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Historical landscape structure affects plant species richness in wet heathlands with complex landscape dynamics

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ABSTRACT

The spatio-temporal dynamics of wet heathlands from two landscapes in high Ardenne (Belgium), as well as the consequences of such dynamics on plant communities were investigated. Past and present destruction and origin of habitat patches have resulted in a complex network of different aged habitat patches. Current specialist and generalist species richness were assessed in 59 patches and analyzed with respect to present and past patch spatial metrics (controlled for habitat quality). Current patch area affected specialist species richness and current patch connectivity influenced both specialist and generalist species richness. Thirteen of the 59 patches were historical patches, i.e. patches that have remained since the 1770s. In these historical patches, including past landscape structure in the analysis explained more of the variability in current species richness than the current landscape structure alone, suggesting the existence of an extinction debt.

1. Introduction

Human activities have impacted landscape structure and function worldwide, and are currently the main factor dictating landscape dynamics in many regions (Baudry and Tatoni, 1993; Goudie, 2005). A common characteristic of human-driven landscape alteration is the destruction and fragmentation of natural and semi-natural habitats (Balmford and Bond, 2005). The most detrimental consequences of landscape fragmentation for plant and animal species includes loss of suitable habitat, progressive habitat patch isolation and increased edge effects at the expense of interior habitats (Andrén, 1994; Fahrig, 2003). Local species extinction rates can be increased and local colonization inhibited due to these pressures on remnant habitat, which consequently reduces species richness. On the other hand, dynamics within human-driven landscapes may also lead to the creation of new habitat patches, resulting in conditions conducive to spontaneous colonization by species from natural or semi-natural environments. Under these conditions, the potential exists for range extension of isolated populations (Collins et al., 1985; Krüger et al., 2002).

From a geographical context, plant species diversity within a habitat type is largely dependent on spatio-temporal landscape patterns, both at the landscape and habitat patch scale (Cousins and Eriksson, 2002; Ricklefs, 2004; Turner et al., 2001). Conceptually, a positive relationship between patch area and species richness has been well established (Bastin and Thomas, 1999; Bruun, 2000; Honnay et al., 1999a). It emphasizes that species in small patches are more susceptible to area-dependent influences, such as genetic and demographic stochasticity (Holsinger, 2000; Pimm et al., 1988). The negative effects of area loss and resulting fragmentation can be reduced when connectivity among habitats is sufficient to maintain propagule dispersal among populations (Brown and Kodric-Brown, 1977; Piessens and Hermy, 2006). However, species response to landscape change exhibits a time lag, and communities which experience habitat destruction and/or creation of new habitat patches may therefore face two unbalanced states with regard to patch (spatial) characteristics: (1) extinction debt (Hanski and Ovaskainen, 2002), or (2) colonization credit (Cristofoli et al., in press). These terms are respectively defined as the mean number of species yet (1) to go extinct in a patch, or (2) to colonize a patch. Both states follow landscape change, and continue until species richness reaches equilibrium with the new spatial properties of the patch. Such unbalanced conditions have important implications for species conservation, since long-term species richness may be over- or underestimated on the basis of current records of species number (Hanski and Ovaskainen, 2002).

Previously widespread wet heathlands and closely associated habitats (i.e. poor fens and bogs) have experienced a marked decline in Western Europe since the 19th century (Webb, 1998). Human activities are largely responsible for this decline, and include peat extraction, anthropogenic afforestation (mainly Norway Spruce

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Picea abies [L.] Karst) and the abandonment of traditional agro-pastoral practices replaced by widespread agriculture (Clicheroux, 1985; Petit and Lambin, 2002; Webb, 2002). This has resulted in habitat fragmentation as well as homogenisation of the landscape matrix. However, thanks to current forest management and successful restoration approaches, wet heathland patches and poor fens have been routinely established (Cristofoli et al., in press). Despite these achievements, a consequence of the dynamic nature of wet heathland communities is the potential for unbalanced states resulting from an extinction debt or a colonization credit. Wet heathlands, poor fens and bogs support very specialised plant and animal species (Lambinon et al., 2004; Rodwell, 1991) and are considered key habitats for biodiversity conservation in the European Community (Annex I of the Habitat Directive 92/43/EEC). Nevertheless, few studies have examined the relationships between species distribution patterns and landscape structure (but see Piessens and Hermy, 2006; Piessens et al., 2005); and studies specifically addressing extinction debt in these habitats are lacking. Piessens and Hermy (2006) suggested that a low species loss rate in highly fragmented north Belgium heathlands may be the result of an extinction debt, but provided no direct test for this hypothesis. However, some studies in semi-natural grasslands have reported evidence of an extinction debt (Gustavsson et al., 2007; Helm et al., 2006) but other studies have not provided supporting data (Adriaens et al., 2006).

The aims of the present study were to investigate and assess the consequences of past and present habitat dynamics on plant community patterns in two high Ardenne landscapes (Belgium). A previous study demonstrated that recently created wet heathland patches did not experience a colonization credit, i.e. species richness in the two landscape patches were similar to that expected at equilibrium given the patch spatial structure (Cristofoli et al., in press). In the present study, we examined the potential for an extinction debt in wet heathland patches.

