathcal{L}]$ , the critical migration radius. RGGs are characterized by a percolation threshold, i.e. a critical value of connectivity,  $\eta_c$ , above which a giant connected component emerges, that is, a compact block of sites from where every individual can move across the landscape.

We explore the whole range of connectivity by dynamically varying the connectivity thresholds from low- to high-connected landscapes (Fig. 6). To explicitly take into account periodic connectivity dynamics, at each generation, two sites  $i$  and  $j$  are connected if their geographic distance,  $d_{ij}$ , is equal to or smaller than a migration radius  $r(t)$  following a periodic, sinusoidal form given (Eq. 1) by:

$$r(t) = \frac{\mathcal{A}}{2}(1 + \sin(2\pi\omega t)), \quad (1)$$

where  $t$  is time measured in generations included in a period  $T$  of oscillation, with  $T = 1/\omega$  (our unit of frequency is thus generations per period of time, GPT,  $T$ ).  $\mathcal{A}$  and  $\omega$  are the amplitude and the frequency of connectivity dynamics determining the temporal fluctuations of the non-negative migration radius. This parametrization allows exploring networks of different sizes, from a network with low connectivity, where the network breaks into many small clusters, to one of high connectivity, where the network is composed of only one giant component.

We measure the relative amplitude of landscape connectivity using  $\mathcal{A}/\mathcal{L}$ , where  $\mathcal{L}$  is the length of the landscape edge. Migration between any pair of sites  $i$  and  $j$  at time  $t$  depends on fluctuations in connectivity and is defined (Eq. 2) by:

$$m_{ij}(t) = \mu P(d_{ij})\theta(r(t) - d_{ij}), \quad (2)$$

where  $\theta(x) = 1$  if  $x \geq 0$  and 0 if  $x < 0$  and  $\mu$  is the local migration rate. Therefore, migration between sites  $i$  and  $j$  occurs only if they are connected, while  $P$  defines the likelihood that a migrant arrives at site  $i$  coming from site  $j$ . Through  $P$ , different migration strategies can be taken into account, selecting from which of the neighboring sites  $j$  the migrant comes. Completely symmetric migration is given by  $P(d_{ij}) = 1/d_{ij}$ , i.e. individuals and populations tend to stay in or return to a particular site (Shtilerman and Lewi 2015, Henry et al. 2016); however, this expression is not normalized. To make the model mathematically consistent, we thus normalize the migration probability among first neighbors and define an asymmetric migration strategy given (Eq. 3) by:

$$P(d_{ij}) = \frac{d_{ij}^{-1}}{\sum_{k \in N_t(i)} d_{ik}^{-1}} \quad (3)$$

where  $N_t(i)$  is the set of the first neighbors of site  $i$  at time  $t$ . In such a scenario, migration events are still inversely proportional to the geographical distance between connected sites, but they are normalized across neighboring sites, at a given time step, reflecting the effect of landscape structure on migration. In this way, we introduce a bias for the migration rate which is dependent on both distance between sites and on their degree, reflecting a potential effect of crowding for

the specific neutral model we are considering. In this case  $K(i, j, t) = P(d_{ij})\theta(d_{ij}, t)$  is our dispersal kernel, i.e. a function defined on the discrete set of neighboring nodes, taking continuous values at every time  $t$ .

Taken together, the fixed parameters within each simulation included in the migration function are local migration,  $\mu$ , frequency,  $\omega$ , and amplitude,  $\mathcal{A}$ , of landscape connectivity and the distance between sites  $i$  and  $j$ ,  $d_{ij}$  (Table 1.) We simulate community dynamics at varying amplitude and frequency using asymmetric migration (Eq. 2, 3, Table 1 for the parameter values explored). To compare predictions between dynamic and static or fixed connectivity, for every dynamic simulation, we also compute a static landscape with mean migration obtained as the time average of the dynamic scenario (Fig. 2). In this way, we can compare predictions between static and dynamic landscapes, avoiding biases towards landscapes with a different number of migration events due to the fluctuations in connectivity.

