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Bridging scales: allometric random walks link movement and biodiversity research

Running headline: Allometric random walks

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Abstract

Integrating mechanistic models of movement and behavior into large-scale movement ecology and biodiversity research is one of the major challenges in current ecological science. This is mainly due to a large gap between the spatial scales at which these research lines act. Here, we propose to apply trait-based movement models to bridge this gap and generalize movement trajectories across species and ecosystems. We show how to use species traits (e.g. body mass) to generate allometric random walks and illustrate in two worked examples how this facilitates general predictions of species-interaction traits, meta-community structures and biodiversity patterns. Thereby, allometric random walks foster a closer integration of movement ecology and biodiversity research by scaling up from small-scale mechanistic measurements to a predictive understanding of movement and biodiversity patterns in different landscapes.

Movement ecology and biodiversity research: from small-scale mechanisms to large-scale patterns

At the landscape scale, movement has broad implications for virtually all patterns in biodiversity and species communities [1–3] (Figure 1). At this spatial scale, new technical advances in tracking have provided big data of unprecedented quality for analyses in vertebrate movement ecology [4]. While this facilitates studies how movement trajectories and biodiversity patterns are related, it requires a complementary understanding of how the underlying physiological, behavioral and trophic processes drive these patterns and their correlations (Figure 1b). In addition, the heavy weight of active tracking tags prevents assessing large-scale movement patterns for most of the invertebrates that dominate natural communities in diversity and abundance [5].

A mechanistic understanding of movement and behavioral processes and their correlations with species traits often takes place at a smaller spatial scale of laboratory or small-scale field experiments [6]. This leaves a large gap between the measurement of movement parameters and landscape patterns in movement and their consequences for meta-communities, food webs, and biodiversity (Figure 1a). Here, we propose to bridge these scales by random-walk models that implement mechanistic movement processes to enable predictions of movement and biodiversity patterns at the scale of larger and more heterogeneous landscapes (Figure 1b). These models can be individual based to account for individual variation in movement and behavior or employ species averages. So far, their systematic development has been hampered by the need for parametrization for all species or even all individuals across species. We suggest to use the traits *body mass* and *locomotion mode* (running, flying, swimming) as predictors of movement capacities to achieve this parameterization of mechanistic walk models. We present a possible way of integrating such traits into random walk models to generate allometric random walks. Furthermore, we demonstrate in two worked examples how to use this approach to predict species-interaction strengths such as attack rates (worked example I) as well as meta-community structures and biodiversity patterns (worked example II, Figure 1b).

Ecological applicability of state-of-the-art movement models

Currently, there is a large gap between movement models and their ecological applicability to natural movement patterns of many species. Random walk models are conceptually simple and therefore widely used, but in their original form conceptualized animals as more or less featureless particles, whereas real animals have different traits, make adaptive decisions, and respond to landscape features. More recent random walk models have included various features of animal behavior [7], and individual-based movement models gain more ecological realism by combining these random walks with an animal's decisions in response to the landscape [1,8]. However, the data needed for developing such models are, despite rapid development in animal tracking technologies [4], still lacking and those that are available are species-specific, so that they cannot be generalized for modeling communities comprising species with substantial variation in traits and consequently movement patterns. Developing models for a general mechanistic understanding of animal movement across many species and the resulting biodiversity patterns at larger spatial scales thus requires a novel trait-based approach.

The allometric approach

The widespread ecological implications of body mass [9] and the Metabolic Theory of Ecology [10] have led to the insight that body mass represents a "super trait" determining many other species traits including physiological rates such as metabolism, growth, reproduction [11,12], interaction strengths with co-existing species [13,14], and also behavioral characteristics [15]. Allometric relationships can thus use one single trait to characterize a species and its other relevant features and can be used to simplify parameterization of community models that often contain too many parameters and species to allow their direct measurements for all species [16]. Consequently, recent community models have integrated allometric scaling relationships that predict parameters depending on the population-average body mass [17,18]. In addition to providing realistic estimates of population parameters across species, this also avoided, by taking into account trade-offs between traits, the fallacy of unrealistic parameter combinations within species (e.g. species with low feeding rates but high biomass production or metabolic rates) that result from random parametrization [19]. These allometric approaches have helped tailor trait-based models with empirically testable predictions that hold across ecosystems [13,18,20]. Despite their predictive success in communities of higher diversity, these population models come at the cost of ignoring (1) variability among the individuals within populations and (2) effects of movement in habitat space including consequences of different landscape structures.

Here, we present a new trait-based framework for movement modeling based on allometric scaling relationships, which helps to achieve a general parameterization across species or even individuals.

