Geomorphic controls on elevational gradients of species richness

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Elevational gradients of biodiversity have been widely investigated, and yet a clear interpretation of the biotic and abiotic factors that determine how species richness varies with elevation is still elusive. In mountainous landscapes, habitats at different elevations are characterized by different areal extent and connectivity properties, key drivers of biodiversity, as predicted by metacommunity theory. However, most previous studies directly correlated species richness to elevational gradients of potential drivers, thus neglecting the interplay between such gradients and the environmental matrix. Here, we investigate the role of geomorphology in shaping patterns of species richness. We develop a spatially explicit zero-sum metacommunity model where species have an elevation-dependent fitness and otherwise neutral traits. Results show that ecological dynamics over complex terrains lead to the null expectation of a hump-shaped elevational gradient of species richness, a pattern widely observed empirically. Local species richness is found to be related to the landscape elevational connectivity, as quantified by a newly proposed metric that applies tools of complex network theory to measure the closeness of a site to others with similar habitat. Our theoretical results suggest clear geomorphic controls on elevational gradients of species richness and support the use of the landscape elevational connectivity as a null model for the analysis of the distribution of biodiversity.

macroecology | complex networks | landscape connectivity | metacommunity theory

The search for the mechanisms determining the distribution of life on Earth has long been, and still is, a challenge of great importance for ecologists and biogeographers. Indeed, developing conservation strategies demands knowledge of *ex ante* and *ex post* biodiversity patterns through their linkage with ecological processes. As a common approach, general patterns in species richness are sought to understand the underlying processes (1–3). One outstanding example is the study of elevational gradients of species richness, the subject of much attention because strong elevational gradients can be observed in any mountainous landscape (4, 5). Among possible drivers, temperature directly controls biological productivity of the community, which, in turn, has been linked to diversity (6). A simplistic association of elevational gradients with temperature gradients in mountainous ecosystems suggests a decline of species richness with increasing elevation (1, 2, 7, 8), echoing the latitudinal decline from the equator to the poles (9). However, such an expectation is clearly inconsistent with empirical observations that often show a hump-shaped rather than a monotonically decreasing pattern (4, 8, 10–12).

A possible explanation is that both productivity versus elevation and species richness versus productivity may be described by nonmonotonic relations (10, 13, 14). At low elevations, in particular, human disturbance may play a major role in reducing biodiversity (15). Whereas several factors [such as temperature, habitat capacity, precipitation, anthropogenic pressure and geometric constraints (1, 5, 15)] change (somewhat) predictably with

elevation, other relevant factors (such as moisture, clear-sky turbidity and cloudiness, sunshine exposure and aspect, wind strength, season length, and exposed lithology) are not elevation-specific (16). Thus, empirical results may hardly sort out general rules unambiguously. Given the multitude of possible confounding factors, theoretical analyses are key to understand elevational gradients of diversity and how biota respond to geophysical drivers and controls (5, 17, 18) [e.g., the foreseen upward shift in plant species optimum elevation (19)].

Here, we identify and analyze three distinctive geomorphic features characteristic of mountainous landscapes that can systematically affect the distribution of species and result in hump-shaped patterns of biodiversity along elevational gradients: (*i*) finiteness of the landscape elevational range; (*ii*) frequency distribution of areal extent at different elevation; and (*iii*) differential elevational connectivity.

Geometrically constrained landscapes are subject to the so-called middomain effect, according to which, if the species' ranges are randomly distributed over a bounded geographic domain free of environmental gradients, ranges would increasingly overlap over the center of the domain (20, 21). Applying the same principle to a finite landscape elevational range would support hump-shaped patterns of local species richness along elevational gradients (e.g., refs. 22–24).

The frequency distribution of elevation in real-life landscapes is distinctly hump-shaped, with the majority of land situated at

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midelevations (Fig. 1 and ref. 25). This pattern is ubiquitous in landscapes shaped by fluvial erosion when a sufficiently large region rather than a single slope or mountain is considered, and the pattern is altered only if large areas outside runoff-producing zones (e.g., large plains) are included in the domain (*Supporting Information*). This pattern is often overlooked (e.g., refs. 1 and 4) because the mountain-cone analogy suggests a monotonically decreasing distribution of elevation. However, mountains are not cones (26) but complex fractal structures. The area of available habitat within a given elevational band may have a direct effect on the diversity of the regional community it hosts [γ-diversity (8, 13, 22, 27, 28)], as predicted by the species–area relationship (29). The area of available habitat may also have an indirect effect on the local species richness [diversity of equal-area plots (i.e., α-diversity)] because local communities can be assembled from a more diverse regional pool of species that are fit to live at similar elevation (28).

