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Linking ecological niche, community ecology and biogeography: insights from a mechanistic niche model

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ABSTRACT

Aim We present a mechanistic niche model that integrates the demography of competing plant species in a metabolic, stochastic framework. In order to explore the model's ability to generate multiple species and community patterns, we assessed trait composition, richness gradients and spatial distributions of species ranges and abundances of simulated communities.

Location Hypothetical, sloped plane.

Methods Stage-structured populations of species differing in traits and habitat requirements competed for space in a grid-based model. Demographic processes (recruitment, reproduction, mortality, dispersal) and resource competition were explicitly simulated. Demographic rates and carrying capacity followed metabolic constraints. We simulated 50 species pools until reaching stable communities. Species pools were initialized with 400 species that had random traits and habitat requirements. The habitat requirements generated potential distributions of richness, range and abundance, whereas the simulations yielded realized distributions.

Results The communities assembled in the simulations consisted of species spread non-randomly within trait space. Potential species richness peaked at mid-elevations, whereas realized richness was slightly shifted towards higher elevations. For 11% of all species, the highest local abundances were found not in the most suitable habitat, but in suboptimal conditions. 53% of all species could not fill the climatically determined potential range. The ability to fill the potential range was significantly influenced by species traits (e.g. body mass and Allee effects) and species richness.

Main conclusions Spatial and trait properties of surviving species and of equilibrium communities diverged from the potential distributions. Realized richness gradients were consistent both with patterns observed in nature and those expected from null models based on geometrical constraints. However, the divergences between potential and realized patterns of richness, ranges and abundances indicate the importance of demography and biotic interaction for generating patterns at species and community levels. Consequently, bias in correlative habitat models and single-species mechanistic models may arise if competition and demography are neglected. Additionally, competitive exclusion provides a mechanistic explanation for the low transferability of single-species niche models. These results confirm the usefulness of mechanistic niche models for guiding further research integrating ecological niche, community ecology and biogeography.

Keywords

Demographic model, interspecific competition, metabolic theory, niche model, process-based stochastic models, range dynamics, species distribution.

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INTRODUCTION

Current niche modelling is dominated by correlative approaches which relate bioclimatic variables to species occurrences (e.g. Guisan & Thuiller, 2005; Wiens & Graham, 2005; Thuiller *et al.*, 2008; Pereira *et al.*, 2010). However, these approaches only describe static patterns (species–habitat equilibrium assumption), do not include mechanisms underpinning species distributions, such as biotic interactions, demography, metabolic constraints or adaptation (Soberón & Peterson, 2005; Thuiller *et al.*, 2008), and often lack a theoretical basis (Cassini, 2011). For example, correlative approaches do not account for transient dynamics, presences generated by source–sink dynamics and extinction debt, or absences due to dispersal limitation (Schurr *et al.*, 2012) or competitive exclusion (Kissling *et al.*, 2012). Hence, although correlative studies are informative for identifying which variables are possibly important for potential species distribution, they are limited in their ability to provide a causal understanding of the processes influencing species distributions (Dormann *et al.*, 2012).

The limitations of correlative approaches have triggered efforts towards mechanistic niche modelling. Until now, mechanistic models have applied methods from different fields, such as animal physiology (e.g. Kearney & Porter, 2004, 2009; Buckley, 2008; Kearney *et al.*, 2008), plant demography (e.g. Keith *et al.*, 2008; Cabral & Schurr, 2010; Pagel & Schurr, 2012; Schurr *et al.*, 2012) and plant phenology (e.g. Morin *et al.*, 2008). Physiological niche models integrate processes such as energy uptake and storage, metabolic rates and behaviour (Buckley, 2008; Kearney & Porter, 2009; Higgins *et al.*, 2012). Phenological niche models simulate life stages and development (Morin *et al.*, 2008), while demographic models simulate population dynamics and dispersal (Cabral & Schurr, 2010; Pagel & Schurr, 2012). Each of these approaches addresses different processes known to affect species distributions (Soberón & Peterson, 2005). Although all these processes interact with each other and may also be influenced by both abiotic factors and biotic interactions, there is no niche model that integrates all these processes and interactions (Kissling *et al.*, 2012). Therefore, models connecting all these processes have great potential to improve our understanding of species distributions.

The integration of multiple processes in a single predictive model is hampered by the parameterization, which may be based either on expert knowledge or on data (Dormann *et al.*, 2012; Hartig *et al.*, 2012; Marion *et al.*, 2012). Parameterization based on data (i.e. inverse modelling) seems currently feasible only for single-species models representing only one aspect of relevant processes (e.g. demography; Pagel & Schurr, 2012). Hence, the parameterization of models linking several ecological components would require an enormous amount of abundance data and detailed biological information for each interacting species. As these data are not currently available and parameterization methods are still in development, mechanistic models are useful theoretical

tools for understanding patterns. Mechanistic models can simulate different processes and a wide array of virtual species by varying parameter values representing ecological traits (e.g. Cabral *et al.*, 2011). These models can also simulate species' behaviour under different model configurations or scenarios (e.g. Keith *et al.*, 2008), and are thus useful tools for exploring biogeographical theories (Gotelli *et al.*, 2009; Colwell & Rangel, 2010; Tello & Stevens, 2011). A potential drawback of adding more processes to a model is that an increased number of parameters and complexity makes interpretation more difficult (Dormann *et al.*, 2012). Nevertheless, considering the urgent demand for a mechanistic understanding of range dynamics, theoretical efforts must somehow proceed (Schurr *et al.*, 2012).

This study aims to improve our understanding of the ecological niche by presenting a novel approach to niche modelling that integrates multiple processes affecting ecological niches (Soberón & Peterson, 2005), namely demographic processes, biotic interactions and metabolic constraints. However, the greater complexity compared to previous niche models means that it is necessary for the model to be able to generate multiple patterns in order to justify its complexity (see Grimm *et al.*, 2005). Therefore, we explore the ability of our proposed model to generate multiple patterns simultaneously at both species and community levels by simulating the demography of virtual species co-occurring on a sloped plane, and ask three questions: (1) Does the trait composition of the equilibrium communities diverge from the random trait composition set at model initialization? (2) Does the species richness of the equilibrium community vary along environmental gradients? (3) Do the species' realized abundance distribution and range diverge from their potential distributions?