We quantify species richness using  $\alpha$ -,  $\beta$ -, and  $\gamma$ -diversity (Whittaker 1960, Leibold and Chase 2018).  $\gamma$ -richness is defined as the total number of species in the landscape, representing diversity at a regional scale;  $\alpha$ -richness is the number of species per site, representing diversity at a local scale (Leibold and Chase 2018); and  $\beta$  is the slope of the  $\alpha$ - and  $\gamma$ -diversity relationship. We divide the landscape into concentric rings with different radii (Fig. 6A–B), and plot  $\alpha$ -diversity per site as a function of the  $\gamma$ -richness of the ring to which the site belongs. We thus produce such  $\alpha$ -to- $\gamma$  plots for the different dynamics explored (Fig. 6C). We have chosen the  $\alpha$  versus  $\gamma$  relationship to compare static and dynamic landscape at different spatial scales (Fig. 3–6). This descriptor allows us to contrast predictions between landscapes with and without fluctuations in connectivity and to figure out which scenario predicts an increase in biodiversity in both high- and low-connected landscapes. All our simulations start with the same species in every site for 100 sites and with 100 individuals in each site for a total population size of  $10^4$  individuals with a novel species entering into the metacommunity,  $v$ , at a rate of  $10^{-4}$ , indicating an introduction of  $\approx 1$  species per generation (Bendif et al. 2019). We run 10 replicates of the same landscape for each combination of dynamical parameters, i.e. varying both  $\mathcal{A}$  and  $\omega$  in Eq. 1 (Table 1), simulating 3000 generations per replicate.

## Results

Our results show that variation in connectivity influences all components of the diversity explored. The mean local and regional species richness follow the sinusoidal form given by the time-dependent periodic fluctuations of the dispersal radius (Eq. 1). Fluctuations in connectivity impact local,  $\alpha$  (Fig. 3), and regional species richness,  $\gamma$  (Fig. 4), in opposite directions. While the local species richness,  $\alpha$ , correlates positively with connectivity (Fig. 3), both below and above the percolation threshold, the opposite occurs with the regional species richness  $\gamma$  (Fig. 4). On the other hand, there

Table 1. Parameters and variables. RGG, random geometric graph.

Symbol	Concept	Value
<i>Fixed parameters</i>		
$\nu$	Regional immigration rate	$10^{-4}$ inds / gen
$S$	Number of sites	$10^2$
$\mathcal{L}$	Length of landscape edge	$10^2$
$J_s$	Number of individuals per site	$10^2$
<i>Local migration parameters</i>		
$\mu$	Local migration rate	[0.01, 0.05, 0.1, 0.2] inds / gen
$\lambda$	Birth rate	$1 - \mu - \nu$
$\omega$	Frequency of landscape connectivity	[0.001 0.002 0.01 0.02 0.1 0.2 1]
$A$	Amplitude of landscape connectivity	[0.075 0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9 1]
$d_{ij}$	Distance between sites $i$ and $j$	Given by the RGG
<i>Local migration variables</i>		
$r(t)$	Migration radius	Eq. 1
$m_{ij}$	Migration rate between sites $i$ and $j$	Eq. 2
$N(i)$	Set of first neighbors of site $i$	Variable
$P(d_{ij})$	Likelihood a migrant arrives at $i$ from $j$	Eq. 3
<i>Measures of species richness</i>		
$\alpha$	Number of species per site	Variable
$\gamma$	Number of species in the landscape	Variable

is no relationship between local (Fig. 3) and regional (Fig. 4) species richness and connectivity dynamics for static landscapes, even if the mean species number is clearly affected by connectivity being below or above the percolation threshold.

Periodic fluctuations in connectivity increase diversity at local and regional levels in comparison to static landscapes despite showing larger fluctuations in species richness (Fig. 5). Landscapes with fluctuating connectivity show, on average, between 10 and 20% more local richness than static landscapes, both below and above the percolation threshold (Fig. 5A, fit using a stepwise function to detect transient and steady state). For regional richness, landscapes with fluctuations in connectivity also show between a 10 and 20% increase above the percolation threshold (Fig. 5B, yellow and purple lines), when compared to static landscapes. Below the percolation threshold, they show a decrease in value, when compared with static landscapes (Fig. 5B, blue and red lines). Taken together, these results suggest that fluctuations in connectivity play an important role in biodiversity dynamics both below and above the percolation threshold, during transient and at steady state, and for local and regional scales (Fig. 3–5).