Finally, a feature potentially capable of shaping elevational diversity patterns is the inherent elevational connectivity of fluvial landscapes. When mapping the fitness, assumed to be elevation-dependent, of three hypothetical species with the same niche width but different niche position [the elevation at which fitness is maximum (30)] over a real mountainous landscape, we find that suitable habitat patches for different species feature very different connectivity (Fig. 2). Valleys (low-elevation sites) and mountain tops (high-elevation sites) form fragmented patches nearly isolated from each other, whereas midelevation sites are both more abundant and more interconnected. Habitat size and connectivity are key determinants of extinction and immigration rates, and thus of diversity, as first predicted by the classic theory of island biogeography (31) and later confirmed by many experimental and theoretical studies (e.g., refs. 32–42). It is thus expected that communities at low (high) elevation, being more isolated, exhibit lower species richness than those at midelevation. This effect has already been discussed for mountain tops (4, 31), and yet isolation of valleys has been so far overlooked, and a comprehensive framework to quantify this effect is missing.

Another limitation of previous studies (e.g., refs. 4, 10, 11, and 13) is that the environmental matrix and the elevational gradients were considered disconnected, and movement and dispersal of organisms across space ignored. Indeed, deriving species distribution patterns directly from elevational gradients of potential drivers implicitly requires the assumption of a 1D landscape (Fig. 1*B*), where all sites at the same elevation share the same characteristics. Such a landscape model is in stark contrast to the complexity of a typical real-life mountainous region (Fig. 1). The hypothesis that the very structure of landscapes can lead to nontrivial diversity patterns, even in the absence of species' preferential elevation or gradients of productivity and habitat capacity, is tested here. To that end, we

simulate ecological dynamics in 3D landscapes using a zero-sum metacommunity model (43, 44) (*Materials and Methods*). The model has been formalized by invoking the minimum set of assumptions principle. Specifically, the following set of rules has been implemented: (*i*) individuals of each species have a fitness (i.e., a competitive ability in this context) that depends on elevation, with all other vital rates being the same; (*ii*) different species have different niche positions but the same niche width (Fig. 2*B*); (*iii*) niche positions are uniformly distributed along the elevational range of the domain, so that there is no preferential elevation at the metacommunity scale; (*iv*) dispersal is isotropic (toward the four nearest-neighbor communities in a regular 2D lattice); and (*v*) the size of local communities is constant over the entire domain (i.e., constant habitat capacity). The above assumptions could be straightforwardly relaxed to mimic more realistic metacommunities. However, this set of assumptions is specifically designed to provide a null model to single out the effect of geomorphic controls of landscape structure on elevational diversity, while deliberately excluding other possible confounding factors.

In addition to real-life landscapes, we run the zero-sum model over synthetic elevation fields derived from optimal channel networks (OCNs) (*Supporting Information*), which are topological structures that minimize a functional describing the total energy dissipated along drainage directions by landscape-forming discharges that hierarchically accumulate toward the outlet of the basin. OCNs are known to systematically reproduce all mutually connected scaling exponents of topological and metric landscape features (25, 45) and are exact steady-state solutions to the landscape evolution equation in the small gradient approximation (46). The use of OCNs has a twofold advantage. First, the use of synthetic elevation fields allows generating consistent replicas of fluvial landscapes in the same domain as the minimization process produces dynamically accessible, yet different, stable states endowed with the same statistical features. Second, OCNs allow producing periodic elevation fields and simulating ecological dynamics over a pseudoinfinite domain, thus avoiding edge effects.

Results

Fig. 3 shows elevational gradients of local species richness (α-diversity) resulting from the simulation of the metacommunity model in real mountainous landscapes at two different scales of analysis. Patterns emerging from a landscape derived from an OCN are reported in Fig. 4. Remarkably, species interacting in an elevation field that embeds the complexity of a real fluvial landscape naturally produce a hump-shaped elevational gradient of species richness (Figs. 3 and 4*D*) even in the absence of gradients of productivity or habitat capacity.

