Land use change and biological invasions collectively threaten biodiversity. Yet, few studies have addressed how altering the landscape structure and nutrient supply can promote biological invasions and particularly invasive spread (the spread of an invader from the place of introduction), or asked whether and how these factors interact with biotic interactions and invader properties. We here bridge this knowledge gap by providing a holistic network-based approach. Our approach combines a trophic network model with a spatial network model allowing us to test which combinations of abiotic and biotic factors can facilitate invasions and in particular invasive spread in food webs.

We numerically simulated 6300 single-species invasions in clustered and random landscapes at different levels of nutrient supply. In total, our simulation experiment yielded 69% successful invasions – 71% in clustered landscapes and 66% in random landscapes, with the proportion of successful invasions increasing with nutrient supply. However, invasive spread was generally higher in random than in clustered landscapes. The latter can facilitate invasive spread within a habitat cluster, but prevent invasive spread between clusters. Low nutrient levels generally prevented the establishment of invasive species and their subsequent spread. However, successful invaders could have more severe impacts as they contribute more to total biomass density and species richness under such conditions. Good dispersal abilities drive the broad-scale spread of invasive species in fragmented landscapes. Our approach makes an important contribution towards a better understanding of what combination of landscape and invader properties can facilitate or prevent invasive spread in natural ecosystems. This should allow ecologists to more effectively predict and manage biological invasions.

Keywords: biological invasions, dispersal, habitat connectivity, land use change, metacommunity, species characteristics
Introduction

Globally, the number of invasive species increases without any sign of saturation (Seebens et al. 2017), raising concern for biodiversity loss and biotic homogenization (Courchamp et al. 2017, Ricciardi et al. 2017). Although invasive species can have profound consequences (both positive and negative) on the ecosystems they invade (David et al. 2017), we lack a clear understanding of which combinations of species, habitat types and landscape structures most effectively facilitate or prevent biological invasions (With 2002, Pantel et al. 2017). Biological invasions are complex processes that consist of several stages (introduction, establishment, dispersal to new sites and subsequent spread; Sakai et al. 2001, With 2002, Pantel et al. 2017). Thus, when and where alien species would successfully invade a new environment depend on several interacting factors, like the ‘invasiveness’ of alien species (determined by certain species characteristics like good dispersal ability, high reproduction rate and generalism; Kolar and Lodge 2001, Sakai et al. 2001, Van Kleunen et al. 2010), but also the native community (Clereau and Mandon-Dalger 2001). A ‘recipient’ community can either be able to resist invasion or facilitate it, depending, for example, on its diversity (Shea and Chesson 2002, Fridley et al. 2007), the strength of the competitive interaction of established competitors (Hart and Gardner 1997), and food web properties (e.g. robustness, connectance, link density, modularity and nestedness; Romanuk et al. 2009, Baijer et al. 2010, Frost et al. 2019).

The ‘invasibility’ of a native community should also increase with unexploited niche space and high nutrient and prey availability (Shea and Chesson 2002, Pantel et al. 2017, Frost et al. 2019) but decrease with the number of predators an invasive species has in the invaded community (enemy release hypothesis; Mitchell and Power 2003). Romanuk et al. (2009), for example, found that generalists, omnivores or herbivores, with few predators, are generally most successful in invading complex food webs. Similarly, Lurgi et al. (2014) could show that in their simulation study larger and more generalist species were the most successful invaders. These examples highlight that species-level network properties, such as trophic position and diet breadth, together with network complexity can play a key role for invasion success (Romanuk et al. 2009, Lurgi et al. 2014, Frost et al. 2019).

Any of the different stages included in the invasion process (introduction, establishment, dispersal, spread) is sensitive to landscape properties. Thus, the spatial configuration of habitat can strongly influence the performance of an invasive species (With 2002, Pantel et al. 2017); for example, the potential for introduction and successful establishment of alien species can depend on the degree of spatial connectivity between its native habitat and the habitat it is invading, the spatial distribution of resources, of other species and of habitat availability and quality (Pantel et al. 2017). The subsequent spread of an invasive species across a novel landscape depends among other factors on the availability of suitable habitat and its spatial connectivity, which in turn depends on the dispersal ability of the invader (With 2002, Hastings et al. 2005). This applies in particular to fragmented patchy landscapes, which can be described as spatial networks, with nodes representing habitat location and edges distance or connectivity (Dale and Fortin 2010; Fig. 1b). By affecting species persistence and species diversity (Hiebeler 2000, Liao et al. 2013a, b, 2016, 2017a, b, 2020), the configuration of habitat can affect also the ‘invasibility’ of the native community (i.e. more diverse native communities should be more resistant to invasions: diversity—invasibility hypothesis; Elton 1958).

In addition to the spatial configuration of habitat, its quality in terms of nutrient availability can be an important determinant for invasion success. High nutrient availability generally causes higher population densities that could facilitate the establishment of invasive populations and thus their further spread through higher emigration rates. Also, nutrient availability in part determines the number of trophic levels a landscape can generally support (Takimoto and Post 2013). A low nutrient availability could thus prevent the establishment of invaders, in particular at higher trophic positions with higher energetic demands. From a network perspective, this means that whether an alien species becomes a successful invader depends on the energy availability in the system to maintain a positive growth rate and the number of links it can establish within the native community (Pantel et al. 2017).

In general, link density and dispersal ability both depend on species characteristics such as body mass and movement mode (Jacob et al. 2011, Hirt et al. 2017a, 2018, Brose et al. 2019), opening up possibilities for trait-based generalizations of model approaches across species, communities and ecosystems. So far, most of our knowledge of biological invasions comes from species-centered and/or trait-based approaches, trying to identify characteristics common to invasive species (Cassey et al. 2004, Blackburn et al. 2009, Van Kleunen et al. 2010, David et al. 2017). Although such approaches often consider abiotic drivers, focusing on particular characteristics and species, they lack ecological complexity in terms of species interactions (David et al. 2017). While recent approaches more often make use of network theory to understand and predict biological invasions and incorporate the multiple directly and indirectly interacting species at different trophic levels (David et al. 2017, Frost et al. 2019 and references therein), they often lack a spatial context (Romanuk et al. 2009, Baijer et al. 2010). As outlined above, however, the spatial context plays a crucial role for invasive species establishment and subsequent spread, and thus, both trophic interactions and spatial dynamics must be taken into account to improve predictions about invasive species and invasive spread.

We here address this issue by combining ecological and spatial networks. Our approach allows us to study which landscape properties render complex food webs more or less susceptible to invasion, and whether these properties interact with certain characteristics of alien species, such as their dispersal ability or trophic position (among others). To do this, we use a bioenergetic meta-food-web model adapted...
from Ryser et al. (2019). Following allometric scaling laws, the model combines feeding and dispersal dynamics of complex food webs in spatially-explicit patchy landscapes. In such landscapes, species persistence largely depends on how well a species can disperse between the habitat patches (its landscape connectivity, Dale and Fortin 2010; Fig. 1b). This connectivity depends on the one hand on the habitat structural connectivity, i.e. how habitat is distributed in a landscape (here clustered or random), but also on the species-specific functional connectivity determined by e.g. dispersal...
Table 1. Local population dynamics. Equations and model parameters.

**Animal population dynamics**

\[
\frac{dA_{i,j}}{dt} = A_{i,j} \sum_{j} e_{j} F_{i,j} - \sum_{j} A_{i,j} F_{i,j} - x_{i} A_{i,j}
\]  

(T1.1)

Rate of change of biomass density of animal species \(i\) on patch \(z\); with conversion efficiency \(e_{j}\) (if \(j\) is a plant, \(e = 0.545\), typical for herbivory; if \(j\) is an animal, \(e = 0.906\), typical for carnivory; Lang et al. 2017); feeding rate \(F_{i,j}\) of consumer \(i\) on resource \(j\) on patch \(z\); metabolic demands per unit biomass for animals \(x = x_{A} m^{0.307}\) with scaling constant \(x_{A} = 0.141\) (the tenfold laboratory metabolic rate measured at a temperature of 20°C to represent field metabolic rates; Ehnes et al. 2011). The first sum goes over all animal and plant resources \(j\) and the second sum over all animal predators \(j\) of animal species \(i\).

