

1 **Information use during movement regulates how fragmentation and loss of**
2 **habitat affect body size.**

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23

24 **Abstract**

25 An individual's body size is central to its behavior and physiology, and tightly linked to its dispersal
26 ability. The spatial arrangement of resources and a consumer's capacity to locate them are therefore
27 expected to exert strong selection on consumer body size.

28 We investigated the evolutionary impact of both the fragmentation and loss of habitat on consumer
29 body size and its feedback effects on resource distribution, under varying levels of information use
30 during the settlement phase of dispersal. We developed a mechanistic, individual-based, spatially
31 explicit model, including several allometric rules for key consumer traits. Our model reveals that as
32 resources become more fragmented and scarce, informed settlement selects for larger body sizes while
33 random settlement promotes small sizes. Information use may thus be an overlooked explanation for
34 the observed variation in body size responses to habitat fragmentation. Moreover, we find that
35 resources can accumulate and aggregate if information on resource abundance is incomplete. Informed
36 movement results in stable resource-consumer dynamics and controlled resources across space.
37 However, habitat fragmentation and loss destabilize local dynamics and disturb resource suppression
38 by the consumer. Considering information use during movement is thus critical to understand the eco-
39 evolutionary dynamics underlying the functioning and structuring of consumer communities.

40

41 **Keywords:** allometry, metabolic theory, body size distributions, eco-evolutionary dynamics, habitat
42 destruction, optimal size

43 **Background**

44 Habitat fragmentation and loss pose severe threats to size diversity at the population and community
45 level, affecting size distributions. Eventually, shifts in size distributions impact ecosystem dynamics
46 (incl. fluxes of nutrients) and functioning [1,2]. As such, a better understanding of the impact of
47 habitat fragmentation and loss on body size distribution through selection is crucial [3].

48 An organism's body size is one of its most comprehensive characteristics. Because of the $\frac{3}{4}$ -scaling
49 rule with metabolic rate, body size is strongly correlated with an array of functional traits, such as
50 ingestion rate, movement speed and developmental time [4,5]. As such, body size represents the
51 outcome of several selective pressures acting on different life history traits, setting boundaries to the
52 ecology, physiology and functioning of an individual [4]. Body size distributions within communities
53 additionally affect intra- and interspecific interactions, important higher-level properties of food webs,
54 and ecosystem functioning [6–9]. Overall, body size can be considered a universal trait constraining
55 ecological and evolutionary dynamics [10,11].

56 Body size distributions are strongly determined by the availability of resources and their distribution
57 across space [12–17]. Hollings' textural discontinuity hypothesis even states that the modes of a body
58 size distribution reflect the foraging scales with the highest resource amounts [15–19]. As habitat
59 fragmentation and destruction progress, the spatial distribution of resources is altered, yet the
60 consequences for (future) body size distributions are unclear. On the one hand, large-bodied
61 individuals may be selected as they have high starvation resistance and are able to cover large
62 distances [4,20,21]. On the other hand, small-sized individuals may have the benefit of short
63 developmental times and low energy requirements [4]. Empirical studies illustrate positive [22–24],
64 negative [25,26] or insignificant [20] effects of fragmentation on average body size within
65 populations. At the community level, shifts in species abundances and therefore size distributions
66 strongly depend on taxonomical group [27]. Despite this variation in empirical results and the absence
67 of a consensus in theoretical work, several theoretical studies have acknowledged a strong dependency
68 of size distributions on habitat configuration [12,28–31]. Habitat fragmentation and loss are
69 considered two distinct processes [32]. Habitat loss results in a decreased percentage of suitable

70 habitat, whereas habitat fragmentation implies a decrease in its spatial autocorrelation [32]. Most
71 experimental studies focus on their joint effect using the term ‘fragmentation’ or ‘landscape
72 simplification’, without assessing the effects of each of these processes independently (e.g. [20,24–
73 27,33] (but see [23] for an exception). This is surprising as the effect of spatial autocorrelation is
74 highest, and therefore most relevant, in landscapes with low percentages of suitable habitat [32].
75 Furthermore, most fragmentation studies focused on mammals and birds and were therefore performed
76 at large spatial scales [34,35]. However, small spatial scales are most important for arthropods that do
77 not disperse via the air or by flying [27,34]. Still, only few empirical studies have investigated changes
78 in arthropod size distributions at such scales (e.g. [20], exception: [27]).

79 Not only resource availability, but also the type of movement and dispersal regulate how populations
80 and communities are spatially structured [36]. High movement frequencies result in spatially coupled
81 populations, whereas low frequencies result in classic metapopulations or -communities [37].
82 Furthermore, movement behavior not only depends on an individual’s body size but also on the
83 information perceived during movement, which enables individuals to continuously update decisions
84 on how far to move and where to settle [38]. The available information differs between organisms,
85 depending on the complexity of their senses. As proven by theoretical studies, some degree of
86 informed settlement already strongly affects spatial dynamics and coexistence compared to random
87 walk [39,40]. Therefore, the effect of informed movement should be incorporated in studies focusing
88 on movement ecology [41].

89 We designed an individual-based, spatially explicit model to study the effect of habitat configuration
90 on the body size distribution of a population or community of arthropods. As the level of information
91 perceived during movement is crucial for movement and therefore body size evolution, we
92 investigated a possible interaction with this trait. We applied a mechanistic approach by incorporating
93 established allometric rules linking body size with movement speed, movement costs, basal metabolic
94 rate, ingestion rate, developmental time, and clutch size into our model. Due to the universal nature of
95 these allometric rules, our conclusions on the effects of fine-grained fragmentation may apply to a
96 wide range of taxa [5].

97 **Methods**

98 The applied model is a spatially explicit, discrete-time model with overlapping generations. One time
99 step corresponds to one day within the lifetime of the consumer. We here took an arthropod-centered
100 approach and parameterized allometric rules for a haploid, parthenogenetic arthropod species feeding
101 on plants (the resource), with a semelparous lifecycle. See table S1.1 for an overview of all
102 parameters applied within the model.

