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Correlations in species richness between taxa depend on habitat, scale and landscape context

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ABSTRACT

Biodiversity indicators are assumed to reflect changes in e.g. species richness of multiple taxa, but correlations in species richness between taxa have often been shown to be weak. However, only few studies are based on data allowing for rigorous tests whether strengths of correlations differ between habitat and landscape factors. We compared strengths of correlations between species richness of butterflies, plants and farmland birds between habitats (semi-natural grasslands, forest verges or field boundaries), spatial scales (0.8 ha, 25 ha and 50 ha) and landscapes differing in heterogeneity and regional land-use intensity. Between habitats, the correlation between butterflies and plants was strongest in semi-natural grasslands. Also concerning butterflies and plants, the correlation was weakest at the 0.8 ha scale, but no consistent scale-dependent patterns were found between plants and farmland birds. In a regional context, butterfly and plant species richness were consistently positively correlated, whereas when involving farmland birds we found correlations between taxa to be weaker and/or not significant in regions with high agricultural land-use intensity and in homogeneous landscapes. In general, species richness was consistently congruent only between butterflies and plants, whereas correlations involving farmland birds were mainly weak and showed contrasting patterns depending on regional context. Increasing landscape heterogeneity thus increased congruence amongst all studied taxa, but in different contexts and due to different underlying mechanisms. Although plants were involved in most of the significant correlations we cannot recommend a particular taxon as a general diversity indicator.

1. Introduction

Increased land-use intensity has resulted in unprecedented declines in global biological diversity (Pereira and Daily, 2006; Pimm and Raven, 2000), but for large areas no data are available to accurately measure these declines (e.g. Jenkins et al., 2003; Kerr et al., 2000). Even in well-studied regions, we lack the necessary information to quantify recent diversity declines of most taxa. Because of limited data availability and resources for biodiversity monitoring, the development of surrogate measures mirroring the state of overall biodiversity has received much attention in the scientific literature (Gaston, 1996; Kerr et al., 2000; Pearman et al., 2006). However, a growing body of research has demonstrated that correlations between taxa are frequently weak (Wolters et al., 2006), casting serious doubts on the general usability of such biodiversity indicators (Rossi, 2011).

According to Wolters et al. (2006), studies on correlations between taxa are biased towards certain taxa and regions. These authors also found that the majority of such studies were based on data collected in grasslands (e.g. Vessby et al., 2002) or forests (e.g. Jonsson and Jonsell, 1999). Only a few studies on correlations between taxa have been carried out in agricultural landscapes (Billeter et al., 2008; Weibull et al., 2003). Agricultural landscapes provide an ideal study system, since they contain both extremely species-rich and species-poor habitats and the determinants of species richness of many taxa are well understood (Kleijn et al., 2009, 2011; Tscharntke et al., 2012).

Strong correlations between taxa in agricultural landscapes would give more confidence in the general applicability of farmland biodiversity indicators. However, as taxa are affected by multiple factors at local, landscape and regional scales (e.g. Billeter et al.,

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2008; Schweiger et al., 2005), the strength of correlations between taxa are also likely to depend on several mechanisms. At rather small scales, local habitat characteristics have strong effects on species assemblages (Ekroos and Kuussaari, 2012; Kuussaari et al., 2007; Öckinger and Smith, 2007). As an example, the species richness of many taxa is likely to be higher in semi-natural grasslands and forest verges than in farmland field boundaries due to e.g. isolation from source populations (Dias, 1996), lower habitat heterogeneity (Tews et al., 2004) and/or higher disturbance caused by agricultural practices (Kleijn and Verbeek, 2000) in the latter habitat. If such factors affect the species richness of multiple taxa in a consistent manner, correlations within habitats can also be expected to depend on habitat type.

The strength of correlations between taxa may also depend on spatial scale independently of habitat factors (Wolters et al., 2006). This can be expected based on species–area relationships, given that species numbers accumulate similarly across taxa (Rosenzweig, 1995). In addition, because species turn-over (beta diversity) is expected to increase with increasing heterogeneity (Ekroos et al., 2010) and spatial scale (Clough et al., 2007), overall species richness of different taxa (gamma diversity across landscape units) may correlate stronger in (a) landscapes with high heterogeneity, and (b) at larger spatial scales, given that common factors drive variation in species richness in several taxa (Benton et al., 2003). On regional scales, differences in between-taxa congruence may arise due to aggregated or disconnected hotspots in species richness (Prendergast et al., 1993).

In this study, we compared correlations between species richness of butterflies, plants and farmland birds in (i) different agricultural habitats, (ii) between spatial scales, (iii) between homogeneous and heterogeneous landscapes, and (iv) between regions characterized by low versus high agricultural land-use intensity. Correspondingly, we expected correlations to be stronger (i) in semi-natural grasslands than in forest verges and field boundaries, (ii) on larger spatial scales (50 ha > 25 ha > 0.8 ha), (iii) in landscapes characterized by higher landscape heterogeneity, and (iv) in regions characterized by low agricultural intensity.