A new framework: trait-based movement models generalize across species

Just like physiological and morphological locomotor traits of animals [21,22], movement parameters such as speed [6,23], migration or dispersal distances [24,25], and home range sizes [26,27] follow allometric scaling relationships. However, environmental conditions such as resource availability or habitat quality may mask body mass effects, which has for example been shown for dispersal distances [28]. Thus, what is realized by animals in nature may differ from the allometric predictions. Nevertheless, the range within which this realized movement occurs has its upper limit at the maximum physiological capacity, meaning that all movement has to be scaled relative to this maximum to allow ecologically meaningful interpretations. This physiological capacity is defined by the maximum speed, which is the fundamental constraint of movement. Recent research has shown that animal maximum speed follows a hump-shaped relationship with body mass [23]. As this pattern holds across taxa and locomotion modes (running, flying, swimming), it provides a powerful tool for understanding the physiological boundaries of animal movement and will therefore form the basis of our framework.

In classical random walk models, the speeds of each individual step are drawn from pre-defined probability distributions and step lengths are obtained by multiplying this speed by time. These probability distributions have either random parameters [29], or they are based on species-specific movement tracks [30]. To obtain non-random distributions of step lengths that are general across species, we suggest including two new trait parameters: *body mass* and *locomotion mode.* Empirical allometric scaling relationships thereby quantify increases in speed with individual body masses for each locomotion mode. As maximum speed follows a hump-shaped relationship with body mass, intermediately sized animals have generally higher speeds and can therefore cover longer distances than smaller or larger ones. Moreover, *locomotion mode* accounts for differences in these allometric scaling relationships between running, swimming and flying organisms. This new framework provides real units of movement and therefore allows species-level predictions of movement trajectories.

Applying the framework

Creating allometric random walks by integrating trait-based steps

The advantage of this framework is the flexibility to integrate the trait-based speeds and step lengths into any desired movement model. Speeds can thereby either be calculated for each time period of a behavioral state separately by applying behavior-specific allometric scaling relationships (e.g. foraging, dispersal or migration speeds; *option 1*) or they can be calculated as proportions of the maximum speed (*option 2*). Here, we chose *option 2* to transform a simple random walk into an allometric random walk (aRW), because it is currently difficult to obtain precise allometric scaling relationships for speeds of different behavioral states, whereas data of high quality are available for maximum speed [23].As many aspects of speed including acceleration and locomotion costs are related to body mass [31,32], we anticipate that the simplifying assumption of all speeds being fixed fractions of maximum speed (*option 2*) could be replaced by more detailed, empirically-established scaling relationships for the different speeds (*option 1*) as soon as they are available (see [6] for an example of invertebrate foraging speed). All speeds are scaled between 0 (resting) and 1 (maximum speed). Speed values are drawn from a two-parameter beta distribution as it is a continuous probability distribution that is defined on the interval [0, 1] (see Supplementary Material for details). To account for the various behaviors, we defined three different beta distributions from which speeds are drawn: one for low speeds such as foraging or exploratory movement (Figure 2a, dashed line), one for intermediate speeds of patch-bridging, dispersal, and migration (travelling speed, Figure 2a, solid line) and one for high speeds as they occur during attack or escape in predator-prey interactions (Figure 2a, dotted line).

Subsequently, the unitless random values drawn from the different beta distributions are multiplied by v_{max}, the species-specific maximum speed, which is derived from the species' body mass and locomotion mode using empirical allometric scaling relationships (Figure 2b). For each species, the dimension of speed is thus scaled between zero and its body-mass dependent maximum speed. Figures 2c and d illustrate the effect of varying the input parameters body mass and locomotion mode using an allometric random walk with foraging speeds. Note that all triplets of trajectories were generated with the same random-number seed and projected on the same spatial landscape scale. Within the same locomotion mode (here: running), intermediate body masses lead to higher speeds (here: foraging speeds) and therefore medium-sized animals have larger step lengths and cover more space in the same amount of time (Figure 2c, middle row) than smaller (Figure 2c, upper row) or larger animals (Figure 2c, lower row). In addition, the locomotion mode affects the spatial scale of movement tremendously with flying animals having higher speeds and covering much more space (Figure 2, lower row) than running (Figure 2d, middle row) or swimming animals (Figure 2, upper row) of the same body mass.

Thus, using allometric random walks provide real units of steps and therefore trait-based movement trajectories. In the following, we will demonstrate possible ways of applying these allometric random walks to predict (1) species-interaction strengths in a homogeneous landscape and (2) large-scale biodiversity patterns in a heterogeneous landscape (patch network). Furthermore, possibilities to include more complex aspects of landscape heterogeneity are discussed.