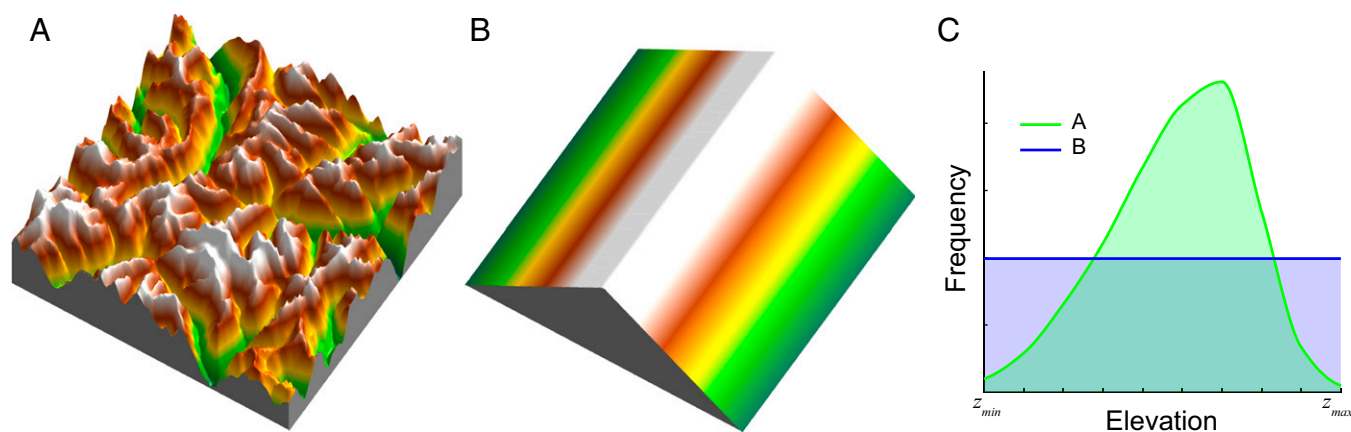Figs. 3 and 4*D* also reveal that sites at the same elevation can host quite a different number of species depending on their

Fig. 1. Comparison between a real-life elevation field (a fluvial landscape in the Swiss Alps, 50 × 50 km²) (*A*) and an oversimplified, 1D elevation field (*B*). (*C*) Frequency distributions of elevation of the two landscapes. Fig. S1 reports other examples.
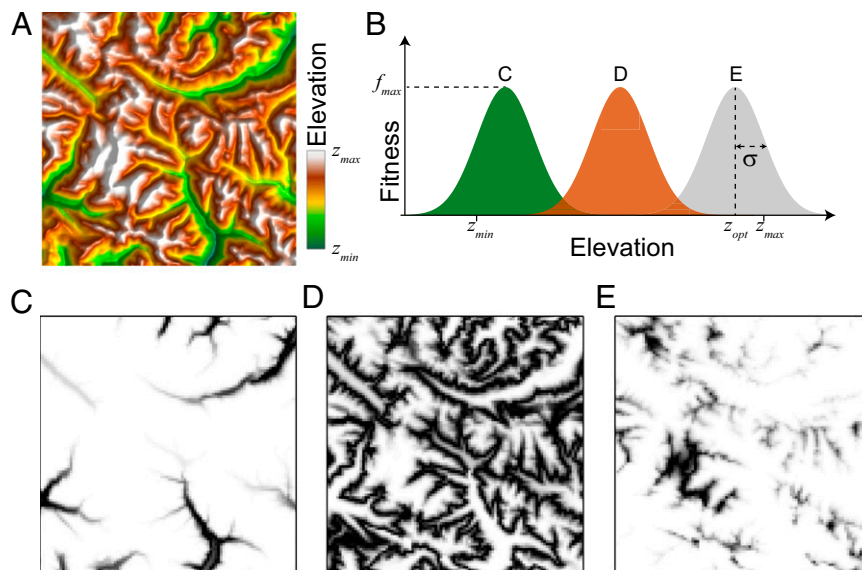
Fig. 2. Habitat maps as a function of elevation. (*A*) A real fluvial landscape (same of Fig. 1*A*). (*B*) Fitness of three different species as a function of elevation. (*C*–*E*) Fitness maps of the three species shown in *B*. Darker pixels indicate higher fitness.