MATERIALS AND METHODS

We implemented a lattice simulation model in C++ based on demographic models for range dynamics (Cabral & Schurr, 2010). This base model was extended to include interspecific competition and a metabolic framework. The following model description follows the 'overview, design concepts, detail' (ODD) protocol for presenting agent-based models (Grimm *et al.*, 2010).

Model description

Purpose

To simulate range and abundance distributions of plant species with a stochastic model that considers demographic processes, interspecific competition for space and metabolic constraints that describe life history trade-offs.

State variables and scales

The model was grid-based, with a grid cell area of 1 km². This was small enough to separate short-distance dispersal

from long-distance dispersal (within and between cells, respectively) and large enough to accommodate discrete populations of several species. The grid represented a sloped plane, with increasing elevation along one axis, mimicking a mountain slope. Elevational levels had equal areas. Each elevational level had a unique mean annual temperature. A difference in one elevational level was considered a difference in temperature of 1 K. Cells could hold as many species as there was space for, but only one population per species. Populations were stage-structured, comprising seeds, juveniles and adults. The main state variables were the space available as well as the seed, juvenile and adult abundances of all species in each cell (see Appendix S1 in Supporting Information). Species had traits and habitat requirements, collectively termed ‘species features’ (Table 1). We assumed time steps of 1 year. The grid dimension and simulation time depended on the experimental design (see ‘Study design’ and Appendix S1), but the model was able to run over long periods of time (thousand years) and large spatial extents (hundreds of km²). The landscape had absorbing boundaries (i.e. individuals dispersing beyond the grid boundaries were lost) and, thus, geometry and edges could have an effect on populations.

Process overview and scheduling

After initialization, processes took place once per time step in the following sequence: population update 1 (sexual maturation, juvenile survival, germination and seed survival), reproduction, dispersal and population update 2 (adult survival, seed bank update).

Input

Model inputs were: (1) a gridded map with a sloped plane, whose elevational levels were converted into temperatures for determining metabolic constraints and the distribution of suitable habitats, (2) mean annual air temperature at the lowest elevational level, T_1 , (3) the species number of the initial source pool, S_{sp} , and (4) intervals (min, max) for each species feature, within which we could draw values from a random uniform distribution (Table 1). The habitat requirements of species were the maximum cell suitability (O), the optimum temperature (T_o) and the temperature envelope or amplitude (T_e). The temperature amplitude accounted for temperature specialization and determined the species potential elevational range or thermal tolerance. Habitat requirements determined the distribution and quality of suitable habitat (see ‘Initialization’). The traits were life form, mean dispersal distance (α), dispersal kernel thinness (p), strength of Allee effects (C), phenology (order placement for each species: 1st – S_{sp} -th) and body masses (B_a for adults, B_y for young or juveniles and B_s for seeds). Life form was the first trait to be drawn, to determine the trait interval from which B_a should be drawn (Table 1). The life forms (trees, shrubs and herbs) of the initial source pool had equal probabilities, according to common percentages found in tropical forests (Cain, 1950). For herbs, we further randomly distinguished between annuals and perennials with equal probabilities. B_y and B_s were functions of B_a (Table 1). The phenology described the order in which species were simulated during each process and model interaction.

Table 1 Species features. The value column gives the interval from which the feature value was randomly drawn (uniform distribution). Additional information is given as observations.

Feature (or parameter)	Value	Observation
Optimum temperature T_o^*	283.15–298.15 K	10–25 °C
Temperature amplitude T_e^*	0–9 K	
Maximum habitat suitability O^*	1%–100%	
Mean dispersal distance α^{**}	0.001–0.05 km	
Dispersal kernel thinness p^{**}	0.1–1 (adimensional)	
Allee effects strength C^{**}	1–0.25 (adimensional) If $C > 0$, re-draw: 0–1000 individuals	When C tends to –1: no Allee effects. If $C > 0$: very strong Allee effects.
Phenology ^{**}	1st– S_{sp} -th	S_{sp} : initial species number
Life form ^{**}	Tree, shrub or herb; Annual or perennial for herbs.	
Adult body mass B_a^{**}	10^1 – 10^3 g for herbs; 10^3 – 10^5 g for shrubs; 10^5 – 10^7 g for trees	
Juvenile body mass B_y^{**}	$B_a/5$	Arbitrary
Seed body mass B_s^{**}	If $B_a < 5.5 \times 10^4$ g, $2.14 \times 10^{-3} B_a^{0.5}$; if $B_a \geq 5.5 \times 10^4$ g, 0.01–30 g.	We estimated the correlation for plants up to 5.5×10^4 g from Hendriks & Mulder (2008). For $B_a \geq 5.5 \times 10^4$ g, we considered seed mass variation of trees (Muller-Landau <i>et al.</i> , 2008).

*Habitat requirement;

**species trait.

Body mass and local temperature determined the area that an adult, $A_{a(i,j)}$, or a juvenile, $A_{y(i,j)}$, of species j in cell i utilizes to exploit resources, being equal to $A_c / (b_A B_j^{-3/4} e^{E/k_B T(i)})$, where A_c is the cell area (10^6 m^2), E the kinetic energy (0.63 eV), k_B Boltzmann's constant, $T(i)$ the temperature in cell i , b_A the proportionality constant for the area exploited by an individual and B_j the body mass of species j . For A_a , we used the adult body mass B_a , whereas for A_y we used B_y . A_a and A_y are fractional areas of single individuals (the fraction occupied only by them). We arbitrarily set $b_A = 0.3 \text{ g}^{3/4}$ individuals to yield, at 303.15 K (30 °C), exploiting areas of 20, 0.6 and 0.02 m^2 per individual for the largest adult trees, shrubs and herbs, respectively. This formula accounted for the increase in metabolism with increasing temperatures (Savage *et al.*, 2004). Consequently, the resources required by an individual increased with temperature, which decreased carrying capacity (Savage *et al.*, 2004).