Worked example I: Predicting species-interaction traits

Allometric random walks help make realistic predictions of species-interaction parameters such as predator-prey attack rates, competition or pollination, which are mainly based on encounter rates. In the following, we will use the example of attack rates that depend on encounters between predator and prey individuals. As encounter rates depend on the length of the path per unit time that is searched and the predator detection range, higher average speeds of animals generally lead to longer paths and thus higher encounter rates as well as higher attack rates [33,34]. Attack rates, in turn, affect interaction strengths and ultimately community attributes such as persistence and stability [35–37] as indicators of local biodiversity. We demonstrate the ability of allometric random walks to predict species-interaction strengths by comparing attack rates generated by individual-based models (IBMs) using a standard (non-allometric) and an allometric random walk. Therefore, we use the model presented by Li et al. 2017 [38] for a standard IBM and modified it following the above described approach to include allometric step lengths (allometric IBM). Both the standard and the allometric IBM include allometric scaling of other parameters such as detection range, maximum feeding capacity and gut clearance rate. The only difference between the two models is that the allometric IBM uses allometric random walks, whereas the standard IBM uses random step length. To be consistent with the empirical data for comparisons, we simulated 11 invertebrate predator-prey pairs in foraging mode with predator body masses ranging from 0.1 - 500 mg, and a predator-prey body-mass ratio of 100 characterizing typical natural invertebrate communities [39,40]. Prey abundance was systematically varied, and we fitted functional responses to the data (see [38] for details). We then analyzed the attack rate in relation to body mass and compared it to published empirical data on attack rates of terrestrial invertebrates [14,41]. The allometric IBM generates the realistic pattern of an increase in attack rate with body mass compared to the flat relationship produced by the standard IBM (Figure S1). The allometric scaling exponent of attack rates using the allometric IBM (0.29) predicts the empirical scaling exponent of attack rates of terrestrial invertebrates (0.3 [41], restricted to empirical data for terrestrial 2D interactions) surprisingly well considering the fact that no calibration was involved. The standard IBM only generates a marginal increase in attack rate with predator body mass (scaling exponent of 0.05), which is caused by allometric scaling of physiological parameters including that larger predators have larger gut sizes and therefore are able to feed longer compared to smaller predators (a property of the model by Li et al. [38]). This effect, however, is partially counteracted by the higher prey body mass of larger predators.

Overall, this worked example illustrates that IBMs with allometric random walks can accurately predict the strengths of species interactions such as attack rates at the small spatial scales of laboratory experiments. Very similar allometric approaches could be used to model other species interactions such as pollination and competition that also depend on encounter rates. Moreover, this allows scaling up to larger areas or even real landscapes and therefore enables mechanistic research on how landscape structures affect species interactions by changing encounter probabilities in different spatial compartments (e.g. patches, refuges or environmental gradients such as altitude). These simulations require accounting for how behavior and movement decisions of individuals respond to landscape structures. Eventually, incorporating these processes in model simulations will yield landscapes of interaction strengths, attack rates and fear, which would enable a better understanding as well as prediction of movement trajectories [42,43]. Moreover, as these interaction strengths have knock-on effects on community persistence, this approach will also allow predicting variation in species diversity across landscape structures.

Worked example II: Predicting meta-community structure and biodiversity patterns

The connectivity of a spatial meta-community network (i.e. the percentage of realized dispersal links between pairs of habitat patches) is generally altered via changing the number of habitat patches (network configuration), which profoundly affects the persistence and dynamics of species within these meta-communities [44]. However, the same spatial network configuration can host different species-specific network connectivities that depend on the species' movement abilities [45,46]. While prior studies have suggested species- and size-specific meta-community networks [45,46], our approach of allometric random walks offers a novel tool to predict the links in these spatial networks based on mechanistic, trait-based processes. As movement speed strongly depends on body mass, the degree of connectivity of a network should also follow an allometric relationship with medium-sized animals covering longer distances [25], which leads to connections between more distant patches [45]. Also, the locomotion mode (flying, running or swimming) should influence the species-specific network connectivity with flying animals being able to connect more distant patches than running ones. Consequently, changes in the spatial network configuration will affect species differently. For instance, increasing the degree of fragmentation (leading to higher distances between patches), will have a stronger effect on small and running animals than on larger or flying animals.

We illustrate this concept of species-specific network connectivities in Figure 3 using a simplified example of our approach, which applies species-averages of all parameters and thus ignores variation across individuals for the sake of simplicity. Future studies, however, can easily realize this approach with individual-based models in which the parameters such as speed and feeding rates vary according to traits of individuals. In our simplified conceptual example, the dispersal links between the patches can be created by running allometric random walks (here simplified to the mean allometric travelling speeds of the species, Fig. 2a) over the maximum travel time through unfavorable habitat. We assume that this maximum travel time should also be body-mass dependent with larger species having lower energetic costs while travelling (lower per unit biomass metabolic rates) and higher energy storage capacities in their body tissue [9]. Thus, larger animals should have more time available for patch-bridging events than smaller ones before they are exhausted or return to the original patch [47]. However, to get accurate quantitative predictions of this scaling relationship, detailed empirical analyses of animal movement between patches and the maximum travel time are needed. In our simplified allometric concept, travelling speeds times maximum travel time yield maximum patch-bridging distances that depend on the body mass of the species. In Figure 3, all patches with distances lower than these allometric patch-bridging distances are linked, which creates species-specific network connectivities (Figure 3a) as well as the corresponding link networks (Figure 3b) and hypothetical link networks in case of a higher degree of fragmentation with several patches removed from the network (Figure 3c). The number of links in the network increases with body mass up to intermediate sizes (Figure 3a, b, c from left to right), but it decreases with increasing fragmentation (Figure 3b vs. c).