**Functional response**

\[
F_{i,j} = \frac{e_{j} \kappa_{i} R_{j}^{1+q} \gamma}{1 + cA_{i,j} + e_{j} \kappa_{i} h_{i} R_{j}^{1+q} + \frac{1}{m_{i}}}
\]  

(T1.2)

Per unit biomass feeding rate of consumer \(i\) on patch \(z\) as a function of its own biomass density, \(A_{i}\) (taking into account the interference competition \(c\), the time lost due to intraspecific encounters, sampled from a normal distribution with mean \(\mu_{c} = 0.8\) and SD \(\sigma_{c} = 0.2\) for each food web) and biomass density of the resource \(R_{j}\) (either animal \(A_{i}\) or plant species \(P_{j}\)) with \(\kappa_{i}\), resource specific capture coefficient (Eq. T1.3); \(h_{i}\), resource-specific handling time (Eq. T1.5); \(\sigma_{j}\), 1/(number of resource species of \(i\)), relative consumption rate accounting for the fact that a consumer has to split its consumption if it has more than one resource species.

**Capture coefficient**

\[
\kappa_{i} = \lambda_{i} m_{i}^{\beta_{i}} m_{j}^{\beta_{j}}
\]  

(T1.3)

Resource specific capture coefficient of consumer species \(i\) on resource species \(j\) scaling the feeding kernel \(L_{j}\) (Eq. T1.4) by a power function of consumer and resource body mass, assuming that the encounter rate between consumer and resource scales with their respective movement speed. We sample the exponents \(\beta_{i}\) and \(\beta_{j}\) from normal distributions (mean \(\mu_{\beta} = 0.42\), SD \(\sigma_{\beta} = 0.05\); \(\mu_{\beta} = 0.19\), SD \(\sigma_{\beta} = 0.04\), respectively; Hirt et al. 2017b). We divide here the group of consumer species into the subgroups of carnivorous and herbivorous species each comprising a constant scaling factor for their capture coefficients \(\lambda_{i}\) with \(l \in \{0, 1\}\) (\(\lambda_{0} = 15\) for carnivorous species; \(\lambda_{1} = 3500\) for herbivorous species). For plant resources \(m_{j}^{\beta_{j}}\) was replaced with the constant value of 1 (as plants do not move).

**Feeding efficiency**

\[
L_{j} = \left(\frac{m_{i} m_{j}^{\beta_{i}}}{m_{j} R_{m}} e^{\left(\frac{m_{i} m_{j}^{\beta_{i}}}{R_{m}}\right)}\right)^{\gamma}
\]  

(T1.4)

Probability of animal \(i\) to attack and capture an encountered resource \(j\) (which can be either plant or another animal), described by an asymmetrical hump-shaped curve (Ricker's function), with width \(\gamma = 2\) centered around an optimal consumer–resource body mass ratio \(R_{m} = 100\), and a maximum of 1. The optimal prey body mass and the location and width of the feeding niche of a predator are parameterized with data from empirical feeding interactions (Brose 2008, Schneider et al. 2016).

**Handling time**

\[
h_{i} = h_{i} m_{i}^{\eta_{i}} m_{j}^{\eta_{j}}
\]  

(T1.5)

The time consumer \(i\) needs to kill, ingest and digest resource species \(j\), with scaling constant \(h_{i} = 0.4\) and allometric exponents \(\eta_{i}\) and \(\eta_{j}\) drawn from normal distributions with means \(\mu_{\eta} = -0.48\) and \(\mu_{\eta} = -0.66\), and standard deviations \(\sigma_{\eta} = 0.03\) and \(\sigma_{\eta} = 0.02\) respectively (Rall et al. 2012).

**Plant population dynamics**

\[
\frac{dP_{i,z}}{dt} = \kappa C_{i} P_{i,z} - \sum_{j} A_{i,j} F_{i,j} - x_{i} P_{i,z}
\]  

(T1.6)

Rate of change of biomass density of plant species \(i\) on patch \(z\); with predation loss \(F_{i,j}\), summed over all consumer species \(j\) feeding on plant species \(i\); metabolic demands per unit biomass for plants \(x = x_{P} m^{0.25}\) with \(x_{P} = 0.138\); intrinsic growth rate \(\kappa = m_{m}^{0.25}\); species specific growth factor \(C_{i}\) (Eq. T1.7).

**Growth factor**

\[
C_{i} = \min \left( \frac{N_{1}}{K_{1,i} + N_{1}}, \frac{N_{2}}{K_{2,i} + N_{2}} \right)
\]  

(T1.7)

Species-specific growth factor of plants determined dynamically by the most limiting nutrient \(l \in 1, 2\); with \(K_{ij}\), half-saturation densities determining the nutrient uptake efficiency assigned randomly for each plant species \(i\) and nutrient \(l\) (uniform distribution within \((0.1, 0.2)\)). The term in the minimum operator approaches 1 for high nutrient concentrations.
ability (which here scales with body mass for animal species). Together, they determine the realized, species-specific spatial network (Hirt et al. 2018; Fig. 1b, gray dashed lines). Depending on habitat density and the degree of clustering (Huth et al. 2014), long distances in clustered landscapes could prevent the spread of invasive species between clusters, depending on their dispersal ability (Fig. 1b). Therefore, we expect higher spread of invasive species in random landscapes (Fig. 1a–b). An increase in nutrient supply might not only facilitate establishment of invasive populations by higher resource availability but also increase the further spread through higher population densities that also yield higher emigration rates (Fig. 1b). This might especially promote the spread of invasive species at high trophic positions in clustered landscapes as they are presumably good dispersers but also depend on a sufficient nutrient supply in the landscape (Post 2002, Takimoto and Post 2013, Ryser et al. 2019). High dispersal ability of invaders is generally associated with high invasion success (Coutts et al. 2011), promoting their spread from the patch of introduction (Fig. 1b, black patch) across the landscape (Fig. 1b, blue and green patches, respectively). Additionally, species-level network properties such as the number of predators (vulnerability) and/or prey (generality) of an invasive species can impact their establishment and further spread across the landscape (Fig. 1b). By combining food webs and networks of habitat patches our approach can improve the understanding of what determines invasion success and invasive spread in realistic ecosystems.

**Methods**

**Model description**

We consider a multitrophic metacommunity consisting of 20 native plant and animal species and one invasive species (which can be a plant or an animal) on 40 homogeneous habitat patches, using a population dynamical approach based on the bioenergetic meta-food-web model by Ryser et al. (2019). The model combines an allometric trophic network model (Schneider et al. 2016) for the body-mass dependence of metabolism, growth and feeding with an allometric spatial network model (Hirt et al. 2018) describing the effect of the allometric scaling of dispersal distance on the realized connections between habitat patches. This means each species is fully characterized by its average adult body mass which determines its metabolic demands, its feeding links, the interaction strengths of these links and its maximum dispersal distance (the latter we here restrict to animals (active dispersers)). For each species, the rate of change in biomass density depends on the difference between its biomass gains due to feeding and immigration, and its biomass losses due to metabolic demands, being preyed upon and emigration. Habitat patches all share the same abiotic conditions and each patch can potentially harbor the full food web including the invader.

