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Multi-scale ecology of insectivorous bats in agricultural landscapes

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ABSTRACT

During the last century, agricultural landscapes have gone through a process of homogenization, driven by the intensification of land use. Homogenization has led to a decline in biodiversity and a degradation of ecosystem services; for instance, biological pest control. Bats have been fairly invisible service providers and the effect of landscape structural changes on them is poorly understood.

We assessed the relative roles of woody habitats and the composition of agricultural landscapes on the diversity and activity of bats in southern Estonia. The study applied a stratified double-point sampling scheme in 30 rural landscape windows comprised of three habitat types, where bats were recorded using automated recording devices. The structure of each stand was described, and the typology of solitary trees, linear objects (alleys and tree-lines) and woodland patches was transformed into a continuous gradient of tree density to simplify the extrapolation of results.

Among 10 species and the *Myotis brandtii*/*mystacinus* complex, *Eptesicus nilssonii* and *Pipistrellus nathusii* prevailed. Species richness and the flight activity of bats were the highest in woodlands, as expected. Linear corridors and solitary trees shared relatively equal richness, while flight activity was three times higher around double-tree-lines (alleys) than around single-tree-lines and solitary trees. Such a pattern was log-linearly related to tree density. Large-scale factors, such as landscape structure and the local species pool, were important drivers for both response indicators; flight activity was additionally dictated by a stand's vertical structure.

We conclude that in order to promote bat diversity and the service potentially provided to agriculture, future agri-environmental schemes should incorporate multi-scale management planning: (i) coordinated establishment or maintenance of alleys and small woodland patches within field complexes over neighbouring farms in the scale of several kilometres; (ii) forming water bodies in the vicinity of woody habitats to improve the landscape quality for bats; and (iii) paying special attention on the preservation of old and low branching trees in each woody habitat type.

1. Introduction

Agricultural landscapes have historically been structurally heterogeneous, consisting of a mosaic of croplands and various semi-natural habitats, which together have supported high natural diversity (Antrop, 2005; Jonsen and Fahrig, 1997; Robinson et al., 2001; Weibull et al., 2000). During the last century, however, the biodiversity has declined because of the intensification of land use, mostly explained by the effect of agro-chemicals and the homogenization of the landscape (Benton et al., 2003; Bianchi et al., 2006; Liira et al., 2008). Homogenization can be viewed on three spatial scales: landscape, field and habitat (patch) scales (Benton et al., 2003). The decline of biodiversity on all three scales has led to severe losses in ecological services, one of which is biological pest control (Bianchi et al., 2006; Weibull et al., 2003). Multiple taxonomic groups provide the pest control service, among which bats are valuable regulators of insect abundance in different crop systems (Boehm et al., 2011; Boyles et al., 2011; Maas et al., 2013; Williams-Guillén et al., 2008). Sometimes the effect of bats on the abundance of pest insects may be even greater than that of birds (Kalka et al., 2008). As bats have been fairly invisible service providers, the effect of landscape structural changes on their populations is poorly understood and the ecological knowledge to promote bats in agricultural landscapes still needs quantified support.

In bat ecology, woody habitats have usually been classified into discrete habitat types within the structural gradient according to their general appearance: solitary trees, tree-lines, alleys and patches (Russ and Montgomery, 2002; Walsh and Harris, 1996). In

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agricultural landscapes, the affiliation of bats' to hedgerows, tree lines and woodland patches differs greatly (Frey-Ehrenbold et al., 2013; Russ and Montgomery, 2002; Vaughan et al., 1997; Walsh and Harris, 1996), but much less is known about the effect of solitary trees in open landscapes (Fischer et al., 2010). Woody habitats have usually been classified into discrete habitat types within the structural gradient according to their general appearance, e.g. solitary trees, tree-lines, patches (Russ and Montgomery, 2002; Walsh and Harris, 1996). In field conditions, bats depend on specific structural properties of these habitats, and as many properties overlap between types, the categorical classification system of woody elements does not sufficiently precisely describe the effect of ecological conditions. For instance, bat abundance correlates not only with the density of trees in the landscape, canopy structure or stand management intensity (Adams, 2012; Boughey et al., 2011; Humes et al., 1999; Patriquin and Barclay, 2003), but also with the length of the linear objects or the area of woodland patches (Frey-Ehrenbold et al., 2013; Fuentes-Montemayor et al., 2011). Habitat structure (internal stand structure and a habitat's general appearance) primarily influences the abundance of prey insects, and that dictates the foraging activity of bats (Burford et al., 1999; Grindal, 1996; Grüebler et al., 2008; Jong and Ahlén, 1991). Therefore, from the perspective concerning bats, internal stand structure (hence-forth 'stand structure') described with continuous variables can be a more adequate approach for the delineation of tree-based habitats than the use of discrete habitat classes (Lumsden and Bennett, 2005). However, from the perspective of landscape planning, the use of habitat types cannot be rejected, and therefore, both approaches should be used in parallel.