Figure 6 summarizes our results to show that fluctuations in connectivity increase local and regional species richness in low- (Fig. 6A) and high- (Fig. 6B) connected landscapes. The slope of the  $\alpha$  to  $\gamma$  relationship,  $\beta$ -richness, changes substantially without and with fluctuating connectivity (Fig. 6C). Turnover is faster below than above the percolation threshold and,  $A$  is faster in static landscapes than in landscapes with fluctuating connectivity, (i.e. compare  $\omega = 1, 100, 500$ , and  $1000$  GPT in Fig. 6). Periodic fluctuations in connectivity increase diversity locally in comparison to static connectivity and sites that have

higher connectivity sustain higher regional species richness than sites with lower connectivity (Fig. 6, compare red with blue sites). Local richness increases beyond the percolation threshold ( $\alpha$ , Fig. 6) without and with fluctuations in connectivity, while regional richness decreases with spatial connectivity above the percolation threshold ( $\gamma$ , Fig. 6, see also Fig. 5B). Furthermore, there is a decrease in local richness towards the periphery of the spatial network, where connectivity is lower, for static and dynamic scenarios (Fig. 6A–B). At high connectivity (e.g. Fig. 6C, above percolation,  $A = 0.2$  L),  $\alpha$  is maximum for medium values of  $\omega$  (e.g.  $\omega = 100$  GPT, where GPT is the number of generations in a period T of oscillation) and it decays for higher values (e.g.  $\omega = 500 - 1000$  GPT). For low-connected landscapes (Fig. 6C, below percolation with  $A = 0.075$  L), there is no giant connected component, i.e. there exist many small clusters in the spatial network (Fig. 6A). In this scenario, the average local richness remains small. These results hold for all values of the frequency of landscape connectivity,  $\omega$ , and of the local migration rate,  $\mu$ ,  $\nu$ , explored (Table 1). In this scenario, the establishment of new species from the global pool is facilitated by low connectivity as we observe the highest regional richness (Fig. 6C).

Metacommunity theory suggests migration and local demography are the main drivers of local richness, while regional immigration and low landscape connectivity are the main drivers determining regional richness. In neutral metacommunity models, regional immigration plays a major role in low-connected landscapes, while migration drives the dynamics in the more connected ones, therefore increasing local richness, but at the cost of decreasing regional species richness. Fluctuations in connectivity alter the trends observed in metacommunities in static and low-connected landscapes. Periods



of 'high' connectivity following the sinusoidal form given by the time-dependent periodic fluctuations of the dispersal radius (Eq. 1) trigger a 10–20% increase in local species richness (Fig. 3A, 4A). The trend is also altered for regional species richness but in the opposite direction. Periods of 'high' connectivity now decrease regional species richness in comparison to landscapes without fluctuating connectivity (Fig. 3B, 4B). Overall, these results suggest that biodiversity dynamics markedly differ between static and dynamic landscapes for a broad range of values of amplitude,  $\mathcal{A}$ , and frequency,  $\omega$ , and of the local migration rate,  $\mu$  (Table 1).

## Discussion

Predictions from theoretical models, field data, and experiments have shown the importance of landscape dynamics for species richness. Many studies have shown that decreasing landscape connectivity increases local richness, but examples of increasing richness with increasing connectivity are also known. These patterns challenge existing metacommunity theory for static landscapes which, below and above given thresholds of low and high connectivity, predicts that low rescue and homogenization decrease species richness (Shtilerman and Lewi 2015, Hock et al. 2017, Leibold and Chase 2018). While landscape connectivity is critical for predicting local richness, studies comparing metacommunities in static and dynamic landscapes, across local and regional scales, are scarce. Our results show that landscapes with static and dynamic connectivity are markedly different in local and regional richness, and thus that fluctuations in connectivity might play a key role in predicting biodiversity dynamics at local and regional scales (Fig. 3–6).