**Local population dynamics**

We distinguish between animal species (trophic levels > 1) and plant species (trophic level 1). For animal species, the rate of change in biomass densities on a patch are determined by biomass gains due to the consumption of plant and/or animals species, biomass losses due to being preyed upon by animals and metabolic demands (first three terms in Eq. 1 and Table 1, Eq. T1.1–T1.5). The rate of change in plant biomass densities on a given patch depends on growth due to the uptake of the two nutrients, mortality through grazing and metabolic losses (first three terms in Eq. 2 and Table 1, Eq. T1.6 and Eq. T1.7). The terms \( E_{i,z} \) (emigration) and \( I_{i,z} \) (immigration) in Eq. 1 and Eq. 2 describe the dispersal dynamics on a given patch as a process of biomass loss due to emigration and biomass gain due to immigration (see Dispersal dynamics and Table 2).

\[
\frac{dA_{i,z}}{dt} = A_{i,z} \sum_j e_j F_{j,i,z} - \sum_j A_{j,z} F_{j,i,z} - x_i A_{i,z} - E_{i,z} + I_{i,z} \text{(animal)} (1)
\]

\[
\frac{dP_{i,z}}{dt} = v_i G P_{i,z} - \sum_j A_{j,z} F_{j,i,z} - x_i P_{i,z} - E_{i,z} + I_{i,z} \text{(plants)} (2)
\]

The energy supply for the food web stems from an underlying nutrient model with two nutrients of different importance that drive the nutrient uptake and therefore the growth rate of the plant populations (Brose 2008, Schneider et al. 2016). The nutrient model consists of two nutrients of different importance, a nutrient turnover rate of 0.25 and a nutrient supply concentration (Table 1, Eq. T1.8). Applying different nutrient supply scenarios, we varied the nutrient supply concentration to obtain oligotrophic, mesotrophic and eutrophic landscapes (‘Generating landscapes’ section). See Table 1 for the corresponding equations and model parameters.

**Dispersal dynamics**

Dispersal between habitat patches is integrated as a dynamic and species-specific process of emigration, traversing through the habitat matrix and immigration. This means biomass flows dynamically between local populations based on the
Table 2. Dispersal dynamics. Equations and model parameters.

**Emigration rate**

\[ E_{iz} = d_{iz} B_{iz} \]  \hspace{1cm} (T2.1)

Emigration rate of species \( i \) from patch \( z \), where \( d_{iz} \) is the dispersal rate of species \( i \) from patch \( z \) (Eq. T2.2), and \( B_{iz} \) is the total biomass density of species \( i \) on patch \( z \).

**Dispersal rate**

\[ d_{iz} = \frac{a}{1 + e^{b(x_{iz} - x_0)}} \]  \hspace{1cm} (T2.2)

The dispersal rate of species \( i \) on patch \( z \), with \( a = 0.1 \) the maximum dispersal rate, \( b \), a parameter determining the slope of the function, \( x_i \), the inflection point determined by the metabolic demands per unit biomass of species \( i \), and \( v_{iz} \), the net growth rate accounting for emigration triggers such as resource availability, predation pressure and inter- and intraspecific competition (Bowler and Benton 2005, Fronhofer et al. 2018). For animals, we set \( b = -10 \), whereas for plants, we set \( b = 10 \). This means, for animals (active dispersers), we let the dispersal rates increase when their net growth rates become negative, whereas for plants (passive dispersers), we let them decrease. In other words, if an animals’ net growth rate is positive, there is no need for dispersal and emigration will be low; but if the local environmental conditions deteriorate, the growing incentives to disperse to better habitat increase the fraction of emigrating individuals (Supporting information). For plants on the other hand, we assume seed production and thus their dispersal rates to be higher when their net growth rates are positive (Supporting information).

**Maximum dispersal distance (animals)**

\[ \delta_i = b_m \delta_i' \]  \hspace{1cm} (T2.3)

Maximum dispersal distance of animal species \( i \), with body mass \( m_i \), scaling exponent \( \epsilon = 0.05 \), determining the slope of the body mass scaling (the positive value accounts for a higher mobility of animals with larger body masses), and intercept \( \delta_i \). We set \( \delta_i = 0.1256 \) so that the largest possible animal species with a body mass of \( m_i = 10^{12} \) has a maximum dispersal range of \( \delta_i = 0.5 \) (half of the length of a landscape with 1 \times 1 side length). An animal species with the smallest possible body mass of \( m_i = 10^2 \) thus has a maximum dispersal range of \( \delta_i = 0.158 \).

**Immigration rate**

\[ I_{iz} = \sum_{m \in N_z} \sum_{n \in N_s} \frac{1 - \delta_{iz}}{1 - \delta_{mn}} \frac{E_{iz}}{1 - \delta_{iz}} \]  \hspace{1cm} (T2.4)

Immigration rate of species \( i \) into patch \( z \), where \( N_s \) and \( N_z \) are the sets of all patches within the dispersal range of species \( i \) on patches \( z \) and \( n \), respectively; \( E_{iz} \) is the emigration rate of species \( i \) from patch \( n \); the term \( (1 - \delta_{iz}) \) is the fraction of successfully dispersing biomass, i.e. the fraction of biomass not lost to the matrix; and \( \delta_{mn} \) is the distance between patches \( n \) and \( z \) relative to species \( i \)'s maximum dispersal distance \( \delta_i \) (Eq. T2.3). The term \( \sum_{m \in N_z} \frac{1 - \delta_{iz}}{1 - \delta_{mn}} \frac{E_{iz}}{1 - \delta_{iz}} \) determines the fraction of biomass of species \( i \) emigrating from source patch \( n \) to target patch \( z \) and depends on the relative distance between the patches, \( \delta_{mn} \), and the relative distances to all other potential target patches \( m \) of species \( i \) on the source patch \( n \), \( \delta_{mn} \). This means more biomass flows between patches that are closer together.

Assuming that larger animals at high trophic positions are more mobile and have higher travel speeds, they can disperse further through the habitat matrix before they need to rest and feed in a habitat patch than smaller animals at lower trophic levels. To this end, we let maximum dispersal distances of animals scale with their body mass \( m_i \) (Table 2, Eq. T2.3). We use scaling parameters, so that the largest possible animal species with a body mass of \( m_i = 10^{12} \) has a maximum dispersal range of \( \delta_i = 0.5 \) (half of the length of a landscape with \( 1 \times 1 \) side length), whereas an animal species with the smallest possible body mass of \( m_i = 10^2 \) has a maximum dispersal range of \( \delta_i = 0.158 \) (Supporting information). In contrast to animals, plant species are assumed to be passive dispersers (e.g. propagated by wind) (Jenkins et al. 2007), and thus, we sampled the maximum dispersal range of each plant species from a uniform probability density within the interval \((0, 0.5)\). This assumption that local population dynamics and dispersal occur at the same timescale (Amarasekare 2008), directly influencing each other (Fronhofer et al. 2018). To this end, we model the emigration rate as a function of the local net growth rate, thereby summarizing resource availability, competition and predator pressure arising from local population dynamics (second last term in Eq. 1 and Eq. 2, Table 2, Eq. T2.1). Immigration rates in turn, depend on the distance an organism has to travel to reach the next habitat patch, its species-specific dispersal range and on the quality of the matrix the habitat patches are embedded in (the habitat matrix) (last term in Eq. 1 and Eq. 2, Table 2, Eq. T2.4). In line with previous theoretical frameworks and empirical observations (Holt 2002, Jetz et al. 2004, Holt and Hoopes 2005, Jenkins et al. 2007, Hirt et al. 2017a), we assume animals to be active dispersers and dispersal ranges to follow allometric scaling laws.
means the best plant disperser can potentially have the same maximum dispersal range as the largest possible animal species. By assigning species-specific maximum dispersal ranges, each species forms its own species-specific spatial network of habitat patches and thus perceives the same landscape differently (Supporting information). We further assume a hostile habitat matrix that does not permit feeding interactions during dispersal and therefore include a distance-dependent dispersal loss. This means biomass is lost to the matrix during dispersal, scaling linearly with the distances traveled and is 100% when the distance between two patches exceeds the maximum dispersal range of an organism. For numerical reasons, we did not allow dispersal flows below $10^{-17}$. See Table 2 for the corresponding equations and model parameters.

