Emergence of Spatially Structured Populations by Area-Concentrated Search

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Abstract

Background: The idea that populations are spatially structured has become a very powerful concept in ecology, raising interest in many research areas. However, despite dispersal being a core component of the concept, it typically does not consider the movement behavior underlying any dispersal.

Methods: Using individual-based simulations in continuous space, we investigate the emergence of a spatially structured population in landscapes with spatially heterogeneous resource distribution and with organisms following a simple area-concentrated search (ACS).

Results: We found that foraging success increased with increasing resource density and decreasing number of resource clusters. In a wide parameter space, the system exhibited attributes of a spatially structured populations with individuals concentrated in areas of high resource density, searching within areas of resources, and 'dispersing' in straight line between resource patches. 'Emigration' was more likely from patches that were small or of low quality (low resource density). 'Looping' from patches was more likely if patches were large and of high quality. With the ACS implemented, individuals tended to move deeper into a resource cluster in scenarios with moderate resource density than in scenarios with high resource density because of more space between resource items.

Conclusion: Our simulations demonstrate that spatial structure in populations may emerge if critical resources are heterogeneously distributed and if individuals follow simple movement rules (such as ACS). Neither the perception of habitat nor an explicit decision to emigrate on the side of acting individuals are necessary for the emergence of spatial structure. Mechanistic models like ours may help to close the gap between movement ecology and spatial ecology theory.

Introduction

The metapopulation concept has been a very powerful one in ecology, raising interest in research areas like dispersal ecology [1–3] or population genetics [4–8]. The concept also had a strong impact on the development of conservation concepts [9–12]. Yet there are also issues about its generality as the occurrence of metapopulations may be restricted to a rather small region in parameter space with many spatially structured populations basically behaving like patchy populations, mainland-island systems, non-equilibrium metapopulations or panmictic populations [13, 14]. Further, the metapopulation concept 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 organisms under investigation have a perception (or a 'concept') of habitat patches or that they at any time 'decide' to emigrate 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 [15–17] even though

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redient 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 [17–19]. Indeed, a rich literature exists of investigating and understanding rules of foraging (movement) at the individual and local level [19–24].

In fact, the 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., 25,26] 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 cause or motivation to move and that they collect and process information to steer their movement; an approach that questions the wide-held assumption in metapopulation models that movement and consequently dispersal would be random. Some authors have already created movement models with some or all of those components of movement [e.g., 18,27–36]. However, we are still only beginning to understand how such rules (or others) might scale up to population and landscape levels, *i.e.*, to the level of metapopulations and other spatially structured populations.

In this article, we propose that features of a spatially structured population and possibly of a metapopulation can emerge if animals follow simple movement rule like an ACS and if critical (and searched) resources are themselves heterogeneously distributed. Other and more sophisticated rules of context dependent movement might have similar effects, however. Here we simulate the movement of foraging organisms in a landscape with clustered resource distribution and explore how this influences the distribution of individuals in space, foraging success and the movement between resource clusters (patches).

Methods

We implement a simple model simulating the movement of resource-searching individuals in a continuous landscape with heterogeneous resource distribution. We investigate how resource distribution affects the spatial distribution (density) of individuals and the movement (dispersal) of individuals between resource clusters. We speculate that a spatially heterogeneous resource distribution and such a simple movement rule are sufficient to generate the different attributes of a spatially structured populations or metapopulation: (i) spatially clustered distribution of individuals in areas of resource concentration ('resource clusters' or 'habitat patches'), (ii) searching behavior within, but straight-line movement outside of habitat patches, (iii) reduced emigration from large and high quality habitat patches vs. elevated emigration from small or poor quality patches. Our simulation ignores birth and death events, but the model implicitly accounts for the (diffuse) effect of competition over resources on

