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Ecological Indicators

Functional connectivity as an indicator for patch occupancy in grassland specialists

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ABSTRACT

Habitat specialists living in metapopulations are sensitive to habitat fragmentation. In most studies, the effects of fragmentation on such species are analyzed based on Euclidean inter-patch distances. This approach, however, ignores the role of the landscape matrix. Recently, therefore, functional distances that account for the composition of the landscape surrounding the habitat patches have been used more frequently as indicators for patch occupancy. However, the performance of functional and non-functional connectivity measures in predicting patch occupancy of such species has never been compared in a multi-species approach.

Here we evaluate the effect of habitat connectivity on the patch occupancy of 13 habitat specialists from three different insect orders (Auchenorrhyncha, Lepidoptera, Orthoptera) in fragmented calcareous grasslands. In order to calculate functional distances we used four different sets of resistance values and rankings. We then modelled species' occurrence using both Euclidean and functional (based on least-cost modelling) inter-patch distances as predictors.

We found that functional connectivity measures provided better results than the non-functional approach. However, a functional connectivity measure that was based on very coarse land-cover data performed even better than connectivity measures that were based on much more detailed land-use data.

In order to take into account possible effects of the landscape matrix on patch occupancy by habitat specialists, future metapopulation studies should use functional rather than Euclidean distances whenever possible. For practical applications, we recommend a 'simple approach' which requires only coarse land-cover data and in our study performed better than all other functional connectivity measures, even more complex ones.

1. Introduction

Land-use change is believed to be the major driver of terrestrial biodiversity loss (Foley et al., 2005; Jetz et al., 2007; Sala et al., 2000). Over the last 150 years, in particular, semi-natural habitats have suffered a severe decline in area due to land-use intensification, abandonment and afforestation (Baur et al., 2006; van Swaay, 2002; WallisDeVries et al., 2002). As a consequence, calcareous grasslands are currently threatened and are therefore protected under the Habitats Directive of the European Union (European Commission, 2007). As these habitats harbour a unique and often very diverse flora and fauna, their destruction has resulted in a rapid loss of species, which still continues (Fahrig, 2003; Kleijn et al., 2011; Krauss et al., 2010; Sang et al., 2010). An interlinked effect of habitat loss is an increase in spatial isolation of the remaining habitat patches (Fahrig, 2003), which can itself contribute to declines of species (Krauss et al., 2003; Roesch et al., 2013).

High extinction rates can particularly be observed for habitat specialists, as they are known to be more sensitive to land-use change than habitat generalists (Brueckmann et al., 2010; Oeckinger et al., 2012). Many highly specialized species build metapopulations, i.e., the regional population consists of several local subpopulations (Biedermann, 2000; Carlsson and Kindvall, 2001; Eichel and Fartmann, 2008; Hanski and Thomas, 1994;

Stuhldreher and Fartmann, 2014) that are inter-connected by migrating individuals (Baguette, 2003; Hill et al., 1996; Schmitt et al., 2006; Zalewski, 2004). Metapopulations have a dynamic population structure that is characterized by local extinctions and recolonizations. The higher the isolation of a subpopulation, the more prone to extinction it becomes and the less likely it is to be re-established (Appelt and Poethke, 1997; Carlsson and Kindvall, 2001; Hanski et al., 1994; Kindvall and Ahlen, 1992; Krauss et al., 2004). In the long-term, this can lead to extinction of the whole metapopulation (van Strien et al., 2011). Consequently, species living in metapopulations are highly affected by habitat fragmentation.

