

Ecography

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Supplementary material

Appendix 1: Model description following the standard ODD protocol.

1. Purpose

The purpose of our model is to simulate community assembly in order to explain and investigate the structure, specifically the individual size distribution (ISD, after White et al. 2007) of herbivorous mammal communities. This is done on the basis of individual physiology and space use characteristics, including the cumulative effects of foraging movement and resource competition between individuals. The model furthermore allows for the investigation of landscape effects (e.g. habitat loss) on community structure in dependence of these mechanisms.

2. Entities, state variables and scales

The model is spatially-explicit and is based on grid-based simulation landscapes. These landscapes, consisting of 257×257 grid cells, each interpreted as 10×10 m, represent the distribution of daily resource production (grid cell values). With increasing model run time (which can be interpreted as assembly history), this available daily resource production in landscape grid cells decreases as more and more mammals incorporate grid cells in their home ranges and consume part of the resources produced (this amount consumed is also calculated as daily consumption).

The model simulates resource-dependent home range formation of individual mammals. These are characterized by their body mass (ranging between 0.005 and 100 kg) and as mammals consuming plant diet (i.e. herbivores and primarily herbivorous omnivores). Moreover, individuals are characterized to be of one of three possible foraging movement types (central place forager CPF, patrolling forager PF, or body mass nomadic forager BNF). Because all individuals have a specific body mass, well established allometric relationships can be used to calculate individual daily resource requirements and specific locomotion cost (per distance moved). Maximum home range size and the share of biomass that an individual can access from the biomass available in each grid cell (both on a daily basis) are also implemented to vary allometrically with body mass (for details see ‘7.1. Submodel: Individual home range search’).

3. Process overview and scheduling

Community assembly is modelled on the basis of three major steps:

- 1) a mammal is assigned a specific body mass, drawn from a continuous, so-called ‘input distribution’.
- 2) for this mammal all suitable grid cells in the landscape are tested as potential central home range cells. This is done by adding grid cells with increasing distance to the potential home range until the food requirements of the animal can be satisfied on basis of the respective area or until an empirically determined (allometric) maximum home range size is exceeded. For each cell that is added to the potential home range during this search process, resource gain from the cell and movement costs (both body mass dependent) associated with inclusion of this cell into the home range are balanced (for detailed description of this model compartment, see below: ‘7.1. Submodel: Individual home range search’). Different types of foraging movement can be incorporated into the modelling framework by a different calculation of movement costs for each home range cell (see below: ‘7.2. Submodel: Foraging Movements’).
- 3) After all suitable grid cells have been tested as potential central cells, and at least one home range search was successful (i.e. the area necessary to cover the mammal’s resource requirements does not exceed the maximum home range size), the animal settles in the smallest of the possible home ranges and the resources within this home range are depleted (by a body mass dependent amount, see above: ‘2. Entities, state variables and scales’, and below: ‘7.1. Submodel: Individual home range search’).

These steps are repeated until a certain level of system saturation (SAT) is reached. This saturation is determined via the amount of available resources that is consumed by the simulated community (for details see below: ‘7.3. Submodel: Community saturation’). Thus, the scheduling of the model is event driven (the ‘arrival’ of individuals and establishment of their home ranges as events), and the time between these events is not explicitly defined. The process of home range search and establishment itself does not have a temporal component either.

4. Design concepts

4.1. Basic principles

A basic concept of the model of individual home range formation in mammal communities are the characterization of individuals by their body mass only, which allows the application of allometric relationships in order to calculate resource needs, specific locomotion costs per distance moved, individual resource availability and maximum home range size.

The search of an individual home range is based on an area minimizing principle adopted from optimal-foraging theory (Mitchell and Powell 2004). The establishment of individual home ranges is controlled by the spatial distribution of available resources as well as by individual physiology and foraging behaviour. The effect of foraging movement type on community structure is systematically tested (see '7.2. Submodel: Foraging movements'). Resource consumption within the home range changes the spatial resource distribution in the landscape and hence implies competition between individual mammals. Community assembly is simulated on the basis of resource production and reduction, individual allometric resource requirements and consumption, as well as foraging movement type (with the respective movement distances), all calculated and balanced on a daily basis.

