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Herb layer extinction debt in highly fragmented temperate forests – Completely paid after 160 years?

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ABSTRACT

The time-delayed extinction of plant species following habitat fragmentation is a well-known phenomenon in ecology. The length of the relaxation time until this 'extinction debt' is paid (i.e., until extinctions cease) depends on the ecosystem, species group and extent of fragmentation. Studies of grassland ecosystems have revealed that plant extirpations after fragmentation can occur rapidly when the degree of fragmentation is high. Studies of extinction debt in highly fragmented forests, however, are lacking. In this study, we evaluated the existence of an extinction debt in the Prignitz, Brandenburg, Germany, where 94% of the semi-natural forests have vanished since 1780. We surveyed the herb-layer species of 104 forest patches and fitted species richness as a function of the historical and present-day patch configurations. Models including the present-day habitat area and connectivity explained the present day species richness better than models including historical patch-configuration variables. There was no significant effect of the historical habitat area on the present day species richness. However, the effect of historical patch connectivity on the richness of forest specialists with short-distance dispersal potential was significant when excluding present-day habitat area from the models and habitat quality and heterogeneity were used as covariables. The extinction debt has largely been paid after approximately 160 years of relaxation time which contrasts with previous studies of temperate forests that have found extinction debts persisting 120–225 years after fragmentation. We demonstrate that extinction debts in temperate forests may be paid off more rapidly if the degree of fragmentation is high.

1. Introduction

Habitat destruction and fragmentation are among the most important threats to biodiversity (Sala et al., 2000; Sax and Gaines, 2003). Although the most dramatic land-cover changes in Central Europe occurred centuries ago (especially when forests that had been more or less continuous were cut for agriculture (Darby, 1956)), there are several indications that historical land-cover changes still affect present-day species richness and community composition (Kuussaari et al., 2009). Land-cover changes can cause a time-delayed loss of species in ecological communities, which is known by the term 'extinction debt' ('ED') (Tilman et al., 1994). Given that species richness was in equilibrium before the habitat destruction event, species will eventually go extinct until the species richness reaches a new quasi-equilibrium. At this time, the ED has finally been paid. The time span from the destruction event until the ED is paid is termed the relaxation time (Kuussaari et al., 2009). Determinations of the magnitudes of an ED and the detection of the processes that influence the magnitudes of ED are important tasks in ecology (Sutherland et al., 2013).

ED has been detected for various species groups and habitats at several spatial scales (Dullinger et al., 2012 (mountain plants); Lira et al., 2012 (small mammals); Brudvig and Damschen, 2011 (pine woodlands); Kuussaari et al., 2009 (review, listing 32 papers where an ED was found)). However, to date, only a few studies have been published for plants of temperate deciduous forests (Paltto et al., 2006; Piessens and Hermy, 2006 (in parts); Vellend et al., 2006). This paucity of studies is surprising because forest herbs are often clonal and are able to persist without sexual reproduction for many decades (Inghe and Tamm, 1985; Cain and Damman, 1997). Thus, a delay in changes in species richness in response to habitat fragmentation could be particularly pronounced in forest ecosystems.

For grassland plants, there are studies with conflicting results. Several authors have found strong evidence for the existence of an ED following habitat fragmentation (Lindborg and Eriksson, 2004; Piqueray et al., 2011), while others did not find any ED (Adriaens et al., 2006; Cousins et al., 2007; Oster et al., 2007). In

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a meta-study, Cousins (2009) noted that, in grassland studies that verified an ED, patches had retained greater than 10% of the target habitat, whereas no evidence for an ED was observed in studies in which patches retained less than 10% ('highly transformed landscape').

For plant communities of temperate deciduous forests, Paltto et al. (2006) (Sweden), Piessens and Hermy (2006) (Belgium) and Vellend et al. (2006) (UK and Belgium) have verified occurrences of an ED. In these studies, the forest covers decreased moderately by 26% in approximately 120 years (Paltto et al., 2006) and by approximately 75% in approximately 210–225 years (Piessens and Hermy, 2006; Vellend et al., 2006). However, there are many regions in Central Europe where the extent of forest area loss was substantially higher (Honnay et al., 1998; Graae, 2000, see also De Frenne et al., 2011). To date, it remains unknown as to whether or not and for how long an ED exists in such highly transformed landscapes. Our objective was to investigate ED in a region where forest area loss was greater than 94% over approximately 200 years. The answers to the questions of whether the ED has been paid or not have broad implications for conservation (Kuussaari et al., 2009; Wearn et al., 2012; Vellend and Kharouba, 2013). In scenarios with an enduring ED, conservation actions can focus on stopping or slowing down extinction processes. If there is no ED, other conservation actions may be more appropriate.

