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Boundary constraints on population dynamics in a percolating habitat

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A B S T R A C T

The spatial distribution of suitable environmental conditions defines a species habitat, and colonization-extinction dynamics within this habitat determine the distribution of species populations. In addition, the success of colonization and the risk of extinction are expected to be influenced by the proximity to habitat boundary. We address here the influence of boundary vicinity for a contact-process model of population dynamics in a percolating habitat lattice. To separate the influence of boundary vicinity from that of fragment area, we investigate population dynamics in the very large spanning cluster of the percolating habitat. The geometry of the spanning cluster varies when habitat density in the lattice is tuned away from the percolation threshold. We expect that the colonization success decreases closer to the boundary, leading to depleted site occupancy in the cluster, and that this effect is even more pronounced near the extinction threshold of the contact process. For the set of suitable sites of the cluster and unsuitable sites next to its boundary, we quantify the boundary density, σ, as the probability to draw a pair of suitable and unsuitable sites. The cluster boundary is most rugged and σ is maximal close to the percolation threshold of the habitat. We expect that the global influence of boundary on population dynamics in the cluster is greater when the boundary is more rugged. We thus investigate population dynamics in the spanning cluster for varying values of σ. We determine the stationary properties of population dynamics in the spanning cluster according to σ and to the species-specific ratio of extinction and colonization rates, denoted r. Using both numerical simulations and a pair-approximation model, we assess global species persistence and site occupancy patterns in the spanning cluster. We show that the extinction threshold r_c depends crucially on σ, i.e., increasing σ limits global species persistence. Furthermore, increasing σ decreases the probability of site occupancy in the spanning cluster. A key result is that this influence extends to sites far from the boundary when r gets close to r_c. Therefore, species that are at risk of extinction are more sensitive to the influence of habitat boundary. These results are of both theoretical and practical interest for understanding and forecasting species viability in heterogeneous and fragmented habitats.

1. Introduction

Understanding the drivers of species distributions is a primary goal in ecology (Elith and Leathwick, 2009). First, suitable environmental conditions define the species habitat where populations can establish and persist. The habitat is classically represented as a binary set of suitable and unsuitable sites. Second, population dynamics are ruled by species colonizing abilities allowing the founding of new populations in the suitable sites of the habitat. Species colonization basically decreases with the distance from source populations. Due to such limited colonization ability, habitat density and configuration determine the outcome of population dynamics. We then expect that the extent and limits of species distributions reflect the combination of habitat structure and species dynamics in space and time (Holt and Keitt, 2000; Holt et al., 2005). Specifically, habitat boundary affects individual organism behaviour and colonization dynamics (Fagan et al., 2009; Schultz and Crone, 2001), species interactions (Cantrell et al., 1998; Fagan et al., 1999; Malcolm, 1994), as well as population viability and extinction (Laurance et al., 1998; Woodroffe and Ginsberg, 1998). The boundary is thus expected to influence colonization-extinction dynamics of populations within the habitat (Holt et al., 2005). We address the issue for a colonization process restricted to the nearest neighbourhood of existing populations (contact process Bascompte and Solé, 1998; Hiebeler, 2000; Houchmandzadeh, 2008; Tilman and Kareiva, 1997). In this case, population dynamics occur across contiguous suitable sites making a habitat cluster. Our aim is to characterize how cluster boundary

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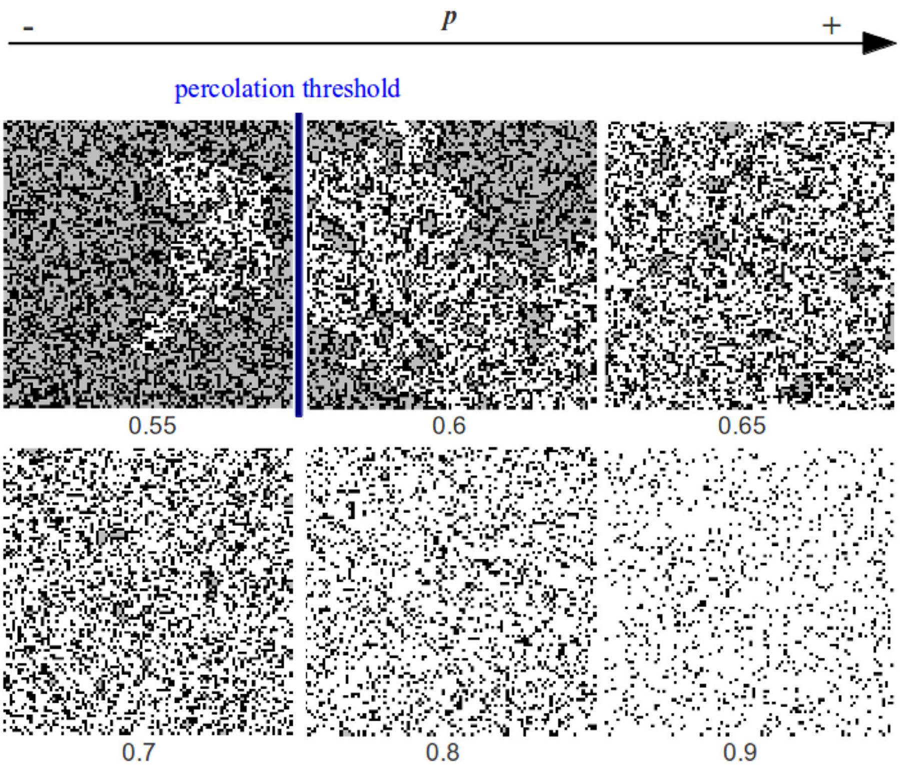