4.2. Emergence

Major model output is the presence of individual mammals of certain body sizes in the community, that is the distribution of individual body masses (or the individual size distribution ISD). In this emerging community all individuals inhabit a home range with a specific location and size. Based on the model algorithms the abundance of individuals of a certain size depends on landscape properties and foraging movement. The same is the case for their home range sizes and locations, which of course additionally depend on the body mass (home range size and location are, however, not in the focus of this study; for more detail regarding this aspect see Buchmann et al. 2011).

4.3. Adaptation

Individual mammals adapt the size of their home range to current resource conditions. If resources are sparse or less spatially concentrated, home ranges have to be larger to fulfil the 'inhabitant's' resource requirements (home range size is, however, not in the focus of this study; for more detail see Buchmann et al. 2011).

4.4. Objectives

The major objective of individual mammals is to minimize the area of their home range.

Technically this is achieved by choosing that location in the landscape to ‘settle down’ which allows for the smallest possible home range.

4.5. Interaction

All individuals in the community interact by consuming and hence competing for the same (type of) resource in the same landscape.

4.6. Stochasticity

Stochastic components in the model are the generated landscapes on the one hand and the (sequence of) body masses drawn from the input distributions. The variability caused by these stochastic model elements is considered by simulating 5 (landscape) replicates for each scenario.

5. Initialization

The model reads in simulation landscapes that are characterized by the spatial autocorrelation of grid cell values (daily resource production) which determines the level of fragmentation of suitable (productive) habitat (Saupe 1988, Hargrove et al. 2002, Körner and Jeltsch 2008). For all simulations we use moderate spatial autocorrelation (Hurst-Factor $H = 0.5$, $\sigma^2 = 30$), i.e. fragmentation remains unchanged. For different habitat loss scenarios, however, landscapes with different area of suitable habitat are used. The (non-0) grid cell values of all landscapes used in simulations follow the same normal distribution (with an average productivity of $6.85 \times 10^{-2} \text{ kg dry biomass} \times \text{grid cell}^{-1} \times \text{day}^{-1}$, oriented towards the productivity of typical shrub lands and grasslands, Whittaker 1975). We generally assume that 20% of this productivity is available to the mammal community (the remainder is assumed to either not be consumable or to be lost to other taxonomic groups, see Buchmann et al. 2011 for analyses of the effects of landscape fragmentation and the share of resources that is available to the community).

Initially, all simulation landscapes are rich in available resources, and do not yet ‘harbour’ any mammals. In the course of the simulation, and successful home range establishments, the community grows and available resources in the landscape get reduced. As input distribution

(out of which individual body masses are drawn), we use for all scenarios a truncated power-law distribution of the form

$$p(M) = \kappa \times M^\eta, \quad (\text{A1.1})$$

with p representing the probability density of a certain body mass M . The normalization constant κ is chosen so that equation A1.1 integrates to 1. As exponent η we use -1.5 for all simulations (a value in the range tested by Buchmann et al. 2011, yielding realistic community structure).

The two major model parameters for all simulation experiments to explore the effects of habitat loss and foraging movement on community structure are set as follows: γ_{PI} , determining the general magnitude of resource use of individuals (for details see ‘7.1. Submodel: Individual home range search’) is set to 0.04; SAT, determining community saturation (see ‘7.3. Submodel: Community saturation’) is set to 0.95 (for sensitivity analysis of both parameters see Appendix A2).

Finally, communities consisting of animals of either of three fundamentally different foraging movement types are simulated for different levels of suitable habitat. These are: central place forager (CPF), patrolling forager (PF) and body mass dependent nomadic forager (BNF) (for details see ‘7.2. Submodel: Foraging movements’).

6. Input data

The model does not use input data to represent time-varying processes, as time is not modelled explicitly.

7. Submodels

7.1. Submodel: Individual home range search

This submodel does not simulate explicit daily behaviour of individuals, but the cumulative effects of resource use and competition in space in combination with foraging behaviour (with corresponding movement costs).