Over a larger body mass scale, the network connectivity increases with body mass following a hump-shaped relationship (Figure 3d). The exact shape of this scaling relationship, however, depends on the interplay of the allometric scaling of maximum travel time and the hump-shaped scaling relationship of speed. A sensitivity analysis varying the exponents showed that the increase in connectivity with body mass from low to intermediate sizes is generally supported, but the effect at higher body masses strongly depends on the assumed scaling of maximum travel time. Hence, research on the allometric scaling of maximum travel time is urgently needed. With higher fragmentation (i.e. larger distances between patches), the increase of the curve is shifted towards higher body masses, implying that species of the same body mass have a lower connectivity in more fragmented landscapes (Figure 3d). This conceptual example is based on two simplifying assumptions. First, we assume that all species regardless of their individual body mass use the same type of patches in the spatial network. However, small species might integrate different patches (e.g. also use smaller patches as habitats) in their spatial networks than large species. Hence, an integration of the allometric scaling of required patch size into allometric spatial networks represents an important future step towards realistic trait-based patch networks. Second, we assume that travel speed is a fixed proportion of maximum speed implying that it also follows a hump-shaped relationship with body mass. However, different realized scaling relationships of travel speed could alter the allometry of network connectivity shown in Figure 3. Overall, allometric random walks can be an important tool to quantitatively predict how species or individuals connect patch networks depending on their traits and how these networks change with ongoing fragmentation. This allows integrating trait-based movement, behavioral decisions, and responses to different landscape structures into predictions of species-specific patch networks.

In the following, we describe a concept how the combination of species-specific patch networks with ecological networks analyses (here: secondary extinction analysis in food webs as an example) could be used for predictions of how strongly biodiversity declines in altered landscapes. We start with an unfragmented landscape (Figure 4, landscape A) and its corresponding features such as biodiversity, body mass-distribution of coexisting species, and food web structure, which can be calculated from the body-mass distribution using feeding kernels for species [18] or individuals as in worked example 1 [38]. In a hypothetical fragmentation scenario, patches are randomly knocked out from the landscape matrix. In this new, fragmented landscape (Figure 4, landscape B), the animals of body mass and locomotion mode as given by the body-mass distribution move according to allometric random walks. Based on the allometries of step lengths and travel times included in the random walk and the allometry of population abundances [48], trait-based extinction probabilities can be calculated. Prior secondary extinction studies have employed a variety of different trait-based extinction probabilities [49,50]. Here, we chose a simple scenario to illustrate the interplay of one of these traditional scenarios, low abundance, with a spatial extinction scenario, in which animals face extinction depending on the number of habitat patches that are still connected in the network (based on species-averaged random walks as in Figure 3). In the simplified spatial extinction scenario, small and large animals will have lower connectivities and a higher probability of extinction in the new landscape than species of intermediate size (Figure 4, extinction scenario B_1). However, the higher population density would in turn decrease extinction probabilities of smaller species (Figure 4, extinction scenario B_2). This implies that the largest species have the highest extinction risk, because of their low abundance and the low connectivity of their spatial networks. The relative extinction risks of small species with high abundances and intermediately-sized species with highly connected spatial networks can vary substantially depending on the allometric scaling exponents of abundance [48] and travel speeds. Moreover, extinction risks can also be affected by patch size and resource abundance. For instance, small animals might survive in only one patch of the network if it is large enough and the resource availability high enough. Scenarios that are more realistic could also include disturbances, and stochastic extinctions or long-distance dispersals. Ultimately, these features can help dovetail the model to the conditions of specific landscapes and communities.

Following the trait-based probabilities for primary extinctions, a new community with new body-mass distribution, food-web structure and lower biodiversity emerges (Figure 4, biodiversity and food web B). Simulations of secondary extinctions will generate a new food web and a community with even lower biodiversity (Figure 4, biodiversity and food web C). Together, this multi-step modeling approach (Figure 4) helps gain mechanistic insights in landscape-scale biodiversity patterns as well as predicted extinction scenarios following habitat fragmentation. Moreover, this concept can easily be transferred to other ecological networks such as plant-pollinator networks [51].

