

1 Emergence of spatially structured populations by  
2 area-concentrated search

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# 13 Emergence of spatially structured populations by area- 14 concentrated search

## 15 Abstract

16 The idea that populations are spatially structured has become a very powerful con-  
17 cept in ecology, raising interest in many research areas. However, despite dispersal  
18 being a core component of the concept, it typically does not consider the movement  
19 behavior underlying any dispersal. Using individual-based simulations in contin-  
20 uous space, we investigate the emergence of a spatially structured population in  
21 landscapes with spatially heterogeneous resource distribution and with organisms  
22 following simple area-concentrated search (ACS); individuals do not, however, per-  
23 ceive or respond to any habitat attributes per se but only to their foraging success.  
24 We investigated effects of different resource clustering pattern in landscapes (single  
25 large cluster vs. many small clusters) and different resource density on spatially  
26 structure of populations and movement between resource clusters of individuals.  
27 As results, we found that foraging success increased with increasing resource den-  
28 sity and decreasing number of resource clusters. In a wide parameter space, the  
29 system exhibited attributes of a spatially structured populations with individuals  
30 concentrated in areas of high resource density, searching within areas of resources,  
31 and 'dispersing' in straight line between resource patches. 'Emigration' was more  
32 likely from patches that were small or of low quality (low resource density), but  
33 we observed an interaction effect between these two parameters. With the ACS  
34 implemented, individuals tended to move deeper into a resource cluster in scenarios  
35 with moderate resource density than in scenarios with high resource density. 'Loop-  
36 ing' from patches was more likely if patches were large and of high quality. Our  
37 simulations demonstrate that spatial structure in populations may emerge if critical  
38 resources are heterogeneously distributed and if individuals follow simple movement  
39 rules (such as ACS). Neither the perception of habitat nor an explicit decision to em-  
40igrate from a patch on the side of acting individuals are necessary for the emergence  
41 of spatial structure.

## <sup>42</sup> keywords

<sup>43</sup> spatially structured population, metapopulation, area-concentrated search, individual-  
<sup>44</sup> based model

# 1 Introduction

The idea of spatially structured population, namely metapopulation, patchy population, mainland-island system, or source-sink systems, has become a very powerful concept in ecology, raising interest in research areas like dispersal ecology (With 2004, Hanski 2012, Lambin et al. 2012) or population genetics (Hastings and Harrison 1994, Harrison and Hastings 1996, Haig 1998, Manel et al. 2003, Montgelard et al. 2014). The concept also had a strong impact on the development of conservation concepts (Thomas 1995, Hanski and Simberloff 1997, Akçakaya et al. 2007, Olivieri et al. 2016). However, these concepts may be more a 'construct' of human observers with their tendency to categorize observations - yet not necessarily reflect the biology underlying the emergence of spatial population structure. In particular, there is no guarantee that the organisms under investigation have a perception (or a 'concept') of habitat patches or that they at any time 'decide' to emigrate from a habitat patch and disperse. Current approaches typically assume the concept to be valid but do not necessarily explain its emergence from first principle.

Another issue with the metapopulation and other spatially structured population concepts is that they do not explicitly account for movement behavior and dispersal that emerges from it (Hanski 1999, Bowler and Benton 2005, Hawkes 2009) even though dispersal is arguably the most important ingredient of the concepts. In particular, it is not guaranteed that dispersal occurs (only) because of the particular 'decision' to disperse, eventually at a certain moment in the life-cycle. Dispersal, i.e. the movement of individuals between habitat patches, may also come about by routine movement, e.g. during foraging. Over the last decades, research has progressed in better understanding what drives the movement of individuals searching for critical resources (Hawkes 2009, Bartoń and Hovestadt 2013, Pyke, 2015). Indeed, a rich literature exists of investigating and understanding rules of foraging movement at the individual and local level (Viswanathan et al. 1999, Benhamou 2007, Plank and James 2008, James et al. 2011, Hills et al. 2013, Pyke 2015).

In fact, searching for some critical commodity like food, mating partners or nest sites may be the motivation underlying the far majority of any movement in mobile animals. Some studies (e.g., Getz and Saltz 2008, Nathan et al. 2008) thus proposed a conceptual framework for movement ecology that considers the interplay among mechanistic components of movement: the internal state, motion, navigation capacities of the individual and the external factors affecting movement. The underlying idea of this and other concepts is the proposition that individuals usually have a

80 cause or motivation to move and that they collect and process information to steer  
81 their movement; an approach that questions the wide-held assumption in metapop-  
82 ulation models that movement and consequently dispersal would be random. Some  
83 authors have already created movement models with some or all of those compo-  
84 nents of movement, e.g., Benhamou (1992), McNamara et al. (2006), Fryxell et al.  
85 (2008), Barton et al. (2009), Bartumeus and Catalan (2009), Van Moorter et al.  
86 (2009), Olsson and Brown, (2010), Reynolds (2012), Avgar et al. (2013), Bartoń  
87 and Hovestadt, (2013), Fagan et al. (2013, 2017) and Fronhofer et al. (2013). How-  
88 ever, we are still only beginning to understand how such rules (or others) might  
89 scale up to population and landscape levels, i.e. to the level of spatially structured  
90 populations.

91 In this article, we propose that features of a spatially structured population and  
92 possibly of a metapopulation can emerge if animals follow simple movement rule like  
93 simple area-concentrated search (ACS) and if critical (and searched) resources are  
94 themselves heterogeneously distributed. Area-concentrated search, also called 'state-  
95 dependent correlated random walk', has been previously used in many ecological  
96 studies (such as Kareiva and Odell 1987, Turchin 1991, Benhamou 1992, 2004, as  
97 the 'Mushroom Hunt Model' in Railsback and Grimm 2012, Bartoń and Hovestadt  
98 2013). According to the ACS, the directionality (correlation) of movement is affected  
99 by e.g. (perceived) habitat attributes per se as in Turchin (1991) or an individual's  
100 internal state (e.g. hunger level, previous foraging success, or recent encounters with  
101 prey). Such models, as well as others with more sophisticated of context dependent  
102 movement might have similar effects, however.