connectivity. Such an effect is further highlighted by analyzing local subplots (Fig. 4*E*). The two quadrants cover very different elevation ranges, and yet they both exhibit similar well-defined midpeak gradients of elevational diversity. Sites at the upper end of the elevational range of the first plot host few species, whereas α-diversity at similar elevation is much higher in the second plot. This difference can be explained by the different connectivity. Sites at the same elevation represent a local mountain top in the first plot, thus poorly connected with sites characterized by similar elevation, whereas in the second plot, the sites lay in the middle of the elevation range, with multiple connections with similar elevations. Therefore, in such systems elevation alone is a poor predictor of species richness, which is instead controlled by the geomorphic organization of the surrounding habitat.

We have sought a measure to quantify the combined effect of the three geomorphic controls on elevational gradients of species richness without resorting to any particular modeling assumptions. To that end, we apply concepts of complex network theory applied to ecology (35, 38–40, 47). The proposed measure, which we term landscape elevational connectivity (LEC) (*Materials and*

Methods and Fig. 5), quantifies the closeness of a site to all others with similar elevation. Such closeness is computed over a graph whose edges represent connections among sites and whose weights are proportional to the cost of spreading through patches at different elevation. Although LEC simply depends on the elevation field and on the niche width, LEC predicts well (Spearman's correlation, $r = 0.79$) the α-diversity simulated by the full metacommunity model (Fig. 4). In particular, LEC is able to capture the variability of diversity hosted at the same elevation, as opposed to a simpler predictor like the elevation frequency ($r = 0.60$; Fig. 4*F*). Simulations over different landscapes and with different parameter sets confirm the main results presented herein (*Supporting Information*).

Discussion

Fluvial networks in runoff-generating areas are naturally fractal (25, 26), owing to the similarity of the networks' parts with the whole. The networks' self-similarity leads to self-affine invariance of the elevation fields owing to the relation between slope and cumulative drainage area, a well-known proxy of landscape-forming hydrological

Fig. 3. Elevational gradients of α-diversity resulting from the application of the zero-sum metacommunity model over two real landscapes derived from the digital elevation model of the Swiss alpine region. The two landscapes cover different areal extents: 625 km^2 (*A*) and 2,500 km^2 (*B*). Blue symbols represent average (circles) and SD (error bars) of α-diversity within elevational bands. Averages over 500 realizations of the metacommunity model are shown. Parameters used are $N = 10^4$, $n = 100$, $\sigma/(z_{max} - z_{min}) = 0.1$, and $\nu = 1$. With this parameter set, the average number of deaths between the emergence of new species into the system is about 3,500.