For each individual, all suitable grid cells are tested for their potential to serve as the centre of a circular home range. Assuming periodic boundary conditions grid cells are added to the home range with increasing distance to the possible core cell. Cells are added and the mammal can gain energy from these cells until the daily energy requirement of the animal is

fulfilled. The latter is calculated as the daily field feeding rate FR. After Nagy (2001) this rate scales for all mammals as

$$FR = 0.055 \times M^{0.74} \quad (\text{kg dry biomass} \times \text{day}^{-1}, M \text{ in kg}). \quad (\text{A1.2})$$

Daily energy gain of an individual IG_i in each cell i is calculated as the part of the daily productivity in each grid cell which is available to the community R_i (note that generally only 20% of the biomass that is produced daily is available to the community for consumption, see ‘5. Initialization’) multiplied by a factor PI. This factor accounts for the part of the available resources in a cell that is exploited on daily average by the individual in case of home range establishment.

$$IG_i = R_i \times PI \quad (\text{kg dry biomass}). \quad (\text{A1.3})$$

The factor PI for individual resource use is implemented to vary with body mass:

$$PI = \gamma_{PI} \times \frac{M^{-0.25}}{0.001 \text{kg}^{-0.25}} \quad (M \text{ in kg}), \quad (\text{A1.4})$$

where the coefficient γ_{PI} , determining the general magnitude of PI, is a systematically tested model parameter. The denominator ($0.001 \text{kg}^{-0.25}$) was chosen to ensure that PI varies between 0 and 1. Such allometric variation of individual resource availability is discussed in the context of the allometry of home range size (e.g. Holling et al. 1992, Haskell et al. 2002, Buchmann et al. 2011).

The net energy gain of individuals IGN_i in each cell i is calculated as

$$IGN_i = IG_i - LC_i \quad (\text{kg dry biomass}), \quad (\text{A1.5})$$

where LC_i , are the locomotion costs of travelling to cell i . Allometric relations for movement costs per unit distance MC are taken from Calder (1996):

$$MC = 10.70 \times M^{0.68} \quad (\text{J} \times \text{m}^{-1}, M \text{ in kg}). \quad (\text{A1.6})$$

We convert MC into the locomotion cost LC_i of reaching grid cell i , using

$$LC_i = \frac{DC_i \times MC}{f} \quad (\text{kg dry biomass}), \quad (\text{A1.7})$$

where DC_i is the average movement distance that has to be travelled on daily average to access resources from this home range cell i (for simplicity and better readability in the paper we only use ‘DC’ for this measure there). As conversion factor f , to express movement costs as equivalent amount of dry biomass, we use $1.00 \times 10^7 \text{ J} \times \text{kg dry biomass intake}^{-1}$, given in Nagy (2001) for non-fermenting herbivores. The method of determining DC_i , the average

daily movement distance for each home range cell, distinguishes three fundamentally different foraging movement types (see next section ‘7.2. Submodel: Foraging movements’).

Cells are sequentially added to the potential home range with increasing distance to the core cell until the animal is satiated ($\sum \text{IGN} \geq \text{FR}$), or until the required area exceeds a maximum home range size. We calculate this upper limit for each body mass as the maximum of the two equations

$$\text{HR}_{\text{max-herb}} = 56.23 \times M^{0.91} \quad (\text{ha, } M \text{ in kg}), \text{ and} \quad (\text{A1.8})$$

$$\text{HR}_{\text{max-omn}} = 47.86 \times M^{1.18} \quad (\text{ha, } M \text{ in kg}), \quad (\text{A1.9})$$

given in Kelt and Van Vuren (2001) as the maximum of a constraint space of home range area for herbivores (Eq. A1.8) and omnivores (Eq. A1.9) (both groups can be assumed to consume the primary production in the model).

If a potential home range fulfils an animal’s resource requirements within this limit, the algorithm records the area and location of this potential home range. Once all suitable cells have been tested as home range centre, the animal settles in the smallest possible home range. This settling means that resources are depleted by IG_i in each grid cell within the home range.

7.2. Submodel: Foraging movements

We distinguish three different general models of foraging behaviour. They differ with respect to the distance (DC_i) which is accounted for movement costs (see eq. A1.6 and A1.7) for integrating any resource patch (landscape grid cell i) into the home range.

7.2.1. Central place forager (CPF)

For this movement approach DC_i (the ‘cost effective distance’ of each home range cell) is calculated as the distance from the respective home range cell (which is added to the home range) to the home range centre. Such implementation can be regarded to represent well central place foragers (CPF), but also other mammals that live in dens or have nests, at least during certain time periods, for example while raising young, and which therefore have a strong focus on one central place in their home range which is visited very frequently (Owen-Smith et al. 2010). This approach was initially proposed by Mitchell and Powell (2004) and was already successfully used in a previous modelling framework to predict community structure, specifically the allometric scaling of home range size and individual abundance (Buchmann et al. 2011). In analogy to this study, the approach is here implemented only

considering suitable grid cells during the home range search, i.e. animals are assumed to not spend energy to go to a cell if this cell does not provide any resources.