103 Here we simulate the ACS movement of foraging organisms in a landscape with  
104 differently clustered resource distribution (single large cluster vs. many small clus-  
105 ters and different resource density) and explore how this influences the distribution  
106 of individuals in space, foraging success, and the movement between resource clus-  
107 ters (patches). We speculate that a spatially heterogeneous resource distribution  
108 and such a simple movement rule are sufficient to generate the different attributes  
109 of a spatially structured population or metapopulation: namely (i) **spatially clus-**  
110 **tered distribution of individuals** in areas of resource concentration ('resource  
111 clusters' or 'habitat patches'), (ii) **different movement pattern inside and out-**  
112 **side patches** – searching behavior within, but straight-line movement outside of  
113 habitat patches, (iii) **emigration rate depending on patch quality** – reduced  
114 emigration from large or high quality habitat patches vs. elevated emigration from  
115 small or poor quality patches. Some authors have explored such movement models

116 previously (e.g. Turchin 1991, Benhamou 1992, 2004, Bartoń and Hovestadt 2013).  
 117 However, they were typically more interested in specifying how such rules affect  
 118 foraging success or movement attributes in different sections of a landscape and not  
 119 so much on the emerging spatial distribution of individuals at the population level.

## 120 2 Material and methods

121 We implement a simple model simulating the movement of resource-searching indi-  
 122 viduals (ACS) in a continuous landscape with heterogeneous resource distribution;  
 123 both, the position of individuals and resources are thus continuous point coordinates.  
 124 We investigate how resource distribution affects the spatial distribution (density) of  
 125 individuals and the movement (dispersal) of individuals between resource clusters.  
 126 Our simulation ignores birth and death events, but the model implicitly accounts  
 127 for the diffuse effect of competition over resources on foraging behavior.

### 128 2.1 Spatial distribution of resources and scenarios

129 We simulated foraging movement in a square landscape of area  $4 \times 10^6$  ( $2000 \times 2000$ )  
 130 squared spatial units with resources distributed within it. In the simulations we cre-  
 131 ated  $k$  resource clusters within the landscape as continuous spatial point pattern  
 132 with points generated by the Matérn Cluster Point Process, using R version 3.5.2,  
 133 library spatstat version 1.58-2 (Baddeley and Turner, 2005). Clusters were gener-  
 134 ated with daughter points (resources) distributed according to a random uniform  
 135 distribution on a disk around parent points with  $g$  as radius of the clusters and  $u$   
 136 as resource density per area unit so that  $\bar{R} = g^2\pi \times u$  was the expected number  
 137 of resource items per cluster, and the expected number of resources items in the  
 138 landscape were thus  $k \times \bar{R}$ . Parent points were distanced at least  $3g$  units apart  
 139 from each other to avoid cluster overlapping. The landscapes were wrapped into  
 140 a torus in both dimensions to avoid edge effects and mimic a landscape of infinite  
 141 dimension. Across scenarios, the number of resource clusters was increased from  
 142  $k = 1$  to  $k = 16$  clusters whereas the radius of clusters ( $g$ ) was reduced from 320  
 143 (at  $k = 1$ ) to 80 (at  $k = 16$ ) so that the total area covered by resource clusters  
 144 was identical in all scenarios (*c.* 8% of total area). The average resource density in  
 145 resource clusters was varied from  $u = 0.01$  to  $u = 1.27$  resources per unit area. A  
 146 summary of all model and simulation parameters and their values can be found in

147 Table 1.

## 148 2.2 Movement rule

149 The movement of each individual was modeled as an ACS. Here we implemented  
150 the simplest of such possible rules, assuming that individual  $i$  moved straighter, the  
151 longer the time interval in which it did not find a food item was, i.e. the longer  
152 the searching time  $\Delta_{S,i}$  was (see Benhamou 1992, reviewed in Bartoń and Hovestadt  
153 2013); generally, such models have been shown to be efficient foraging strategies (e.g.  
154 Benhamou, 1992; Pyke 2015). Comparable movement was, for example, observed  
155 in starved amoeboid cells that move rather straight whereas well-fed cells moved  
156 changed direction much more frequently (van Haastert and Bosgraaf 2009) but just  
157 as well in mammal species (Auger-Méthé et al. 2016). At any moment  $t$ , and for any  
158 moving individual  $i$ , the turning angle between two consecutive steps was determined  
159 by drawing a random value from a wrapped normal distribution (Jammalamadaka  
160 and SenGupta 2001) with mean 0 and standard deviation  $d_{i,t}(\Delta_{S,i})$  calculated as

$$d_{i,t}(\Delta_{S,i}) = d_{min} + (d_{max} - d_{min}) \cdot \left(1 - \frac{\Delta_{S,i}^\alpha}{(\Delta_{S,i}^\alpha + h^\alpha)}\right) \quad (1)$$

161 Consequently,  $d_{i,t}$  ranges between  $d_{min} = 0.01$  (nearly straight-line movement)  
162 when  $\Delta_{S,i} \gg h$  and  $d_{max} = 1$  when  $\Delta_{S,i} = 0$ , i.e. when the individual just found  
163 a food item. In the latter case, the movement became highly uncorrelated, and  
164 the individual performed area-concentrated search. The parameter  $\alpha$  is a shape  
165 parameter (in our simulations always  $\alpha = 3$ ), and  $h$  is the half-saturation constant  
166 (always  $h = 200$ ). The effects of parameter  $\alpha$  and  $h$  on  $d_{i,t}$  and on foraging success  
167 were described in Bartoń and Hovestadt (2013). We also tested different values  
168 of  $h$  and  $\alpha$  in this study but found that these two parameters did not strongly  
169 affect results. We thus kept these two parameter values constant in all simulations.  
170 Examples of movement paths of individuals from simulations are shown in Figure 1.