103 **The landscape**

104 The landscape is a cellular grid of 100 by 100 cells and is generated using the Python package NLMpy
105 [42]. Each cell within the landscape has a side length (SL) of 0.25 m and therefore a total surface of
106 0.0625 m^2 . Within the landscape, a distinction is made between suitable and unsuitable habitat. Only
107 within suitable habitat, the resource is able to grow. When testing the effect of landscape
108 configuration, the proportion of suitable habitat (P) and habitat autocorrelation (H) were varied
109 between landscapes. Habitat availability increases with P , whereas habitat fragmentation decreases
110 with H . The following values were assigned to P : 0.05, 0.20, 0.50 or 0.90. H equaled either 1 (in all
111 four cases), 0.5 (when P equaled 0.05 or 0.20) or 0 (when P equaled 0.05). As such, highly fragmented
112 landscapes with a high amount of suitable habitat were not included in the analysis as these rarely
113 occur in nature [43].

114 **The resource**

115 Resources are not individually modeled but by a logistic growth model for each habitat cell. Local
116 resource biomass is represented as the total energetic content of resource tissue within that cell ($R_{x,y}$ in
117 joules). This resource availability grows logistically in time depending on the resource's carrying
118 capacity (K) and intrinsic growth rate (r). In any cell, a fixed amount of resource tissue (E_{nc} , in Joules,
119 fixed at I J) is non-consumable by the consumer species, representing below-ground plant parts. As
120 such, E_{nc} is the minimum amount of resource tissue present within a suitable cell, even following local
121 depletion by the consumer species.

122 **The consumer**

123 All consumers are individually modelled within the landscape. The consumer has two life stages: a
124 juvenile and adult life stage. Within a day, both stages have the chance to execute different events (see
125 Figure 1).

126 First, an individual nourishes its energy reserve by consumption. Second, the energy reserve is
127 depleted by the cost of daily maintenance (i.e. basal metabolic rate) and the cost of movement. To
128 assess the effect of informed settlement on our results, three different types of movement (see below)
129 were implemented within the model. Third, juveniles may further deplete the energy reserve by
130 growth, eventually resulting in maturation if they approximate their adult size (W_{max}). Resources that
131 were not utilized are stored within the energy reserve. Adults can only reproduce if their internally
132 stored energy (E_r) exceeds a predefined amount. As the consumer species is semelparous, adults die
133 after reproduction. How body size affects each of these events is explained in supplementary material
134 part 1.

135 Individual body size at maturity (W_{max} , in kg) is coded by a single gene. Adult size is heritable and
136 may mutate with a probability of 0.001 during reproduction. A new mutation is drawn from the
137 uniform distribution [$W_{max} - (W_{max}/2)$, $W_{max} + (W_{max}/2)$] with W_{max} referring to the adult size of the
138 parent. New mutations may not exceed the predefined boundaries [0.01g, 3g] that represent absolute
139 physiological limits. As such, our minimum adult size corresponds to the size of a small grasshopper
140 such as *Tetrix undulata* (0.01 g) and the maximum size (3 g) to that of some longhorn beetles
141 (Cerambycidae), darkling beetles (Tenebrionidae), scarab beetles (Scarabaeidae) or grasshoppers
142 (Acrididae). New variants of this trait may also originate by immigration (see further). Mutation
143 enables fine-tuning of the optimal body size, whereas immigration facilitates fitness peak shifts.

144 **The movement phase**

145 *Emigration rate*

146 Whether an individual moves depends on the ratio of the amount of energy present within a cell
147 ($R_{x,y}$) relative to the maximum amount of energy that can be consumed by all consumers present

148 within that cell. This latter factor is determined by calculating the sum of all individuals' daily
149 ingestion rates within that cell ($\sum i_{max_{x,y}}$).

150 By assuming a symmetric competition, the probability of moving (p) is equal for all individuals
151 present within the same cell and is calculated by (based on [44]) :

$$152 \quad p = 1 - \frac{R_{x,y}}{\sum i_{max_{x,y}}} \quad \text{if } \frac{R_{x,y}}{\sum i_{max_{x,y}}} < 1 \quad (\text{eq. 1})$$

$$153 \quad p = 0 \quad \quad \quad \text{if } \frac{R_{x,y}}{\sum i_{max_{x,y}}} \geq 1$$

154

155 *Determining cell of destination*

156 As one time step in our model corresponds to one day, we do not model the movement behavior of an
157 individual explicitly but instead, estimate the total area an individual can cover during a day in search
158 for resources. This total area an individual can search during a day is called its foraging area which is
159 circular and is defined by a radius (*rad*, see further). The center of an individual's foraging area
160 corresponds to its current location. Overall, the size of an individual's foraging area increases with its
161 size [4,21] and is recalculated daily by taking into account an individual's optimal speed (v_{opt}),
162 movement time (t_m) and perceptual range (d_{per}). The cost of movement includes the energy invested
163 by an individual in prospecting its foraging area, and is therefore independent of the final cell of
164 destination.

165 An individual's average speed of movement (v_{opt} , in meters per second) is calculated by means of the
166 following allometric equation, derived for walking insects [4,45]:

$$167 \quad v_{opt} = 0.3 \cdot W^{0.29} \quad (\text{eq. 2})$$

168 With W referring to the weight of an individual in kg, not including the energy stored in its energy
169 reserve. The time an individual invests in movement per day (t_m , in seconds) is maximally 1 hour. In
170 case too little internally stored energy (E_r) is present to support movement for one hour, t_m is
171 calculated by:

172
$$t_m = \frac{E_r}{c_m} \text{ (eq. 3).}$$

173 c_m refers to the energetic cost of movement (in joules per second) and is calculated by the following
174 formula, which is based on running poikilotherms [4,45]:

175
$$c_m = (0.17W^{0.75} + 3.4W) \text{ (eq. 4).}$$

176 Independent of the cell of destination, the cost of moving during the time t_m ($t_m \cdot c_m$) is subtracted from
177 an individual's energy reserve. Based on t_m and v_{opt} , the total distance an individual covers at day t
178 (d_{max}) is determined:

179
$$d_{max} = v_{opt} \cdot t_m \text{ (eq. 5)}$$

180 Next, the perceptual range of an individual is determined by means of the following relationship:

181
$$d_{per} = 301W + 0.097 \text{ (eq. 6)}$$

182 For simplicity, this relationship is linear and based on the assumption that the smallest individual
183 (0.01g) has a perceptual range of 0.10 m and the largest individual (3g) a perceptual range of 1m. The
184 effect of this relationship has been tested (see supplementary material part 4). Moreover, the positive
185 relationship between body size and perceptual range or reaction distance has been illustrated over a
186 wide range of taxa, including arthropods (supplementary information of [46]).