**Generating food webs**

We generated five native food webs, each with 20 species, by randomly sampling the log10 body mass $m_i$ of each species from a uniform probability density from the inclusive interval $(2, 12)$ for animal species, and from the inclusive interval $(0, 6)$ for plant species (see the Supporting information for the scaling relationship between body mass and trophic level). In this manner, we also determine the unique body mass (and dispersal range) of the invasive species $k$ using the specified intervals for plants and animals respectively. Drawing species’ body masses and the dispersal ranges of plant species at random makes the model inherently stochastic, but from thereon, all other steps are completely deterministic. We account for the stochastic nature of the algorithm by which food web topologies are created (Schneider et al. 2016) by generating five model food webs, each with a unique randomly sampled set of species body masses. For each food web, we simulate 21 single-species invasions of which five assume plant invaders and 16 animal invaders that differ in their body mass, trophic position and dispersal range. See the Supporting information for two exemplary food webs before and after invasion.

**Generating landscapes**

To test the effect of the spatial habitat configuration (landscape structure) on invasion success, we generated a total of 20 landscapes with a side length of $1 \times 1$, each comprising 40 habitat patches. In half of them, we distributed patches randomly in the landscape by sampling their $x$- and $y$-coordinates from a uniform distribution within the limits $(0, 1)$ (random landscapes). In the other half, we randomly distributed patches into eight habitat clusters, each comprising of five closely positioned patches (clustered landscapes). To do this, we first sampled the $x$- and $y$-coordinates of eight patches from a uniform distribution within the limits $(0, 1)$, under the condition that there is a minimum distance of 0.3 between them. Then we close position four patches around each of these eight patches by drawing their $x$- and $y$-coordinates from a truncated normal distribution between 0 and 1 with a mean of $x_{1\ldots8}$ and $y_{1\ldots8}$, respectively, and a standard deviation of 0.03. See Fig. 1c for the quantitative differences between clustered and random landscapes (distributions of cluster coefficients respectively nearest neighbor distances). Assigning each landscape different levels of nutrient supply concentrations $S_l$ further allowed us to test the effects of fertilization on invasion success. We applied three nutrient supply scenarios, yielding in total six distinct landscape categories: random/clustered-oligotrophic ($S_0 = 0.1$), random/clustered-mesotrophic ($S_0 = 1$) and random/clustered-eutrophic ($S_0 = 1000$). See Table 1, Eq. T1.8 for further information regarding the nutrient dynamics.

**Invasion simulations**

We simulated invasions using a three-step process:

1. First, we initialize the native food web by randomly sampling the initial biomass densities $B_{i,0}$ of each species $i$ on any given patch $z$ from a uniform probability density within the intervals $(0, 10)$. To start the simulations with some differences in species composition across patches, we initialize on each patch only 60% of all species from the native web (initial $\beta$-diversity), which we draw on each patch at random under the condition that at least one basal species is initialized on each patch, and that the full native web exists in the regional species pool. We further initialize on each patch two nutrients $N_l (l \in 1,2)$ of different importance and depending on the nutrient supply scenario, nutrient supply concentrations of $S_0 = 0.1$ (oligotrophic), $S_0 = 1$ (mesotrophic) and $S_0 = 1000$ (eutrophic); holding them constant over all patches.

2. Starting from these random initial conditions, we numerically simulate the feeding and dispersal dynamics of the native meta-food-web for 5000 time steps. This means we integrate the bioenergetic model formulated in terms of ordinary differential equations described in the ‘Methods’ section using procedures of the SUNDIALS CVODE solver ver. 2.7.0 in C++ (backward differentiation formula with absolute and relative error tolerances of $10^{-10}$) (Hindmarsh et al. 2005). In short, the rate of change in biomass density of any species $i$ on any patch $z$, $B_{i,z,t}$, depends on the difference between its biomass gains due to feeding and immigration, and its biomass losses due to metabolic demands, being preyed upon and emigration. For the equations and parameterization see Table 1 and 2. Depending on the combination of food web, landscape and nutrient scenario, the dynamics reach equilibrium or a stationary state after a couple of hundred time steps with no evidence for alternative stable states.

3. In the third step, at $t = 5000$ we introduce the invasive species $k$ on the upper most left patch in the landscape (the ‘introduction patch’ $x$, black patch in Fig. 1b) by initializing it with a biomass density of $B_{k,x,0} = 5$, the mean of the uniform probability density from which we draw the initial biomass densities of the native species. We then continue to compute the dynamics of the now invaded meta-food-web for another 5000 time steps, using the same parameterization.
Following this three-step process, we simulated for each native food web 21 single-species invasions on 20 landscapes and three nutrient supply scenarios, yielding a total of 6300 simulations. All code was programmed in C++ and R ver. 3.5.1 (<www.r-project.org>). We ran simulations on a high-performance cluster using a 64-bit platform (Schnicke et al. 2019).

**Invader characteristics**

In addition to the species characteristics we used as input parameters (body mass $m_k$ (log10-transformed) and dispersal range $\delta_k$), we evaluated for each invader $k$ four species-level network properties to describe their typical interaction structure within the native food web at the time of introduction ($t = 5000$): the prey-averaged trophic level $T_k$, defined as one plus the mean trophic level of all the invader’s resource species, thereby assigning plant species trophic level 1 (Williams and Martinez 2004); the degree of omnivory $O_k$, expressing the variance in trophic levels of a consumer’s prey; generality $G_k$ (prey counts); and vulnerability $V_k$ (predator counts). We calculated $T_k$ and $O_k$ using the function `TrophicInd` of the `NetIndices` package in R ver. 3.5.1 (Kones et al. 2009), and normalized both $G_k$ and $V_k$ by dividing the number of prey respectively predator species by the total number of extant species in the meta-food-web at $t = 5000$.

**Invasion success**

An invasion process was labeled as successful if an invader $k$ reached stationary persistence in at least one patch in addition to the ‘introduction patch’ $x$ (on which $k$ was initialized with a biomass density $B_{k,x} = 5$ at $t = 5000$). We counted a patch $x$ as successfully invaded if $k$’s biomass density post-simulation at $t = 10000$, $B_{k,x}$, exceeded the extinction threshold of $10^{-20}$. To quantify an invader’s ability to spread across a new environment (invasive spread), we calculated the fraction of successfully invaded patches in a landscape at $t = 10000$ (excluding the ‘introduction patch’). Additionally, we evaluated the biomass density of an invader in the landscape, $B_k$, relative to the total biomass density of all species in the landscape, $B$, at $t = 10000$.

**Analyses and data visualization**

We checked for correlation between the initialized $\beta$-diversity at $t = 0$ (we did not initialize all species on all patches) and the $\beta$-diversity that emerged by simulating feeding and dispersal dynamics for 10 000 time steps (none detected; Supporting information). Further, we removed 1115 simulations for which we could not calculate meaningful trophic levels (animal invaders without prey) and used the remaining 5185 simulations for further analysis. We generated boxplots with the `ggplot2` package in R ver. 3.6.3 (Wickham 2016) to illustrate the impacts of spatial habitat configuration and nutrient availability on invasion success, and the proportion of invader biomass density in a landscape. To compare the group means of clustered and random landscapes, we used pairwise t-tests, separately for each level of nutrient supply. Using the same kind of boxplot, we illustrate the impact of each invader characteristic (body mass, dispersal range) and species-level network property (trophic level, omnivory, generality, vulnerability) on invasive spread, separately for each landscape type and nutrient level. For the purpose of illustration, we combined invasive species into groups, separately for each trait and species-level network property. To do this, we rounded invader body masses, $m_k$, and degree of omnivory, $O_k$, up to the nearest multiple of 0.2, dispersal ranges, $\delta_k$, normalized generality, $G_k$, and normalized vulnerability, $V_k$, up to one decimal place, and prey-averaged trophic levels, $T_k$, up to the nearest integer. To illustrate the number of observations in the groups, we displayed boxes with widths proportional to the square-roots of the number of observations in each group. We fitted generalized linear mixed-effect models with binomial distribution and logit link function to relate each invader characteristic to the fraction of invaded patches (invasive spread), using the function `glm` of the `lme4` package in R ver. 3.6.3 (Bates et al. 2015). For each invader characteristic, we fitted six models, one for each combination of landscape type and nutrient scenario as fixed effects, with food web ID (1–5) as random factor to account for their different network properties. To make the effect sizes comparable, we z-transformed each invader characteristic, using the function `scale` in R ver. 3.6.3.