## 171 2.3 Foraging

172 At each time step, each individuals moved one step according to the movement rule  
173 described above. Individuals were moved in a random sequence to avoid priority  
174 benefits. The step length of movement ( $p$ ) was constant and equal to 1 spatial  
175 unit. After movement, an individual immediately found all resource items within

its perception radius ( $c = 1$  spatial unit, identical to the step length). All resource items within this radius were 'foraged' and removed (the individual maintained its position, however). Following a movement step, the value of  $\Delta_{S,i}$  for each individual was increased to  $\Delta_{S,i} + 1$  in case an individual did not find a resource item, but was reset to  $\Delta_{S,i} = 0$  whenever the individual found a food item, thus initiating the ACS as described above.

After movement of all individuals, removed resource items were replaced by a same number of new items placed randomly as daughter points of randomly selected parent points according to the rules explained above (global replacement). With this global replacement we implemented a global equilibrium assumption between resource production (regrowth) and consumption yet nonetheless allowing for the more short term depletion (competition) effects due to intense local harvesting.

## 2.4 Simulations and analysis

For each parameter combination (resource density and cluster size, see above), we carried out ten replicates on ten independently created landscapes. In each simulation, eighty individuals were released at random coordinates within resource clusters. Their  $\Delta_{S,i}$  value was set to  $\Delta_{S,i} = 500$  at the beginning of a simulation so that individuals started with nearly straight line movement. The initial direction of each individual was randomly selected from a uniform distribution between 0 and  $2\pi$ . At each time step, individuals moved and foraged resource items as described above. All individuals were allowed to move for 10,000 steps, but all analyses described below are based on data collected over the last 2000 movement steps only.

At the beginning of each simulation, the expected number of resource items per cluster was equal to  $\bar{R}$  (see above). Due to the global replacement of foraged resource items, the total number of resource items in the landscape was kept constant and consequently the average number of resource items per cluster remained at  $\bar{R}$ . However, the number of items in a single cluster could vary over time and degrade if the cluster was harvested intensively, i.e. by many individuals at the same time.

Effects of resource density and cluster size on the distribution of individuals and spatially structure of the system – including metapopulation structure – were evaluated in this study. For graphical presentation, the grand mean and its standard deviations of ten replicates are shown in figures with calculations based on the averages calculated across all individuals within single replicates. Foraging and



209 movement behavior of individuals in different scenarios were compared according to  
210 (1) foraging success (=proportion of time steps when an individual harvests one or  
211 more resource item) and (2) total number of different clusters from which resource  
212 items were collected.

213 We defined immigration as a moment when an individual entered the area of a  
214 cluster (radius around a parent point) even without foraging success and emigration  
215 as the moment when an individual left away from this area. For analyzing the dura-  
216 tion of movements within and between clusters, we noted the moments of emigration  
217 from, respectively of immigration into patches. For (3) duration of visits to a patch  
218 ('patch visitation time'), we counted the time between moment of immigration to  
219 emigration and for (4) duration of 'patch searching time', we counted time between  
220 moment of emigration to immigration for each individual incidence. The data also  
221 allowed to calculate (5) the number of emigration events/individual. If an individual  
222 foraged and moved away from a resource cluster and later returned to the same clus-  
223 ter to forage again, we counted this as two different clusters visited in our analysis;  
224 this is justified in a torus-world where individuals can return to a certain position  
225 by once walking around the torus. However, the emigration events also contained  
226 short excursions away and back to a cluster similar to 'foray loops' (a succession of  
227 progressively larger ellipsoidal loops) previously described in Conradt et al. (2003)  
228 and McIntire et al. (2013). We thus separated (6) excursions of less than 200 steps  
229 as 'foray loops' from 'long-distance emigration events' in our analyses.

230 Fronhofer et al. (2012) proposed three broad criteria that were observed in previ-  
231 ous studies of classical metapopulations: (i) patch occupancy is between 5% - 85% as  
232 a metapopulation is a network of occupied and empty patches; (ii) the turnover-rate  
233 (changes from extinct to occupied and vice versa) is between 10-40%; (iii) Migration  
234 between patches must be intermediate as a metapopulation is neither a panmictic  
235 population (no structure among populations, correlated population dynamics) nor a  
236 collection of completely isolated habitat patches. For comparison between our sys-  
237 tem and classical metapopulation structure, we thus measured (7) patch occupancy  
238 (proportion of time patches contained at least one individual), (8) the percentage of  
239 individuals located in clusters (9) the number of 'successful' migration events, i.e.  
240 transitions from one cluster to another and finally (10) the percentage of emigration  
241 events where individuals failed to reach a patch including the patch of origin. For  
242 the analysis (9), individuals that never entered a patch within the last 2000 time  
243 steps were excluded.

## 244 3 Results

### 245 3.1 Foraging behavior and foraging success

246 In this study, we investigated the emergence of spatially structured population in  
247 the simulations with a simple movement rule of individuals in the system, the area-  
248 concentrated search, in patch landscape with clustered resource distribution. We  
249 could indeed observe features of spatially structured populations and even metapop-  
250 ulation in some scenarios of our systems.

251 Examples of movement of individual in different scenarios are shown in Figure 1.  
252 In concordance with the principles underlying the ACS, two types of movement can  
253 be recognized in our simulations - searching for (or 'dispersing between') resource  
254 clusters and foraging within resource clusters. Straight line movement primarily  
255 (and obviously) occurred in the 'matrix areas' between resource clusters whereas  
256 foraging - characterized by more uncorrelated movement - occurred within resource  
257 clusters.