187 The foraging area of an individual is circular and its radius (rad , in m) is calculated by taking into
188 account the total distance the individual has covered during the day and the individual's perceptual
189 range (see supplementary material part 2 for an explanation of this formula):

190
$$rad = \sqrt{\frac{2 \cdot d_{max} \cdot d_{per} + \pi \cdot d_{per}^2}{\pi}} \text{ (eq. 7).}$$

191 In order to avoid artifacts of applying the continuous variable rad to a grid-based landscape, a random
192 value drawn from the following uniform distribution, $[-0.5 \cdot SL, 0.5 \cdot SL]$, is added to rad .

193 The selection process for finding a new location within this foraging area depends on the selective
194 ability of the individual. Here, we make a distinction between three types of selection procedures
195 during movement.

196 *Case 1- Uninformed movement*

197 Within this scenario, movement is completely uninformed. As such, no distinction can be made
198 between matrix and habitat. Within the foraging area, the new location is randomly sampled.

199 *Case 2- Partially informed movement*

200 Here, an individual is able to distinguish matrix from habitat and will always prefer the latter above
201 the former. An individual will sample its location randomly from the suitable cells within its foraging
202 area.

203 *Case 3- Informed movement*

204 Here, an individual moves to the cell with the highest amount of resources within its foraging area.

205 **Immigration**

206 The frequency with which immigrants arrive in the landscape is described by q . This variable is fixed
207 at one per 100 days. The process of determining an immigrant's adults size is similar as during
208 initialization (see below). An immigrant is always introduced within a suitable cell and its energy
209 reserve contains just enough energy to survive the first day.

210 **Metapopulation and metacommunity perspective**

211 By applying an individual-based approach, we were able to include intra-specific size variation and
212 stochasticity within our model. This approach in conjunction with the assumption of asexual
213 reproduction and equivalent ontogenetic and interspecific scaling exponents [47,48], implies that our
214 results can be interpreted both at the metapopulation and metacommunity level.

215 **Initialization:**

216 Per parameter combination, 10 simulations were run. At the start of a simulation, adult individuals
217 were introduced with an average density of two individuals per suitable cell. The adult weight of each

218 individual (W_{max}) was determined by drawing the value for $\log(W_{max})$ from an even distribution
219 between -5 and -2.522878745. Also, each initialized individual carried enough energy within its
220 energy reserve to survive the first day. Initial resource availability per cell corresponded to the
221 maximum carrying capacity. Because of computational limitations, total runtime differed between
222 simulations. For an overview, see supplementary material part 3.

223 Data analysis

224 During each simulation, we traced changes in the mean amount of resources per cell, total number of
225 adults and juveniles, average adult weight (W_{max}) and the coefficient of variation, skewness, and
226 kurtosis of the consumer's adult weight (W_{max}) distribution. Every 500 time steps, the value of W_{max} of
227 maximum 50 000 randomly sampled individuals was collected.

228 Variability

229 In order to infer the temporal stability of the community at different scales we calculated the α , β_2 and
230 γ variability for each simulation run. This calculation is based on samples of total consumer biomass
231 every 10 time steps during the final 100 time steps of a simulation within 100 pre-selected, suitable
232 cells. α variability is a measure of the local temporal variability and is calculated by

$$233 \quad \alpha_{CV} = \left(\frac{\sum_m \sqrt{w_m}}{\sum_m \mu_m} \right)^2 \text{ (eq. 8)}$$

234 with w_m referring to the temporal variance and μ_m to the temporal mean of population or community
235 consumer biomass in cell m [49]. The temporal variability at the metapopulation or metacommunity
236 scale or γ variability was calculated by:

$$237 \quad \gamma_{CV} = \frac{\sum_{m,n} w_{mn}}{(\sum_m \mu_m)^2} \text{ (eq.9)}$$

238 with w_{mn} referring to the temporal covariance of population or community biomass between cells m
239 and n [49]. Finally, β_2 variability or asynchrony-related spatial variability was determined by:

$$240 \quad \beta_2 = \alpha_{CV} - \gamma_{CV} \text{ (eq. 10).}$$

241

242 Reproductive success and movement

243 Throughout the final 600 days of a simulation, 1000 eggs were randomly selected to be followed
244 during their lifetime. The movements and reproductive success of the resulting consumer individuals
245 were recorded.

246 Sensitivity Analysis

247 A thorough sensitivity analysis was conducted. See supplementary material part 4 for an overview of
248 the tested parameters and their effects.

249 Results

250 A clear interaction with information use is observed when studying the effect of habitat fragmentation
251 and loss on the average body mass of a consumer population or community (Fig 2). Individuals are
252 larger with increasing loss of habitat when movement is fully informed (Fig 2). This effect is enforced
253 by increasing habitat fragmentation (Fig 2). When P equals 0.05, $H=0$ and movement is informed,
254 15% of the population does not belong to the smallest size class. Although these larger individuals are
255 lower in abundance than the smallest individuals, they represent a large fraction of total consumer
256 biomass (60%). In contrast, average body mass decreases with habitat fragmentation when movement
257 is uninformed (Fig 2). No clear pattern is observed when movement is partially informed. Still,
258 individuals tend to be smallest within the landscape type with P equaling 0.05 and $H=1$ and small
259 individuals do not occur when P equals 0.05 and $H=0$ (Fig 2 & 3). When comparing body sizes
260 between movement types, individuals with informed movement are the smallest (Fig 2).

261 The narrowest body size distributions, reflected by the high level of kurtosis, occur in the landscapes
262 with high percentages of suitable habitat (P equaling 0.50 or 0.90) when movement is informed (Fig 3
263 and S5.4). Overall, most distributions are right-skewed, except for the distributions with partially
264 informed movement, which tend to be neutrally skewed (Fig 3 and S5.11). Because the uninformed

265 and partially informed strategy become identical when P approaches one, body size distributions are
266 similar when movement is partially informed or uninformed when P equals 0.9 (Fig 3).

267 As informed movement results in the selection of the smallest individuals, the highest abundances are
268 observed in these simulations (Fig S5.9). Also, the chance of moving during a day is largest when
269 movement is informed (Fig S5.5). Large individuals can occur in all landscape types when movement
270 is partially informed and in landscapes with a high percentage of suitable habitat when movement is
271 uninformed. Total lifetime is longest in those simulations having the largest individuals (Fig S5.8). As
272 large individuals move further than small individuals (Fig S5.6), their total distance covered during
273 one lifetime is also larger (Fig S5.7).

