Landscape and Urban Planning 130 (2014) 149–158

Contents lists available at ScienceDirect

Landscape and Urban Planning

journal homepage: www.elsevier.com/locate/landurbplan

Research Paper

A spatially explicit empirical model on actual and potential ancient forest plant diversity in a fragmented landscape

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HIGHLIGHTS

- Habitat continuity and suitability explain AFS richness in sample plots.
- AFS richness is predicted for present-day forest and currently open landscapes.
- The predictive map can serve for conservation and restoration purposes.

ARTICLE INFO

Article history:
Received 21 June 2013
Received in revised form 7 July 2014
Accepted 12 July 2014

Keywords:
Connectivity
Generalized additive model (GAM)
Multi-temporal GIS
Historical ecology
Land-use change
Environmental planning

ABSTRACT

Spatio-temporal forest cover changes often cause a change of forest plant species diversity. Slow colonizing ancient forest plant species (AFS) can be negatively affected, as they depend to a certain degree on the continuity of the forest cover in space and time. The implementation of conservation and restoration strategies for AFS can be supported by a map that represents the actual AFS diversity of the current forest, as well as the potential AFS diversity that open land can achieve when converted to forest. To create such a map for Flanders (northern Belgium), an empirical model was constructed using spatially explicit data on habitat suitability and continuity. The model calculated a high AFS diversity for suitable mesophilous sites covered by forest in 1775 and in the early 20th century. Sites near a concave edge of a forest patch in 2000, either inside or outside forest, were also rated high. This is the first operational landscape model on AFS diversity that can be used to select hotspots of AFS diversity in the present-day forest and sites with a high restoration potential in the open landscapes. Application of the AFS diversity map on a local scale should include additional information on linear landscape elements, soil conditions and forest management, as we assume that these factors account for a high proportion of the unexplained deviance.

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1. Introduction

Many forest organisms are slowly colonizing habitat specialists and the most studied species in this respect are vascular plants called ancient forest plant species (AFS) (Hermy, Honnay, Firbank, Grashof-Bokdam, & Lawesson, 1999). AFS are, by definition, found more frequently in ancient forest – sites as far as we know continuously covered by forest – than in recent forest that was converted to other land-use for some time (Rackham, 1980). AFS depend on a long and continuous forest land-use and they suffer from habitat loss and fragmentation at a rate that exceeds the slow colonization capacities of AFS (Vellend, 2003; Verheyen, Vellend, Van Calster, Peterken, & Hermy, 2004). Spatio-temporal disruptions can result into a highly fragmented forest cover with a variable recovery level of forest vegetation (Verheyen, Fastenaekels, Vellend, De Keersmaeker, & Hermy, 2006).

The recovery of forest vegetation at former agricultural sites is a slow process and largely depends on the connectivity with source populations of AFS (Baeten, Hermy & Verheyen, 2009; Baeten, Jacquemyn, et al., 2009; Brunet, 2007; Brunet et al., 2011). For this reason conservation of remaining ancient forest is seen as a

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http://dx.doi.org/10.1016/j.landurbplan.2014.07.006
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priority (Peterken, 1977; Vellend, 2003; Wulf, 2003). The AFS number in recent forest is positively influenced by physical contact with ancient forest (Honnay, Hermy, & Coppin, 1999; Peterken & Game, 1984). However, the quality of the landscape matrix can be important as well. Relic populations of AFS can survive forest clearance in fringe relics, hedges or tree rows, that support vegetation recovery following reforestation (Honnay, Hermy, & Coppin, 1999). Furthermore, hedgerows and tree rows can function to some extent as habitat corridors for AFS (Corbit, Marks, & Gardescu, 1999; Endels, Adriaens, Verheyen, & Hermy, 2004; Wehling & Diekmann, 2009).

AFS diversity is not only explained by habitat continuity and connectivity, but also by habitat suitability, that can be influenced by natural and by anthropogenic factors. The number of AFS is dependent of habitat type (De Keersmaeker et al., 2013; Hermy et al., 1999). The highest diversity of AFS in NW Europe is found in forest habitat on mesophilous sites (Hermy et al., 1999). However, more than other forest habitat types, mesophilous forest was cleared and converted to agricultural land during the past centuries (De Keersmaeker, 2013; Wulf, Sommer, & Schmidt, 2010). AFS diversity of the remaining mesophilous forest habitat can also decline by anthropogenic habitat degradation (Baeten, Bauwens, et al., 2009; Baeten, Hermy, Van Daele, & Verheyen, 2010; Decocq et al., 2004; Van Calster et al., 2008). As a result of habitat loss and degradation, the recovery of recent forest can be inhibited as well (Baeten et al., 2010; Vellend, 2003).

