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Decisive environmental characteristics for woody regrowth in forest edges – Patterns along complex environmental gradients in Southern Sweden

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ABSTRACT

Early and late successional stages of forest edge development were studied across long, complex environmental gradients in order to disentangle and assess the woody species composition and functional traits' relations to abiotic and biotic environmental characteristics at site and landscape scale. Data were sampled from 78 randomly stratified locations along a 610-km railway corridor between the cities of Stockholm and Malmö, Sweden, and subsequently analysed in multiple steps of unconstrained, constrained and partial constrained ordination and variation partitioning. Different analytical methods were applied at each step and only the environmental characteristics that repeatedly showed significant impacts on woody species composition were selected for analysis of average weighted community traits to provide verification and a more detailed understanding. Following this approach, 10 environmental characteristics were identified as decisive for the woody species composition of the forest edges. The variation partitioning revealed a marked shift in the relative explanatory power of the environmental variables in relation to the succession of the forest edges. In the early successional stage, the abiotic variables related to site productivity (as reflected by field layer type and soil moisture) and climate (humidity and altitude) dominate, while in the late successional stages of forest edges more complex patterns evolved due to hierarchical and dynamic filter effects, where biotic variables reflecting structural aspects at site (forest edge profile, canopy stratification and canopy cover) and landscape (forest continuity and the shape and contrast of edges in the surrounding landscape) level were equally important as the abiotic variables. We concluded that management efforts in early succession stages of forest edges should depart from basic abiotic gradients of site fertility and moisture; and that it is crucial to incorporate vegetation structure variables at site and landscape level into long-term management planning.

1. Introduction

In infrastructure environments, such as railway corridors and roadsides, clearing of forest edges is increasingly practised to eliminate the risk of windblown trees falling on the rail and road, improve visibility, decrease shade and support species related to early successional stages (e.g. Ballard et al., 2007; Bramble et al., 1985; Buckley et al., 1997; Non and de Vries, 2013; Rühle, 1995; Rydberg and Falck, 2000).

During two record storms with hurricane-force winds in 2005 and 2007, falling trees on rail tracks and power-lines caused severe damage to the Swedish railway system. Therefore, the Swedish Transport Administration obtained legislation in 2008 to expand the railway corridor from 10 to 20 m from the rail banks and to clear the forest edge in the new part of the corridor. Since then, forest has been cleared along more than 4000 km of Swedish railway line (Swedish Transport Administration, 2015).

While the old management corridor (OMC; 0–10 m from rail bank) must be kept free of woody vegetation to ensure good sight conditions, the long-term goal for the new management corridor (NMC; 10–20 m from rail bank) is to successively manage the woody regrowth, i.e. spontaneously established trees and shrubs,

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so that suitable forest edge composition and structures develop over time.

However, there is a lack of comprehensive studies of the interaction between environmental characteristics and woody community assembly of forest edges across long environmental gradients. Thus, the relative impact and interrelationship at different successional stages between abiotic site characteristics and climate (Larsen and Nielsen, 2007; Oliver and Larson, 1996), the surrounding landscape structure and its relations to species dispersal (Grashof-Bokdam, 1997) and browsing mechanisms (Kie et al., 2002) and how this can inform and guide management and planning strategies of forest edges remains unclear.

While relationship between woody species and environmental characteristics over long environmental gradients have been studied for forest stands (e.g. Lawesson and Skov, 2002; Lawesson and Oksanen, 2009) and helped inform management decisions (e.g. Larsen and Nielsen, 2007), previous forest edge studies have mainly documented the edges' many effects on environmental characteristics and organisms (e.g. Hamberg et al., 2009; Kollmann and Buschor, 2003; Williams-Linera, 1990). In the present study we reversed the perspective and examined how traits of woody species in forest edges relate to intrinsic environmental characteristics (Grime, 2006; Kleyer et al., 2012) and how the woody community assembles in relation to environmental characteristics over long environmental gradients. Such knowledge will be crucial for predicting the response to different management scenarios, and thus ultimately for sound decision-making.

We use 'environmental characteristics' hereafter as an umbrella term for spatially varying abiotic and biotic variables of the environment, operating at varying scale from site level to overall landscape composition and configuration. Among the abiotic variables, we distinguish soil variables from climate variables. Among the biotic variables, we restrict the focus to vegetation structure variables at site and landscape level.

Plant-available nutrients and water provide the resources underlying plant growth and form the basis for biotic interactions through competition and facilitation (Callaway and Walker, 1997; Connell and Slatyer, 1977; Grime, 2001). In forestry, there is a long tradition of using direct and indirect measures of these soil variables to determine site productivity, often in the form of a 'site index' (e.g. Hägglund and Lundmark, 2007a; Puettmann et al., 2008).