Many studies on ED use historical and present-day patch configuration to model present-day species richness (Kuussaari et al., 2009). However, species richness also depends on the habitat quality and habitat heterogeneity (Honnay et al., 1999; Dumortier et al., 2002; Wulf and Kolk, 2014). The omission of these environmental factors may lead to false conclusions: A weak, but true habitat-loss-induced ED may remain undetected, or a non-existent ED may be erroneously confirmed although in fact correlations of patch configuration with environmental factors are the reason for significant results. Here, we aim to study the effects of including environmental variables when quantifying the ED.

Species do not respond to land-use changes in the same way. Several studies have revealed that forest specialists are prone to fragmentation effects (Dupre and Ehrlen, 2002; Kolb and Diekmann, 2004; Jamoneau et al., 2011; Rodríguez-Loinaz et al., 2012) and are overall more dependent on patch configuration than generalists (Dupre and Ehrlen, 2002; Kimberley et al., 2014). Specialists often have slow metapopulation dynamics, i.e. a high persistence and limited dispersal abilities, which may support delayed extinctions (Vellend et al., 2006; Hylander and Ehrlén, 2013). The analysis of trait-defined groups that represent species with slow metapopulation dynamics can give further knowledge about which specialists contribute most to an ED. A precondition is that the considered trait attributes make species respond to the spatial configuration of habitats because only then such species can constitute an ED induced by area loss and fragmentation. It has been shown that in forest ecosystems clonal species, species with low numbers of seeds per ramet and species with a short-distance dispersal potential are especially dependent on patch configuration and that such species also have low rates of colonization and a high level of persistence (Dupre and Ehrlen, 2002; Kolb and Diekmann, 2005; Kimberley et al., 2014).

Hence, we hypothesize that (a) the historical habitat area and degree of patch connectivity are better predictors for present-day species richness than present-day habitat area and patch connectivity and, in consequence, that the ED has not been paid; (b) forest specialists contribute more to an ED than generalists; (c) specialists with an extensive clonal growth, a low seed production and a short distance dispersal potential are most highly influenced by the historical patch configuration.

2. Material and methods

2.1. Study area

Our study was conducted in the Prignitz region (4217 km^2, 52°42′N–53°23′N, 11°15′E–12°43′E), which is located in the western portion of the federal state of Brandenburg, North-Eastern Germany (Fig. 1).

The region has an overall flat terrain with elevations ranging from 10 to 150 meters locally and is mainly subject to intensive agricultural land use. The primary soil types are Eutric Cambisols, Haplic Stagnosols and Haplic Gleysols that have developed on glaciofluvial sand deposits and loamy ground moraines (Stackebrandt et al., 1997). The mean annual temperature is 9.2 °C. The mean annual precipitation is 574 mm (DWD, 2014, Kyritz weather station). The primary forest types are large, Scots-pine (*Pinus sylvestris*)-dominated plantations, deciduous or mixed forests with oak (*Quercus robur*) and beech (*Fagus sylvatica*), and alder forests (*Alnus glutinosa*). The deciduous and mixed deciduous forests cover 18.8% of the total forested area, while the coniferous forests contribute 78.3% (see Table A.2 for the proportions of specific deciduous forest types). The area of the deciduous forest patches ranges from approximately 0.3 ha to 275 ha. The majority of the patches are less than two ha in size. These patches are often scattered within large agricultural fields.

2.2. Land-use history

Comparisons of historical and present-day patch configurations require comprehensive data on land-use history. We used the historical Schmettau map created from 1767 to 1787 at a scale of 1:50 000 (hereafter, 1780) and the Prussian government map created from 1875 to 1915 at a scale of 1:25,000 (hereafter, 1880) to derive the forest distribution during these time periods. The forest patch configuration in 1780 was used in our species richness models (sections 2.5 and 2.7). The forest distribution in 1880 was used

Fig. 1. Location of the study area in Prignitz, Brandenburg, Germany.