As spatio-temporal forest cover changes and habitat degradation put a high pressure on AFS diversity, there is a need for tools that can support conservation and restoration projects. Strategies for conservation of forest plant species diversity have been explored several times, e.g. in the framework of the SLOSS (a single large or several small) discussion (Game & Peterken, 1984; Hokkanen, Kouki, & Komonen, 2009; Honnay et al., 1999a). The operationalization of conservation strategies requires thorough species inventories (Hokkanen et al., 2009), that are mostly only available for a selected, relatively small number of forest patches.

The aim of this study was to build a model using spatially explicit explanatory variables that can predict AFS richness on a scale and resolution that are beyond the limits of what is possible by means of field surveys. As argued above, such a model requires maps on habitat suitability and on forest continuity, both of which are available for our study area. However, we also aimed to create a map that can be used to forecast the recovery potential of open land, when converted to forest. As the historical landscape structure can explain the recovery rate of post-agricultural forest, we wanted to include connectivity measures calculated on separate historical and present-day forest maps instead of measures only calculated on the remaining ancient forest (AF). We aimed to create a spatially explicit model and for this reason explanatory connectivity measures had to be quantified for the whole study area, not only for forests. As far as we know, an operational landscape model of this kind has not been constructed before.

2. Methods

2.1. Study area

This study covered most of Flanders (northern Belgium, 13,500 km^2). The climate is mild with little regional variation. Average monthly minimum and maximum temperatures equal 2.5 °C and 17.0 °C, respectively, and mean annual precipitation amounts to 852 mm according to the Royal Meteorological Institute (www.meteo.be). The altitude increases from sea level in the West to ca. 290 m in the East. The north of Flanders is flat or undulating and relic hills up to 150 m are present in the southwest and the center. Topsoils mainly consist of pleistocene aeolian sand and loess deposits that result in soils with a high silt loam content. The silt loam content gradually increases from the north to the south. Flanders has been densely populated for a long time and it is assumed that forest cover was already low in medieval times and in many cases even in the Roman era (Tack, van den Bremt, & Hermy, 1993). At the end of the 18th century, forest cover equalled 10.8% of the total area. Absolute changes were low since that time and the forest cover occupied 10.6% of the total area of Flanders in 2000. However, after 1775 many forests on soils with a high silt loam content were converted to farmland, which resulted into a decline by approximately 50% of the area covered by forest on these sites. This area loss was counterbalanced by the conversion of heathland and waterlogged soils to forest in the 19th and 20th century. As a result of these spatio-temporal forest cover changes, only approximately 16% of the forest cover in 2000 is called ancient forest in Flanders, i.e. forest continuously present since 1775 when the first maps for the whole area were drawn (De Keersmaeker, 2013).

2.2. Response data

We intended to explain AFS number for a relative large area, counted in grid-based sample plots that are representative for the total forest cover in our study area. These data were provided by the Flemish forest inventory, a systematic sampling of forests containing an inventory of vegetation at the nodes of a 1 km × 1 km grid (Waterinckx & Roelandt, 2001). Grid nodes that were covered by forest, were visited between 1997 and 1999 for this purpose. Vegetation at these grid nodes was inventoried in 16 m × 16 m (256 m^2) sample plots, using the Braun–Blanquet sampling scale (Waterinckx & Roelandt, 2001). Sample plots at a distance of less than 200 m from the border of the study area were omitted, as not all explanatory variables could be calculated at closer distance (explained below).

We calculated from this vegetation samples ($n = 1121$) the number of species that are considered AFS according to a European compilation list (Hermy et al., 1999). The number of AFS in forest vegetation is not only determined by forest history, but is also highly dependent of natural site conditions (see above). To reduce zero-inflation of the dataset, we removed samples located on sites that are unsuitable for mesophilous forest habitat according to the potential natural vegetation (PNV) map of Flanders (De Keersmaeker et al., 2013). PNV is the most mature forest vegetation that can be expected and the map depicts the suitability of a site for five PNV types (Table 1). The two selected PNV types (AP and FC in Table 1) are mesophilous forest habitat with a high number of AFS, including several habitat specialists that are frequent in one PNV type but scarce in others. AFS, in particular habitat specialists, are scarce in other PNV types that were not selected (Table 1). As a result of this selection, 737 sample plots were removed, most of which counted less than four AFS (Appendix A). Seven sample plots with extreme values of explanatory variables were also removed, so 377 samples on sites with a potential for mesophilous forest were used for modeling.

2.3. Explanatory data

The explanatory variables were derived from five types of source data (Table 2): eight connectivity measures were calculated on maps with forest cover at four time slices, four connectivity measures were calculated on a cadastral map, two habitat suitability indices were extracted from the PNV map, slope was derived from a digital terrain model (DTM), and three variables were the result of an interpretation of land use on eight maps that cover the time period between 1775 and 2000. Names of explanatory variables are indicated by capitals hereafter (Table 2). Contrary to the 15 other variables that are spatially explicit, the three

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