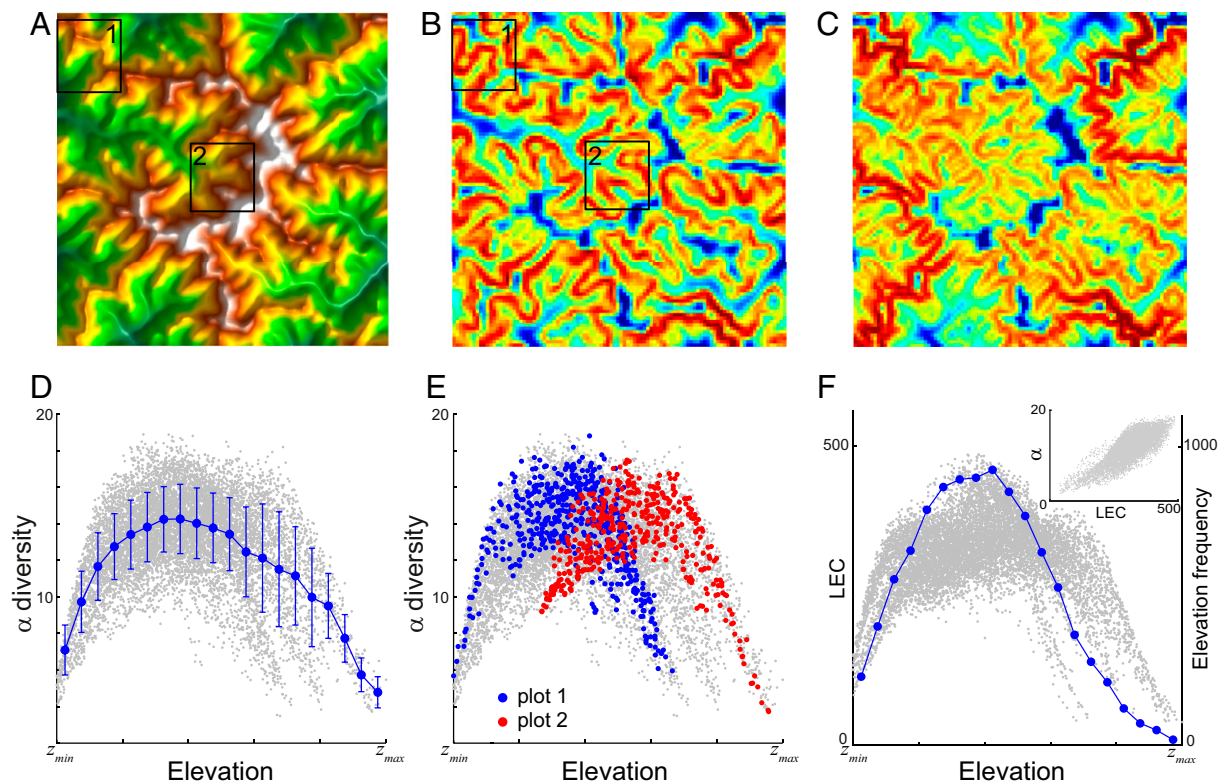**Fig. 4.** Local species richness (α-diversity) patterns resulting from the metacommunity model applied to an elevation field derived from an OCN. (*A–C*) Maps of the elevation field (*A*), α-diversity (*B*), and LEC (*Materials and Methods*) (*C*). Color code in *B* and *C* goes from blue (low values) to red (high values). (*D*) α-Diversity as a function of site elevation (gray dots). Symbols are as in Fig. 3. (*E*) Same as *D*, where points belonging to the two subplots indicated in *A* and *B* are highlighted. (*F*) LEC (gray dots) and elevation frequency (blue dotted line) as a function of site elevation. (*F*, *Inset*) Relationship between LEC and α-diversity. The replicable domain (an OCN) is obtained by imposing four outlets to otherwise periodic boundaries (Fig. S2). Averages over 500 realizations of the metacommunity model are shown. Parameters are as in Fig. 3. Results for different landscapes and for different parameter sets are reported in Figs. S3–S6.

events (*Supporting Information*). Fluvial landforms thus show deep similarities across many orders of magnitude despite great diversity of their drivers and controls (e.g., relief, exposed lithology, geology, vegetation, or climate) (25). The universality of the main attributes of the fluvial landscape naturally lends itself to the quest for general patterns of the ecological dynamics that such landscapes host (41, 42, 48–54).

The α-diversity map shown in Fig. 4*B* reveals a clear spatial pattern with valleys and mountain tops characterized by lower species richness. All three geomorphic factors described before simultaneously concur to the formation of such pattern. The first factor is related to the finiteness of the landscape elevational range: sites at midelevation can potentially be colonized by species that live at (and are fit for) higher and lower elevations, whereas sites at the lowest (highest) extreme are only subject to the colonizing pressure from higher (lower) elevations. In addition to this boundary effect, the geomorphic structure of fluvial landscapes results in a midelevation peak in both area and connectivity across the landscape, both of which can promote diversity. We have specifically designed a set of simulations to disentangle the role of these three factors (*Supporting Information*). Results show that without any of these effects, the model predicts no gradients of diversity. Each geomorphic factor produces, independently or in combination with others, a hump-shaped pattern of species richness. Moreover, the differential elevational connectivity characteristic of fluvial landscapes results in a marked variability of diversity for the same elevation.

The results shown in Figs. 3 and 4 reveal that similar mid-peak elevational gradients of diversity can be observed at different scales of observation even if the domains span different elevational ranges. This pattern is a direct consequence of the self-affine fractal structure of fluvial landscapes that reproduces statistically similar

elevational fields (properly rescaled) at every scale of observation. Results also show that, when the scale of observation is enlarged, different hump-shaped patterns are blended together, possibly producing a confounding effect (Fig. 4*E*), especially if the analysis is limited to the average diversity as a function of elevation. This feature might help in understanding why elevational diversity is often found to be dependent on the scale of observation (10, 11, 15).

