RESEARCH ARTICLE

The analysis of spatio-temporal forest changes (1775–2000) in Flanders (northern Belgium) indicates habitat-specific levels of fragmentation and area loss

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Received: 26 February 2013 / Accepted: 11 November 2014 / Published online: 25 November 2014 - Springer Science+Business Media Dordrecht 2014

Abstract

Introduction Spatio-temporal forest changes can have a progressive negative impact on the habitat of species that need forest continuity, i.e. the continuous presence of forest. Long-term species data that demonstrate such an impact are often not available. Instead we applied a spatial analysis on maps of the historical and present-day forests, by calculating landscape indices that explain forest plant species diversity.

Methods We digitized for this purpose, forests in Flanders (northern Belgium, \sim 13,500 km2) at four time slices (1775, 1850, 1904–1931, 2000) and created a map of forest continuity in 2000. The ecological relevance of the analysis was further enhanced by a site classification, using a map of potential forest habitat types based on soil–vegetation relationships.

Electronic supplementary material The online version of this article (doi[:10.1007/s10980-014-0119-7\)](http://dx.doi.org/10.1007/s10980-014-0119-7) contains supplementary material, which is available to authorized users.

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Results Our results indicated that, between 1775 and 2000, forests occupied 9.7–12.2 % of the total study area. If continuity was not taken into consideration, forest fragmentation slightly increased since 1775. However, only 16 % of the forest area in 2000 remained continuously present at least since 1775 and is therefore called ancient forest (AF). Moreover, connectivity of forest that originated after 1775, called recent forest, was low and only 14 % was in physical contact with AF. The results were habitat-specific as forest on sites that are potentially suitable for a high number of slow-colonizing species, e.g. ancient forest plants, were affected most. Conclusion We discuss that a GIS analysis of this kind is essential to provide statistics for forest biodiversity conservation and restoration, in landscapes with a dynamic and heterogeneous forest cover.

Keywords Connectivity · GIS · Historical ecology · Historical maps - Land-use change - Land-use reconstruction - Landscape metrics - Recovery potential

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Introduction

Many forest organisms depend on forest continuity, as observed for certain lichens (Fritz et al. [2008](#page-11-0)), springtails (Ponge et al. [2006\)](#page-12-0), beetles (Assmann [1999;](#page-11-0) Desender et al. [1999](#page-11-0)), and vascular plants called ancient forest species (Hermy et al. [1999](#page-11-0)). The association of these species with a continuous presence of forest is explained by the slow formation of suitable habitat (e.g. old-growth structures) or by poor dispersal capacities (Nordén and Appelqvist [2001](#page-12-0)). Spatio-temporal forest changes can therefore result into progressive loss, fragmentation or degradation of habitat of species that depend on forest continuity.

Historical maps can be used to quantify spatiotemporal forest changes at a regional scale, and for a long period of time (e.g. Foster [1992](#page-11-0); Wulf et al. [2010\)](#page-12-0). The direct impact of spatio-temporal habitat changes on biodiversity requires information on historical species composition, e.g. by public land surveys used in Northern America (see Batek et al. [1999;](#page-11-0) Hall et al. [2002](#page-11-0); Bolliger et al. [2004](#page-11-0)) and Australia (Fensham and Fairfax [1997](#page-11-0)). If such information is not available, landscape indices calculated on digitized maps could be used as a proxy. The relationships between species diversity, forest plants in particular, and habitat size, continuity, and connectivity are well studied (e.g. Peterken and Game [1984](#page-12-0); Honnay et al. [2002;](#page-11-0) Jacquemyn et al. [2003](#page-11-0); Vellend [2003\)](#page-12-0). Landscape indices that explain species diversity according to these specific studies can be calculated on spatially explicit forest maps that cover a wide area and a long period of time. By doing so, the impact of spatio-temporal changes on forest habitat can be quantified without using species data.