274 At the local and inter-patch scale, temporal variability of total consumer biomass is highest when
275 movement is informed (Fig S5.1 and S5.2). However, at the landscape scale, no clear distinction
276 between movement types in temporal variability is observed (Fig S5.3). Still, the landscape type with
277 $P = 0.05$ and $H = 1$ is most variable at the landscape scale when movement is uninformed or partially
278 informed (Fig S5.3). This explains why two out of the ten simulations with partially informed
279 movement went extinct for this landscape type.

280 Finally, when movement is informed, resource and consumer dynamics at the landscape scale are very
281 stable (Fig S7.5). During a simulation, resources are always spread according to a consistent,
282 homogeneous pattern within the landscape (Fig S7.2). On the contrary, when movement is uninformed
283 or partially informed, resource and consumer dynamics fluctuate strongly in time (Fig S7.1). In
284 addition to these temporal fluctuations, resources are either homogeneously (Fig S7.4) or
285 heterogeneously (Fig 7.3) distributed in space. In some simulations, fluctuations in spatial resource
286 dynamics (homogeneous or heterogeneous spread of resources) correspond with shifts in average size
287 of the consumer (Fig S7.8). However, this is not always the case (Fig S7.9). When movement is
288 informed, resources are only heterogeneously distributed when the landscape is strongly fragmented
289 and contains a low percentage of suitable habitat (Fig S7.6). In this case, resource and consumer
290 dynamics are more unstable (Fig S7.7).

291 Discussion

292 Several theoretical models have investigated how consumer-resource dynamics are affected by
293 nonrandom settlement [39,40], body size distributions [8,14,31,50], spatial habitat configuration [51–
294 54], and more specifically, landscape fragmentation [55]. However, only a few studies combined these
295 research interests in an integrated manner [12,29,30]. Our study is unique as it investigates how body
296 size distributions of a consumer population or community evolve in response to landscape
297 fragmentation and habitat loss, while taking into account the level of informed settlement.

298 Our model provides a mechanistic understanding of optimal body size distributions and shows that
299 individuals should become larger with increasing fragmentation and loss of habitat when movement is
300 informed, smaller when movement is uninformed and be almost invariant when movement is partially
301 informed. Information use during settlement has a critical impact as it is related to multiple costs
302 during dispersal [56]. When movement is informed, individuals should be able to trace resource
303 availability within the landscape, preventing local resource accumulation. This is in line with our
304 observation that overall, average resource amounts are lowest when movement is informed (Fig
305 S5.10). As such, informed movement results in stable resource amounts and consumer numbers at the
306 landscape scale (Fig S7.5). If resources are homogeneously distributed in space, even small
307 individuals are guaranteed to find resources within their proximity if they are capable of informed
308 movement. As these small individuals have the shortest developmental time, they have a large
309 selective advantage over large individuals and dominate the population when P is high. When P is
310 low, and especially when H is low as well, a small but stable number of large individuals are able to
311 coexist within the landscape as only large individuals are able to trace isolated patches with resources.
312 These patches are out of reach for the smallest individuals, which remain within non-isolated patches.
313 The sensitivity analysis highlights that when the relative mobility of the smallest individuals is
314 decreased, only larger individuals survive when P and H are low; these findings highlight the role of
315 the trade-off associated with body size with regard to movement (efficiency) and metabolic efficiency.
316 Our finding contradicts that of another theoretical study by Buchmann (2013) [29], who concluded
317 that habitat destruction and fragmentation resulted in a relatively higher frequency of small individuals

318 of mammals and birds. Assuming that mammals' and birds' movement is informed, we predict the
319 opposite pattern. This inconsistency may result from differences in model design as their model did
320 not include any resource-consumer dynamics and therefore local colonization-extinction events, which
321 are crucial in shaping body size distributions. Moreover, it did not link body size with developmental
322 time, which drives the selection of small individuals.

323 On the contrary, when movement is implemented as uninformed or partially informed, individuals do
324 not observe local resource quantity, allowing for resources to accumulate. This results in
325 heterogeneous spatial distributions of the resource. Moreover, resource and consumer dynamics
326 fluctuate strongly in time when movement is not informed (Fig S7.1). When few resources are
327 available within the landscape with large P , there is selection in favor of those individuals that can
328 reach these few patches with resources first (Fig S7.11). Therefore, large individuals can invade the
329 population or community resulting in large-sized equilibria. However, when resources are highly
330 abundant within the landscape, small-sized individuals can reinvade as they have the shortest life cycle
331 and increase fastest in number (Fig S7.10), shifting the equilibrium towards small-sized individuals
332 again. Hence, when P is high, a dynamic equilibrium involving two alternative states is observed: one
333 state with small individuals and one state with large individuals [57]. These shifts do not occur when
334 immigration from outside the landscape is turned off, which highlights the significance of immigration
335 as a mechanism maintaining fundamental genetic variance [3]. Some rate of immigration is realistic as
336 open communities are the rule rather than exception in nature [1,58].

337 When movement is uninformed, individuals decrease in size with decreasing levels of suitable habitat.
338 As large individuals move further, they have the highest chance of ending up outside suitable habitat.
339 This risk is even more elevated when the landscape is less autocorrelated, resulting in even smaller
340 individuals. When P equals 0.50 and movement is uninformed, the equilibrium with only small
341 individuals is almost never achieved. Probably, at this particular ratio of suitable versus unsuitable
342 habitat, gaps of unsuitable habitat are relatively easily crossed by large individuals whereas small
343 individuals rarely manage to cross such gaps (see supplementary material part 6). This mechanism
344 might be comparable to the mechanism allowing for emigration-mediated coexistence in food webs:

345 the competitive strength of a strong competitor is lowered by its emigration, enabling coexistence with
346 a weaker competitor [39].