As a proof of concept, we have presented results based on nearest-neighbor dispersal to highlight the role of elevational connectivity. Indeed the effect of elevational isolation is expected to be reduced as dispersal limitation decreases because species can overcome elevational constraints with long-distance dispersal (e.g., dispersing from one mountain top to another without going through unfavorable lower elevation habitats). Moreover, we have assumed that the landscape can be uniformly colonized, whereas real-life habitats are often composed by patches with different spatial connectivity and size (33). Spatial and elevational connectivities can interact in a complex ways to shape diversity patterns. The modeling framework proposed can be easily generalized to accommodate both fragmented habitats and generic dispersal kernels, and the framework has the potential to effectively describe how spatial and elevational connectivities shape diversity in complex 3D landscapes.

Our exploration of metacommunity patterns suggests that the specific spatial arrangement of sites at different elevation in fluvial landscapes suffices in inducing mid-peak elevational gradients of species richness without invoking specific assumptions, except that each species is fit for a specific elevation. In this framework, an elevation-dependent fitness applied to a real-life landscape translates into a fragmented habitat map (Fig. 2). Such conceptualization lends itself to the application of classic concepts of metacommunity dynamics (33, 55), according to which habitat size and connectivity are
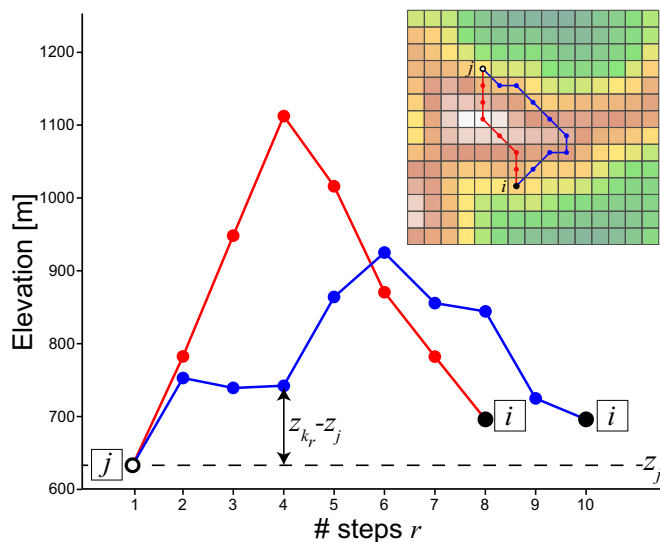
Fig. 5. Computation of LEC. Examples of two possible paths connecting site j to i (*Inset*) with the corresponding elevational profile. Although the blue path is longer, the associated cost ($\sum_{r=2}^{L}(z_{k_r} - z_j)^2$) is smaller than that of the red path because the blue path travels through sites with elevations more similar to that of the starting point (z_j).

key drivers of biodiversity. We thus expect different metacommunity models to produce similar results. For this reason, we have developed a measure, LEC, that subsumes the geomorphic controls on elevational diversity without resorting to any particular biodiversity model.

Intermediate elevations hold, on average, higher LEC (Fig. S6), and this statistical property might explain the hump-shaped elevational gradients of mean species richness widely observed in nature. We do not dismiss as negligible other potential drivers of diversity, including those that often covary with elevation (e.g., habitat capacity, productivity, human disturbance). However, we argue that these drivers may act on top of the unavoidable effects provided by the geomorphic controls. A general consensus has been achieved on the fact that the analysis of elevational diversity should not seek one single overriding force but rather understand how different factors covariate to synergistically shape the observed patterns (4, 5). Our results strongly suggest that fluvial geomorphology likely has an important, yet thus far overlooked, role in driving emergent diversity elevational patterns.