258 We represent foraging success of each individual by the proportion of time steps  
259 when an individual encountered resources (Figure 2A). Foraging success increased  
260 with increasing resource density and decreasing number of resource clusters. Overall,  
261 individuals were more successful in a landscape with a single large resource cluster  
262 than in landscapes with many small clusters even though the total area covered by  
263 the clusters in different scenarios was equal. This effect was more pronounced at  
264 low resource density than at high resource density (e.g. at  $u = 0.01$ , the foraging  
265 success in the one-cluster scenario was approximately 64-fold higher than that in  
266 16-cluster scenario while this difference was approximately 13-fold at  $u = 1.27$ ).  
267 When resource clusters were small and/or resource density was low, individuals often  
268 moved through clusters without encountering resource items within their perceptual  
269 range and thus maintaining their straight searching movement. In other words,  
270 individuals eventually did not 'recognize' the presence of a resource aggregation if  
271 resource density was rather low and clusters were small.

272 We generally expected that individuals would stay and forage longer for resources  
273 within a patch and also find new patches faster when resources were dense but our  
274 simulations provided more complex results. The mean number of clusters from which  
275 resources were collected was mostly  $< 1$  (this value included individuals that did  
276 not successfully reach a resource cluster) and smaller than the number of clusters

they entered because some individuals did not detect resource item within clusters (Figure 2B). In the small cluster scenarios (16 and 8 clusters), the number of clusters harvested continuously increased with increasing resource density (Figure 2B). In line, the average patch visitation time increased (Figure 3A) and patch searching time decreased with increasing resource density (Figure 3B) as expected. However, in the scenarios with only few, large clusters (1-4 clusters) the response was more complex: the number of clusters harvested and patch visitation time showed a uni-modal response and patch searching time showed a U-shaped response.

For better understanding the emergence of this uni-modal response we analyzed – just for the one-cluster scenarios – the position of individuals within the resource cluster at the last time step. We found that the mean positions of individuals in scenarios with moderate resource density were closer to the center point (parent point) than those in scenarios with high and low resource density (Figure 4). In other words, individuals tended to penetrate deeper into a resource cluster (move closer to the patch center) with moderate resource density than in a cluster with high resource density because they were less likely to encounter a resource item near the edge of the cluster upon arrival than in high resource density scenarios. Consequently, the chance to move away from a cluster briefly after it was found was lower in the scenarios with intermediate resource density. In scenarios with high resource density, individuals foraged mainly close to the edge of a cluster with the associated risk of eventually leaving that cluster.

### 3.2 Emigration and spatially-structured population properties of the system

The number of emigration events for each individual increased with resource density and number of resource clusters in the landscape (Figure 5A). Individuals in small cluster scenarios tended to emigrate more frequently than individuals in large cluster scenarios, in particular if resource density was high. However, not all of these emigration events resulted in permanently leaving a resource cluster so that individuals eventually returned to the cluster they just left before, resulting in a 'foray loop' (cf. Conradt et al. 2003). Using an arbitrary cut-off level of 200 time steps to separate between 'permanent emigration' and foray loops we recognize that with increasing resource density a larger proportion of emigration episodes falls into the foray loop category (Figure 5B). Note that this finding also explains the apparent contradiction between Figures 2B and 5A. The results show that long-distance emigration

311 events occurred more often at low resource density and small cluster size whereas  
 312 foray loops were observed more often at high resource density and the proportion  
 313 of foray loops generally increased with decreasing number of clusters (increasing  
 314 cluster size).

315 Generally, we could observe attributes of a spatially structured population in our  
 316 system as described above, i.e spatially clustered distribution of individuals, different  
 317 movement pattern inside and outside patches, and emigration rate depending on  
 318 patch quality and size. When analyzing our simulation results for the emergence of  
 319 classical metapopulation properties (as described in Fronhofer et al. 2012), we found  
 320 mean patch occupancy lower than 85% only in five scenarios, i.e. with 8 clusters and  
 321 resource density  $u = 0.01$  and in scenarios with 16 clusters and  $u \leq 0.08$  (Figure  
 322 6A), scenarios where the distribution of individuals across the whole landscape was  
 323 still nearly random (close to the expected percentage of individuals in clusters if they  
 324 were randomly distributed  $\approx 8\%$ ; Figure 6B). With increasing resource density and  
 325 cluster size individuals increasingly concentrated within resource clusters ('habitat').  
 326 For example, if 50% of individuals reside inside resource clusters that cover just 8% of  
 327 the total area, the 'population density' inside cluster is already 11.5 times larger than  
 328 in the surrounding matrix. In passing we note that these results completely deviate  
 329 from those predicted by the diffusion approximation outlined by Turchin (1991, see  
 330 also Patlak 1953a,b); for more details on underlying reasons see discussion. However,  
 331 for the scenarios with few clusters, the response to resource density was uni-modal  
 332 due to the increasing emigration probability mentioned before. The highest number  
 333 of successful patch changes per individual was observed in scenarios with many  
 334 clusters and low resource density and this value decreased with lower number of  
 335 clusters and higher resource density (Figure 6C) and was almost or equal to zero  
 336 at  $k \leq 2$ . In turn, the proportion of individuals outside patches and never finding  
 337 a patch within the 2000 time steps was also largest when resource density was low  
 338 (Figure 6D).

## 339 4 Discussion

340 In our simulations, we use a simple movement model (ACS) on the one hand and  
 341 landscapes with more or less spatially concentrated resource distribution on the  
 342 other to simulate a collective of foraging individuals; the simulated populations  
 343 show attributes of a spatially structured population as emergent properties. As

344 such, the emergence of of spatial structure cannot be a very surprising outcome as  
 345 already common sense would make us expect that animals tend to concentrate in  
 346 areas where critical resources are aggregated (up to population densities  $\approx 65$  times  
 347 larger inside clusters than outside - Figure 6B). This observation here is similar to  
 348 the work of Peter Turchin (1991) who in fact provided a one-dimensional solution  
 349 for the problem. Nonetheless, we see a value in our simulations in making clear  
 350 that neither the perception of a patch-matrix dichotomy, nor spatial memory or any  
 351 complex decision rules for emigration are needed to generate spatial heterogeneity  
 352 in the distribution of individuals. Further, the simulations implemented here also  
 353 generate more specific patterns that are expected to emerge in spatially structured  
 354 population systems, i.e. that individuals are more likely to emigrate from small vs.  
 355 large resource clusters (*viz.* patches) and with greater probability from poor quality  
 356 (low resource density) than from high quality clusters (but see below).