**Results**

**Abiotic factors**

Numerically simulating biological invasions in meta-foodwebs in landscapes that differ in their spatial configuration of habitat and nutrient supply shows that both landscape properties affect invasion success. In total, approximately 68.5% of all simulated 6300 invasion processes led to successful invasions (i.e. at least one patch in addition to the ‘introduction patch’ was successfully invaded). We find this fraction to be higher in clustered landscapes than in random landscapes (approximately 70.9% and 65.7%, respectively; Supporting information), with the differences being most pronounced in mesotrophic landscapes (Fig. 2a, second column). Accounting for the spread of an invader across the landscape, our results point towards a reversed pattern (Fig. 2b, Supporting information): in mesotrophic and most of all in eutrophic landscapes, invasive species could invade more patches in landscapes in which habitat was scattered across the landscape than in landscapes in which habitat was clumped into clusters (with long distances between them). We found that invader biomass density relative to the total biomass density in the landscape decreased with nutrient supply (Fig. 2d) – although the total biomass density in the landscape was increasing with nutrient supply (Fig. 2c). This concerned both clustered and random landscapes, showing comparable fractions of total and relative invader biomass density (Fig. 2d). In our simulations, oligotrophic landscapes could in general only support few species at low trophic
Invasive species can invade more patches in random landscapes than in clustered landscapes (Fig. 2b).

**Influence of biological characteristics of invaders**

In addition to the influence of landscape type and nutrient supply, our simulations show that invasive spread (defined as the spread of an invader across a new environment) varies among invasive species depending on their characteristics (Fig. 3, Supporting information). In accordance with our expectations, we found dispersal range of an invader to be the most important predictor for invasive spread. Invaders with long distances between habitat clusters, whereas in random landscapes with generally higher invasion success the benefit arising from high dispersal ability was less pronounced, in particular under eutrophic nutrient conditions (Fig. 3b, third column, Supporting information). Besides dispersal ability, the realized trophic level of an invader in the native web at the time of introduction affected its spread across a landscape. In eutrophic landscapes, we found the fraction of invaded patches to increase with trophic level (apart from plant species) (Fig. 3c, third column). Whereas in mesotrophic landscapes, animal invaders at higher trophic levels ($T_k > 4$) were limited in their spread, particularly in random landscapes (Fig. 3c, second column, second row). For animal species, both dispersal ability and trophic level scale with body mass, and so the effects of the trophic level could be confounded with the increase in dispersal range with trophic level, provided that nutrient availability does suffice to support them. Supporting this, we found a huge variance in the invasive spread of plant invaders with body mass independent dispersal ranges ($T_k = 1$) (Fig. 3c).
Figure 3. Influence of biological characteristics of invaders. Invasive spread (measured as the fraction of invaded patches) in landscapes varying in their spatial configuration of habitat and nutrient availability in response to invasive species characteristics and species-level network properties: (a) body mass (log10-transformed), (b) dispersal range, (c) prey-averaged trophic level, (d) omnivory index, (e) generality (normalized prey counts) and (f) vulnerability (normalized predator counts). Columns indicate nutrient availability in a landscape; rows the spatial configuration of habitat. Boxplots show the quantiles (25–50–75%) with whiskers showing the 95% CI and box widths are displayed proportional to the square-roots of the number of observations in the groups. Species-level network properties were assessed at the time of introduction ($t=5000$). The fraction of invaded patches was evaluated post-simulation at time $t=10\,000$, counting a patch as successfully invaded when the biomass density of the invader exceeded the extinction threshold of $10^{-20}$. See the Supporting information for the corresponding effect sizes and p-values obtained by fitting generalized mixed-effect models for each invader characteristic and combination of landscape type and nutrient level.
The degree of omnivory, $O_k$, expresses the variance in trophic levels of a consumer’s prey ($O_k = 0$ indicates plant species). For animal invaders, we found the fraction of invaded patches to increase with increasing degree of omnivory (Fig. 3d, first row). In other words, animal invaders that feed on preys at several trophic levels tend to invade more patches than invaders feeding on species from similar trophic groups. This effect was more pronounced in random than in clustered landscapes, especially under eutrophic conditions (Fig. 3d, second row, third column). We found similar trends for invader generality, $G_k$ (normalized prey counts, not accounting for their trophic level) (Fig. 3e). The effect of vulnerability, $V_k$ (normalized predator counts), on the fraction of invaded patches also varied among landscape structures and nutrient availability, showing different trends for clustered and random landscapes (Fig. 3f). In clustered landscapes, invader vulnerability only marginally affected its invasive spread, whereas in random landscapes, invaders with few predators had an advantage over invaders that are consumed by more native species.

**Discussion**

Invasive species are a major component of global change (Seebens et al. 2017) that can (permanently) alter ecosystem structure and functioning (Murphy and Romanuk 2014, Mollot et al. 2017). Biological invasions are complex processes that depend on a number of interdependent factors acting over a wide range of spatial scales (With 2002, Pantel et al. 2017), including the spatial structure of a landscape, abiotic environmental conditions, species interactions and invasive species characteristics. To account for these factors at both the local and landscape scale we here combined an allometric trophic network model (Ryser et al. 2019) with an allometric spatial network model (Hirt et al. 2018). This allowed us to study how the landscape properties underlying food webs and the invader properties determine invasion success and invasive spread in different landscape structures. Our simulation experiment yielded on average approximately 68.5% successful invasion processes, i.e. the invasive species established itself on at least one patch in addition to the patch on which it was introduced, corresponding closely to the invasion success rates both Hewitt and Huxel (2002) and Romanuk et al. (2009) found in their studies simulating invasions in non-spatial food webs (50–60% and 47%, respectively). While Romanuk et al. (2009) provided insights into how invader characteristics and native food web properties relate to invasion success (for the latter see also Baiser et al. 2010), Hewitt and Huxel (2002) focused on invasion resistance in (multi-trophic) communities depending on the number of invaders (one and two) and initial biomass densities. Although these studies underlined the important role of trophic interactions in invasion success, they neglected the influence of landscape structure that can impose strong constraints on food web dynamics (Gravel et al. 2016, Ryser et al. 2019). Specifically, invasive species have been shown to spread more rapidly in fragmented landscapes (Sakai et al. 2001). One historic example, for instance, is the brown-headed cowbird, an avian brood parasite, whose spread accelerated in response to forest clearing (Sakai et al. 2001). Our simulations support the important role of the spatial context, showing a higher fraction of successful invasions in clustered than in random landscapes (71% respectively 66%), whereas invasive spread was generally higher in the latter. Both measures strongly depended on sufficient nutrient availability as well as invader characteristics, with good dispersal abilities being most important for large-scale invasive spread.