The presence of bat species at a certain landscape element depends not only on the habitat's internal properties, but also on the availability of species in the larger region, i.e. there are also landscape-scale factors. Bats move nightly between several habitat patches over a range of several kilometres, and therefore, landscape structure can be as important as properties of a habitat patch and the habitat's internal structure (Akasaka et al., 2012; Davidson-Watts et al., 2006; Flaquer et al., 2009; Hillen and Veith, 2013). A down-scale relationship like this is synonymous with a species pool effect, which initially involves large-scale factors determining the size of the local species pool, and secondly a filtering effect at smaller scale, by which interaction between habitat properties and species preferences defines a species selection from the local pool into the habitat spot (Cornell and Lawton, 1992; Ricklefs, 1987; Zobel, 1997).

We examined relationships between the multi-scale complex of ecological drivers affecting bats around woody objects (alleys, tree-lines and solitary trees) in open agricultural landscapes. Assuming that forests and parks are the main source habitat of a local species pool, we hypothesized that species richness and the flight activity of bats both will decline from woodlands towards single trees. However, the effect of habitat properties and the landscape structure around habitats will be revealed only after considering the size of locally available species pool. Therefore, we evaluated the relative roles of potential factors in three spatial scales: landscape, habitat element (field-scale from the point of view of agricultural planning) and the internal structure of a habitat (Fig. 1).

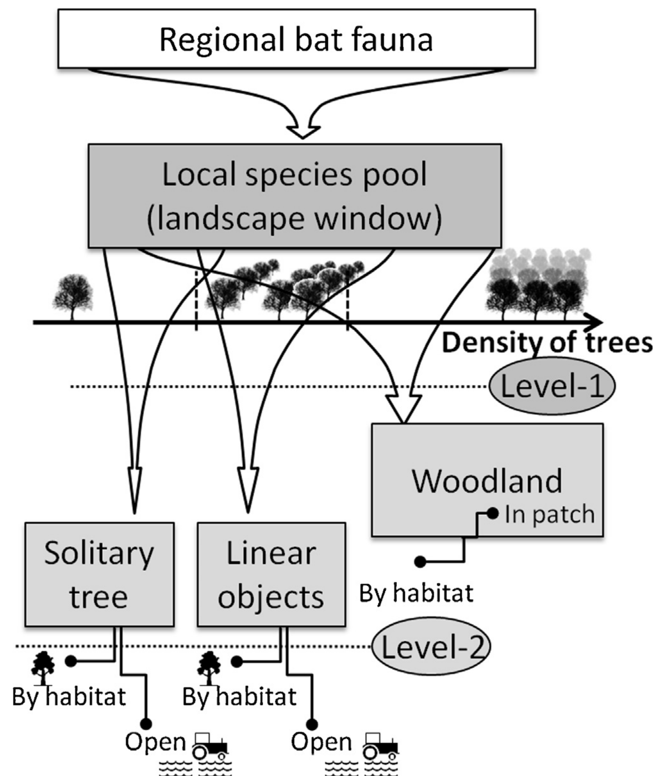

Fig. 1. Scheme of hierarchical interrelations of bat species richness across spatial scales.

2. Materials and methods

2.1. Study area and timing

Bat species richness and their relative abundance were surveyed using a stratified double-point survey methodology in 30 agricultural landscape windows in southern Estonia. The maximum diameter of a landscape window was 3 km, although most were smaller. The distance between windows was kept larger than the diameter of the windows to keep observations as independent as possible. Windows were selected to cover a wide range of landscape complexes, i.e. windows were selected with a variable abundance of woodlands and water bodies. Each window included a minimum mix of at least one of each category of sampling site types (see Fig. 1): (i) 37 instances of a woody landscape object of a solitary tree or an isolated copse; (ii) 46 instances of a woody landscape object of a linear landscape element (a single line of trees line or an alley of two parallel tree lines) and (ii) 38 instances of the nearest mature woodland patch, park or forest. Sometimes, a second survey point in one of the habitat types was used, if it was structurally different and was located in a different part of the window. All forests and parks were selected by the dominance of deciduous trees. The survey was conducted between the end of May and the end of July 2012.

Sampling sites comprised of two 'simultaneously-recording' microphones (sampling points); one located in or near a woody habitat and the other in an open area (Fig. 1). The study used automated bat recording devices SM2BAT and SM2BAT+ (Wildlife Acoustics Inc.) with a two-channel recording setup with a sampling rate of 192 kHz. Microphones were fixed to 2.5 m rods and pointed in opposite directions approximately 40 m apart to avoid any overlap in their detection radii. The placing of the two microphones differed between the categories of sampling site. One of the two microphones in the woodland sampling site was placed inside the woodland and the other in an open area at 5 m distance from the woodland's edge (agricultural field or clear-cut area). In survey sites located at linear objects or solitary trees the first microphone was placed adjacent to the key object and the second in the open field (crop-land or grassland). Dual recording was expected to emphasise a local contrast between the woody habitat and the neighbouring open area. Sampling lasted from 22:30 to