357 As expected, a reduction of the number of clusters (larger cluster at the same  
 358 time) and/or an increase resource density leads to more foraging success of each  
 359 individual and also affects movement pattern of individuals. In the scenarios with  
 360 high resource density or larger cluster, individuals tend to stay long within a patch  
 361 and perform more area-concentrated search than straight line movement. Such  
 362 effects of resource density and resource spatial arrangement on movement strategies  
 363 and foraging success were also observed in previous studies (Kareiva and Odell 1987,  
 364 Benhamou 1992, Scharf et al. 2009, Bartoń and Hovestadt 2013). Note that in our  
 365 scenarios the tendency to remain in a resource aggregation is only driven by the  
 366 attributes of the ACS but does not require that individuals respond to or even  
 367 recognize (suitable) habitat per se as is the underlying assumption in e.g. Turchin  
 368 (1991). It also does not require that individuals apply different rules of movement  
 369 to habitat and matrix or that individuals ever take a decision to emigrate from a  
 370 habitat patch. Saying so, we do not want to exclude and even suggest that animals  
 371 typically forage with more sophistication than we assume in our model, e.g. that  
 372 they utilize environmental cues, e.g. habitat suitability, that indicate that finding  
 373 resources would be more likely in a certain region or base movement decisions on  
 374 experience and spatial memory (as e.g. in Avgar et al. 2013, Fronhofer et al. 2013).

375 Interestingly, the greatest foraging success occurred in scenarios with a single  
 376 resource cluster and highest resource density, but individuals did not stay longest  
 377 within patches in this scenario: contrary to expectation, the longest residence times  
 378 were observed in scenarios with moderate resource density, in particular in the sce-  
 379 narios with few, larger clusters. An underlying reason is that individuals tended to

380 stay nearer to patch edges if resource density was very high and did not move as  
 381 far into a patch (approaching the patch center) compared to individuals in scenar-  
 382 ios with moderate resource density. Therefore, they tended to leave patches more  
 383 often than in the other scenarios. Particularly with high resource concentration,  
 384 many emigrations resembled foray loops, however, where individuals return to the  
 385 same patch (Conradt et al. 2003, McIntire et al. 2013). On the other hand, with  
 386 very low resource density individuals often moved through resource clusters without  
 387 encountering (perceiving) resources at all and consequently maintaining a very di-  
 388 rected walk and leaving the patch quickly again. Emigration events as well as foray  
 389 loops might become rarer if individuals were to apply more sophisticated movement  
 390 rules than those implemented here, e.g. when using memorized knowledge about  
 391 patch location (Fryxell et al. 2008, Van Mooter et al. 2009, Avgar et al. 2013,  
 392 Fagan et al. 2013), knowledge about patch quality (Olsson and Brown 2010), im-  
 393 proved perception range (Avgar et al. 2013, Johnston and Painter 2019) or applying  
 394 smarter Bayesian movement decision rules (Fronhofer et al. 2013). Indeed, in some  
 395 preliminary simulations we found that even a simple ACS with a delayed change in  
 396 movement randomness after encountering a resource item resulted in deeper pene-  
 397 tration into resource clusters and longer patch residence times. Adding any of such  
 398 behavioral components might lead to edge 'avoidance' and a more 'organized' and ef-  
 399 ficient resource utilization from clusters and should lead to a decrease in emigrations  
 400 and foray loops in scenarios with high resource density.

401 We show that our system with simple area-concentrated search develops prop-  
 402 erties of a spatially structured population over a wide parameter range but never  
 403 matches the more strict attributes of a classical metapopulation (*sensu* Fronhofer  
 404 et al. 2012). A patch occupancy below 85% emerged in simulations with multiple  
 405 patches (8 and 16 patches) and low resource density (Figure 6A). However, in these  
 406 scenarios individuals were hardly aggregating into resource clusters (Figure 6B) –  
 407 that is, the distribution of individuals across the landscape was more or less random  
 408 and not showing signs of spatial structure at all. More importantly, we find interest-  
 409 ing interaction effects between number of resource clusters and resource density on  
 410 the one hand and emerging population density inside and outside aggregations on the  
 411 other. Our findings thus completely deviate from those predicted by Turchin (1991)  
 412 who based predictions, however, on a model where individuals modulate direction-  
 413 ality of movement based on the perception of habitat and not of resource items.  
 414 In fact, with the constant values for step length and duration as assumed in our  
 415 simulations, Turchin's analytical equations calculate an even density of individuals  
 416 inside and outside habitat (resource clusters, indicated by the hatched line in Figure

417 6B) - a prediction we could validate by implementing simulation rules that exactly  
418 match those assumed by Turchin. To some degree the difference in our findings and  
419 those predicted by Turchin may be a consequence of that we implemented circular  
420 resource cluster whereas Turchin assumed a one-dimensional transition between  
421 habitat and non-habitat (i.e. habitat stripes) but we think that the far more important  
422 reason for the difference between our findings and Turchin's predictions is the  
423 difference in the movement rules implemented – changing movement directionality  
424 (to lower) when encountering habitat in Turchin's model but changing directionality  
425 when detecting a resource item in our model.

