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Research paper

The influence of landscape fragmentation, expressed by the 'Effective Mesh Size Index', on regional patterns of vascular plant species richness in Lower Saxony, Germany

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HIGHLIGHTS

- Effects of landscape fragmentation on plant species richness patterns.
- Fragmentation measured using Effective Mesh Size Index (m_{eff}).
- Fragmentation geometries need to be carefully chosen.
- M_{eff} is a good proxy of neophyte but not of native plant species richness.

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ABSTRACT

Landscape fragmentation has been identified as a major threat to biodiversity worldwide. Several landscape metrics have been developed to quantify the extent of fragmentation, of which the Effective Mesh Size Index (m_{eff}) is one of the most widely used. However, its relevance for analysing the effect of fragmentation on biodiversity patterns has been rarely tested. We analysed the explanatory power of m_{eff} for richness patterns of different groups of vascular plant species (all species, and species groups by naturalisation and threat status) in Lower Saxony, Germany, by using a grid of 1386 analysis units. Since we assumed species richness to be influenced by abiotic conditions and spatial autocorrelation, we used variation partitioning to separate the effects of these variables from that of fragmentation. We tested five types of m_{eff} based on various fragmentation geometries. We found that m_{eff} largely influenced richness of neophytes and, to a lesser extent, that of archaeophytes whilst the richness of native species was only slightly affected and threatened species were not affected. All species groups, except threatened species, showed a negative correlation with m_{eff}, i.e. richness was highest in highly fragmented and lowest in less fragmented grid cells. We conclude that m_{eff} is a meaningful tool to explain richness patterns of non-native plant species, if relevant fragmentation geometries are chosen, but not of native and threatened plant species. Our approach may help future studies to determine correct fragmentation geometries to use with m_{eff} and may facilitate the unravelling of fragmentation impacts on the landscape-scale.

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1. Introduction

The term 'landscape fragmentation' describes both the process of the subdivision of a large continuous patch into smaller and more isolated fragments, as well as the state of a landscape (Forman, 1995). As soon as the effect of fragmentation on the biota is concerned, frequently also the term 'habitat fragmentation' is applied.

Besides general habitat loss and decline in habitat quality, fragmentation has been identified as a major threat to biodiversity worldwide (Honnay, Jacquemyn, Bossuyt, & Hermy, 2005; Jaeger 2000; Krauss et al., 2010; Kuussaari et al., 2009). In Central Europe, habitat change accelerated in course of urbanisation and industrialisation in the late 19th and early 20th century (Krause & Culmsee, 2013; Tscharntke, Klein, Kruess, Steffan-Dewenter, & Thies, 2005) and has been reinforced by the advent of the common agricultural policy of the EU since the 1950s (Krause, Culmsee, Wesche, Bergmeier, & Leuschner, 2011; Stoate et al., 2001). However, landscape development in Central Europe currently does not appear to be following a clear trend, and we observe complex and diverse landscapes as a result of multi-layered historical and current land

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use practices (Vos & Meekes, 1999). This, in turn, results in differences in the fragmentation intensity between neighbouring landscapes and in a more or less strong gradient of fragmentation on the regional and supra-regional scales.

The analysis of landscape fragmentation is an important aspect of landscape ecological research (Haila, 2002). Different indices for the quantification of landscape fragmentation have been introduced, such as the 'Number of Undissected Areas', 'Bowens Landscape Dissection Index' (Bowen & Burgess, 1981), 'Splitting Index' (Jaeger, 2000) and 'Effective Mesh Size' (Jaeger, 2000). All of these indices provide a spatially differentiated assessment of the fragmentation of a region (Jaeger, 2000). By evaluating these four plus an additional four indices, Jaeger (2000) found that 'Effective Mesh Size' (m_{eff}) is the most appropriate fragmentation measure due to its "mathematical characteristics and its intuitive interpretation" (Jaeger 2000; p. 127). The index quantifies the probability that two randomly chosen points in a study area are connected (Girvetz, Thorne, Berry, & Jaeger, 2008) and has frequently been used to quantify landscape fragmentation, e.g. in Europe (EEA, 2011), Germany (Esswein & Schwarz-von Raumer, 2004, 2006; Jaeger, Esswein, Schwarz-von Raumer, & Müller, 2001; Walz, 2005), Italy (Moser, Jaeger, Tappeiner, Tasser, & Eiselt, 2007), Switzerland (Jaeger et al., 2008), the USA (Girvetz et al., 2008) and China (Li et al., 2010).

In Germany, m_{eff}, in combination with an index that quantifies the number of undissected areas (>100 km^2) with low traffic intensity, is used by the government to quantify landscape fragmentation for environmental reporting (BMU, 2007). However, despite its frequent application and the fact that m_{eff} has been proposed as an ecologically relevant indicator (Girvetz et al., 2008; Jaeger, 2000; Jaeger et al., 2008), it has been rarely used to analyse the effect of landscape fragmentation on biodiversity (but see Li et al., 2010 who analysed mammal species richness in relation to m_{eff} in China). Strand et al. (2007) suggested that studies investigating the direct effect of landscape fragmentation (expressed in terms of fragmentation metrics) on biodiversity should be undertaken, because indicators that quantify landscape fragmentation are more useful if they can be directly linked to possible impacts on species diversity and distributions.