Demographic (germination, sexual maturation, reproductive and density-independent mortality) rates of species j in cell i followed the metabolic theory (Brown *et al.*, 2004; Savage *et al.*, 2004; Marbà *et al.*, 2007; McCoy & Gillooly, 2008):

$$\text{Rate}_{(i,j)} = b_0 B_j^{-1/4} e^{-E/k_B T(i)} \quad (1)$$

where b_0 is the proportionality constant of the respective rate. Proportionality constants vary between taxa and between biogeographical regions (Brown *et al.*, 2004). The selection of values for the constants is explained in the following sections.

Initialization

The simulation was initialized by reading in the grid map and the species pool. Each species received a lineage ID (from 1 to S_{sp}) and a habitat suitability matrix, H . Habitat suitability of species j in cell i , $H_{(i,j)}$, was truncated between 0 and 1 ($0 \leq H_{(i,j)} \leq 1$) following $H_{(i,j)} = O_{(j)} - ((O_{(j)}/T_{e(j)})(|T(i) - T_{o(j)}|))$.

Species germinated where $H_{(i,j)} > 0$, which occurred in cells with $T(i)$ within the species' thermal tolerance determined by the optimum temperature (T_o) and the temperature amplitude (T_e), $T_o(j) \pm T_{e(j)}$. A dispersal kernel D was initialized for each species by generating a two-dimensional discrete Clark's 2Dt kernel (Clark *et al.*, 1999), based on the parameters α and p . Long-distance dispersal ability increased with fatter kernel tails (decreasing p). Clark's 2Dt kernel describes dispersal near and far from a source and is a particularly suitable kernel for modelling short- and long-distance dispersal simultaneously (Nathan & Muller-Landau, 2000). This kernel also allowed the systematic inclusion of dispersal parameters in our analyses. We did not associate dispersal ability with seed mass because long-distance dispersal often happens by non-standard means of dispersal (Higgins *et al.*, 2003; Nathan, 2006). For each species, the abundance matrixes for adults, N_a , juveniles, N_y , and seeds, N_s , were initialized. N_a and N_y started empty, whereas for each cell i , $N_{s(i)} \sim \text{Uniform}(110,000)$. The matrix with the area occupied by all individuals of all species, A_t , was also initialized.

Population update 1

Firstly, the area occupied by all individuals of all species in cell i was calculated as $A_{t(i)} = \sum_j (N_{a(i,j)} A_{a(i,j)} + N_{y(i,j)} A_{y(i,j)})$. Population updates followed the phenological species order and were stochastic processes. Transition rates were converted to probabilities following the function: $F(\text{transition rate}) = 1 - (1 - \text{transition rate})^{q/t}$, where t is the time interval for the transition rate (1 year) and q the cycle length of our Markov model (1 year). Abundance matrixes were then updated sequentially by (A) turning juveniles to adults, (B) applying density-independent mortality to the remaining juveniles, (C) germinating seeds, and (D) applying seed mortality.

(A) $N_{a(i,j)} = N_{a(i,j)} + \text{Binomial}(N_{y(i,j)}, F(g_{r(i,j)}))$, where $g_{r(i,j)}$ is the transition rate from juvenile to adult of species j in cell i , given by equation 1, with $B_{y(j)}$ as body mass and b_{gr} being the proportionality constant specific for g_r . We arbitrarily set $b_{gr} = 3.53 \times 10^9 \text{ g}^{1/4} \text{ year}^{-1}$ to yield, at 303.15 K, $g_r = 1$ for the lightest herb juvenile. $A_{t(i)}$ was re-calculated. If $A_{t(i)} > A_c$, the exceeding adults were excluded from $N_{a(i,j)}$ until $A_{t(i)} = A_c$.

(B) $N_{y(i,j)} = \text{Binomial}(N_{y(i,j)} - \text{Binomial}(N_{y(i,j)}, F(g_{e(i,j)})), 1 - F(m_{y(i,j)}))$, where $m_{y(i,j)}$ is the juvenile mortality rate of species j in cell i , given by equation 1 with $B_{y(j)}$ as body mass and $b_{mort,y}$ being the specific proportionality constant for juvenile mortality rate. We set $b_{mort,y} = 3.53 \times 10^9 \text{ g}^{1/4} \text{ year}^{-1}$ to yield, at 303.15 K, $m_y = 1$ for the lightest herb juvenile. $A_{t(i)}$ was re-calculated.

(C) $N_{y(i,j)} = N_{y(i,j)} + \text{Binomial}(N_{s(i,j)}, F(g_{e(i,j)}))$, where $g_{e(i,j)}$ is the germination rate of species j in cell i , given by equation 1 with $B_{y(j)}$ as body mass and b_{ge} being the specific proportionality constant for g_e . We arbitrarily set $b_{ge} = 8.5 \times 10^9 \text{ g}^{1/4} \text{ year}^{-1}$ to yield, at 303.15 K, $g_e = 1$ for the lightest herb seed (lighter seeds germinate faster, Norden *et al.*, 2009). $A_{t(i)}$ was re-calculated. If $A_{t(i)} > A_c$, the exceeding juveniles were excluded from $N_{y(i,j)}$ until $A_{t(i)} = A_c$.

(D) $N_{s(i,j)} = \text{Binomial}(N_{s(i,j)} - \text{Binomial}(N_{s(i,j)}, F(g_{e(i,j)})), 1 - F(m_{s(i,j)}))$, where $m_{s(i,j)}$ is the seed mortality rate of species j in cell i , given by equation 1 with $B_{s(j)}$ as body mass and $b_{mort,s}$ being the specific proportionality constant for seed mortality rate. We set $b_{mort,s} = 8.5 \times 10^9 \text{ g}^{1/4} \text{ year}^{-1}$ to yield, at 303.15 K, $m_s = 1$ for the lightest herb seed. The exclusion (i.e. death) of germinating and maturing individuals due to lack of available space mimicked self-thinning mechanisms and generated density-dependent mortality (Antonovics & Levin, 1980). Annual herbs germinated and reached maturity within the same time step.