**Invasion success and spread depend on landscape properties**

Testing different landscape structures (clustered and random distribution of habitat) and levels of nutrient supply (oligotrophic, mesotrophic and eutrophic), our simulations yielded different patterns for invasion success (at least one patch in addition to the introduction patch is invaded) and invasive spread (the fraction of invaded patches in a landscape) depending on the spatial habitat configuration and level of nutrient supply. This highlights the important role landscape properties play for the establishment and further spread of invasive species, supported by previous theoretical and empirical studies (Sakai et al. 2001, Williamson and Harrison 2002, With 2004, Hastings et al. 2005). In clustered landscapes, long distances between habitat clusters appear to limit the spread of invasive species across the landscape, but very short distances within a cluster seem to facilitate invasions within a cluster. In contrast, randomly distributed habitat generally shows higher fractions of invaded patches, provided there was sufficient nutrient supply. This is to some extent in support of the observations made by Havel et al. (2002), who found that lakes closer to source lakes tended to be more invaded by an exotic water flea than more isolated lakes (based on data collected from 152 Missouri lakes, USA over seven years). In these lake ecosystems, however, they did not find an effect of lake fertility (but see, Mata et al. 2013), whereas in our simulation experiment, an increase in nutrient supply enhanced invasion success and invasive spread. In our framework, landscapes with high nutrient availability could in general accumulate more biomass, particularly at high trophic levels and thus increase the number of trophic levels a landscape can support, thereby also benefiting invasive species (particularly at high trophic positions). Oligotrophic conditions on the other hand reduced the number of species and trophic levels able to persist, and thus, prevented invasion success and invasive spread due to energy limitation, in particular of species at higher trophic positions (despite good dispersal abilities). This suggests that in oligotrophic landscapes invader dispersal ranges and other invader characteristics are less important than energetic limitations in explaining the strong negative response of higher trophic levels to nutrient deprivation. This is supported by Ryser et al. (2019) who found comparable patterns in their work, showing that habitat isolation induced bottom--up energy limitation can drive top species extinctions.
in complex meta-food-webs. Interestingly, however, in oligotrophic landscapes we found the highest fractions of invader biomass density relative to the overall biomass density in the landscape. In other words, although oligotrophic landscapes can generally support only few species at low trophic positions and in general lower biomass, if successful, an invader makes up a high fraction of biomass in the invaded system. This might indicate that in oligotrophic landscapes invaders could have more severe impacts as they make up a larger proportion of biomass density and species compared to mesotrophic and eutrophic landscapes, provided that they can establish themselves under such restricted conditions.

**Invader properties are important**

Species characteristics are key determinants for local and spatial processes, this also applies to biological invasions and invasive spread. In our simulations, invader properties, and in particular dispersal ability, strongly influenced the fraction of patches an invader could successfully invade. This supports previous theoretical and empirical studies showing that invader properties are important determinants for invasion success (Sakai et al. 2001, Mata et al. 2013, Mollot et al. 2017), and can be more important than properties of the native community (e.g. the structure of the recipient food web; Romanuk et al. 2009). In our simulation experiment, we found dispersal ability to be the best determinant for broad-scale invasive spread in fragmented landscapes, followed by trophic level (excluding trophic level 1, i.e. plant species; Fig. 3b–c. Supporting information). In our model, we let both animal dispersal ability and trophic level increase with body mass (active dispersers), whereas for plant species (trophic level 1) we assume passive dispersal and thus body mass independent dispersal ranges that were drawn at random. This means that based on our model setup invaders with good dispersal abilities (which can either be randomly selected plants with long-distance seed dispersal or large animals at high trophic positions with large dispersal ranges) can connect more patches in a landscape (Supporting information), giving them an invasion advantage over species with low dispersal abilities. We further found an increase in the fraction of invaded patches with trophic level (except for plant species at trophic level 1). Note however, that based on our model assumptions, both animal dispersal range and trophic level scale with body mass, which is supported by empirical patterns and previous theoretical frameworks (Holt 2002, Holt and Hoopes 2005, Jenkins et al. 2007, Riede et al. 2011, Hein et al. 2012, Hirt et al. 2018). Although our modelling choice finds empirical and theoretical support, it creates an advantage for invasive species at higher trophic levels in fragmented landscapes. As a result, animals at high trophic positions can spread further than animals at lower trophic levels, which also applies to plant invaders with long-distance seed dispersal (selected at random). This is an important consideration as the assumed scaling relationship between dispersal ability and trophic level does not apply to all systems (Beisner et al. 2006, Pedersen et al. 2016) and in real ecosystems, many invaders are in fact at low trophic level. Therefore, in our simulations we attribute the strong relationship between the invasive spread of animals and trophic level to their good dispersal abilities rather than to their trophic position. This is further supported by our finding that invasive spread strongly varies among plant invaders at trophic level 1, suggesting that in our simulations dispersal range and not trophic level drive invasive spread. Although based on our model set up we attribute the larger invasive spread of species at higher trophic levels mostly to their large dispersal ranges, trophic position has been shown to strongly relate to the invasiveness of a species in non-spatial food webs (Romanuk et al. 2009, Howeth et al. 2016). Whereas Romanuk et al. (2009) found species at lower trophic positions or with small shortest food chain length (the dominant energy pathway of species; Williams and Martinez 2004) to be better invaders, Howeth et al. (2016) identified species at top trophic levels (in their case, invertivore-piscivore and piscivore species) as the invaders with the most severe ecological impacts. Together with the established correlation between larger dispersal distances and trophic level (Holt 2002, Jetz et al. 2004, Holt and Hoopes 2005, Jenkins et al. 2007, Hirt et al. 2017a) this can have severe impacts on native communities, for example, by increasing top-down pressure.

The spatial configuration of habitat determines which habitat patches a species can connect, i.e. its spatial network (Hirt et al. 2018), pointing towards an interaction with the biological characteristics allowing an invasive species to spread across a new environment. For a given landscape, detailed knowledge of the properties of a potential invader, in our simulations most importantly its dispersal ability relative to distances in the landscape, can be extremely valuable to reliably predict and prevent invasive spread (Sakai et al. 2001, Mata et al. 2013). The importance of long-distance dispersal for invasive spread in fragmented landscapes has also been highlighted by With (2004). However, human activities and above all human transport processes, for example, by car, truck or boat greatly facilitate biological invasions and invasive spread, e.g. due to long-distance dispersal of exotic non-native species with high biomasses such as the movement of Argentine ants by cars and trucks, or of zebra mussels by boats (Hastings et al. 2005, Wilson et al. 2009). Also, omnivory and generality, both indicating a broad resource variety, can to some extent relate to invasive spread (although less pronounced than dispersal ability and trophic level). Simulating species invasions in non-spatial food webs yielded similar results (Romanuk et al. 2009), suggesting that variables that reflect the interaction between an invader and the invaded community (e.g. trophic position, generality and omnivory) can govern invasion success in complex ecological networks (Romanuk et al. 2009, David et al. 2017). For vulnerability, i.e. the number of species an invader is preyed upon, we found opposite trends, however, these are rather weak. This could indicate that the number of predators an invader is preyed upon is less important in determining its success and spread than having a broad feeding niche, but more importantly, good dispersal abilities.
Model specifications and future directions

Our approach to modelling invasions in meta-food-webs allows examining how species interactions, abiotic environmental conditions and landscape properties together determine invasion success and spread in fragmented landscapes. Our framework is based on a tested and realistic allometric trophic network model and metacommunity theory and very general. For example, it can be used to study the effects of various additional properties (in terms of landscape, invader and native food web properties) on invasion success and invasive spread but also to explore how invaders impact native meta-food-webs. Due to indirect effects present in ecological networks, the invasion of a species can entail a cascade of subsequent changes. Furthermore, with all model parameters based on allometric principles, our modelling approach can be simply adapted to other trophic networks such as empirical food web structures (Brose et al. 2019) or other food web models (Williams and Martinez 2000, Petchey et al. 2008). Also, empirical patch networks or other dispersal mechanisms could be incorporated in the future. Environmental heterogeneity (differences among patches) can influence all stages of the invasion process—introduction, establishment, dispersal and further spread (reviewed by With 2002). Thus, patch heterogeneity should influence the patterns we found. Furthermore, we here introduce each invasive species with a biomass density of $B_i = 5$ at $t = 5000$, which is rather high compared to the biomass densities of native species at $t = 5000$. This is in line with empirical research showing that invasive species often are introduced with high densities due to human activities, such as ballast water release (Hastings et al. 2005, Wilson et al. 2009). Although in our simulations initial (invader) biomass densities do not affect the observed patterns (Supporting information), introducing invasive species with much lower biomass densities compared to the equilibrium densities of native species might change the results (Hewitt and Huxel 2002). Moreover, if introduced on patches with oscillating population dynamics, the time of introduction and biomass density might play an important role. Another aspect of our simulations that may affect the generality of our results lies in the way we generate native food webs, in which invasive species have a ‘free’ niche space they can settle into. Also, we tested only single-species invasions that are introduced once. Future work would be needed to assess the influence of different initial biomass densities at different time steps, as well as waves of invasions or multi-species invasions. In this study, we did not extensively test the parameter space for fixed, arbitrary values that we assigned for a number of parameters (but see Ryser et al. 2019 for the corresponding sensitivity analyses for dispersal parameters). Furthermore, most studies taking a (non-spatial) network perspective in invasion biology so far focused on identifying network properties that relate to the ‘invisibility’ of the resident community and how they are affected by invasive species (Romanuk et al. 2009, Baiser et al. 2010, Frost et al. 2019). The focus of our work was on identifying which combination of landscape properties and invasive species characteristics and species-level network properties determine invasion success and invasive spread in meta-food-webs, thereby addressing an important but understudied avenue in invasion biology (Frost et al. 2019).