426 We did not calculate turnover rates in this study as we were simulating in (ap-  
427 proximately) continuous time so that calculation of turn-over would depend on an  
428 arbitrary decision on the time-window over which to make such calculation; the turn-  
429 over concept applies better in long-term studies and in populations with a distinct  
430 dispersal phase. Instead, a more meaningful criterion is the frequency of successful  
431 patch changes as a measure of gene flow and possible patch recolonization or rescue.  
432 The number of successful patch changes (emigration from one and immigration into  
433 another resource patch) was indeed quite low (Figure 6C), but this values can only  
434 be interpreted in relation to the total period covered by our scenarios. For example,  
435 if we assume that a single time step in this simulation (the time an individual needs  
436 to pass through its perceptual radius) is five minutes, the two thousand time steps  
437 analyzed cover a period of approximately 7 days. Further assuming that animals are  
438 active only 12h a day (e.g. because they are nocturnal) and do not move during more  
439 than 1/2 of their active time, the period covered would correspond to *c.* 2-3 weeks,  
440 a value that is reasonable for the expected life-span of many adult insects. Based on  
441 these assumptions we thus find that in many of our simulations only a small fraction  
442 of individuals (mostly  $< 20\%$ ) successfully 'dispersed' from one habitat cluster to  
443 another during their life-time. This infrequent dispersal events emerged despite the  
444 fact that we did not assume a mortality risk for individuals moving outside habitat,  
445 e.g. due to exhaustion or predation. In this regard our simulations indeed meet  
446 the metapopulation criterion defined by Fronhofer et al. (2012) but as explained  
447 above, the patch occupancy criterion is only satisfied in those scenarios that showed  
448 at best weak symptoms of spatial structure. Our results thus support the idea that  
449 spatial population structure covers a continuum in terms of patch occupancy and  
450 migration rate (Harrison and Taylor 1997, Ovaskainen and Hanski 2004) but that  
451 true classical metapopulation attributes rarely emerge as long as external factors do  
452 not lead to the sudden extinction of local populations (Venable and Brown 1993,  
453 Travis and Dytham 1998, Fronhofer et al. 2012).

454 In this study, we varied patch structure (many small patches to single large patch  
 455 and low to high resource density) but within a scenario all patches were identical.  
 456 Creating landscapes with resource clusters of variable attributes might enable us to  
 457 investigate the emergence of spatially structure in populations in other landscape  
 458 settings, e.g. settings that show attributes of a mainland-island system (Harrison  
 459 1991) or a system with varying patch quality (resource density) like in source–sink  
 460 systems (Pulliam 1988). It must also be mentioned that we did not investigate the  
 461 effect of the two parameters  $\alpha$  and  $h$ , but previous studies showed that our choice of  
 462 parameter values is adequate to result in good foraging success in a broad spectrum  
 463 of parameters for the spatial distribution of resources (*cf.* Bartoń and Hovestadt  
 464 2013 for more details). Generally, a decrease of the half-saturation constant  $h$  should  
 465 lead to an increase in emigration rates and a reduction of patch residence times.

466 In this model, we assumed no birth and death events in the population because  
 467 we simulated only short ecological time interval and we avoided complexity caused  
 468 by birth and death process, such as population dynamics. By excluding natality and  
 469 mortality, we also did not include factors that might affect the spatial structure, such  
 470 as dispersal mortality, starvation, or environmental stochasticity (Chaianunporn and  
 471 Hovestadt 2012, 2019, Fronhofer et al. 2012). Including these factors, emigration  
 472 rates and spatial population structure in this system would presumably change. In  
 473 addition, a full model should in fact also account for a proper resource dynamics, e.g.  
 474 by either simulating abiotic resources with a constant supply rate (patch specific)  
 475 or by implementing it as a prey population with its own population dynamics.

## 476 5 Conclusions

477 In this study, we implement a model of organism with area-concentrated search as  
 478 a foraging movement rule moving in a continuous landscape with aggregated re-  
 479 source distribution. Although we do not include population dynamics (birth and  
 480 death) into the system, the simulated collective of individuals expresses proper-  
 481 ties of spatially structured populations as emergent properties. Models like this  
 482 can be used to improve our understanding of the mechanisms underlying the emer-  
 483 gence of population spatial structure but could also be applied – given we know  
 484 the rules of movement – to foresee the effects of landscape changes *viz.* changes in  
 485 resource distribution on (endangered) populations. Furthermore, the model could  
 486 be extended by adding components that affect population dynamics, e.g. disper-



487 sal mortality, environmental stochasticity, heterogeneous patch quality, or varying  
488 natality and mortality, for help us to gain more understanding about population  
489 change in heterogeneous landscape. Mechanistic models like ours may help to close  
490 the gap between movement ecology and spatial ecology theory.

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## 498 Data Availability Statement

499 The data and the code of the simulation model that support the findings of this  
500 study are openly available in "Dryad" at <https://doi.org/10.5061/dryad.n8pk0p2xr>.

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654 *lution of Metapopulations*. Elsevier, pp. 23–44.

## 655 6 Table

656 Table 1: Definition and ranges of parameters values used.

Symbol	Description	Values
$k$	number of resource clusters within the landscape	16, 8, 4, 2, 1
$g$	radius of clusters corresponding to $k$	80, $80\sqrt{2}$ , 160, $160\sqrt{2}$ , 320
$u$	resource density	varied ( $0.01 \leq u \leq 1.27$ resources items per unit area)
657 $d_{min}$	minimum value for correlation of turning angles of consecutive steps	0.01
$d_{max}$	maximum value for correlation of turning angles of consecutive steps	1 (corresponds to straight line movement)
$\alpha$	shape parameter	3
$h$	half-saturation constant	200
$p$	step length of movement	1
$c$	perception radius	1