347 In case of partially informed movement, no clear effect of habitat loss and fragmentation on body size
348 is visible. Still, average body weight is smallest when very few suitable cells are present and they are
349 strongly aggregated ($P = 0.05$, $H = 1$). Consequently, all cells are within reach of the smallest
350 individuals, lowering the advantage of large individuals. Only within this scenario, two out of ten
351 simulations went extinct, indicating that small individuals are vulnerable to extinction under these
352 circumstances. In this scenario, small individuals might go extinct as (i) they have low probability of
353 locating cells with high resource abundance (versus a scenario with informed movement) and (ii)
354 experience strong competition (versus a scenario with uninformed movement). These reasons also
355 explain why small individuals do not occur in any simulation in which the little available habitat is
356 spread widely across the landscape ($P = 0.05$ and $H = 0$), as then even fewer cells are reachable for the
357 smallest individuals. Therefore, large individuals invade the landscape as they can also access the
358 more isolated cells.

359 Type of movement not only has a large influence on resource distribution, but also on the spatial
360 structuring of populations or communities. When movement is informed, consumers move more often
361 than when movement is partially informed or uninformed. Movement events can either occur at faster
362 or slower rates than local food web dynamics, resulting in spatially coupled populations (e.g. foraging
363 behavior) or classic metapopulation dynamics (e.g. extinction, colonization events), respectively [59].
364 As such, we might conclude that patches have a higher tendency of being spatially coupled when
365 movement is informed, than when movement is partially informed or uninformed.

366 Our sensitivity analyses showed that our model results were robust. Only immigration rate and growth
367 speed of the resource affect the outcome. When the growth speed of the resource and thus productivity
368 is lowered, no large individuals are observed in any simulation and many simulations go extinct. As
369 large individuals need a minimum amount of resources to survive, they are no longer able to persist.
370 When immigration rate is deactivated, large individuals completely disappear in some scenarios (e.g.

371 when $P = 0.90$, $H = 1$ and movement is uninformed) as they occur at much lower abundances than
372 small individuals and are therefore more susceptible to drift. However, when large individuals remain
373 in a certain scenario without immigration, the strength of selection in favor of these large individuals
374 is illustrated.

375 **Conclusions**

376 Empirical inconsistencies in body size responses to habitat loss and fragmentation have so far been
377 attributed to differences in scale [22] and in the suitability of the matrix [27] and whether an
378 equilibrium was obtained (e.g. extinction time lags) [20]. Our model provides an alternative
379 explanation: the level of informed movement. Moreover, it highlights the relevance of not only habitat
380 loss but also of fragmentation, since the latter reinforces the effect of the former. Importantly, our
381 model reveals that habitat fragmentation and loss lead to a possible introduction of large individuals or
382 species when settlement is informed and a disappearance of large individuals when settlement is
383 uninformed. Our results are of great relevance to conservation management. Not only body size
384 distributions are affected by habitat fragmentation but also the distribution of resources (changing
385 from homogeneous to heterogeneous) and stability of consumer-resource dynamics (from stable to
386 unstable), implying an elevated extinction risk.

387 **Competing interests**

388 We have no competing interests.

389 **Authors' contributions**

390 DB, TH and JH conceived the ideas and designed methodology; JH designed the model; DB, MLV,
391 TH and JH analyzed the data; DB, MLV and JH led the writing of the manuscript.

392

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398 References

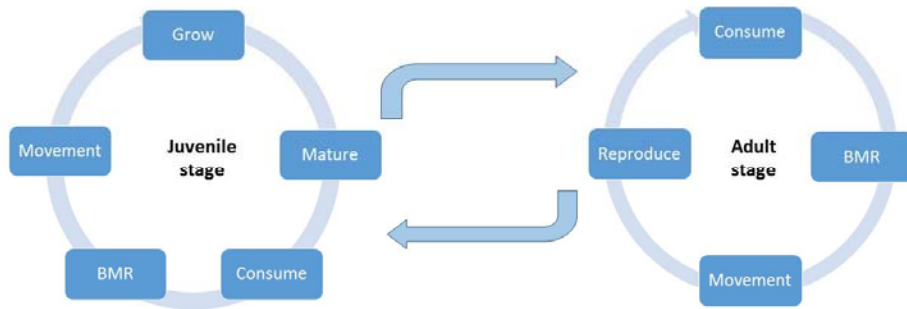
- 399 1. Gounand I, Harvey E, Little CJ, Altermatt F. 2017 Meta-Ecosystems 2.0: Rooting the Theory
400 into the Field. *Trends Ecol. Evol.* **xx**, 1–11. (doi:10.1016/j.tree.2017.10.006)
- 401 2. Séguin A, Harvey É, Archambault P, Nozais C, Gravel D. 2014 Body size as a predictor of
402 species loss effect on ecosystem functioning. *Nature* **4**, 4616. (doi:10.1038/srep04616)
- 403 3. Vellend M. 2010 Conceptual Synthesis in Community Ecology. *Q. Rev. Biol.* **85**, 183–206.
404 (doi:10.1086/652373)
- 405 4. Peters RH. 1983 *The ecological implications of body size*. Cambridge: Cambridge university
406 press. See <http://books.google.com/books?id=OYVxiZgTXWsC>.
- 407 5. Brown JH, Gillooly JF, Allen AP, Savage VM, West GB. 2004 Toward a metabolic theory of
408 ecology. *Ecology* **85**, 1771–1789. (doi:10.1890/03-9000)
- 409 6. Fritschie KJ, Olden JD. 2016 Disentangling the influences of mean body size and size structure
410 on ecosystem functioning: An example of nutrient recycling by a non-native crayfish. *Ecol.*
411 *Evol.* **6**, 159–169. (doi:10.1002/ece3.1852)
- 412 7. Yvon-Durocher G, Allen a. P. 2012 Linking community size structure and ecosystem
413 functioning using metabolic theory. *Philos. Trans. R. Soc. B Biol. Sci.* **367**, 2998–3007.
414 (doi:10.1098/rstb.2012.0246)
- 415 8. Brose U, Williams RJ, Martinez ND. 2006 Allometric scaling enhances stability in complex
416 food webs. *Ecol. Lett.* **9**, 1228–1236. (doi:10.1111/j.1461-0248.2006.00978.x)
- 417 9. Bartholomew G, Grinnell A, Jorgensen C, White F. 1982 Energy metabolism. In *Animal*
418 *Physiology: Principles and Adaptations*, pp. 57–110. New York: MacMillon.
- 419 10. Llandres AL, Marques GM, Maino JL, Kooijman SALM, Kearney MR, Casas J. 2015 A
420 dynamic energy budget for the whole life-cycle of holometabolous insects. *Ecol. Monogr.* **85**,
421 353–371. (doi:10.1890/14-0976.1)
- 422 11. Applebaum SL, Pan TCF, Hedgecock D, Manahan DT. 2014 Separating the nature and nurture
423 of the allocation of energy in response to global change. *Integr. Comp. Biol.* **54**, 284–295.
424 (doi:10.1093/icb/icu062)
- 425 12. Ritchie ME, Olff H. 1999 Spatial scaling laws yield a synthetic theory of biodiversity. *Nature*
426 **400**, 557–60. (doi:10.1038/23010)
- 427 13. Allen CR, Garmestani AS, Havlicek TD, Marquet PA, Peterson GD, Restrepo C, Stow CA,
428 Weeks BE. 2006 Patterns in body mass distributions: sifting among alternative hypotheses.
429 *Ecol. Lett.* **9**, 630–643. (doi:10.1111/j.1461-0248.2006.00902.x)