Reproduction

Following the phenological species order and for each grid cell, the number of seeds produced by species j in cell i ($S_{p(i,j)}$) was calculated followed the Beverton–Holt model (Beverton & Holt, 1957) extended for Allee effects (Courchamp *et al.*, 2008; Cabral

& Schurr, 2010): $S_{p(i,j)} = (N_{a(i,j)}R_{\max(i,j)})/(1 + k(N_{a(i,j)} - c)^2)$, where $R_{\max(i,j)}$ is the maximum reproductive rate of species j in cell i , k is a modified carrying capacity and c a modified Allee threshold (Cabral & Schurr, 2010). $R_{\max(i,j)}$ was given by formula (1) with $B_{a(j)}$ as body mass and $b_{R\max}$ being the proportionality constant specific for R_{\max} . $b_{R\max}$ was $1.5 \times 10^{12} \text{ g}^{1/4} \text{ year}^{-1}$, in agreement with herb data (Hendriks & Mulder, 2008). k was given by $k = 4(R_{\max(i,j)} - m_{a(i,j)})/(m_{a(i,j)}(K_{(i,j)} - C_{t(i,j)}))^2$, and c by $c = C_{t(i,j)} + \sqrt{((R_{\max(i,j)} - m_{a(i,j)})/(m_{a(i,j)}k))}$, where $m_{a(i,j)}$ is the adult mortality rate, $K_{(i,j)}$ is the carrying capacity and $C_{t(i,j)}$ is the Allee threshold of species j in cell i . $m_{a(i,j)}$ was given by equation 1 with $B_{a(j)}$ as body mass and $b_{\text{mort},a}$ being the specific proportionality constant for adult mortality rate. We set $b_{\text{mort},a} = 5.25 \times 10^9 \text{ g}^{1/4} \text{ year}^{-1}$ to yield, at 303.15 K, $m_a = 1$ for the lightest adult herb. $C_{t(i,j)}$ was given by $C_{t(i,j)} = C_{(j)}K_{(i,j)}$ if $C_{(j)} < 0$, or $C_{t(i,j)} = C_{(j)}$ if $C_{(j)} > 0$, where $C_{(j)}$ is the strength of Allee effects on species j . $K_{(i,j)}$ was given by the local available space (corrected for habitat suitability and area occupied by non-conspecifics) divided by the area exploited by an adult of species j : $K_{(i,j)} = ((A_c - (A_{t(i)} - (N_{a(i,j)}A_{a(i,j)} + N_{y(i,j)}A_{y(i,j)}))) / A_{a(i,j)}) H_{(i,j)}$. This shows, jointly with the density-dependent mortality (see ‘Population update 1’), how space was used as an interaction currency (Kissling *et al.*, 2012).

Dispersal

The number of seeds of species j arriving in cell z was $S_{d(z,j)} = D_{(z,i)}S_{p(i,j)}$, where $D_{(z,i)}$ is the per-seed probability of dispersal from cell i to cell z .

Population update 2

Abundance matrices were updated by (A) applying density-independent mortality to adults, $N_{a(i,j)} = \text{Binomial}(N_{a(i,j)},$

$1 - F(m_{a(i,j)}))$, and (B) incrementing seed bank, $N_{s(i,j)} = N_{s(i,j)} + \text{Poisson}(S_{d(i,j)})$.

Output

The output included N_a , N_y , N_s , parameter values and the lineage ID of all species.

Study design

We ran the model for 50 different species pools (replicates), with $T_1 = 298.15 \text{ K}$ (25 °C) and $S_{sp} = 400$ species. We limited the spatial scale to a sloped plane of 15×15 cells (225 km²), with elevational level 1 at the bottom of the grid (e.g. lowlands) and the elevational level 15 at the top. This grid supported species with different range sizes (15–225 km²) and habitat locations. Patterns remained stable after the last extinctions (from species with slow demographic dynamics, e.g. trees), which occurred around the 5000th time step. Therefore, we ran each species pool for 10,000 years, which was enough time for the community to reach an equilibrium (i.e. quasi-stationary) state. We simulated both whole communities and each species individually.

Analyses

We addressed the study questions with several analyses, mostly focusing on the simulation of whole communities (Table 2). For the first question, coexistence of ecologically different species in the equilibrium communities was assessed by comparing the number of species along each species trait.

For the second question, we calculated species richness for each cell by counting the number of species. The potential

Table 2 Study questions and analyses. We first tested variables for normality with a Shapiro–Wilk test. Because most of the variables were not normally distributed, we performed Wilcoxon rank tests for paired samples. For generalized linear models (GLM), the maximum model included all two-way interactions between adult body mass and other factors. To obtain minimal adequate models, we stepwise removed non-significant terms from the maximum model (Crawley, 2007). We applied significance levels of 5% for all analyses.

Question	Analyses
(1) Do the equilibrium trait composition diverge from the initial, random trait composition?	(1) Comparing* number of surviving species over trait space
(2) Does species richness vary along environmental gradients?	(2) Comparing** realized and potential richness gradients
(3) Do the realized range and abundance distributions diverge from their potential distributions?	(3a) GLM with quasibinomial error distribution investigating whether range filling (realized/potential range ratio) was influenced by surviving species richness (max. 1 when species were simulated alone), habitat requirements (O , T_o and T_e), species traits (B_a , C , α , p and being annual or not) and their two-way interactions with B_a (except for being annual or not); (3b) Comparing** realized and potential abundance distributions; (3c) Comparing*** realized and potential elevational levels with highest abundance

*Simultaneous tests for linear models with multiple comparisons of means using Tukey contrasts that are robust under non-normality, heteroscedasticity and variable sample size (Herberich *et al.*, 2010);

**Kolmogorov–Smirnov test;

***Wilcoxon rank tests for paired samples.

richness was calculated by overlapping the suitable habitats (potential ranges) of the species for both initial and equilibrium communities, whereas the realized richness was calculated by overlapping abundance distributions of the species in the equilibrium communities (i.e. realized ranges).