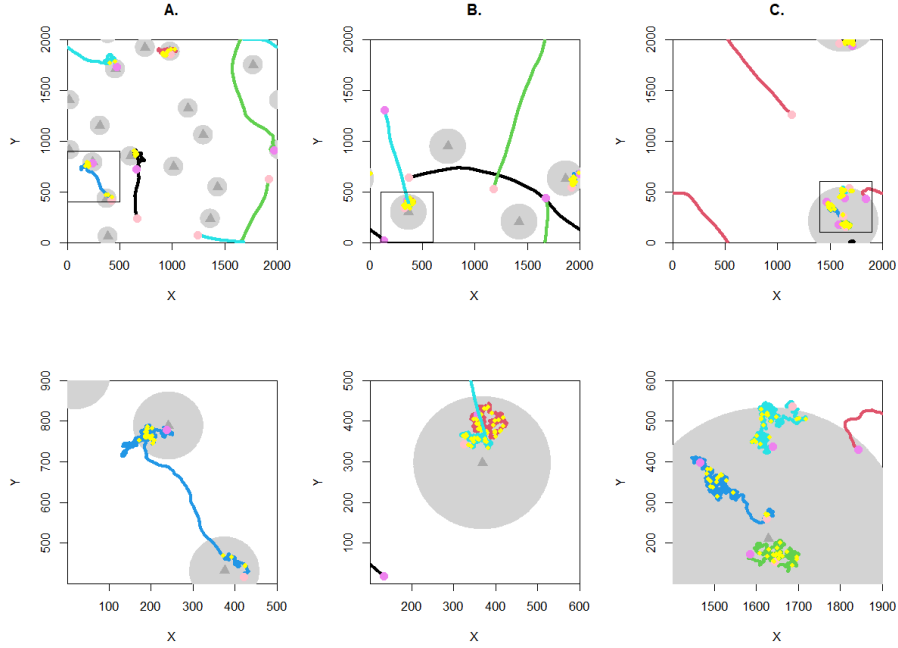


Figure 1: Examples of movement path of five individuals (five different color lines) in the landscape of different scenarios from last 2000 time-steps. Pink points indicate the starting position of the movement, yellow points show the positions where resource items were harvested and purple points are the end position of the movement. Large grey circles present the position and size of resource clusters and the grey triangles show the positions of parent points. Upper figures present the movement paths in the whole landscape and lower figures indicate the movement paths in a section of the square area in the upper figures: (A) Scenario with 16 clusters ( $k = 16$ ) with size of 80 units ( $g = 180$ ) and resource density of 0.16 ( $u = 0.16$ ) resources per unit; (B)  $k = 4$ ,  $g = 160$ ,  $u = 0.16$ ; (C)  $k = 1$ ,  $g = 320$ ,  $u = 0.16$ .



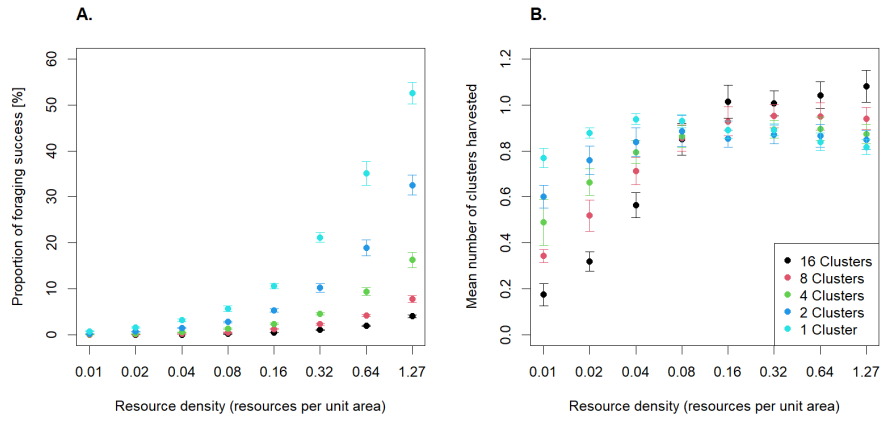


Figure 2: (A) Percentage of movement (time) steps with foraging success (harvesting one or more resource items) calculated over the last 2000 time steps and plotted over resource density. (B) Total number of clusters from which resource items were harvested during the last 2000 time steps plotted over resource density.

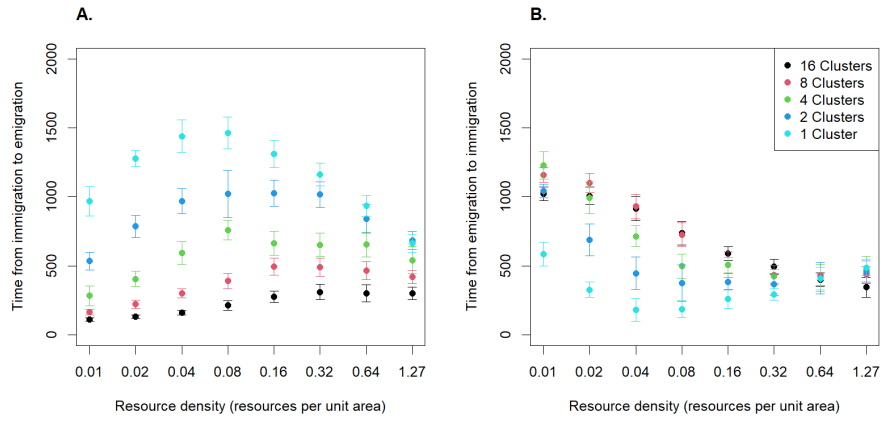


Figure 3: (A) Averaged duration of visits to a resource cluster (time from immigration to emigration) and (B) averaged duration of patch searches (time from emigration to immigration) during the last 2000 time steps plotted over resource density.