Fig. 1. Simulated habitat lattices over a gradient of suitable habitat density p. Unsuitable sites are shown in black, while the other sites are suitable. The largest habitat cluster in white represents the spanning cluster when $p > p_c$, where p_c is the percolation threshold. Other habitat clusters are shown in gray. The spanning cluster rapidly occupies the overall habitat when p increases above the percolation threshold.

influences species persistence and population density in the cluster.

The influence of cluster boundary is intertwined with the effect of cluster area, insofar as the probability that a site of the cluster is close to the boundary increases when area decreases. Because cluster area also influences population dynamics and species persistence (Etienne and Nagelkerke, 2002; Ovaskainen, 2001), distinguishing the effects of cluster area and of cluster boundary is needed but still challenging (Ewers and Didham, 2006; Fletcher et al., 2007). Previous works addressed the influence of habitat fragmentation on population dynamics, based on some synthetic metrics of habitat structure, such as density and aggregation in habitat lattices (e.g., Ellner, 2001; Hiebeler, 2000; Liao et al., 2013). A habitat lattice can include a number of clusters with varying size and boundary geometry. A gradient of habitat structure in terms of global habitat density or aggregation in the lattice then does not allow assessing the respective influences of cluster size and boundary geometry on population dynamics. Our objective is to address the specific influence of boundary geometry, irrespective from the influence of cluster size. Therefore, we need (i) to define a single habitat cluster with large-enough size to prevent finite-size effects on population dynamics, (ii) and to make vary its boundary geometry.

Percolation theory is a general framework that allows characterizing a range of binary habitat geometries on a lattice (Boswell et al., 1998; Gardner et al., 1987; Huth et al., 2014). The percolation threshold represents an abrupt change of habitat structure when decreasing habitat density, from a habitat dominated by a very large cluster of contiguous habitat sites, called spanning or percolating cluster, to an archipelago of small habitat clusters (Turner et al., 2001). In the limit of an infinite lattice, the spanning cluster is an infinite and unfragmented set of suitable sites, and the perimeter-to-area ratio of this cluster varies continuously when tuning habitat density above the percolation threshold (Leath and Reich, 1978; Peters et al., 1979; Stauffer and Aharony, 1994). In finite simulated lattices, the spanning cluster is not infinite but still very large, so that we expect little influence of finite habitat area and can specifically address the influence of varying boundary geometry on population dynamics.

We consider the spanning cluster of a percolating habitat plus the unsuitable sites next to its boundary. We define an index of boundary density, denoted σ, as the probability that a pair of neighbouring sites includes a suitable site of the spanning cluster and an unsuitable site. The greater σ is the more rugged is the boundary, and the more likely is a site of the cluster to be close to the boundary. We consider a gradient of spanning clusters with varying σ values, and a contact-process model of spatial population dynamics within the cluster. We address whether and how (i) species persistence in the cluster is altered along the gradient, and (ii) the probability of site occupancy varies within the cluster according to the distance from the boundary. Our basic hypothesis is that limited availability of colonization sources affects species persistence, globally, and the occurence of populations in sites close to habitat boundary, locally. Furthermore, near the critical extinction threshold of the contact process, long-range correlations in spatial occupancy are known to occur (Bascompte and Solé, 1996). Therefore, we expect that the influence of boundary is more and more long-range within the cluster when the contact process is closer to its extinction threshold. In order to address the local influence of boundary, we consider a pair-approximation model of population dynamics such that the occupancy state of contiguous pairs of sites is analyzed in addition to local occupancy state (Hiebeler, 2000; Iwasa, 2000; Matsuda et al., 1992). Pairs of suitable-unsuitable sites represent the boundary of the spanning cluster and we analyze the steady-state occupancy of these pairs compared to suitable-suitable pairs farther from the boundary. We address the spatial extent of boundary influence by analyzing site occupancy as a function of the distance from the boundary.

2. Material and methods

2.1. Spanning cluster of a percolating habitat

We randomly select in a square lattice a proportion p of sites (state h) constituting the habitat of a given organism, while the remaining proportion $1 - p$ represents unsuitable sites (state $\bar{h}$). Such lattice model was previously proposed as a baseline to represent a variety of landscape configurations (Gardner et al., 1987), and their spatial properties have been extensively investigated in physics and ecology in the context of percolation theory (Stauffer and Aharony, 1994; Turner