The macroclimate sets the frame for plant utilisation of available water and nutrients in the soil. The macroclimate is often shaped by complex gradients such as altitude that capture multiple variables (Jansen and Oksanen, 2013), e.g. the sum of evapotranspiration and precipitation (humidity) and the length and temperature of the growing season. However, microclimate variables such as amount of solar radiation, and thus also temperature and evapotranspiration as affected by slope and geographical orientation, are reported to strongly influence the macroclimate effect on forest edge composition (Matlack and Litvaitis, 1999).

Over millennia, woody species have developed different functional traits in order to adapt to abiotic characteristics of shade, nutrient supply, soil pH, water supply, temperature, etc. (Grime, 2001; Niinemets and Valladares, 2006). However, compared with forest interiors and open land, forest edge structure modifies such abiotic variables (Hamberg et al., 2009; Williams-Linera, 1990) through changes in temperature (Geiger, 1965; Matlack, 1993), nutrient deposition (Weathers et al., 2001), available light (Matlack and Litvaitis, 1999) and wind penetration (Ruck et al., 2012). The forest edge structure also affects the movement and abundance of different animal species, which can give rise to biotic regulations through changes in herbivory disturbance, e.g. browsing (Wirth et al., 2008) and propagule predation (Guzmán-Guzmán and Williams-Linera, 2006; Kollmann and Buschor, 2003). The structure of the forest edge has also been shown to affect seed-rain of species with zoochory dispersal traits and other propagule vectors (Sarlöv-Herlin and Fry, 2000; Wiström and Nielsen, 2014).

Numerous landscape ecology studies have shown that the dispersal of propagules is affected not only by the forest edge structure itself, but also the vegetation structures in the surrounding landscape (e.g. Grashof-Bokdam, 1997). Furthermore, the landscape structure affects wildlife communities and related grazing and browsing patterns (Kie et al., 2002; Wirth et al., 2008), which can have a great influence on woody species composition.

In this study, we disentangled and assessed the influence of these many environmental characteristics on woody species composition and traits in forest edges along the main railway line between Stockholm (the capital) and Malmö (the third largest city in Sweden), distinguishing: (1) the early successional stage in the NMC and (2) the later successional stage of the remaining old forest edge stand. This railway, which is 610 km in length, runs through the hemi-boreal forest region and northern part of the nemoral forest region and provides extensive and complex environmental gradients. Along these gradients, we sought to:

- Identify environmental variables that are decisive for the composition of woody species of forest edges.
- Assess the relative importance of soil, climate, vegetation and landscape structure characteristics for the woody species composition of forest edges.
- Identify associations between the environmental characteristics identified and traits of woody species in forest edges.

2. Material and methods

The Södra stambanan (Southern main line, henceforth denoted SML) between Stockholm and Malmö runs from latitude 55.609814 to 59.330497N and longitude 13.00115 to 18.05603E. On its way through Southern Sweden, it passes through six of the 10 geographical strata defined for Sweden within the monitoring programme NILS (Gallegos Torell, 2011). It ranges in altitude from 0 to 336 m above sea level, providing a vegetation period (days with average temperature above 5 °C) ranging from 184 to 233 days. The accumulated annual temperature sum varies from 1272 to 1789 degree-days and the overall climate is slightly humid, with mean annual precipitation of 600–900 mm. Overall, there is slightly positive mean precipitation after subtraction of evapotranspiration during the vegetation period, which ranges between 33 and 156 mm with an overall decreasing trend towards the east.

The soil type varies widely and includes both glacial till and sedimentary soils spanning from clayish to coarse sandy and gravel types. The dominant land cover is forest, with the total cover comprising 45% (conifer 26%, deciduous 8%, mixed 4%, clear-cut/regenerating forest 7%). All background environmental data were retrieved from national GIS data for the 1000-m buffer around SML (© Lantmäteriet, i2014/764; © Naturvårdsverket, i2014/764; © SMHI i2014/00764).

2.1. Overview of data retrieval

A field inventory was conducted at the end of the growing season in 2011, i.e. 3–4 growing seasons after expansion of the management corridor from 10 to 20 m from the track. Using the definition of forest edges adopted in the National Inventory of Landscapes in Sweden (NILS) (Gallegos Torell, 2011), 78 sites were located along the railway corridor using stratified random sampling (see Fig. 1). Sites bordering recently clear-cut forest stands