A multitude of man-made landscape elements, including urban, industrial and traffic infrastructure, can cause landscape fragmentation, resulting in patchy landscapes with generally small remaining natural or semi-natural habitat fragments. Depending on the specific biological traits of the species, very different landscape elements, including even (near-)natural ones, can be considered fragmentation elements (see EEA, 2011; Girvetz et al., 2008). When assessing fragmentation at the landscape scale, fragmentation elements (also termed fragmentation geometries) should therefore be carefully chosen.

The fragmentation of habitats may result in an increasing isolation of plant or animal subpopulations that inhabit the patches. Habitats colonised by different subpopulations of the same species are isolated if genetic exchange is constrained because the area between the patches is too large, or too impermeable, to be overcome by pollination or dispersal events (Poschlod et al., 1997). The loss of genetic variation, in turn, may hamper the species' ability to respond to changing environmental conditions (Booy, Hendriks, Smulders, Groenendael, & Vosman, 2000) and the populations may thus become threatened with extinction. Numerous studies examined the effect of habitat fragmentation on plant and animal assemblages at the local and landscape scales (see for an overview Debinski & Holt, 2000; Fahrig, 2003). Frequently, the size of and the isolation of or connectivity between patches were used as measure of fragmentation (e.g. Cousins, Ohlson, & Eriksson, 2007; Helm, Hanski, & Pärtel, 2006), yet none of these studies applied the Effective Mesh Size Index.

The effects of landscape fragmentation on species richness may vary depending on the species groups considered (Ewers & Didham, 2006). Certain species, particularly those spreading along linear landscape elements or associated with man-made habitats, like many neophytes as well as archaeophytes frequently occurring in productive agricultural areas (Kühn, Brandl, May, & Klotz, 2003; Schmiedel, Schacherer, Hauck, Schmidt, & Culmsee, 2011), may benefit from landscape fragmentation (Botham et al., 2009; Dark 2004; Deutschewitz, Lausch, Kühn, & Klotz, 2003; Honnay, Piessens, Landuyt, Hermy, & Gulinck, 2003). In contrast, species as e.g. (threatened) native species depending on undisturbed (semi-)natural habitats may be adversely affected by fragmentation events (Ewers & Didham, 2006).

The overall objective of our study was to investigate whether the frequently used Effective Mesh Size Index (m_{eff}) is a suitable measure to explain vascular plant species richness on the landscape scale. We used the state of Lower Saxony, Germany, as a model region as it hosts a high diversity of landscapes differing in habitat composition and structural complexity (cp. Schmiedel, Bergmeier, & Culmsee, 2015). Therefore, we expected a long gradient in fragmentation across the study area. Furthermore, the area is particularly suitable due to the availability of extensive data collected in a state-wide mapping program on the distribution of vascular plants with a resolution of c. 30 km^2 (NLWKN 1982–2003, Garve, 2007). Thus, high quality plant distribution data was available for a region that is more or less homogeneous in climate and biogeographical history, so that we considered the same regional species pool throughout the studied landscapes. We used different subsets of fragmentation geometries (FGs) and also different subsets of the regional plant species pool, dependent on the naturalisation and threat status of the species, in order to investigate the underlying patterns in plant species distributions as responses to different fragmenting landscape elements.

Specifically, we hypothesised that:

(1) Landscape fragmentation, expressed as Effective Mesh Size (m_{eff}), varies in space, which results in a gradient in the degree of fragmentation within the sample of landscape units used in this study.
(2) The choice of fragmentation geometries that are used for the calculation of m_{eff} is of major importance for explaining plant species richness patterns on the landscape scale.
(3) Plant species richness varies between landscape units along the fragmentation gradient, with the explanatory power of the Effective Mesh Size differing between different groups of species dependent on their naturalisation (natives, archaeophytes and neophytes) and threat status (threatened vs. non-threatened).

2. Methods

2.1. Study area

The study was carried out in Lower Saxony, Germany (47,500 km^2, Fig. 1). As a result of the variety in relief and bedrock, colonisation history and current land use are diverse across north-western Germany (Behre, 2008). Lower Saxony harbours a relatively large number of different habitats, which include natural coastal and forest-dominated landscapes, structured and homogeneous agricultural landscapes, and densely populated areas (Gharadjedaghi et al., 2004).

The coastal area in the north is dominated by Holocene marine deposits, while the lowlands were formed during the Pleistocene. The landscape of the uplands is shaped by Mesozoic and Palaeozoic bedrocks. From the coast in the north to the uplands in the south-

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