Spatial distribution of resources and scenarios

We simulated foraging movement in a square landscape of area 4×10^6 squared spatial units (2000 x 2000) with resources distributed within it. In the simulations we created k resource clusters within the landscape as continuous spatial point pattern with points generated by the Matérn Cluster Point Process, using R version 3.5.2, library spatstat version 1.58-2 [37]. Clusters were generated with daughter points (resources) distributed according to a random uniform distribution on a disk around parent points with g as radius of the clusters and u as resource density per area unit so that $\bar{R} = g^2 \pi \times u$ was the expected number of resource items per cluster and the expected number of resources items in the landscape were thus $k \times \bar{R}$. Parent points were distanced at least $3g$ units apart from each other to avoid cluster overlapping. The landscapes were wrapped into a torus in both dimensions to avoid edge effects and mimic a landscape of infinite dimension.

Across scenarios, the number of resource clusters was increased from $k = 1$ to $k = 16$ clusters whereas the radius of clusters (g) was reduced from 320 (at $k = 1$) to 80 (at $k = 16$) so that the total area covered by resource clusters was identical in all scenarios (c. 8% of total area). The average resource density in resource clusters was varied from $u=0.01$ to $u=1.27$ resources per unit area. A summary of all model and simulation parameters and their values can be found in Table 1.

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	$0.01 \leq u \leq 1.27$ resources items per unit area
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)
α	Shape parameter	3
h	Half-saturation constant	200
p	Step length of movement	1
c	Perception radius	1

Movement rule

The movement of each individual was modeled as an ACS (also called 'state-dependent correlated random walk'; [18,38–40]). According to the ACS, the directionality (correlation) of movement is affected by an individual's internal state (e.g., hunger level) or its previous foraging success. Here we implemented the simplest of such possible rules, assuming that individual i moved straighter, the longer the time interval in which it did not find a food item was, i.e., the longer the searching time $\Delta_{S,i}$ was (reviewed in Bartoń and Hovestadt (2013) [18], see Benhamou (1992) [39]). At any moment t , and for any moving individual i the turning angle between two consecutive steps was determined by drawing a random value from a wrapped normal distribution [41] with mean 0 and standard deviation $d_{i,t}(\Delta_{S,i})$ calculated as

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

Consequently, $d_{i,t}$ ranges between $d_{min} = 0.01$ (nearly straight-line movement) when $\Delta_{S,i} \gg h$ and $d_{max} = 1$ when $\Delta_{S,i} = 0$, i.e., when the individual just found a food item. In the latter case, the movement became highly uncorrelated, and the individual performed an area-concentrated search. The parameter α is a shape parameter (in our simulations always $\alpha = 3$), and h is the half-saturation constant (always $h = 200$). The effects of parameter α and h on $d_{i,t}$

and on foraging success were described in [18]. We also tested different values of h and in this study but found that these two parameters did not strongly affect results. We thus kept these two parameter values constant in all simulations. Examples of movement paths of individuals from simulations are shown in Fig. 1.

Foraging

At each time step, each individual moved one step according to the movement rule described above. Individuals were moved in a random sequence to avoid priority benefits. The step length of movement (p) was constant and equal to 1 spatial unit. After movement, an individual immediately 'searched' for resource items within its perception radius ($c = 1$ spatial unit, identical to the step length). Any 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).

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

For analyzing the duration of movements within and between clusters, we noted the moments of emigration from, respectively of immigration into patches. For (3) duration of visits to a patch ('patch visitation time'), we counted the time between moment of immigration to emigration and for (4) duration of 'patch searching time', we counted time between moment of emigration to immigration for each individual incidence. We defined immigration as a moment when an individual entered the area of a cluster (radius around a parent point) even without foraging success and emigration as the moment when an individual left away from this area. The data also allowed to calculate (5) the number of emigration events/individual. If an individual foraged and moved away from a resource cluster and later returned to the same cluster to forage again, we counted this as two different clusters visited in our analysis; this is justified in a torus-world where individuals can return to a certain position by once walking around the torus. However, the emigration events also contained short excursions away and back to a cluster similar to 'foray loops' (a succession of progressively larger ellipsoidal loops) previously described in [42, 43]. We thus separated (6) excursions of less than 200 steps as 'foray loops' from 'long-distance emigration events' in our analyses.