Synthesis and outlook

Biological invasions are a major component of global change that can cause biodiversity loss and biotic homogenization (Courchamp et al. 2017, Ricciardi et al. 2017). Providing reliable predictors of whether introduced species are able to persist in a new environment and of further spread is crucial to improve invasive species management and should also be valuable for ecological theory. Yet, despite its relevance, our ability to predict which combinations of species, habitats and landscape structures facilitate or prevent biological invasions remains limited. We addressed this issue with a holistic, network-based approach built on a bioenergetic meta-food-web model and integrating direct and indirect effects arising from local population dynamics and spatial processes. From our simulation experiment the following important conclusions arise: 1) in fragmented landscapes, invader dispersal ability is the best predictor for invasive spread; 2) the differences we find among our simulations emphasize the importance to jointly consider landscape properties (e.g. the distribution of habitat and nutrient availability), species interactions and invader characteristics; 3) our results stress the importance of the spatial network structure to predict invasion success and invasive spread, provided there is sufficient nutrient supply in the landscape. More generally, our work shows that understanding invasion success and more importantly, invasive spread, depends on the circumstances when information on network structure should be complemented with invasive species characteristics. This is highly relevant considering the rapidly progressing land use change and its consequences. Distances between suitable habitat patches expand and landscapes become increasingly fragmented and isolated (Haddad et al. 2015), comparable to the clustered landscapes we simulated here. Furthermore, land use changes can cause landscape eutrophication, e.g. due to enhanced fertilization, but also can lead to nutrient deprivation. As shown by our results, all these factors can facilitate invasion success and invasive spread in complex systems. However, studies that jointly address abiotic and biotic drivers at scales beyond the local habitat are scarce, although urgently needed. We here provide one promising direction for invasion biology for a better understanding of the interplay between landscape properties, resident communities and invasive species, which is extremely important to identify potential invaders and mitigate their impacts.

Acknowledgements – We thank François Muñoz for helpful and constructive comments on our manuscript; we thank the EcoNetLab and TheoBio for discussions and statistical support, in particular Benjamin Rosenbaum, György Barabás and Anna Eklöf. We carried out numerical work on the high-performance computing cluster EVE of the Helmholtz Centre for Environmental Research (UFZ) and iDiv; we thank the EVE staff for their support. Open Access funding enabled and organized by Projekt DEAL.
Funding – This study was financed by the German Research Foundation (DFG) in the framework of the research unit FOR 1748 – Network on Networks: The interplay of structure and dynamics in spatial ecological networks (RA 2339/2-2, BR 2315/16-2) and FOR 2716 – Spatial community ecology in highly dynamic landscapes: from island biogeography to metacommunities [DynaCom] (BR 2315/21-1). Further, we gratefully acknowledge the support of iDiv funded by the German Research Foundation (DFG-FZT 118, 202548816).

Conflict of interest – The authors declare no competing interests.

Author contributions

Johanna Häussler: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Methodology (lead); Project administration (lead); Software (lead); Validation (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). Ulrich Brose: Conceptualization (equal); Funding acquisition (lead); Methodology (supporting); Supervision (lead); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). Remo Ryser: Methodology (supporting); Software (supporting); Validation (supporting); Writing – original draft (supporting); Writing – review and editing (supporting).

Data and code availability

Data and code to reproduce our results can be found at: <https://github.com/johannahae/invasive_spread>.

References

Amarasekare, P. 2008. Spatial dynamics of foodwebs. – Annu. Rev. Ecol. Evol. Syst. 39: 479–500.
Baiser, B. et al. 2010. Connectance determines invasion success via trophic interactions in model food webs. – Oikos 119: 1970–1976.
Bates, D. et al. 2015. Fitting linear mixed-effects models using lme4. – J. Stat. Softw. 67: 1–48.
Beisner, B. E. et al. 2006. The role of environmental and spatial processes in structuring lake communities from bacteria to fish. – Ecology 87: 2985–2991.
Blackburn, T. M. et al. 2009. The role of species traits in the establishment success of exotic birds. – Global Change Biol. 15: 2852–2860.
Bowler, D. E. and Benton, T. G. 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. – Biol. Rev. 80: 205–225.
Brose, U. 2008. Complex food webs prevent competitive exclusion among producer species. – Proc. R. Soc. B 275: 2507–2514.
Brose, U. et al. 2019. Predator traits determine food-web architecture across ecosystems. – Nat. Ecol. Evol. 3: 919–927.
Cassey, P. et al. 2004. Global patterns of introduction effort and establishment success in birds. – Proc. R. Soc. B 271: S405–S408.
Clergeau, P. and Mandon-Dalger, I. 2001. Fast colonization of an introduced bird: the case of Pycnonotus jocosus on the Mascarene Islands. – Biotropica 33: 542–546.

Courchamp, F. et al. 2017. Invasion biology: specific problems and possible solutions. – Trends Ecol. Evol. 32: 13–22.
Courtts, S. et al. 2011. What are the key drivers of spread in invasive plants: dispersal, demography or landscape: and how can we use this knowledge to aid management?. – Biol. Invas. 13: 1649–1661.
Dale, M. R. T. and Fortin, M. J. 2010. From graphs to spatial graphs. – Annu. Rev. Ecol. Evol. Syst. 41: 21–38.
David, P. et al. 2017. Chapter One – Impacts of invasive species on food webs: a review of empirical data. – In: Bohan, D. A. et al. (eds), Networks of invasion: a synthesis of concepts. Academic Press, Vol. 56 of Advances in Ecological Research, pp. 1–60.
Ehnes, R. B. et al. 2011. Phylogenetic grouping, curvature and metabolic scaling in terrestrial invertebrates. – Ecol. Lett. 14: 993–1000.
Elton, C. S. 1958. The ecology of invasions by animals and plants. – Univ. of Chicago Press.
Fridley, J. D. et al. 2007. The invasion paradox: reconciling pattern and process in species invasions. – Ecology 88: 3–17.
Fronhofer, E. A. et al. 2018. Bottom–up and top–down control of dispersal across major organisinal groups. – Nat. Ecol. Evol. 2: 1859–1863.
Frost, C. M. et al. 2019. Using network theory to understand and predict biological invasions. – Trends Ecol. Evol. 34: 831–843.
Gravel, D. et al. 2016. Stability and complexity in model metacommunities. – Nat. Commun. 7: 12457.
Haddad, N. M. et al. 2015. Habitat fragmentation and its lasting impact on Earth’s ecosystems. – Sci. Adv. 1: e1500052.
Hart, D. and Gardner, R. A. 1997. A spatial model for the spread of invading organisms subject to competition. – J. Math. Biol. 35: 935 – 948.
Hastings, A. et al. 2005. The spatial spread of invasions: new developments in theory and evidence. – Ecol. Lett. 8: 91–101.
Havel, J. E. et al. 2002. Estimating dispersal from patterns of spread: spatial and local control of lake invasions. – Ecology 83: 3306–3318.
Hein, A. M. et al. 2012. Energetic and biomechanical constraints on animal migration distance. – Ecol. Lett. 15: 104–110.
Hewitt, C. L. and Huxel, G. R. 2002. Invasion success and community resistance in single and multiple species invasion models: do the models support the conclusions? – Biol. Invas. 4: 263–271.
Hiebeler, D. 2000. Populations on fragmented landscapes with spatially structured heterogeneities: landscape generation and local dispersal. – Ecology 81: 1649–1661.
Hindmarsh, A. C. et al. 2005. SUNDIALS. – ACM Trans. Math. Softw. 31: 363–396.
Holt, R. M. et al. 2017a. A general scaling law reveals why the largest animals are not the fastest. – Nat. Ecol. Evol. 1: 1116–1122.
Holt, R. M. et al. 2017b. The little things that run: a general scaling of invertebrate exploratory speed with body mass. – Ecology 98: 2751–2757.
Hirt, M. R. et al. 2018. Bridging scales: allometric random walks link movement and biodiversity research. – Trends Ecol. Evol. 33: 701–712.
Holt, R. and Hoopes, M. 2005. Food web dynamics in a metacommunity context: modules and beyond. – Univ. of Chicago Press.
Holt, R. D. 2002. Food webs in space: on the interplay of dynamic instability and spatial processes. – Ecol. Res. 17: 261–273.
Howeth, J. G. et al. 2016. Predicting invasiveness of species in trade: climate match, trophic guild and fecundity influence establishment and impact of non-native freshwater fishes. – Divers. Distrib. 22: 148–160.