To test the third question, we compared potential and realized ranges and abundance distributions of each species using the following set of analyses. We calculated the ratio between realized and potential ranges (hereafter 'range filling'; Svenning & Skov, 2004) and investigated factors influencing this ratio. We also calculated range filling from the results of single-species simulations. To investigate abundance distributions for each species, we used the equilibrium distribution of adults along an elevational gradient sample. A sample consisted of one grid cell per elevational level (e.g. Nogués-Bravo *et al.*, 2008) located centrally within the sloped plane. Realized elevational distributions of adult abundances were compared to potential distributions. The distribution of potential abundances was assumed to correlate with the habitat suitability (given by H). Finally, we investigated whether the elevational level with the highest abundance diverged from the elevational level with the species' highest habitat suitability.

RESULTS

From the total of 20,000 initial species in all 50 runs, 17,725 species (88.6%) supported viable populations in equilibrium communities. The mean number of surviving species in the equilibrium community was 352 per initial pool of 400 species (range 316–370; standard deviation, SD = 13 species).

In general, compared to the initial communities, there were significantly more species in the equilibrium communities with large adult body sizes (statistics in Fig. 1a), no Allee effects (Fig. 1b), intermediate-to-low mean dispersal distances (Fig. 1c), large temperature amplitudes (Fig. 1d) and maximum habitat suitability greater than 20% (Fig. 1e).

The potential species richness was hump-shaped along the elevational gradient, peaking in mid-elevations (Fig. 1f, panels i–ii). Realized species richness in the community simulations was slightly shifted towards higher elevations (Fig. 1f, panel iii), but was not significantly different from the potential gradients. There were no shifts in realized richness compared to potential richness in single-species simulations.

The realized ranges of 9462 species (53% of all species) were smaller than their potential ranges (Fig. 2a–c) in community simulations, whereas only 31% of single-species simulations resulted in smaller realized ranges. Range filling was more variable for lowland species (Fig. 2d). Range filling decreased significantly with dispersal kernel thinness, strength of Allee effects, optimum temperature, temperature amplitude and for annuals, but increased with adult body mass, mean dispersal distance and total species richness at the equilibrium community (Table 3). There were significant interactions of body mass with dispersal kernel thinness, strength of Allee effects, mean dispersal distance, optimum

temperature, temperature amplitude and total species richness in determining range filling (Table 3). These interactions indicate that the negative impacts of dispersal kernel thinness and Allee effects on range filling were mostly experienced by herbs, whereas the negative impacts of optimum temperature and temperature amplitude as well as the positive impacts of mean dispersal distance and maximum habitat suitability were mostly experienced by trees. The interaction between body mass and surviving species richness was more complex, with the effect of species richness on range filling changing from positive for herbs to negative for trees.

For 2024 species (11.4% of all species), the abundance distribution along the elevational gradient in community simulations was significantly different from the expected abundance distribution described by their habitat suitability (Kolmogorov–Smirnov tests in Table 2). 41% of these species had their abundance distribution shifted towards higher elevations, 32% to lower elevations and 27% had their abundance distribution symmetrically shrunk. Considering all species in community simulations, the elevational level with the highest abundance (mean = 8.6, SD = 4.6) was significantly higher (Wilcoxon rank test: $V = 2.3 \times 10^7$, $P < 0.001$) than the elevational level with the optimum temperature (mean = 8.2, SD = 4.3). There were no abundance shifts in single-species simulations.

DISCUSSION

Emerging patterns and study questions

Regarding our first study question, equilibrium communities did indeed diverge from the initial random species pools, and the number of species was not evenly distributed within the range of some traits, as it was at initialization (Fig. 1). However, values covering the entire range of the potential trait space (Table 1) were present in surviving species (Fig. 1), probably because of the high proportion of surviving species. For example, there were species over the entire spectrum of dispersal ability (Table 1, Fig. 1; see also Olivieri *et al.*, 1995). The unexpected lower survival of herbs is likely to reflect the large cell size and absence of disturbances. Additional exploratory simulations indicated that the lower survival of herbs compared to shrubs and trees disappeared with smaller cell areas and the addition of disturbances (results not shown). In these exploratory scenarios, smaller or unviable shrub and tree populations left more space available, allowing the establishment and viability of herb populations. Future research using such simulations to investigate community assembly rules would benefit from exploring viable trait combinations (Götzenberger *et al.*, 2011; Pakeman *et al.*, 2011).

Answering our second question, gradients of species richness along environmental gradients diverged little between initial and equilibrium communities. Potential species richness peaked at mid-elevations. This was expected from the