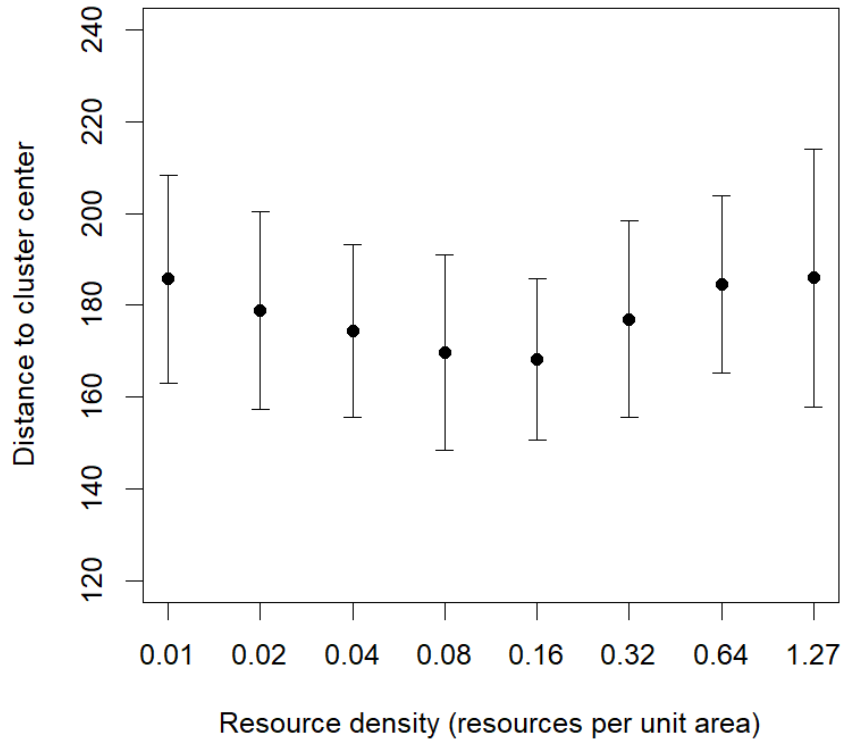


Figure 4: (A) Averaged distance between the current location of an individual in cluster at the last time step and the parent point of the cluster (patch center) from the scenario with single cluster (patch radius = 320 spatial unit) plotted over resource density.

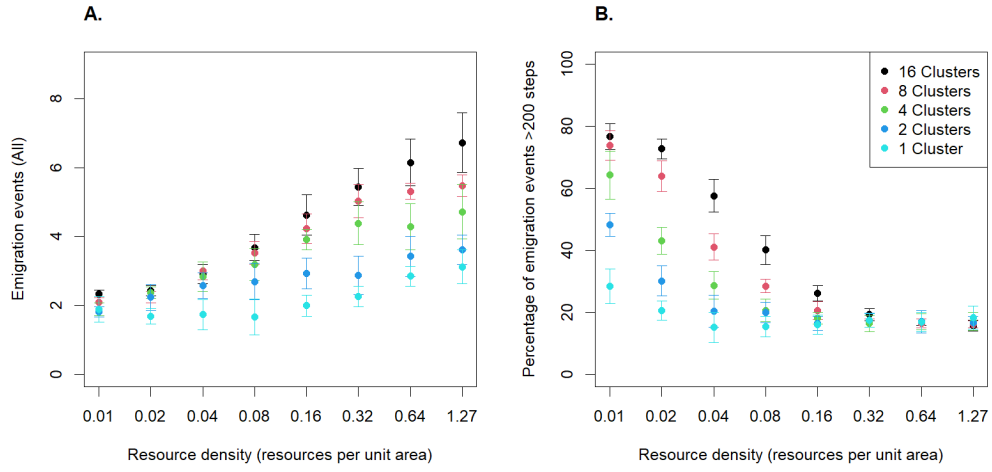


Figure 5: (A) The averaged number of emigration events per individual over the last 2000 time steps and (B) The percentage of emigration events that were longer than 200 steps (permanent emigration) plotted over resource density.

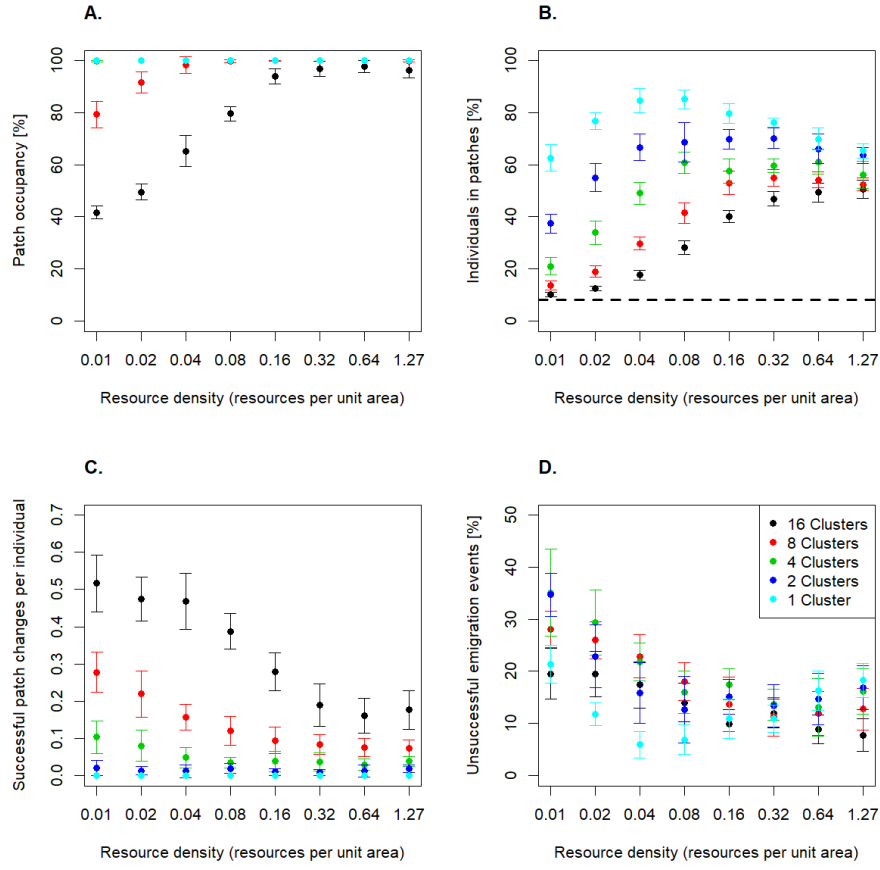


Figure 6: (A) averaged percentage of patch occupancy, (B) averaged percentage of individuals in clusters, (C) average number of successful patch changes per individual and (D) the proportion of individuals that never reach a patch (all values were calculated during the last 2000 time steps) plotted over resource density. The dashed line in (B) shows the expected percentage of individuals in clusters if they were randomly distributed.