Outlook & Conclusion

In this conceptual framework, we highlighted the importance of including trait-based step lengths in movement models to make more realistic predictions of movement and biodiversity patterns at the landscape scale. We focused on the basic principle of including body-mass and locomotion-mode dependent speeds in these models, a basis to which important extensions can be added (see Outstanding Questions). These include (1) other important functional and behavioral traits and (2) other aspects of landscape heterogeneity. First, functional traits affecting animal space use such as hunting modes (sit-and-wait vs. cursorial) [52] or feeding types (e.g. predator vs. herbivore) [6,26] as well as other behavioral facets such as animal personality (e.g. boldness) [53] could be added to this concept. Second, also abiotic conditions and landscape structures play an important role in shaping the space use of animals [54]. By supplying different distributions and qualities of resources or by providing refuge places, the landscape structure actively changes movement speeds, detection efficiencies, and ultimately the type and strengths of predator-prey interactions. Moreover, the spatial arrangement of the individual habitat domains (habitat space that predator and prey use while foraging) can alter predator-prey interactions and even shift the direction of predatory effects [55–57]. Schmitz et al. 2017 [57] developed an elegant approach on how to calculate the overlap between these habitat domains by assessing individual predator and prey movement trajectories. Using allometric random walks could represent an easy way of producing multiple realistic species-specific predator-prey movement scenarios, in which the individuals exhibit behavioral responses to the abiotic (e.g. habitat structure) and biotic (presence of prey or predators) characteristics of the landscape. This will help make general predictions on predator-prey interactions across landscapes of varying structure and heterogeneity. Moreover, large-scale effects on predator-prey interactions could be assessed on a landscape-complexity gradient. For instance, impacts of movement corridors, barriers, or hiding places on functional responses in simple agricultural vs. more structured landscapes could be identified and finally provide important information on the persistence of species communities. How these additional aspects of landscape heterogeneity (e.g. barriers, environmental gradients) affect the step length distributions of the allometric random walk needs to be explored in future studies, but it is likely that generic trait-based relationships can be devised (see Outstanding Questions). Eventually, all these processes do not only constrain the behavior and interactions between species but indirectly also link to biodiversity patterns of landscapes.

Bridging between the spatial scales of (1) movement and behavioral processes and (2) movement and biodiversity patterns requires the implementation of trait-based movement models, as we cannot determine all relevant movement parameters for all species. We present the new framework of allometric random walks and its potential to fill this gap by being empirically realistic yet general across species. On the one hand, they represent the movement of real species better than random walks with stochastic parameters. On the other hand, they can be generalized more easily across species and communities than walk models based on tedious measurements of species-specific movement parameters. Therefore, this novel approach will provide realistic yet also generalized predictions and critically important mechanistic understanding of large-scale movement and biodiversity patterns.

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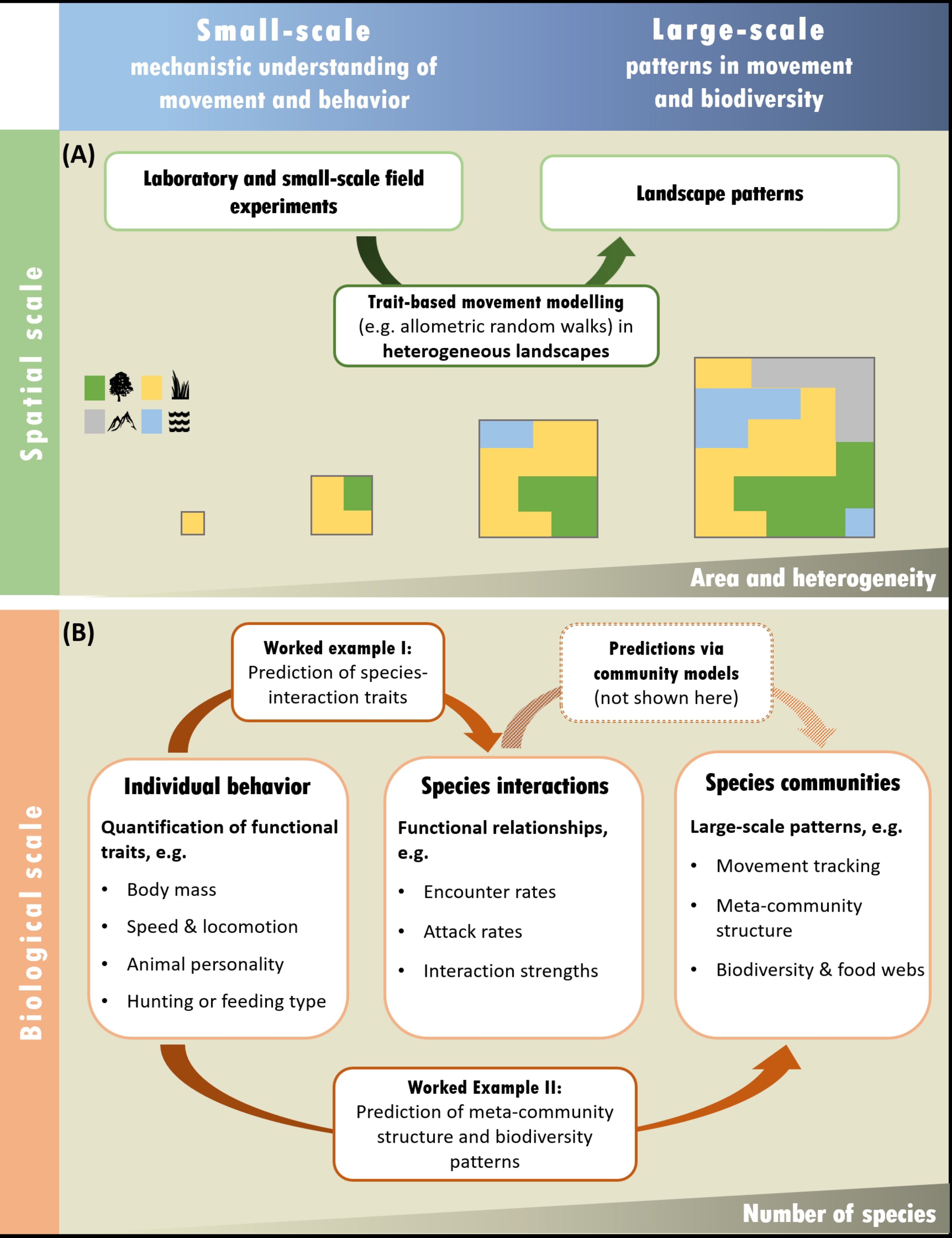
Figure 1: The different scales of processes and patterns in movement ecology and biodiversity research. (a) The spatial scale: a mechanistic understanding of movement and behavioral processes takes place at a laboratory or small-scale experimental scale while movement and biodiversity patterns are mainly described at larger scales of heterogeneous landscapes. This gap can be bridged by parameterizing movement models to obtain trait-based models such as allometric random walks, which are introduced in the course of this study. **(b)** The scale of biological organization: by integrating parameters of individual behavior (e.g. speed) into movement models, species-interaction traits such as attack rates and interaction strengths can be predicted (see worked example I) and possibly scaled up to larger areas or heterogeneous landscapes to gain a mechanistic understanding of how landscape structures affect predator-prey interactions and consequently community persistence and diversity. Furthermore, parameterized movement models can be used to directly predict meta-community structures and assess the effects of habitat fragmentation and landscape heterogeneity on food webs and biodiversity patterns (see worked example II).