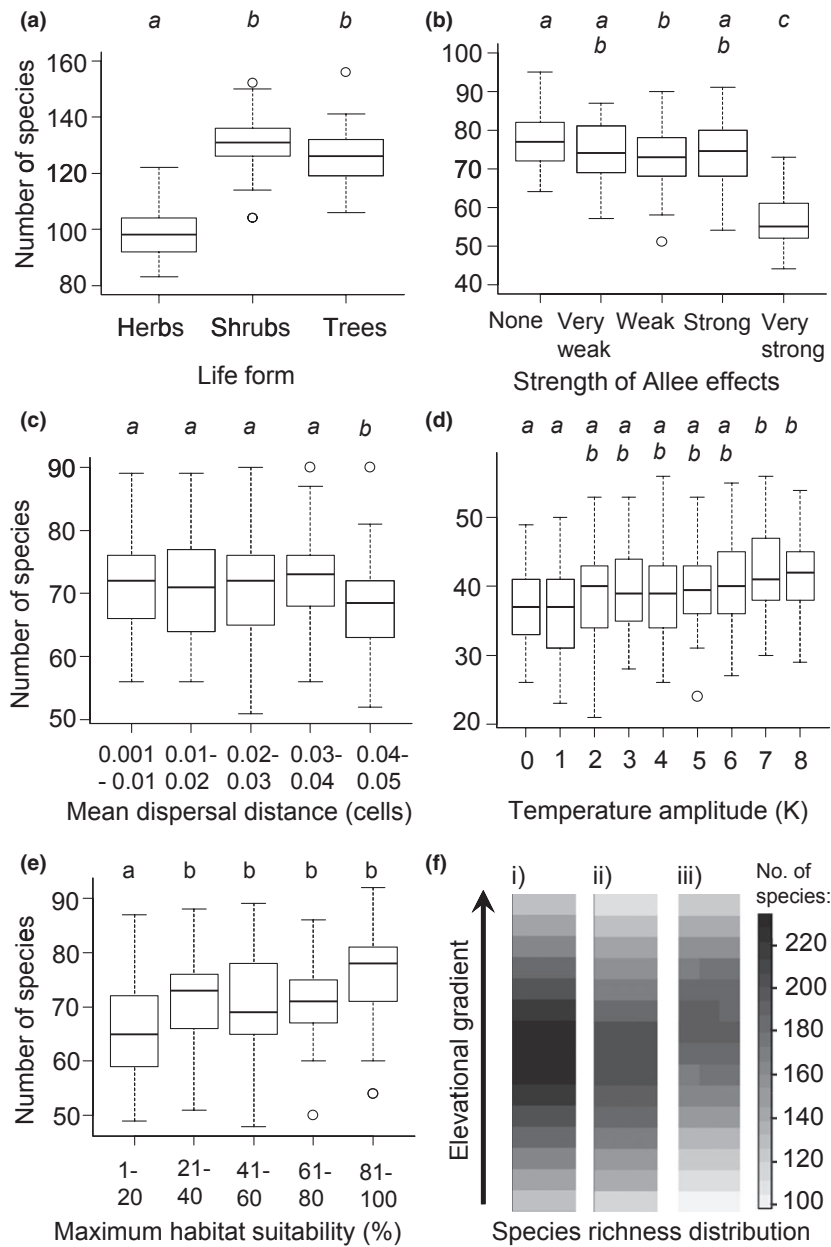


Figure 1 Number of species within the trait and physical spaces. (a) Life form, based on adult body mass (see Materials and Methods). (b) Strength of Allee effects, where no Allee effects means that the Allee effects strength C is equal or close to the inverse of carrying capacity, whereas very strong means $C > 0$. (c) Mean dispersal distance. (d) Temperature amplitude. (e) Maximum habitat suitability (percentage of the cell area that is suitable for a given species). Panels (a)–(e) considered species in the equilibrium community ($n = 50$ replicate species pools). Note that the number of species over the trait space at initialization was even distribution within the range of each trait. (f) Average spatial distribution of species richness: (i) potential richness at initialization, (ii) potential richness in equilibrium community, and (iii) realized richness in equilibrium community. Whiskers represent 1.5 interquartile range and circles are outliers. Parameter values not connected by the same letter (top of each panel) were significantly different according to simultaneous tests for general linear models with multiple comparisons of means using Tukey contrasts that are robust under non-normality, heteroscedasticity and variable sample size (Herberich *et al.*, 2010).

random placement of suitable habitats, which generates the highest overlap of ranges at the landscape centre simply due to geometrical constraints (mid-domain effects; Colwell & Lees, 2000). Interestingly, realized richness gradients were slightly shifted from the potential gradients (Fig. 1f). This suggests that realized richness gradients are highly influenced

by the initial distribution of suitable habitat. There were no clear geometrical constraints in the horizontal direction (Fig. 1f and Fig. 2a,b). When simulating a mid-domain-based null model (Tello & Stevens, 2011) for comparison, we also obtained species richness peaking at the landscape centre, but decreasing in all directions, not only with higher or lower

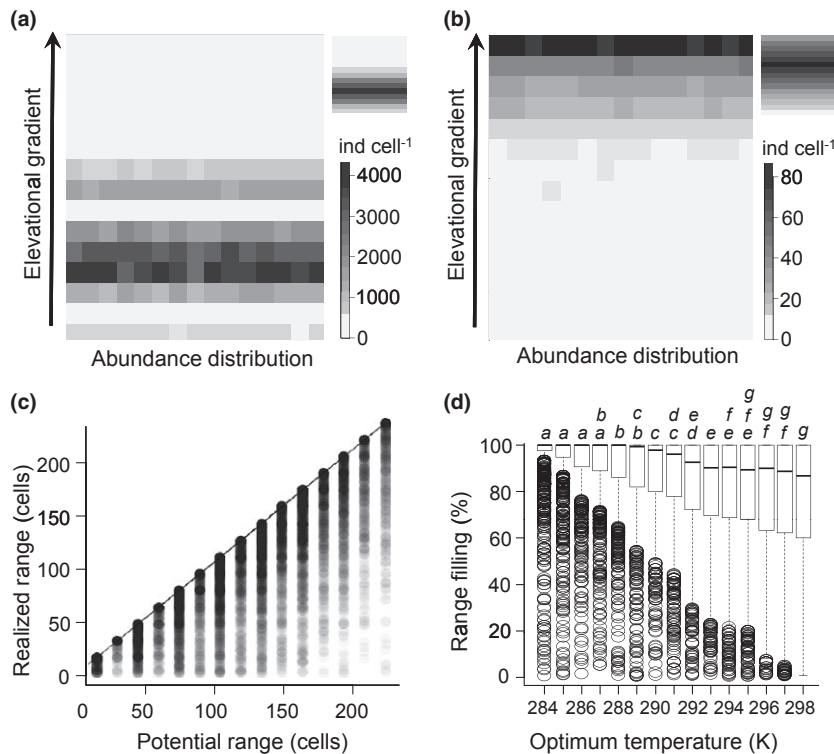


Figure 2 Spatial patterns of ranges and abundances. (a–b) Examples of realized and potential (inset at the top right of each panel) range and abundance distributions. (a) Species features: life form = shrub; $B_a = 4.7 \times 10^3$; $T_o = 293.15$ K; $T_c = 4$ K; $O = 70\%$; $\alpha = 0.02$ km; $P = 0.3$; $C = -0.8$. (b) Species features: life form = tree; $B_a = 7.7 \times 10^6$; $T_o = 288.15$ K; $T_c = 8$ K; $O = 5\%$; $\alpha = 0.019$ km; $P = 0.68$; $C = -0.66$. The colour gradient of the potential range inset represents the habitat suitability (%) from 0 (light grey at the top row) to the maximum habitat suitability (black). (c) Potential versus realized range. (d) Range filling versus optimum temperature. Line in (c) represents the identity function between potential and realized values. Letter coding at the top of panel (d) associates groups that are not significantly different (Herberich *et al.*, 2010).

elevation (results not shown). Nevertheless, area seems to have a negative effect on richness when temperatures are set higher, due to lower carrying capacities, and/or when cell grain is smaller, due to smaller local populations (results not shown).