Connecting empirical patterns of local species richness to fluctuations in landscape connectivity can, however, be more challenging. This would require taking into account sampling factors at different spatiotemporal resolutions, to quantitatively evaluate predictions from empirical metacommunities in landscapes with fluctuating connectivity dynamics (i.e. low local versus high regional richness at low connectivity, Fig. 3, 4) and to compare empirical patterns of species richness across studies (i.e. local richness might decrease or increase with low connectivity). Unfortunately, empirical studies rarely combine data of landscape connectivity with biodiversity surveys. A major challenge in future biodiversity studies will be to integrate different data sources including both landscape connectivity and biodiversity surveys, to test the extent to which dynamics affect local and regional biodiversity (Chase et al. 2018).

Our results also show that fluctuations in connectivity in low-connected landscapes (i.e. below percolation threshold, Fig. 6A) cannot rescue the species going to extinction in isolated clusters. In this scenario, the difference between biodiversity in static and dynamic landscapes decreases until zero when all sites are isolated. On the other boundary, dynamic connectivity in high-connected landscapes (i.e. above percolation, Fig. 6B), increases homogenization, and although

differences between landscapes with static and dynamic connectivity still occur, these differences tend to zero for a fully connected spatial network. The maximum difference between static and dynamic landscapes occurs around the percolation threshold, where the coexistence of large and small components in the spatial network allows the rescue of new species arrivals, triggered by a 'migration pump' driven by pulses in connectivity (Fig. 3, 4). The maximum difference between static and dynamic connectivity around the percolation threshold in local and regional species diversity suggests that migration may lead to a much quicker increase in species abundance than it takes for neutral drift for species to go extinct. This pattern resembles the mechanism underlying the storage effect. Favorable periods last for a much longer time than unfavorable ones, leading to a strong frequency dependence and a migration pump effect with species richness accumulating faster than going to extinction due to the fluctuations in connectivity in the landscape.

A next step in comparing theoretical expectations in landscapes with and without fluctuating connectivity is to quantitatively compare models and patterns by calibrating the model for the characteristic time of the metacommunity, related to the individual time scales of the biological processes in consideration, e.g. by comparing the characteristic time of dispersal  $\tau_\mu = 1/\mu$ , or to the characteristic time of regional immigration,  $\tau_\nu = 1/\nu$ , in relation to the time scale of landscape connectivity ( $T = 1/\omega$ ). We could then have predictions of the model using different orders of magnitude for the biological,  $\tau_\mu$ ,  $\tau_\nu$ , and physical processes,  $T$  and have a clearer, more quantitative comparison, also when landscape dynamics is not merely periodic, but characterized by different dominant frequencies (Ontiveros et al. 2021). In this respect, in weather prediction studies, it is standard to use and develop statistical methods aimed at predicting patterns in fluctuating environments (Sigrist et al. 2015).

Varying environments are an important factor in predicting empirical patterns of single and multiple species communities (Chesson and Warner 1981, Lande et al. 2003). Many recent extensions of neutral biodiversity theory have considered environmental stochasticity in addition to demographic stochasticity to predict the empirical patterns of species diversity (Alonso et al. 2015, Kalyuzhny et al. 2015b, Azaele et al. 2016). Environmental stochasticity in static landscapes can predict the short-term population fluctuations and the similarity decay with time while retaining predictions for the species abundance distributions (Kalyuzhny et al. 2015a). On the other side, at larger spatiotemporal scales, patch and fluctuations in connectivity accounting for fluctuations in habitat availability and plate tectonics, respectively, might be playing a major role in predicting diversity and hot spot patterns on many taxa (Leprieur et al. 2016). An open challenge for further extending the neutral theory is to combine environmental stochasticity to connectivity and site dynamics. In this regard, our model highlights the need for taking into account changes in connectivity dynamics to test new predictions in metacommunity theory about species diversity. Our results are

based on the assumption of fixed patch size and a large and diverse pool of species with homogeneous regional immigration dynamics for all our landscape simulations. Our neutral dynamics in homogeneous landscapes might only apply to small-scale metacommunities. Further work exploring diversity patterns incorporating habitat variability, together with connectivity fluctuations at broader spatial scales with a much less diverse regional pool, can provide the appropriate scales where fluctuations in connectivity have an important role in explaining diversity (Marske et al. 2023).