Landscape dynamics are complex. Therefore, we first provided a detailed analysis of wet heathlands and closely associated habitat spatial and temporal landscape changes over the past 250 years. Furthermore, the distinct contributions of habitat destruction and origins to landscape dynamics were investigated for four time periods. We subsequently analyzed the relationships between present and past landscape structure and plant species richness, and tested for an extinction debt in historical wet heathland patches.

2. Materials and methods

2.1. Study site

The study site was 797 km^2 (50°N, 5°E) in size and included two landscapes in the Belgian Ardenne, separated by a large valley (Plateau de Saint-Hubert and Plateau des Tailles, 400–650 m a.s.l., respectively; Fig. 1). Although highly fragmented, this region supports one of the last substantial areas of bogs, poor fens and wet heathlands in Belgium. The delimitation of these habitats relies on peat depth and is restricted to nutrient poor, relatively acidic and poorly drained soil conditions (Bakker and Berendse, 1999; Gimmingham, 1972). The habitats are developed under azonal climatic conditions characterised by cold winters (average winter temperature: 0.4 °C) and high precipitation (1150 mm/year), typical of Belgian plateaus.

2.2. Landscape analysis

Current (2006) and past landscape structure of target habitats were assessed using geographic information systems (GIS, ArcGIS 8.3, ESRI, 2002). Five topographical maps dating from the

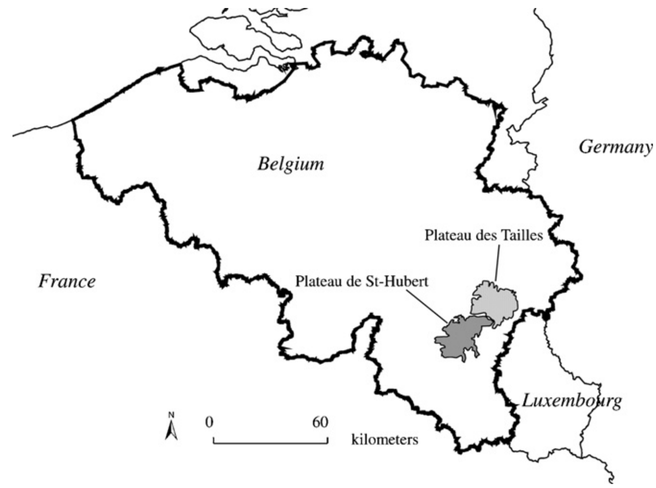

Fig. 1. Study area location (Plateau de Saint-Hubert and Plateau des Tailles) in Belgium.

(1) 1770s (1:11 520; De Ferraris); (2) 1880s (1:20 000; Belgian Military Cartographic Institute); (3) 1950s (1:20 000; Belgian National Geographical Institute); (4) 1970s (1:10 000; Belgian National Geographical Institute); and (5) 2006 (1:10 000; Regional Research Centre for Nature, Forest and Wood) were digitised. Although the cartographical documents we used to evaluate landscape dynamics spanned a long period of time, the date ranges can be considered comparable in terms of spatial resolution. Documents that covered the 1880s, 1950s, 1970s and 2006 covered minimal patch area of similar size (100 m^2). The cartographical document from the 1770s was the first topographical map of the region. We found the document to exhibit decreased accuracy yet hold valuable information regarding early landscape characteristics. Feature classes were made homogeneous across the multiple maps and three classes, i.e. bogs, poor fens and wet heathlands were retained to delimit habitat patches. However, the first four maps did not distinguish wet and dry heathlands because soil drainage was not always explicitly circumscribed. A potential habitat map for target communities was subsequently created based on soil properties (derived from the Walloon digital soil map, FSAGx, 2004) and altitude. Heathland patches located outside potential sites (i.e. xeric and mesic heathlands) were excluded from the study. Heathlands, poor fens and bogs are intricate communities and form a mosaic of habitats; therefore the respective habitat maps were merged to form one single habitat category, termed a 'complex of wet heathlands'.

The spatial structure of target habitats was assessed using the following quantitative metrics, estimated for each of the five map dates and for each plateau: total habitat area, number of patches, patch area, patch connectivity (Hanski's *S* index in the Incidence Function Model index (Hanski, 1994), referred to as IFM *S* index) and patch isolation (Euclidian distance from a patch border to its 'nearest neighbour'). The IFM *S* index was computed using edge-to-edge distances between all the patches, i.e. between all the possible source populations in the landscape (Moilanen and Nieminen, 2002). IFM *S* index calibration parameters followed the recommendations and values of Moilanen and Nieminen (2002) used in recent plant studies, i.e. $\alpha = 1$ (Adriaens et al., 2006; Bruun, 2000; Kolb and Diekmann, 2005; Lindborg, 2007). The metrics were calculated separately for new and old patches for each map date. For a given date, an old patch was defined as a habitat patch observed at the study site that was also present on the former map, and a new patch was one absent on the former map but currently observed at the study site. We determined the annual rate of target habitat destruction or creation during four time periods (1770–1880; 1880–1950; 1950–1970 and 1970–2006) as habitat contraction (destroyed area