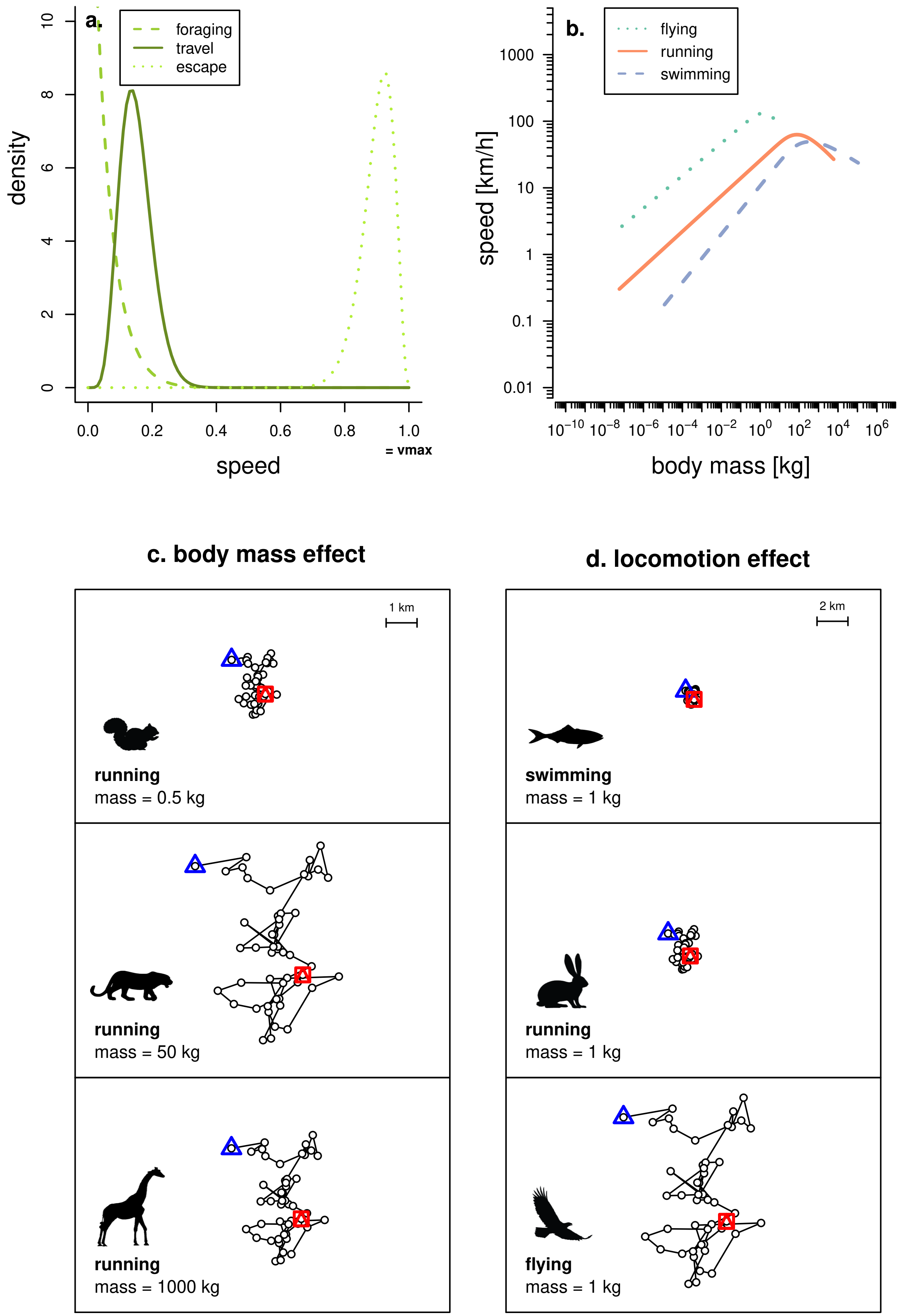
Figure 2: Effects of body mass and locomotion mode on movement trajectories in an allometric random walk. (a) The three beta distributions from which speeds are drawn for different behaviors (see Supplementary Material for details). (b) Allometric scaling relationships of maximum speed (Hirt et al. 2017) for the different locomotion modes. (c) Effect of body mass on the movement trajectory of an allometric random walk with foraging speeds. (d) Effect of the locomotion mode on the movement trajectory of an allometric random walk with foraging speeds. Note that all triplets of trajectories were generated by using the same seed for random numbers and are projected on the same spatial landscape scale.