2. Methods

2.1. Study design and field work

The field data were collected in 102 separate 25-ha study units situated pair-wise (i.e. 51 study unit pairs) in Southern and Central mainland Finland (in 2001) and in the Åland islands (in 2002). The landscapes were situated in five agricultural regions with differences in agricultural land use and degree of specialization (Fig. 1). Agriculture in the Southern and South-Western regions was specialized into cereal production, whereas the other three regions (Åland, Eastern and Western regions) had higher proportions of mixed farming and the study units were characterized by higher landscape heterogeneity (Luoto, 2000). Here, these regions are referred to as regions with high agricultural land-use intensity (Southern and South-Western regions, $n = 25$ study unit pairs) and low agricultural land-use intensity (Åland, Eastern and Western regions, $n = 26$ study unit pairs). We use the term “agricultural land-use intensity” in the context of describing landscape structure (“landscape complexity” sensu Persson et al., 2010) and not the intensity of agricultural practices.

The study unit pairs were chosen amongst four 25-ha candidate landscapes within randomly selected rectangular 100-ha grid cells ($n = 51$). In order to maximize local variability in landscape structure, the most and least heterogeneous 25-ha squares within each 100-ha grid cell were selected as study units. Heterogeneous study units had significantly lower arable field cover than homogeneous study units in both regions with high agricultural land-use intensity (mean ± SD = 53.15 ± 18.67% versus 76.13 ± 16.61%; Welch Two Sample t-test, $t = 4.60$, df = 47.36, $P < 0.0001$) and low agricultural land-use intensity (38.96 ± 13.57% versus 52.21 ± 21.53%; $t = 2.65$, df = 42.16, $P = 0.01$). Likewise did homogeneous study units ($t = 4.45$, df = 46.89, $P < 0.0001$) and heterogeneous study units ($t = 3.1$, df = 43.75, $P = 0.003$) have higher arable field cover in regions with high agricultural land-use intensity.

Plants and butterflies were individually recorded in six 50-m long transects (width 1 m for plants and 5 m for butterflies) placed in non-crop habitats in each 25-ha study unit ($n = 612$). However, in six study units data were available for both plants and butterflies

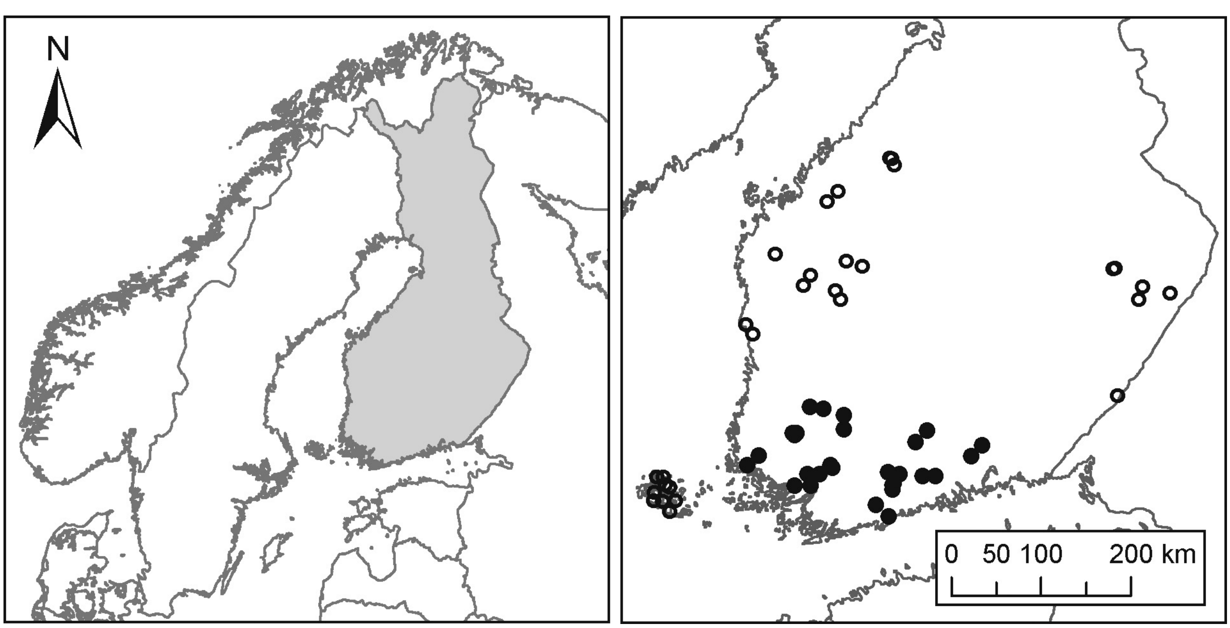

Fig. 1. Location of the study unit pairs in Southern and Central Finland. The regions with high agricultural land-use intensity (Southern and South-Western regions; $n = 25$) are shown with filled symbols, whereas the regions with low agricultural land-use intensity (Åland, Eastern and Western regions; $n = 26$) are shown with open symbols.