A well-established method for measuring the degree of isolation of populations is Hanski's connectivity index (Hanski, 1999). It yields better results than other connectivity measures such as percentage habitat cover or distance to the next suitable habitat (e.g. Brueckmann et al., 2010; Moilanen and Nieminen, 2002). The index uses the distances of the focal patch to the occupied patches in the surrounding area, the size of the occupied patches in the surroundings and the average dispersal distance of the focal species. Although this approach has proven useful in several studies (e.g. Anthes et al., 2003; Binzenhofer et al., 2008; Carlsson and Kindvall, 2001; Krauss et al., 2004), when based on Euclidean distances it ignores the landscape matrix. This matrix represents the structural configuration of the landscape between the focal patch and the patches in the surrounding (Ricketts, 2001). The major effects of the matrix on the accessibility of a patch have already been shown by several studies dealing with the concept of functional connectivity (e.g. Richard and Armstrong, 2010; Watts and Handley, 2010; review by Sawyer et al., 2011; Sutcliffe et al., 2003). Functional connectivity has also been established as an indicator for landscape fragmentation (Hernández et al., 2015) and uses functional (least-cost) rather than Euclidean distances. While most of the studies that adopt this functional approach focus on landscape ecology (i.e. landscape connectivity, least-cost corridors and/or migration zones), functional connectivity is rarely analyzed in the context of metapopulation ecology (i.e. patch connectivity). In addition, the few studies that investigate the influence of functional connectivity on species' occurrence deal with single species rather than groups of species, which is why the results are often not applicable to other species (cf. Doerr et al., 2011).

Functional distances can be calculated using least-cost modelling. This method assigns a specific resistance value to each land-cover type in the matrix (Adriaensen et al., 2003; Chardon et al., 2003). Land-cover types favouring dispersal are allocated lower resistance values than those that hinder movement (Kraemer et al., 2012). In least-cost modelling, the length of a potential dispersal corridor is traded off against the sum of the resistance values encountered along that corridor. Hence, the functional distance describes the accumulated cost that is demanded of an individual to cover the least costly path between two habitat patches.

Even though Hanski's index is widely used in metapopulation ecology (see above), to our knowledge it has only once been combined with least-cost modelling: Verbeylen et al. (2003) achieved good results with this method. However, the authors emphasize a need for further research, especially with regard to resistance values.

This study presents a multi-species approach using 13 species from three different insect orders (Auchenorrhyncha, Lepidoptera, Orthoptera). We modelled species' occurrences using the classical approach (based on Euclidean inter-patch distances) on the one hand and the functional approach (based on least-cost modelling) on the other hand. We tested four different sets of resistance values and rankings for the functional approach. In each case, habitat connectivity was calculated using Hanski's index. Specifically, the following questions were addressed:

(1) Does the functional approach lead to better results than the classical approach?
(2) Which method of assigning resistance values and rankings to land-cover types has the highest explanatory power?
(3) Which approach of modelling habitat connectivity is most suitable in practical applications?

2. Material and methods

2.1. Study organisms

As study organisms we chose four Auchenorrhyncha (*Batracomorphus irroratus*, *Goniagnathus brevis*, *Kosswigianella exigua*, *Neophilaenus albipennis*), six butterfly (*Argynnis aglaja*, *Cupido minimus*, *Erynnis tages*, *Hesperia comma*, *Melitaea aurelia*, *Satyrium spini*) and three Orthoptera species (*Metrioptera brachyptera*, *Phaneroptera falcata*, *Stenobothrus lineatus*) (Table 1). Due to their high sensitivity to environmental changes, the three groups are well-suited for ecological studies (Auchenorrhyncha: Achtziger et al., 2014; Nickel and Hildebrandt, 2003; butterflies: Fartmann et al., 2013; Orthoptera: Fartmann et al., 2012). All study organisms

Table 1
Study organisms and their developmental stages searched for during the study period (April to September).

Study organisms	Study period				
	Late April	Late May	Late June	July/August	Early September
(a) Auchenorrhyncha					
Batracomorphus irroratus			Adult	Adult	Adult
Goniagnathus brevis	Adult	Adult	Adult	Adult	Adult
Kosswigianella exigua	Adult	Adult	Adult	Adult	Adult
Neophilaenus albipennis		Adult	Adult	Adult	Adult
(b) Lepidoptera					
Argynnis aglaja			Adult		
Melitaea aurelia			Adult/egg	Larva	Larva
Cupido minimus		Adult/egg	Adult/egg	Adult/egg	
Erynnis tages		Adult/egg	Egg/larva		
Hesperia comma				Adult/egg	Egg
Satyrium spini				Egg	Egg
(c) Orthoptera					
Phaneroptera falcata		Nymph	Nymph	Nymph/adult	Adult
Stenobothrus lineatus		Nymph	Nymph/adult	Adult	Adult
Metrioptera brachyptera	Nymph	Nymph	Nymph	Nymph/adult	Adult