Figure 3: Species-specific landscape connectivity over a fragmentation gradient. **(a)** An exemplary naturally fragmented landscape with different species-specific connectivities for four example animals of different body masses (low to intermediate). **(b)** Corresponding link network to the landscape connectivity in **a**. **(c)** Link network with a higher degree of fragmentation: patches B, D, F, I, K, and L have been removed from the network. **(d)** Landscape connectivity

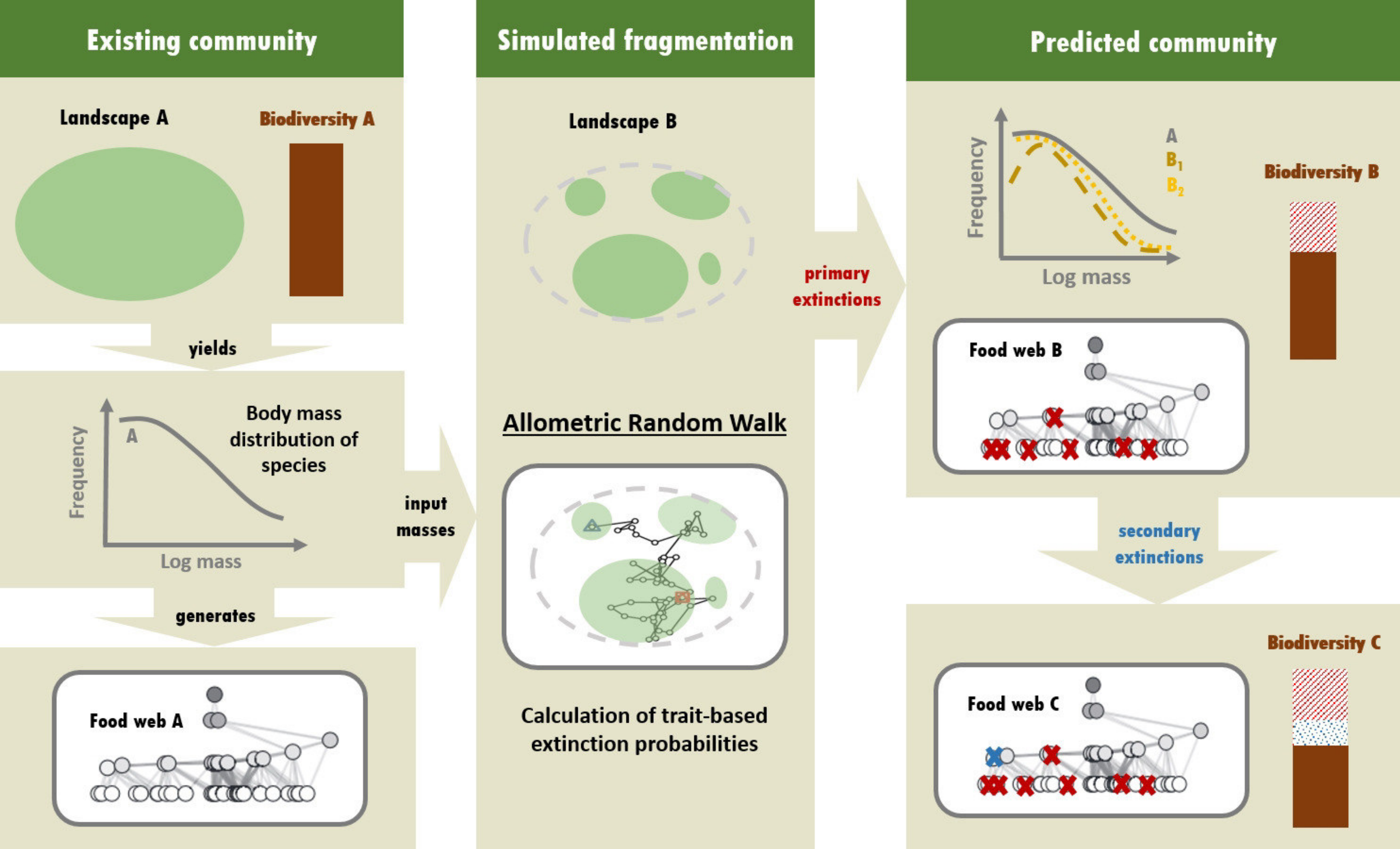
over a continuous body mass range (given as the percentage of realized links in the network). The degree of fragmentation increases from link network A to B to C. Link network A and B correspond to the networks in **b** and **c**. In the additional link network C, patches A, D, G, I, M, O and Q have been removed.