Fronhofer et al. (2012) [14] proposed three broad criteria that were observed in previous studies of classical metapopulations: (i) patch occupancy is between 5% - 85% as a metapopulation is a network of occupied and empty patches; (ii) the turnover-rate (changes from extinct to occupied and vice versa) is between 10-40%; (iii) Migration between patches must be intermediate as a metapopulation is neither a panmictic population (no structure among populations, correlated population dynamics) nor a collection of completely isolated habitat patches. We thus measured (7) patch occupancy (proportion of time patches contained at least one individual), (8) the percentage of individuals located in clusters (9) the number of 'successful' migration events, *i.e.*, transitions from one cluster to another and finally (10) the percentage of emigration events where individuals failed to reach a patch including the patch of origin. For the analysis (9), individuals that never entered a patch within the last 2000 time steps were excluded.

Results

Foraging behavior and foraging success

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

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

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

We generally expected that individuals would stay and forage longer for resources within a patch and also find new patches faster when resources were dense, but our simulations provided more complex results. The mean number of clusters from which resources were collected was mostly <1 (this value included individuals that did not successfully reach a resource cluster) and smaller than the number of clusters they entered because individuals did not detect resource item within clusters (Fig. 2B). In the small cluster scenarios (16 and 8 clusters), the number of clusters harvested continuously increased with increasing resource density. In line, the average patch visitation time increased (Fig. 3A) and patch searching time decreased with increasing resource density (Fig. 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 a U-shaped response. Note that the duration of patch visits and searching was counted based on individuals entering or leaving a cluster radius independent of foraging success.

For better understanding the emergence of this uni-modal response we analyzed, just for the 1 cluster scenario, the position of individuals that were located within the resource cluster at the last time step for each resource density. 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 (Fig. 4). In other words, individuals tended to move deeper into a resource cluster with moderate resource density than in a cluster with high resource density because they were less likely to encounter upon arrival a resource item near the edge of the cluster. 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 leaving again the cluster.

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 (Fig. 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, with increasing resource density a smaller proportion of emigration events were >200 time steps so that individuals often returned into the patch of origin ('foray loops'; Fig. 5B); note that this explains the apparent contradiction between Figure 2B and 5A. The results showed that long-distance emigration events occurred more often at low resource density and small cluster size whereas foray loops occurred more often at high resource density and the proportion of foray loops generally increased with decreasing number of clusters (increasing cluster size).

When analyzing our simulation results for the emergence of metapopulation properties (as described in Fronhofer et al. (2012) [14]), we found mean patch occupancy lower than 85% only in five scenarios, i.e., with 8 clusters and resource density $u=0.01$ and in scenarios with 16 clusters and $u \leq 0.08$ (Fig. 6A), scenarios where the distribution of individuals across the whole landscape was still nearly random (close to the expected percentage of individuals in clusters if they were randomly distributed – the value was calculated from the area of the cluster divided by total area of the landscape $\approx 8\%$). With increasing resource density and cluster size individuals increasingly concentrated within resource clusters ('habitat'; Fig. 6B). For example, if 50% of individuals reside inside resource clusters that cover just 8% of the total area, the 'population density' inside cluster is already 11.5 times larger than in the surrounding matrix. However, for the scenarios with few clusters, the response to resource density was uni-modal due to the increasing emigration probability mentioned before. The highest number of successful patch changes per individual was observed in scenarios with many clusters and low resource density and this value decreased with lower number of clusters and higher resource density (Fig. 6C) and was almost or equal to zero at ($k < 2$). In turn, the proportion of individuals outside patches and never finding a patch within the 2000 time steps was also largest when resource density was low (Fig. 6D).