- 430 14. Milne BT, Turner MG, Wiens JA, Johnson AR. 1992 Interactions between the fractal geometry
431 of landscapes and allometric herbivory. *Theor. Popul. Biol.* **41**, 337–353. (doi:10.1016/0040-
432 5809(92)90033-P)
- 433 15. Holling CS. 1992 Cross-Scale Morphology, Geometry, and Dynamics of Ecosystems. *Ecol.*
434 *Monogr.* **62**, 447–502. (doi:10.2307/2937313)
- 435 16. Borthagaray AI, Arim M, Marquet PA. 2012 Connecting landscape structure and patterns in
436 body size distributions. *Oikos* **121**, 697–710. (doi:10.1111/j.1600-0706.2011.19548.x)
- 437 17. Nash KL, Allen CR, Barichiev C, Nyström M, Sundstrom S, Graham NAJ. 2014 Habitat
438 structure and body size distributions: Cross-ecosystem comparison for taxa with determinate
439 and indeterminate growth. *Oikos* **123**, 971–983. (doi:10.1111/oik.01314)
- 440 18. Gagné SA, Proulx R, Fahrig L. 2008 Testing Holling’s textural-discontinuity hypothesis. *J.*
441 *Biogeogr.* **35**, 2149–2150. (doi:10.1111/j.1365-2699.2008.02031.x)
- 442 19. Raffaelli D, Hardiman A, Smart J, Yamanaka T, White PCL. 2016 The textural discontinuity
443 hypothesis: An exploration at a regional level. Shortened version: Exploring Holling’s TDH.
444 *Oikos* **125**, 797–803. (doi:10.1111/oik.02699)
- 445 20. Davies KF, Margules CR, Lawrence JF. 2000 Which traits of species predict population
446 declines in experimental forest fragments? *Ecology* **81**, 1450–1461. (doi:10.1890/0012-
447 9658(2000)081[1450:WTOSPP]2.0.CO;2)
- 448 21. Tscharrntke T, Brandl R. 2004 Plant- Insect Interactions in Fragmented Landscapes. *Annu. Rev.*
449 *Entomol.* **49**, 405–430. (doi:10.1146/annurev.ento.49.061802.123339)
- 450 22. Warzecha D, Diekötter T, Wolters V, Jauker F. 2016 Intraspecific body size increases with
451 habitat fragmentation in wild bee pollinators. *Landsc. Ecol.* **31**, 1449–1455.
452 (doi:10.1007/s10980-016-0349-y)
- 453 23. Jauker B, Krauss J, Jauker F, Steffan-Dewenter I. 2013 Linking life history traits to pollinator
454 loss in fragmented calcareous grasslands. *Landsc. Ecol.* **28**, 107–120. (doi:10.1007/s10980-
455 012-9820-6)
- 456 24. Fietz J, Weis-Dootz T. 2012 Stranded on an island: consequences of forest fragmentation for
457 body size variations in an arboreal mammal, the edible dormouse (*Glis glis*). *Popul. Ecol.* **54**,
458 313–320. (doi:10.1007/s10144-012-0310-0)
- 459 25. Renauld M, Hutchinson A, Loeb G, Poveda K, Connelly H. 2016 Landscape Simplification
460 Constrains Adult Size in a Native Ground-Nesting Bee. *PLoS One* **11**, 1–11.
461 (doi:10.1371/journal.pone.0150946)
- 462 26. Sumner J, Moritz C, Shine R. 1999 Shrinking forest shrinks skink: Morphological change in
463 response to rainforest fragmentation in the prickly forest skink (*Gnypetoscincus*
464 *queenslandiae*). *Biol. Conserv.* **91**, 159–167. (doi:10.1016/S0006-3207(99)00089-0)
- 465 27. Braschler B, Baur B. 2016 Diverse effects of a seven-year experimental grassland
466 fragmentation on major invertebrate groups. *PLoS One* **11**, 1–20.
467 (doi:10.1371/journal.pone.0149567)
- 468 28. Milne BT. 1992 Spatial Aggregation and Neutral Models in Fractal Landscapes. *Am. Nat.* **139**,
469 32–57. (doi:10.1086/285312)
- 470 29. Buchmann CM, Schurr FM, Nathan R, Jeltsch F. 2013 Habitat loss and fragmentation affecting
471 mammal and bird communities—The role of interspecific competition and individual space
472 use. *Ecol. Inform.* **14**, 90–98. (doi:10.1016/j.ecoinf.2012.11.015)