The slight shift of realized richness towards high elevations in our community models (Fig. 1f, panel iii) is the result of competition pressure and metabolic constraints. This is indicated by the lack of a richness shift in single-species simulations (i.e. no interspecific competition) and in simulations without the influence of temperature distribution on metabolic rates (i.e. by applying the same temperature over the entire grid for metabolic functions, but keeping temperature gradients to calculate suitable habitats; results not shown). Our results agree with some previous work on elevational richness gradients. For example, physiological effects on elevational richness patterns have been reported for ferns (Kessler *et al.*, 2011). Furthermore, hump-shaped elevational gradients of species richness are common in nature (Rahbek, 1995; Lomolino, 2001; Nogués-Bravo *et al.*, 2008). Colwell & Rangel (2010) showed that hump-shaped elevational gradients of species richness can be produced by optimizing species-level processes, like speciation and extinction, to match field data. Our model ignores speciation and has extinction

emerging from demographic stochasticity, but can generate similar richness patterns from processes at the population level. Moreover, hump-shaped richness patterns have traditionally been interpreted as originating from geometrical constraints, from the effects of elevational changes in the environment (e.g. temperature, humidity or pristine habitat), or from a combination of both (McCain, 2004; Brehm *et al.*, 2007; Nogués-Bravo *et al.*, 2008; Kessler *et al.*, 2011). Hence, further theoretical studies should elaborate a specific study design to investigate richness gradients (Sanders & Rahbek, 2012).

In answer to our third question, the simulation of demography and competition generated large discrepancies between potential and realized range and abundance distributions. More than half of the species could not fill their potential range (Fig. 2a–c). This suggests that many species identified as specialists from field observations may in fact be generalists. In addition, there was a strong effect of species properties and species richness on range filling (Table 3). This suggests that realized ranges may be influenced by interspecific competition (due to species richness) and by species properties not related to environmental conditions (e.g. Allee effects; Keitt *et al.*, 2001). Consequently, correlative niche models must be interpreted with caution, as they do not

Table 3 Factors affecting range filling. Generalized linear models considered 17,725 species and were fitted with quasi-binomial distribution (maximum model in Table 2). The minimal adequate model was obtained through chi-square values by stepwise removing non-significant terms at $P < 0.05$ significance level (Crawley, 2007). Model covariants were standardized through z-transformation. The maximum model had $R^2 = 0.23$ and the minimal adequate model $R^2 = 0.22$.

Model term	Effect size \pm standard error	t-value
Intercept	1.8 \pm 0.01	***
Adult body mass, B_a	0.25 \pm 0.02	***
Dispersal kernel thinness, p	-0.24 \pm 0.01	***
Strength of the Allee effects, C	-0.62 \pm 0.01	***
Mean dispersal distance, α	0.18 \pm 0.01	***
Being annual	-0.38 \pm 0.01	***
Optimum temperature, T_o	-0.14 \pm 0.01	***
Temperature amplitude, T_e	-0.18 \pm 0.01	***
Surviving species richness	0.26 \pm 0.01	***
Interaction B_a : p	-0.09 \pm 0.01	***
Interaction B_a : C	0.14 \pm 0.01	***
Interaction B_a : α	0.03 \pm 0.01	*
Interaction B_a : T_o	0.10 \pm 0.01	***
Interaction B_a : surviving species richness	-0.57 \pm 0.01	***

* $0.01 < P < 0.05$

*** $P < 0.001$.

explicitly consider species properties or biotic interactions. This caution might be especially relevant for spatially restricted species with strong conservation appeal, which may actually have broad ecological tolerances but be unable to fill their potential range due to demographic constraints or biotic interactions (Soberón & Peterson, 2005). Ultimately, this could be experimentally tested or observed during species invasions. For example, niche 'shifts' have been reported from invasive species when comparing native and invaded ranges, revealing low transferability of correlative niche models (e.g. Broennimann *et al.*, 2007; Gallagher *et al.*, 2010). The ecological constraints found to limit range filling in our study offer a theoretical and mechanistic explanation for this low degree of transferability of correlative approaches (Gallagher *et al.*, 2010; Dormann *et al.*, 2012).

Several species were most abundant at elevational levels higher than the optimal level determined by their habitat requirements. This was probably due to the alleviated competitive pressure caused by higher carrying capacities at lower temperatures (Savage *et al.*, 2004). This indicates that species can reach their highest abundances under suboptimal environmental conditions (McGill, 2012). Abundance peaks in habitats with suboptimal conditions have been observed in Iberian ibex (Acevedo *et al.*, 2008), large marsupials (Ritchie *et al.*, 2009) and trees (McGill, 2012), in all cases possibly due to biotic interactions (Acevedo *et al.*, 2008; Ritchie *et al.*, 2009; Cassini, 2011). Hence, both correlative habitat models and single-species mechanistic models may produce biased predictions for the species niche, depending on how often the observed abundance distributions are constrained by

demographic processes and biotic interactions (Soberón & Peterson, 2005; Soberón & Nakamura, 2009). In summary, the possibility of both low range filling and abundance shifts to suboptimal conditions invalidates the theoretical principle underpinning correlative and single-species mechanistic models – that the probability of occurrence is directly related to habitat suitability (habitat matching rule; Cassini, 2011).

Effects of model assumptions

The observed patterns of community trait composition, richness gradients, range filling and abundance distributions appeared relatively robust to variation in model structure, study design and constants. This was supported by exploratory simulations (results not shown). For example, we obtained similar patterns using more complex landscapes (e.g. pyramidal mountain), temperatures oscillating through time, different initial species number and different values for metabolic constants. If speciation or invasion was included, better competitors could appear and increase competition pressure, resulting in stronger elevational range shifts, lower range filling and an even greater extinction rate for poor competitors.