Recent studies have shown that persistence in metapopulations is enhanced when dispersal is pulsed in landscapes with a high rate of patch turnover (Reigada et al. 2015). These results suggest that fluctuations in landscape connectivity, driven by migration pumps or pulses, could predict stronger deviations from static landscapes after accounting for both connectivity dynamics and patch turnover dynamics. In food webs, daily, monthly, and annual cycles in foraging activities play key roles in maintaining complex communities, and recent results show that each cycle does not have a strong stabilizing effect independently, but that it enhances community persistence when combined with other rhythms (Mougi 2021). On the regional immigration and speciation side, most metacommunity studies accounting for explicit landscape dynamics (i.e. plate tectonics, geodynamics, and mountain formation) have also assumed simple point mutation speciation dynamics (Leprieur et al. 2016, Descombes et al. 2018, Pontarp et al. 2019). Therefore, the effects of more realistic regional immigration or speciation scenarios on biodiversity dynamics in dynamic landscapes remain mostly unknown.

## Conclusion

Our study attempts to integrate metacommunity dynamics into the field of chronobiology and geochronology. Chronobiology is the part of biology that examines biological processes following periodic cycles and their adaptation to solar- and lunar-related rhythms. Major recent advances in chronobiology have occurred in many biological processes like physiology, hibernation, mating, migration, and the circadian and circannual cycles, as the most empirically supported cycles (Helm et al. 2017). Geochronology, as the part of geology analyzing climate cycles for reconstructing geologic time for understanding ancient climate change and for evaluating the history of our solar system (Meyers and Malinverno 2018), has been used only rarely to predict macroecological patterns. Merging metacommunity dynamics and geochronobiology by connecting chronobiology and geochronology to explore the interactions between periodic and aperiodic cycles and biological processes (Fig. 1) is one of the most exciting but also most challenging avenues for understanding biodiversity dynamics at different spatiotemporal scales.

Our study might also help to further extend chronobiology to life history and to migration traits, for example,

by accounting for intraspecific trait variation in the adaptive response to fluctuations in landscape connectivity, to study the effect of periodic cycles on range contractions and expansions on biodiversity dynamics in the context of global change. These extensions might bring new insights into the causes of biodiversity fluctuations in rapidly changing landscapes. Our study is a first step to show that biodiversity dynamics in landscapes with periodic fluctuating connectivity might strongly deviate from biodiversity dynamics in static landscapes, even in the case of a simple neutral model. This approach is the most conservative starting point to compare the scenarios emerging in these two types of landscapes. Further, including non-periodic fluctuations in landscape connectivity, multiple overlapping environmental forcing, and environmental stochasticity, might predict much stronger deviations and more complex biodiversity dynamics in both local and regional species richness.

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**Gian Marco Palamara:** Conceptualization (supporting); Methodology (supporting); Writing – original draft (equal); Writing – review and editing (equal). **Alejandro Rozenfeld:** Formal analysis (lead); Methodology (lead); Writing – original draft (equal); Writing – review and editing (equal). **Charles N. de Santana:** Conceptualization (equal); Methodology (supporting), Writing – original draft (equal). **Jan Klecka:** Conceptualization (supporting); Methodology (supporting); Writing – original draft (equal); Writing – review and editing (supporting). **Rodrigo Riera:** Writing – review and editing (equal). **Victor M. Eguíluz:** Conceptualization (supporting); Methodology (equal); Writing – original draft (equal); Writing – review and editing (equal). **Carlos J. Melián:** Conceptualization (lead); Formal analysis (equal); Funding acquisition (lead); Methodology (equal); Writing – original draft (equal); Writing – review and editing (equal).

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## Data availability statement

Data are available from the Github Repository: <https://github.com/melian009/Dynalands> (Palamara et al. 2023).

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