- 473 30. Buchmann CM, Schurr FM, Nathan R, Jeltsch F. 2012 Movement upscaled - the importance of
474 individual foraging movement for community response to habitat loss. *Ecography (Cop.)*. **35**,
475 436–445. (doi:10.1111/j.1600-0587.2011.06924.x)
- 476 31. Etienne RS, Olff H. 2004 How Dispersal Limitation Shapes Species-Body Size Distributions in
477 Local Communities. *Am. Nat.* **163**, 69–83. (doi:10.1086/380582)
- 478 32. Fahrig L. 2003 Effects of Habitat Fragmentation on Biodiversity. *Annu. Rev. Ecol. Evol. Syst.*
479 **34**, 487–515. (doi:10.1146/132419)
- 480 33. Lomolino M V., Perault DR. 2007 Body size variation of mammals in a fragmented, temperate
481 rainforest. *Conserv. Biol.* **21**, 1059–1069. (doi:10.1111/j.1523-1739.2007.00727.x)
- 482 34. Gonzalez A, Chaneton EJ. 2002 Heterotroph species extinction , abundance in an
483 experimentally biomass dynamics fragmented microecosystem. *J. Anim. Ecol.* **71**, 594–602.
484 (doi:10.1046/j.1365-2656.2002.00625.x)
- 485 35. Debinski DM, Holt RD. 2009 Review□: A Survey and Overview of Habitat Fragmentation
486 Experiments Survey and Overview of Habitat Fragmentation Experiments. *Conserv. Biol.* **14**,
487 342–355. (doi:10.1046/j.1523-1739.2000.98081.x)
- 488 36. Fronhofer EA, Kubisch A, Hilker FM, Hovestadt T, Poethke HJ. 2012 Why are
489 metapopulations so rare? *Ecology* **93**, 1967–1978. (doi:10.1890/11-1814.1)
- 490 37. Amarasekare P. 2016 Evolution of dispersal in a multi-trophic community context. *Oikos* **125**,
491 514–525. (doi:10.1111/oik.02258)
- 492 38. Fronhofer EA, Hovestadt T, Poethke HJ. 2013 From random walks to informed movement.
493 *Oikos* **122**, 857–866. (doi:10.1111/j.1600-0706.2012.21021.x)
- 494 39. Amarasekare P. 2010 Effect of non-random dispersal strategies on spatial coexistence
495 mechanisms. *J. Anim. Ecol.* **79**, 282–293. (doi:10.1111/j.1365-2656.2009.01607.x)
- 496 40. Melián CJ, Křivan V, Altermatt F, Stary P, Pellissier L, De Laender F. 2015 Dispersal
497 Dynamics in Food Webs. *Am. Nat.* **185**, 157–168. (doi:10.1086/679505)
- 498 41. Nathan R, Getz WM, Revilla E, Holyoak M, Kadmon R, Saltz D, Smouse PE. 2008 A
499 movement ecology paradigm for unifying organismal movement research. *Proc. Natl. Acad.
500 Sci.* **105**, 19052–19059. (doi:10.1073/pnas.0800375105)
- 501 42. Etherington TR, Holland EP, O’Sullivan D. 2015 NLMpy: A python software package for the
502 creation of neutral landscape models within a general numerical framework. *Methods Ecol.
503 Evol.* **6**, 164–168. (doi:10.1111/2041-210X.12308)
- 504 43. Neel MC, McGarigal K, Cushman SA. 2004 Behavior of class-level landscape metrics across
505 gradients of class aggregation and area. *Landsc. Ecol.* **19**, 435–455.
506 (doi:10.1023/B:LAND.0000030521.19856.cb)
- 507 44. Poethke HJ, Hovestadt T. 2002 Evolution of density- and patch-size-dependent dispersal rates.
508 *Proc. Biol. Sci.* **269**, 637–45. (doi:10.1098/rspb.2001.1936)
- 509 45. Buddenbrock W V. 1934 Uber die kinetische und statische Leistung grosser und kleiner Tiere
510 und ihre bedeutung für dem Gesamtstoffwechsel. *Naturwissenschaft* **22**, 675–680.
- 511 46. Pawar S, Dell AI, Van M. Savage. 2012 Dimensionality of consumer search space drives
512 trophic interaction strengths. *Nature* **486**, 485–489. (doi:10.1038/nature11131)
- 513 47. Moses ME, Hou C, Woodruff WH, West GB, Nekola JC, Zuo W, Brown JH. 2008 Revisiting a

- 514 model of ontogenetic growth: estimating model parameters from theory and data. *Am. Nat.* **171**,
515 632–645. (doi:10.1086/587073)
- 516 48. West GB, Brown JH, Enquist BJ. 2001 A general model for ontogenetic growth. *Nature* **413**,
517 628–631. (doi:10.1038/35098076)
- 518 49. Wang S, Loreau M. 2014 Ecosystem stability in space: α , β and γ variability. *Ecol. Lett.* **17**,
519 891–901. (doi:10.1111/ele.12292)
- 520 50. Ritterskamp D, Bearup D, Blasius B. 2016 Emergence of evolutionary cycles in size-structured
521 food webs. *J. Theor. Biol.* **408**, 187–197. (doi:10.1016/j.jtbi.2016.08.024)
- 522 51. Massol F, Gravel D, Mouquet N, Cadotte MW, Fukami T, Leibold MA. 2011 Linking
523 community and ecosystem dynamics through spatial ecology. *Ecol. Lett.* **14**, 313–323.
524 (doi:10.1111/j.1461-0248.2011.01588.x)
- 525 52. Economo EP, Keitt TH. 2008 Species diversity in neutral metacommunities: A network
526 approach. *Ecol. Lett.* **11**, 52–62. (doi:10.1111/j.1461-0248.2007.01126.x)
- 527 53. Carrara F, Altermatt F, Rodriguez-Iturbe I, Rinaldo A. 2012 Dendritic connectivity controls
528 biodiversity patterns in experimental metacommunities. *Proc. Natl. Acad. Sci.* **109**, 5761–5766.
529 (doi:10.1073/pnas.1119651109)
- 530 54. Holt R, Hoopes M. 2005 *Food Web Dynamics in a Metacommunity Context: Modules and
531 Beyond*.
- 532 55. Liao J, Bearup D, Blasius B. 2017 Food web persistence in fragmented landscapes. *Proc. R.
533 Soc. B Biol. Sci.* **284**, 20170350. (doi:10.1098/rspb.2017.0350)
- 534 56. Delgado MM, Barton KA, Bonte D, Travis JMJ. 2014 Prospecting and dispersal: their eco-
535 evolutionary dynamics and implications for population patterns. *Proc. R. Soc. B Biol. Sci.* **281**,
536 20132851–20132851. (doi:10.1098/rspb.2013.2851)
- 537 57. Bell G, Fortier-Dubois É. 2017 Trophic dynamics of a simple model ecosystem. *Proceedings.
538 Biol. Sci.* **284**, 20171463. (doi:10.1098/rspb.2017.1463)
- 539 58. Massol F, Altermatt F, Gounand I, Gravel D, Leibold MA, Mouquet N. 2017 How life-history
540 traits affect ecosystem properties: effects of dispersal in meta-ecosystems. *Oikos* **126**, 532–546.
541 (doi:10.1111/oik.03893)
- 542 59. Amarasekare P. 2008 Spatial Dynamics of Foodwebs. *Annu. Rev. Ecol. Evol. Syst.* **39**, 479–
543 500. (doi:10.1146/annurev.ecolsys.39.110707.173434)