Discussion

In our simulations, we use a simple movement model on the one hand and landscapes with more or less spatially concentrated resource distribution on the other to simulate a collective of foraging individuals; the simulated populations show attributes of a spatially structured population as emergent properties. As such, the emergence of spatial structure cannot be a very surprising outcome as already common sense would make us expect that animals tend to concentrate in areas where critical resources are concentrated (up to population densities approx. 65 times larger inside clusters than outside - Fig. 6B). Nonetheless, we see a value in our simulations in making clear that neither the perception of a patch-matrix dichotomy nor any particular (decisions) rules for emigration are needed to generate spatial heterogeneity in the distribution of individuals. Further, the simulations implemented here also generate more specific patterns that are expected to emerge in spatially structured population systems, i.e., that individuals are more likely to emigrate from small vs. large resource clusters (*viz.* patches) and with greater probability from poor quality (low resource density) than from high quality clusters (but see below).

Foraging behavior and foraging success

As expected, a reduction of the number of clusters (larger cluster at the same time) and/or an increase resource density leads to more foraging success of each individual and also affects movement pattern of individuals. In the scenarios with high resource density or larger cluster, individuals tend to stay long within a patch and perform more area-concentrated search than straight line movement. Such effects of resource density and resource spatial arrangement on movement strategies and foraging success were also observed in previous studies [18, 39, 44]. Note that in our scenarios the tendency to remain in a resource aggregation is only driven by the attributes of the ACS but does not require that individuals respond to or even recognize (suitable) habitat *per se*. It also does not require that individuals apply different rules of movement to habitat and matrix or that individuals ever take a decision to emigrate from a habitat patch. Saying so, we do not want to exclude and even suggest that animals typically forage with more sophistication than we assume in our model, e.g., that they recognize environmental cues indicating that finding resources would be more likely in a certain region or base movement decisions on experience and memory [as examples in 34,45].

Interestingly, the greatest foraging success occurred in scenarios with a single resource cluster and highest resource density, but individuals did not stay longest within patches in this scenario: contrary to expectation, the longest residence times were observed in scenarios with moderate resource density, in particular in the scenarios with few, larger clusters. An underlying reason is that individuals tended to stay nearer to patch edges if resource density was very high and did not move as far into a patch (approaching the patch center) compared to individuals in scenarios with moderate resource density. Therefore, they tended to leave patches more often than in the other scenarios. Particularly with high resource concentration, many emigrations resembled foray loops, however, where individuals return to the same patch [42, 43]. On the other hand, with very low resource density individuals often moved through resource clusters without encountering resources at all and consequently maintaining a very directed walk and leaving the patch quickly again. Emigration events as well as foray loops might become rarer if individuals were to apply more sophisticated movement rules than implemented here, e.g., when using memorized knowledge about patch location [28, 31, 34, 35], knowledge about patch quality [32], improved perception range [34, 46] or applying smarter Bayesian movement decision rules [45]. Indeed, in some preliminary simulations we found that even a simple ACS with a delayed change in movement randomness after encountering a resource item resulted in deeper penetration into resource clusters and longer patch residence times. Adding any of such behavioral components might lead to edge 'avoidance' and a more 'organized' and efficient resource utilization from clusters and should lead to a decrease in emigrations and foray loops in scenarios with high resource density.

We show that our system with a simple area-concentrated search develops properties of a spatially structured population over a wide parameter range but never matches the stricter attributes of a metapopulation [*sensu* 14]. A patch occupancy below 85% emerged in simulations with multiple patches (8 and 16 patches) and low resource density (Fig. 6A). However, in these scenarios individuals were Loading [MathJax]/jax/output/CommonHTML/jax.js g. 6B) – that is, the distribution of individuals across the