Figure 4: Predicting biodiversity loss due to fragmentation in natural landscapes by applying allometric random walks. An existing community in landscape A with biodiversity A holds a certain body-mass distribution A of species. Using feeding kernels *[18]*, the corresponding food web (food web A) can be generated from this distribution. In a hypothetical fragmented landscape B, species-averaged allometric random walks (body masses are derived from the frequency distribution) allow calculating trait-dependent extinction probabilities in the new landscape. These primary extinctions yield a new community with a different body-mass distribution. B_1 illustrates the spatial extinction scenario where intermediately sized animals have the highest connectivity potential and therefore lowest extinction risk; scenario B_2 additionally includes abundances, with higher abundances reducing the extinction probability of small species. These new body-mass distributions then yield a new food web structure (food web B) and biodiversity (biodiversity B). Subsequent biodiversity loss can be predicted by simulating secondary extinctions in the food web (food web C and biodiversity C). Note that food webs B and C represent meta food webs, whereas detailed predictions of local food webs require model simulations.


Small-scale
mechanistic understanding of movement and behavior
Large-scale
patterns in movement and biodiversity
Spatial scale
(A)
Laboratory and small-scale field experiments
Landscape patterns
Trait-based movement modelling (e.g. allometric random walks) in heterogeneous landscapes
Area and heterogeneity
Biological scale
(B)
Worked example I: Prediction of species-interaction traits
Predictions via community models (not shown here)
Individual behavior
Quantification of functional traits, e.g.
• Body mass
• Speed & locomotion
• Animal personality
• Hunting or feeding type
Species interactions
Functional relationships, e.g.
• Encounter rates
• Attack rates
• Interaction strengths
Species communities
Large-scale patterns, e.g.
• Movement tracking
• Meta-community structure
• Biodiversity & food webs
Worked Example II: Prediction of meta-community structure and biodiversity patterns
Number of species


a.
foraging
travel
escape
density
0
2
4
6
8
10
0.0
0.2
0.4
0.6
0.8
1.0
= vmax
speed
b.
flying
running
swimming
speed [km/h]
0.01
0.1
1
10
100
1000
10^{-10} 10^{-8} 10^{-6} 10^{-4} 10^{-2} 10^{0} 10^{2} 10^{4} 10^{6}
body mass [kg]
c. body mass effect
1 km
running
mass = 0.5 kg
running
mass = 50 kg
running
mass = 1000 kg
d. locomotion effect
2 km
swimming
mass = 1 kg
running
mass = 1 kg
flying
mass = 1 kg


Increase in body mass M
Allometry of landscape connectivity
Natural Landscape
Increase in fragmentation
Habitat patches
Link Network A
Link Network B
M = 0.01 kg
M = 1 kg
M = 5 kg
M = 20 kg
a)
b)
c)
d)
Link Network A
Link Network B
Link Network C
landscape connectivity [percentage realized links]
body mass [kg]
0.0
0.2
0.4
0.6
0.8
1.0
0.001
0.01
0.1
1
10
100
1000


Existing community
Landscape A
Biodiversity A
yields
Frequency
Log mass
A
Body mass distribution of species
generates
Food web A
input masses
Simulated fragmentation
Landscape B
Allometric Random Walk
Calculation of trait-based extinction probabilities
primary extinctions
Predicted community
Frequency
Log mass
A
B1
B2
Biodiversity B
Food web B
secondary extinctions
Biodiversity C
Food web C

Outstanding Questions

- How can other important functional and behavioral traits of species (besides body mass and locomotion mode) be integrated in movement models?
- What are the consequences of functional and behavioral traits or differences in animal personalities for large-scale movement trajectories, meta-community structures and biodiversity patterns?
- How may landscape structure and heterogeneity affect movement parameters and ultimately predator-prey interactions?
- Is there an interaction between landscape structures and the movement behavior depending on the individual’s functional and behavioral traits?
- What are the consequences of predator avoidance behavior for movement trajectories, individual ranges and meta-population structures?

Highlights

- Research on movement processes and biodiversity patterns are two currently dominating ecological disciplines yet they are still difficult to link.
- This is because research on biodiversity patterns and movement trajectories mainly take place at a large landscape scale, whereas mechanistic research on movement and behavior is carried out at smaller laboratory or field-experimental scales.
- Generating trait-based movement models by including species traits (such as body mass or locomotion mode) as predictors of movement capacities will help to bridge this gap across spatial scales.