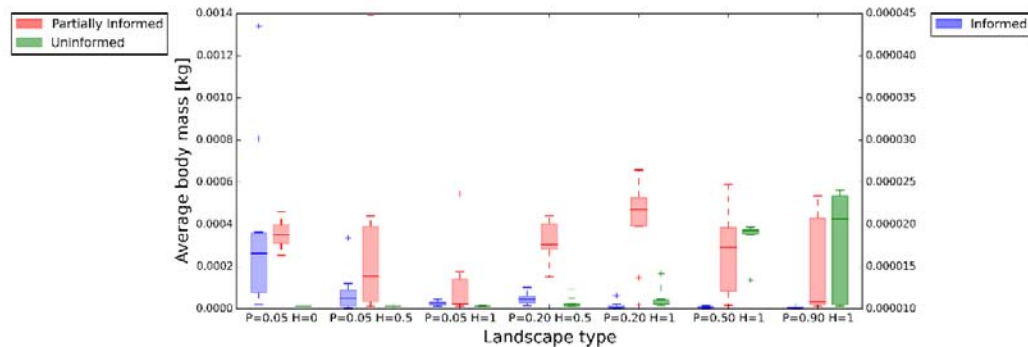
544 **Figures**



545

546 Figure 1: A comparison of daily events for the juvenile and adult stage of the consumer. BMR stands

547 for the basal metabolic rate costs.



548

549 Figure 2: The effect of habitat fragmentation and destruction on average adult body mass of the

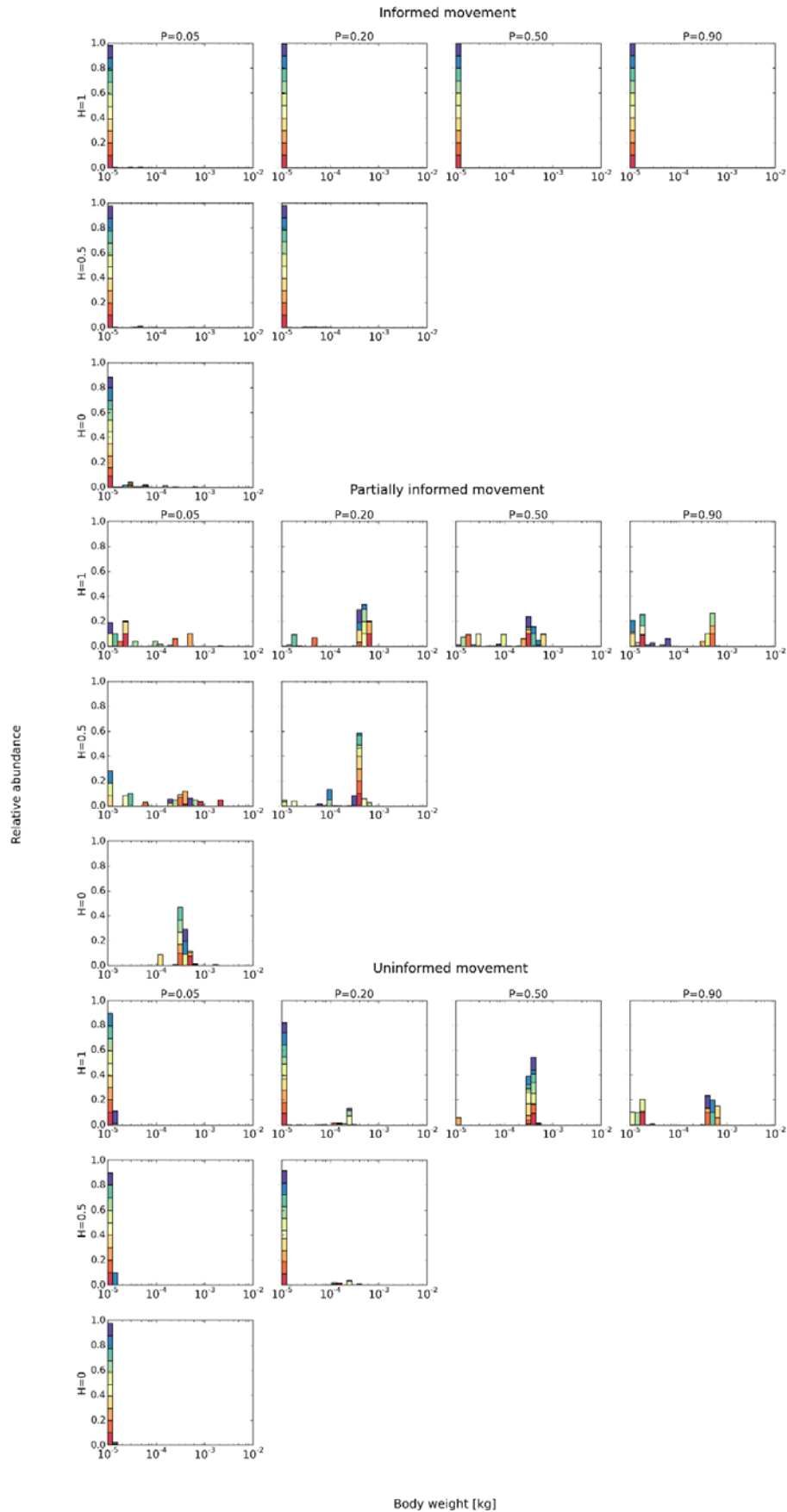
550 consumer(s) for each of the three types of information use during movement (informed, partially

551 informed or uninformed). The configuration of suitable habitat within a landscape is described by

552 means of P (percentage of suitable habitat) and H (level of autocorrelation). Note the different axis

553 scales for partially informed and uninformed movement on the one hand, and informed movement on

554 the other.



556 Figure 3: The effect of habitat fragmentation and destruction on the adult body size distribution of a
557 consumer population or community, with movement of the consumer informed, partially informed or
558 uninformed. The configuration of suitable habitat within a landscape is described by P (percentage of
559 suitable habitat) and H (level of autocorrelation). Each color represents the outcome of a single
560 simulation. In total, ten simulations were run per scenario.

561