7.2.2. Patrolling forager (PF)

A contrasting alternative foraging movement strategy is implemented by calculating the ‘cost-effective distance’ DC_i for each home range cell as the average distance from neighbouring cells (i.e. 1.207 grid units or 12.07 m). This approach reflects animals that are patrolling their home range, without frequently returning to the central place, but which are feeding ‘on the way’. In this movement model of a ‘patrolling forager’ (PF), all grid cells (including non-productive) are considered for the home range search (the non-productive bear costs without providing resources), because on such a patrolling forage trip, non-productive cells are also assumed to be visited.

7.2.3. Body mass dependent nomadic forager (BNF)

This BNF foraging movement approach considers the body mass dependence of daily movement distance (DMD). Therefore, the sum of the ‘cost-effective distances’ of all home range cells ($\sum DC_i$), i.e. the total distance that is accounted for locomotion costs on daily average for any individual, shall follow the same relationship with body mass as the one found for DMD of non-carnivores (Garland 1983). This is achieved by modifying the PF approach by calculating DC_i as

$$DC_i = \frac{\text{daily accounted distance}}{\text{number of cells } i \text{ in home range}} . \quad (\text{A1.10})$$

As numerator of this equation, we use Garland’s (1983) allometric equation. The denominator we calculate by combining reported allometric relationships for home range size of mammals (the mean of coefficients and exponents; herbivores and omnivores: Harestad and Bunnell 1979, Ottaviani et al. 2006; herbivores: Holling 1992).

Thus, in our modelling context equation A1.10 translates to

$$DC_i = \frac{(875 \text{ m} \times M^{0.22})}{(1107 \text{ cells } i \times M^{1.05})} = 0.79 \times M^{-0.83} \quad (\text{in meter per cell, } M \text{ in kg}). \quad (\text{A1.11})$$

7.3. Submodel: Community saturation

Individual mammals get assigned a body mass drawn from the input distribution and a home range search is performed. In case of home range establishment of individuals the community

grows and resources in the landscape get more and more reduced. The amount of resources consumed by the community shows a saturation response with model runtime (comparable to the saturation response of the number of animals in the community shown by Buchmann et al. 2011, however, saturating even more quickly). Simulations were executed (i.e. animals were drawn from the input distribution and for each, a home range search was performed) until 5,000 consecutive individuals were unable to establish a home range (because the resources in the landscape were already too low). This value could be safely assumed to represent 100% saturation, since no more change of the amount of consumed resources could be recognized, already at lower values than 5,000. The respective amount of consumed resources was thus used (as 100%) to calculate the resource level corresponding to the community saturation aimed for in simulation scenarios (e.g. 95%), which was then used as termination criterion for these simulations.

Appendix 2: Model validation and sensitivity analysis

Figure A2.1 shows that model predictions for the vast majority of scenarios agree well with empirical data, independently of the foraging movement model applied. For simulations investigating the effect of habitat loss on community structure, we used values of the two major model parameters ($\gamma_{PI} = 0.04$ and $SAT = 0.95$) that lead to good agreement between model predictions and independent data (allometry of home range size: Harestad and Bunnell 1979, Ottaviani et al. 2006, Holling 1992, exponent of ISD: Burbidge and McKenzie 1989, Brown and Nicoletto 1991, for derivation of values see Buchmann et al. 2011). Model responses to variation in these two parameters are discussed in detail in Buchmann et al. 2011. Variation in DC allometry (to account for considerable variability in the data of daily movement distance and home range size, see Methods) has a negligible effect on model predictions (Fig A2.1).

The caveat for the BFN movement model is that allometric scaling of home range size is needed as an input to calculate DC. Technically, the model may therefore not be used to predict allometric relationships of home range size. Results of home range scaling produced by this model and the sensitivity of these results to model parameters were, however, not markedly different from the results of the PF movement model. The fact that BNF and PF movement models only differ with respect to a body mass dependent factor for DC indicates that the body mass dependent implementation of DC only affects body mass composition of the community and its reaction to habitat loss, but not the home ranges of individuals.