landscape was more or less random and not showing signs of spatial structure at all. We did not calculate turnover rates in this study as we were simulating in (approximately) continuous time so that calculation of turn-over would depend on an arbitrary decision on the time-window over which to make such calculation; the turn-over concept applies better in long-term studies and in populations with a distinct dispersal phase. Instead, a more meaningful criterion is the frequency of successful patch changes as a measure of gene flow and possible patch recolonization or rescue. The number of successful patch changes (emigration from one and immigration into another resource patch) was indeed quite low (Fig. 6C), but these values can only be interpreted in relation to the total period covered by our scenarios. For example, if we assume that a single time step (the time an individual needs to pass through its perceptual radius) is five minutes, the 2000 time steps analyzed cover a period of approximately 7 days. Further assuming that animals are active only 12h a day (e.g., because they are nocturnal) and do not move during more than 1/2 of their active time, the period covered would correspond to *c.* 3-4 weeks, a value is not unreasonable for the expected lifespan of many adult insects. Based on these assumptions we thus find that in many of our simulations only a small fraction of individuals (mostly <20%) successfully 'dispersed' from one habitat cluster to another during their lifetime. This infrequent dispersal events emerged despite the fact that we did not assume a mortality risk for individuals moving outside habitat, e.g., due to exhaustion or predation. In this regard our simulations indeed meet the metapopulation criterion defined by Fronhofer et al. (2012) [14] but as explained above, the patch occupancy criterion is only satisfied in those scenarios that showed at best weak symptoms of spatial structure. Our results thus support the idea that spatial population structure covers a continuum in terms of patch occupancy and migration rate [47, 48] but that true metapopulation attributes rarely emerge as long as external factors do not lead to the sudden extinction of local populations [14, 49, 50]. Unfortunately, only few empirical studies focused on resource density *per se* on emigration and immigration rate. For several insect species, the density of nectar sources or host plants has a negative effect on emigration and possibly a positive effect on immigration [51–53] and possibly increases patch occupancy [54–56].

In this study, we varied patch structure (many small patches to single large patch and low to high resource density) but within a scenario all patches were identical. Creating landscapes with resource clusters of variable attributes might enable us to investigate the emergence of spatially structure in populations in other landscape settings, e.g., settings that show attributes of a mainland-island system [13] or a system with varying patch quality (resource density) like in source–sink systems [57]. It must also be mentioned that we did not investigate the effect of the two parameters α and h , but previous studies showed that our choice of parameter values is adequate to result in good foraging success in a broad spectrum of parameters for the spatial distribution of resources (*cf.* Bartoń and Hovestadt (2013) [18] for more details). Generally, a decrease of the half-saturation constant h should lead to an increase in emigration rates and a reduction of patch residence times.

In this model, we assumed no birth and death events in the population. By excluding natality and

dispersal mortality, starvation, or environmental stochasticity which were reported to influence dispersal probability and spatial population structure [14, 58, 59]. A full model should in fact also account for a proper resource dynamic, e.g., by either simulating abiotic resources with a constant supply rate (patch specific) or by implementing it as a prey population with its own population dynamics.

Conclusions

In this study, we implement a model of organism with an area-concentrated search as a foraging movement rule moving in a continuous landscape with aggregated resource distribution. Although we do not include population dynamics (birth and death) into the system, the simulated collective of individuals expresses properties of spatially structured populations as emergent properties. Models like this can be used to improve our understanding of the mechanisms underlying the emergence of population structure but could also be applied – given we know the rules of movement – to foresee the effects of landscape changes *viz.* changes in resource distribution on (endangered) populations. Furthermore, the model could be extended by adding components that affect population dynamics, e.g., dispersal mortality, environmental stochasticity, heterogeneous patch quality, or varying natality and mortality.

Declarations

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Author contributions

TC, TH designed the study; TC developed and carried out the simulations, performed the analysis and wrote an initial draft of the manuscript; all authors contributed to the revisions of the manuscript, read, and approved the final manuscript.

Ethics approval and consent to participate

Not applicable

Consent for publication

Not applicable

Competing interest

The authors declare that they have no competing interest.

Availability of supporting data

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The datasets supporting the conclusions of this article are available upon request from the corresponding author.

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Figures

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) with size (g) of 80 units and resource density (u) of 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 average 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.