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Habitat Heterogeneity Hypothesis and Edge Effects in Model Metacommunities - Marked Manuscript

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5 Abstract

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Spatial heterogeneity is an inherent property of any living environment and is expected to favour biodiversity due to a broader niche space. Furthermore, edges between different habitats can provide additional possibilities for species coexistence. Using computer simulations, this study examines metacommunities consisting of several trophic levels in heterogeneous environments in order to explore the above hypotheses on a community level. We model heterogeneous landscapes by using two different sized resource pools and evaluate the combined effect of dispersal and heterogeneity on local and regional species diversity. This diversity is obtained by running population dynamics and evaluating the robustness (i.e., the fraction of surviving species). The main results for regional robustness are in agreement with the habitat heterogeneity hypothesis, as the largest robustness is found in heterogeneous systems with intermediate dispersal rates. This robustness is larger than in homogeneous systems with the same total amount of resources. We study the edge effect by arranging the two types of resources in two homogeneous blocks. Different edge responses in diversity are observed, depending on dispersal strength. Local robustness is highest for edge habitats that contain the smaller amount of resource in combination with intermediate dispersal. The results show that dispersal is relevant to correctly identify edge responses on community level.

⁶ Keywords: ecotone, foodweb, population dynamics, simulation, space.

7 1. Introduction

Most organisms live in a spatially heterogeneous environment. Combining this general observation 8 with classical niche theory (for a review see for example Leibold [1]) leads to the so-called habitat g heterogeneity hypothesis [2]. This idea was first discussed in order to explain the latitudinal gradient 10 in species diversity. Species diversity increases from the poles to the equator. This can be explained by 11 the hypothesis that a diverse (heterogeneous) environment offers more possible niches, thereby allowing 12 more species to coexist. The habitat heterogeneity hypothesis has been successfully tested in various 13 empirical studies across different biomes and taxa, for reviews see for example [3, 4]. Recently Harpole et 14 al. showed that the addition of nutrients that are otherwise limiting, decreases species diversity in plant 15 communities [5]. Reversing this observation means that diversity is higher in systems with more limiting 16 factors because more niches can be occupied. Those systems can be viewed as more heterogeneous in 17 their environmental conditions. 18

Related to the habitat heterogeneity hypothesis is ecological edge theory [6, 7, 8]. Edge theory states 19 that species abundance can differ between boundaries¹ of adjacent habitats and "core areas" inside a 20 habitat. Ries and Sisk developed a framework for explaining species abundance at ecological edges [9]. 21 The key information for determining the edge effect of a species in this framework is the distribution of 22 its resources. This is related to the underlying mechanisms of "resource mapping": a change in a species 23 resource distribution will induce a change in the species abundance itself. By determining if a resource 24 is either supplementary or complementary, species abundance at the edge can be predicted. This thesis 25 was successfully tested on several species from different biomes and taxa [10]. However it is still not clear 26 how it scales up to food web or even metacommunity level. One assumption of this bottom-up theory is 27 that "resource mapping" should also cascade up through trophic levels in a food web (chain). Wimp et 28

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¹also called ecotones or simply edges [7]

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