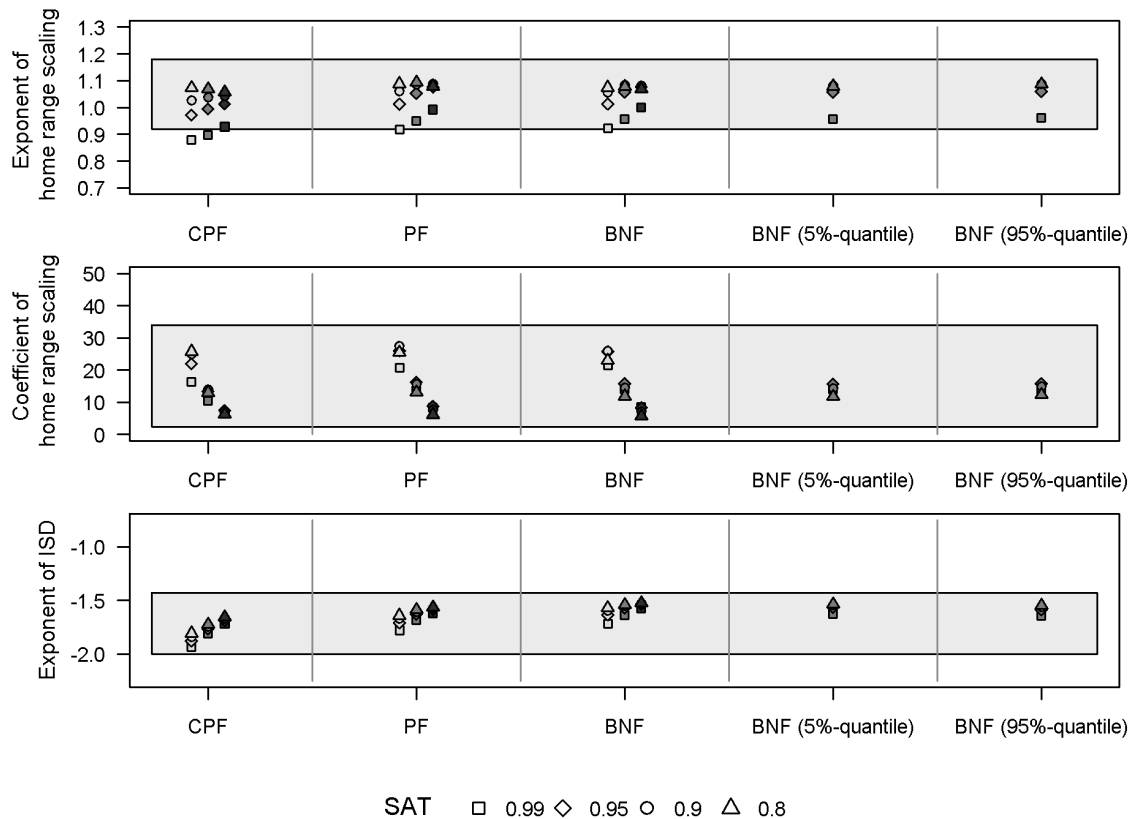


Figure A 2.1. Validation and sensitivity analysis of the allometric community model of individual home range formation with three different foraging strategies (central place forager CPF, patrolling forager PF and body mass dependent nomadic forager BNF) and of variation of the allometric equation of DC (the locomotion cost-effective distance for each home range grid cell, see Methods) for the BNF model ($S = 0.15$, $H = 0.5$, in analogy to Buchmann et al. 2011). Model results are shown for three major output variables characterizing the allometry of home range size and the exponent of the individual size distribution (ISD) of the community, predicted by the model. Symbols characterize different community saturation SAT (legend) and grey scale values stand for the coefficient of the allometric equation of individual resource availability γ_{PI} (light grey 0.02, medium grey 0.04, and dark grey 0.08, for the effect of variation of DC calculation only γ_{PI} of 0.04 was tested). Grey boxes show the range of comparable empirical data for mammals (allometry of home range size: Harestad and Bunnell 1979, Ottaviani et al. 2004, Holling 1992, exponent of ISD: Burbidge and McKenzie 1989, Brown and Nicoletto 1991, for derivation of values see Buchmann et al. 2011).

References

- Brown, J. H. and Nicoletto, P. F. 1991. Spatial scaling of species composition - body masses of north-american land mammals. - *Am. Nat.* 138: 1478-1512.
- Burbidge, A. A. and McKenzie, N. L. 1989. Patterns in the modern decline of Western Australia's vertebrate fauna: causes and conservation implications. - *Biol. Conserv.* 50: 143-198.