Divergences to the presented community trait composition occurred in harsher environments (e.g. with disturbances, 5-cell-wide landscapes, higher initial species number and/or cell area of only 4×10^4 m²). Under these conditions, fewer species survived and there were stronger effects of habitat suitability and temperature amplitude and stronger Allee effects. There were also fewer species with large body mass (unviable populations due to smaller areas and disturbances) and fewer species with high dispersal ability. Such selection for reduced dispersal was probably influenced by the absorbing boundaries. This was because with smaller cell grains, high dispersal ability reduces the viability of populations due to seed loss at the boundaries. Making the boundaries periodic (seeds dispersing out of one edge reappear on the opposite edge) changed communities only in scenarios with smaller landscape and cell areas. In such unrealistic scenarios, tree populations were unviable, whereas survival over the entire trait space was enhanced (excluding body mass). The higher survival of non-tree species in these scenarios was probably because dispersal was not affected by the periodic edges, whereas there was enough space for viable populations.

The results of low range filling and elevation-shifted abundance distributions were robust to changes in model assumptions. However, in harsh environments (e.g. involving smaller areas, absorbing boundaries, disturbances, invasion and/or evolutionary processes), we would expect the few surviving species to exclude most of their competitors and fill their potential range without abundance shifts. Furthermore, the richness patterns seemed to be affected by assumptions determining the habitat requirements of species and consequent distribution of their suitable habitats. For example, we observed species richness peaking in lowlands when we set the species temperature amplitude to be lower and

peaking at highlands with higher temperature amplitudes. Finally, although not investigated, divergences in the presented patterns can be expected when varying metabolic constants independently for each species and ignoring life history trade-offs. Such theoretical scenarios may generate communities dominated by unrealistic 'super plants', e.g. a species with low mortality, with high recruitment and reproduction and exploiting few resources.

Model relevance, limitations and potentials

Our approach is the first mechanistic model of range dynamics that integrates key demographic processes with biotic interaction in a metabolic framework. This mechanistic model overcomes limitations present in correlative and in single-species mechanistic approaches. For example, the inclusion of competition for area allowed us to apply the Hutchinsonian niche concept in its full extent by considering both scenopoetic (density-independent, e.g. temperature and habitat suitability) and bionomic (density-dependent and competition-mediated, e.g. space) variables (*sensu* Hutchinson, 1978). Therefore, our model integrates Grinnellian (scenopoetic variables) and Eltonian (bionomic variables) niche concepts (Chase & Leibold, 2003; Soberón, 2007). This is important because most niche models claim to describe the Hutchinsonian niche, but largely ignore bionomic variables.

We have demonstrated that, for niche models, it is possible to link important processes that describe the niche (e.g. demographic, metabolic and interaction processes). Other multi-species approaches simulating communities also link several processes, but they do not investigate range dynamics and apply more simple demographic submodels (including dispersal) than presented here. For example, models of forest dynamics include, at small spatio-temporal scales, physiological processes, interspecific competition and simplistic demographic assumptions (Huth & Ditzer, 2000; Purves & Pacala, 2008; Hurr *et al.*, 2010). In contrast, vegetation models concentrate on metabolic and phenological constraints on plant functional types at large scales (e.g. Prentice *et al.*, 1992; Cramer *et al.*, 2001; Sitch *et al.*, 2003; Reu *et al.*, 2011; Hartig *et al.*, 2012). All these approaches may offer alternative routes for simultaneously modelling the range dynamics of multiple species.

Most limitations of our model originate from its complex mechanistic framework and include difficult parameterization and computational demand. However, the generation of multiple patterns compensated for the model's complexity. Each resulting pattern can be further investigated with more detailed experimental designs and with appropriate data for validation. Such multiple possibilities for model validation improve parameterization and calibration (Wiegand *et al.*, 2003; Grimm *et al.*, 2005). Currently, inverse modelling is virtually impossible for models like ours as it requires time series of life-stage abundances for all species in a given area, which are very labour-intensive to collect in the field (Jeltsch *et al.*, 2008; Schurr *et al.*, 2012). Such scarcity of data ham-

pers the simultaneous validation of multiple patterns. For example, realized richness gradients are common in the literature, but they do not incorporate range or abundance distributions. Consequently, a simulation design addressing richness gradients can only use richness data for validation. Therefore, we suggest the monitoring of local abundances in preference to collecting only richness data, as richness and ranges can be derived from them. Additionally, demographic data could validate metabolic rates, whereas laboratory experiments assessing ecological amplitudes (e.g. for temperature) could validate potential distributions.

Although our study was limited to a moderate number of species over a relatively small landscape, advances in computer science will soon enable more extensive simulation experiments. This will allow a better appraisal of model uncertainty originating from metabolic constants and model structure (parameter and model uncertainties, respectively, *sensu* Jeltsch *et al.*, 2008). Nevertheless, our simulation design already considered variation in predictions by investigating random species pools, and thus random species-level parameter combinations. Additionally, our model considered demographic stochasticity arising from the probabilistic mortality, stage transitions and dispersal events.

Finally, in addition to the issues we have addressed here, a wide range of further theoretical questions could be investigated with our approach. This is possible because simulation experiments can investigate not only the theory underpinning the chosen functions and submodels (Schurr *et al.*, 2012), but also the theory regarding emergent properties. For example, it is possible to investigate how range dynamics and richness patterns vary under different combinations of reproduction, dispersal or metabolic functions. Patterns at biogeographical scales can also be investigated using our approach, including Rapoport's rule, species-area relationships and predictions of island biogeographical models. Therefore, our approach offers a valuable tool for improving the mechanistic understanding of ecological niches, especially with the increasing push to link species niches to community and biogeographical theory (McGill *et al.*, 2006; Whittaker & Kerr, 2011; Wiens, 2011).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 State variables and model specifications.

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BIOSKETCHES

Juliano Sarmiento Cabral is interested in processes and factors influencing species distribution and coexistence at various scales, including spatio-temporal dynamics of abundances and ranges.

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Editor: Steven Higgins

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