Materials and Methods

Zero-Sum Metacommunity Model. The model assumes a system of N local communities, organized in an equally spaced 2D lattice in which each cell is characterized by its elevation. Each local community assembles n individuals. The system is assumed to be at saturation [zero-sum assumption (43)]. Thus, at any time, the system is populated by $N \cdot n$ individuals belonging to S different species. Each species is characterized by a specific elevational niche that expresses, in this context, how the species' competitive ability varies with elevation. This relationship is modeled by a Gaussian suitability function (30):

$$f_i(z) = f_{max_i} e^{-\frac{(z-z_{opt_i})^2}{2\sigma_i^2}},$$

where $f_i(z)$ reflects the competitive ability of the individuals of species i at elevation z, z_{opt_i} is the niche position (30) of species i [i.e., the elevation where $f_i(z)$ equals its maximum f_{max_i} (Fig. 2B)], and σ_i controls the dispersion of the Gaussian function. A neutral approach is adopted (43), save for the effects of elevation on fitness, in that the analysis is limited to the case where all species have the same parameters $\sigma_i = \sigma$ and $f_{max_i} = f_{max}$, as well as the same fertility, death, and dispersal rates. Ecological interactions among individuals are simulated as follows. At each time step, a randomly selected

individual dies and is replaced by an offspring of one of the individuals living in either the same community or one of the four nearest-neighbor communities (von Neumann neighborhood) or by the offspring of an additional individual, belonging to a species not currently present in the system. This additional competitor is added with probability ν at every time step. z_{opt_i} of the new competitor is drawn from a uniform distribution spanning twice the relief of the system to avoid edge effects (Fig. S7A). The introduction of new species is aimed at modeling both speciation and immigration from external communities (43, 56). The offspring replacing the dead individual is randomly selected with a probability proportional to the scores $f_i(z)$ of all of the candidate colonizing offsprings evaluated at the elevation z of the local community of the dead individual. The system is initially populated by one single species and is simulated until a statistically steady state is reached ($\sim 10^4$ generations, where a generation is $N \cdot n$ time steps). Periodic boundaries conditions are prescribed. Model results do not depend on the actual elevation range ($[z_{min}, z_{max}]$) but only on the ratio $\sigma/(z_{max} - z_{min})$. Moreover, f_{max} does not affect the simulated dynamics, and it has thus been set to 1.

LEC. The LEC LEC_i of site i can be expressed as

$$LEC_i = \sum_{j=1}^{N} C_{ji},$$ [1]

with C_{ji} being a measure of the closeness of site j to i in terms of elevational connectivity. Such a measure should quantify how easily a species living in patch j can spread and colonize patch i. Because the fitness is assumed to be elevation-dependent, C_{ji} depends on how often a species, assumed to be adapted to the elevation of j, z_j, needs to travel outside its optimal fitness range in the path from j to i. C_{ji} thus depends on the elevation field but also on the width of the species niche, here described by the parameter σ. Indeed, for high σ, species are free to spread throughout the system regardless of elevational constraints. Conversely, for low σ, species are constrained to spread following paths with similar elevation without the ability to cross elevational barriers. LEC subsumes the combined effect of the three geomorphic factors: bounded elevational range, frequency distribution of areal extent at different elevation, and differential elevational connectivity.

The closeness C_{ji} can be expressed as

$$C_{ji} = \max_{p \in \{j \to i\}} C_{ji,p},$$ [2]

where $C_{ji,p}$ is a measure of the closeness of community j to i along path p. The overall closeness C_{ji} is defined as the maximum value of $C_{ji,p}$ along all of the possible paths p form j to i (see the graphical representation in Fig. 5). $C_{ji,p}$ is assumed to be proportional to the product of the probabilities of making each step of the path p. Let $p = [k_1, k_2, \ldots, k_L]$, $k_1 = j$, $k_L = i$ be the sites comprised in a path p form j to i. $C_{ji,p}$ can be expressed as

$$C_{ji,p} = \prod_{r=2}^{L} e^{-\frac{(z_{k_r} - z_j)^2}{2\sigma^2}}.$$ [3]

In Eq. **3**, the exponential form is proportional to the fitness that species adapted to site j have in site k_r.

From an operational viewpoint, C_{ji} is computed by focusing on the quantity

$$-\ln C_{ji} = \frac{1}{2\sigma^2} \min_{p \in \{j \to i\}} \sum_{r=2}^{L} (z_{k_r} - z_j)^2,$$ [4]

where the log-transformation maintains extremal properties. For each site j, a graph is built with edges representing all possible nearest-neighbor connections among sites and weights equal to the square of the difference between the site elevation and z_j. The Dijkstra algorithm (57) is then used to find the shortest path from j to all other sites.

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