Appendix 3: Exemplary individual size distributions (ISD) of simulated communities

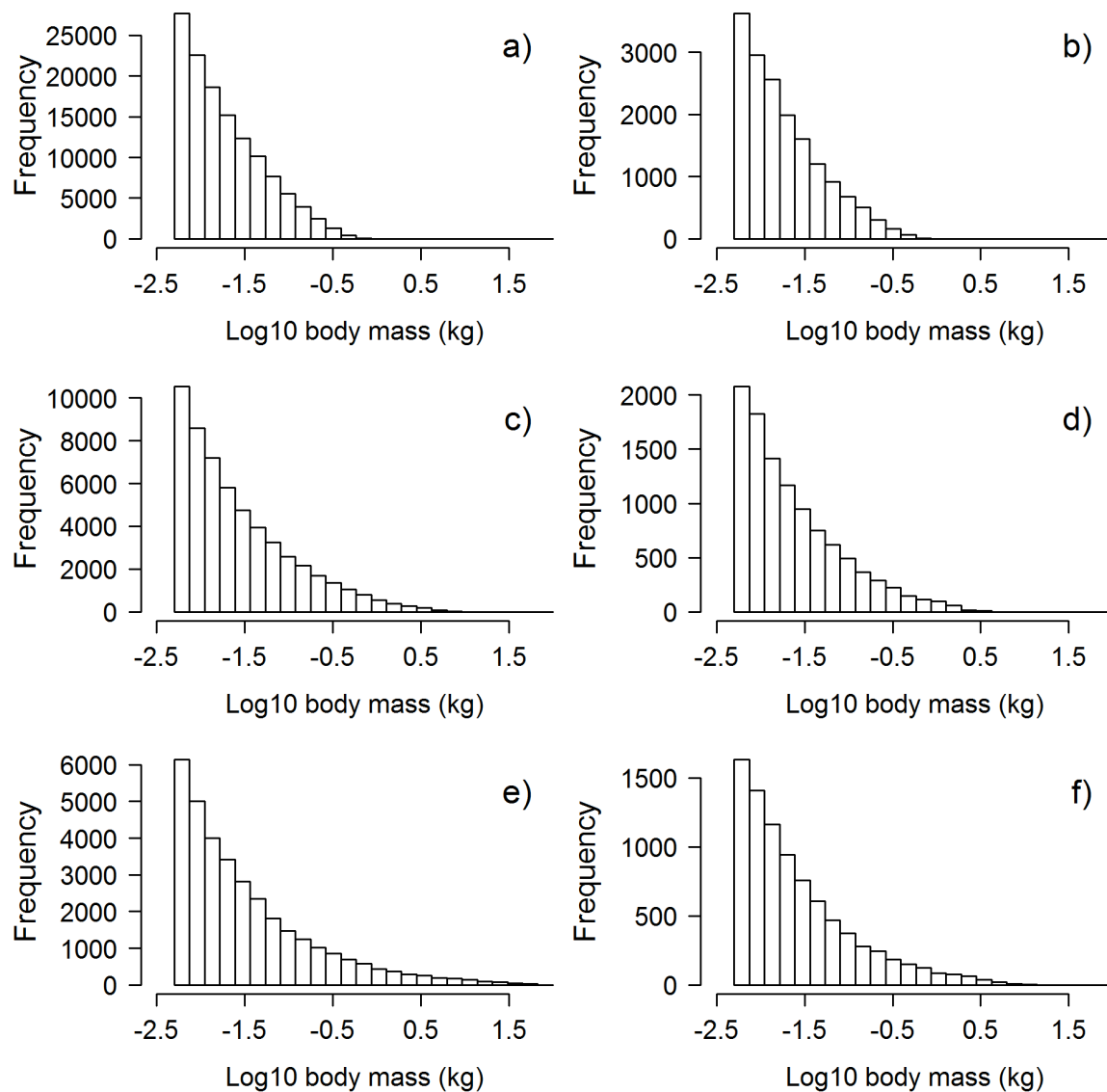


Figure A3.1. Sample individual size distributions (ISD) of simulated communities: left column: suitable area 75%, right column: suitable area 10%; a and b) central place forager CPF, c and d) patrolling forager PF, e and f) body mass dependent nomadic forager BNF.