Huth, G. et al. 2014. Correlated percolation models of structured habitat in ecology. – Physica A 416: 290–308.

Jacob, U. et al. 2011. The role of body size in complex food webs: a cold case. – In: Belgrano, A. (ed.). The role of body size in multispecies systems. Academic Press, Vol. 45 of Advances in Ecological Research, pp. 181–223.

Jenkins, D. G. et al. 2007. Does size matter for dispersal distance?. – Global Ecol. Biogeogr. 16: 415–425.

Jetz, W. et al. 2004. The scaling of animal space use. – Science 306: 266–268.

Kolar, C. S. and Lodge, D. M. 2001. Progress in invasion biology: predicting invaders. – Trends Ecol. Evol. 16: 235–245.

Kones, J. K. et al. 2009. Are network indices robust indicators of food web functioning? A Monte Carlo approach. – Ecol. Model. 220: 370–382.

Lang, B. et al. 2017. Temperature and consumer type dependencies of energy flows in natural communities. – Oikos 126: 1717–1725.

Liao, J. et al. 2013a. Modelling plant population size and extinction thresholds from habitat loss and habitat fragmentation: effects of neighbouring competition and dispersal strategy. – Ecol. Model. 268: 9–17.

Liao, J. et al. 2013b. Species persistence in landscapes with spatial variation in habitat quality: a pair approximation model. – J. Theor. Biol. 335: 22–30.

Liao, J. et al. 2016. An extended patch-dynamic framework for food chains in fragmented landscapes. – Sci. Rep. 6: 33100.

Liao, J. et al. 2017a. Diverse responses of species to landscape fragmentation in a simple food chain. – J. Anim. Ecol. 86: 1169–1178.

Liao, J. et al. 2017b. Robustness of metacommunities with omnivory to habitat destruction: disentangling patch fragmentation from patch loss. – Ecology 38: 42–49.

Liao, J. et al. 2020. The role of omnivory in mediating metacommunity robustness to habitat destruction. – Ecology 101: e03026.

Lurgi, M. et al. 2014. Network complexity and species traits mediate the effects of biological invasions on dynamic food webs. – Front. Ecol. Evol. 2: 36.

Mata, T. M. et al. 2013. How invader traits interact with resident communities and resource availability to determine invasion success. – Oikos 122: 149–160.

Mitchell, C. and Power, A. G. 2003. Release of invasive plants from fungal and viral pathogens. – Nature 421: 625–627.

Mollot, G. et al. 2017. Chapter Two – The effects of invasive species on the decline in species richness: a global meta-analysis. – In: Bohan, D. A. et al. (eds), Networks of invasion: a synthesis of concepts. Academic Press, Vol. 56 of Advances in Ecological Research, pp. 61–83.

Murphy, G. E. P. and Romanuk, T. N. 2014. A meta-analysis of declines in local species richness from human disturbances. – Ecol. Evol. 4: 91–103.

Pantel, J. H. et al. 2017. Chapter Six – 14 questions for invasion in ecological networks. – In: Bohan, D. A. et al. (eds), Networks of invasion: a synthesis of concepts. Academic Press, Vol. 56 of Advances in Ecological Research, pp. 293–240.

Pedersen, E. J. et al. 2016. Empirically motivated ecological theory. – Am. Nat. 187: E117–E128.

Petchey, O. L. et al. 2008. Size, foraging and food web structure. – Proc. Natl Acad. Sci. USA 105: 4191–4196.

Post, D. M. 2002. The long and short of food-chain length. – Trends Ecol. Evol. 17: 269–277.

Rall, B. C. et al. 2012. Universal temperature and body-mass scaling of feeding rates. – Phil. Trans. R. Soc. B 367: 2923–2934.

Ricciardi, A. et al. 2017. Invasion science: a horizon scan of emerging challenges and opportunities. – Trends Ecol. Evol. 32: 464–474.

Riede, J. O. et al. 2011. Stepping in Elton’s footsteps: a general scaling model for body masses and trophic levels across ecosystems. – Ecol. Lett. 14: 169–178.

Romanuk, T. N. et al. 2009. Predicting invasion success in complex ecological networks. – Phil. Trans. R. Soc. B 364: 1743–1754.

Ryser, R. et al. 2019. The biggest losers: habitat isolation deconstructs complex food webs from top to bottom. – Proc. R. Soc. B 286: 20191177.

Sakai, A. K. et al. 2001. The population biology of invasive species. – Annu. Rev. Ecol. Syst. 32: 305–332.

Schneider, F. D. et al. 2016. Animal diversity and ecosystem functioning in dynamic food webs. – Nat. Commun. 7: 12718.

Schnicke, T. et al. 2019. EVE – high-performance computing cluster. – Helmholtz-Zentrum für Umweltforschung GmbH – UFZ, Leipzig.

Seebens, H. et al. 2017. No saturation in the accumulation of alien species worldwide. – Nat. Commun. 8: 14435.

Shea, K. and Chesson, P. 2002. Community ecology theory as a framework for biological invasions. – Trends Ecol. Evol. 17: 170–176.

Takimoto, G. and Post, D. M. 2013. Environmental determinants of food-chain length: a meta-analysis. – Ecol. Res. 28: 675–681.

Van Kleunen, M. et al. 2010. A meta-analysis of trait differences between invasive and non-invasive plant species. – Ecol. Lett. 13: 235–245.

Wickham, H. 2016. ggplot2: elegant graphics for data analysis. – Springer.

Williams, R. and Martinez, N. 2000. Simple rules yield complex food webs. – Nature 404: 180–183.

Williams, R. J. and Martinez, N. D. 2004. Limits to trophic levels and omnivory in complex food webs: theory and data. – Am. Nat. 163: 458–468.

Williamson, J. and Harrison, S. 2002. Biotic and abiotic limits of the spread of exotic revegetation species. – Ecol. Appl. 12: 40–51.

Wilson, J. R. et al. 2009. Something in the way you move: dispersal pathways affect invasion success. – Trends Ecol. Evol. 24: 136–144.

With, K. A. 2002. The landscape ecology of invasive spread. – Conserv. Biol. 16: 1192–1203.

With, K. A. 2004. Assessing the risk of invasive spread in fragmented landscapes. – Risk Anal. 24: 803–815.