An important step in this approach is the assessment of forest continuity, by means of a GIS analysis on historical and present-day forest maps (Foster [1992](#page-11-0); Wulf et al. [2010](#page-12-0); Andrieu et al. [2011](#page-11-0); Skalos et al. [2012\)](#page-12-0). Ancient forest (AF) can thus be discriminated from recent forest (RF). AF have remained continuously present, whereas RF were established on open land (Spencer and Kirby [1992](#page-12-0)). The quantification and location of AF is highly important for forest policy, management and conservation as they are considered as biodiversity hotspots (Spencer and Kirby [1992](#page-12-0); Wulf [2003\)](#page-12-0). Such a GIS analysis can also provide information on the continuity and connectivity of RF. The age of a RF explains the recovery level and RF in physical contact with AF can recover faster than isolated RF (Peterken and Game [1984;](#page-12-0) Honnay et al. [2002;](#page-11-0) Vellend [2003](#page-12-0); Jacquemyn et al. [2003;](#page-11-0) Verheyen et al. [2006](#page-12-0)).

When potential effects of spatio-temporal forest changes are studied, it is appropriate to include a habitat typology as well. As different forest habitat types share only a limited pool of common species, habitat heterogeneity can further constrain species migration and forest recovery. This assumption was applied to explain forest plant species diversity in dynamic and heterogeneous landscapes (Jacquemyn et al. [2001](#page-11-0); Verheyen et al. [2006](#page-12-0)).

Spatial explicit studies that aimed to quantify longterm forest changes at a regional scale were performed in Europe (Sereda and Lukana [2009;](#page-12-0) Wulf et al. [2010](#page-12-0); Skalos et al. [2012](#page-12-0)) and northern America (Iverson [1988;](#page-11-0) Hall et al. [2002\)](#page-11-0). Some studies mapped forest changes with a high spatial and temporal resolution and also determined forest continuity (Wulf et al. [2010;](#page-12-0) Skalos et al. [2012\)](#page-12-0), but they did not apply a habitat typology. Other studies reconstructed eighteenth or nineteenth century vegetation in northern America (Batek et al. [1999](#page-11-0); Hall et al. [2002;](#page-11-0) Bolliger et al. [2004\)](#page-11-0), Australia (Fensham and Fairfax [1997](#page-11-0)), and Europe (Wulf and Rujner [2011\)](#page-12-0). Whereas these studies quantified the historical area and reconstructed the species composition of habitat types, they did not study the impact of spatio-temporal changes on habitat continuity and connectivity.

We aimed to study the potential impact of spatiotemporal forest changes on forest habitat at a regional scale $({\sim}13,500 \text{ km}^2)$ and for a long time period (1775–2000). We intended to use for this purpose landscape indices that explain forest plant species diversity, as indicated by previous research. We hypothesized that the impact of spatio-temporal forest changes could be habitat-specific and included for this reason a site classification into the GIS analyses.

Methods

Study area

This study covered most of Flanders (13.500 km^2) , a region in northern Belgium (Fig. [1](#page-2-0)). Three municipalities of Flanders were excluded as they were not Fig. 1 Location of Flanders (dark grey area) in northern Belgium (dark grey outline) and in western Europe (light grey area)

represented by the oldest map. The climate of Flanders is mild, with little regional variation. Average monthly minimum and maximum temperatures equal 2.5 and 17.0 \degree C, respectively, and annual precipitation amounts to 852 mm according to the Royal Meteorological Institute [\(www.meteo.be](http://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.

As climatic variability is low, natural forest vegetation composition is mostly explained by soil conditions (De Keersmaeker et al. [2013](#page-11-0)). Topsoils mainly consist of pleistocene aeolian sand and loess deposits. The silt loam content gradually increases from the north to the south. Heathland or forests soils on sand mostly are Arenosols or Podzols (IUSS Working Group WRB [2006](#page-11-0); Dondeyne et al. [2012](#page-11-0)). When covered by forest, vegetation on acid sandy soils and soils with an intermediate silt loam content is classified as an acidophilus forest vegetation dominated by English and sessile oaks (Quercion robori-petraeae) (Table [1](#page-3-0)). Soils with a high silt loam content that are covered by forest, have a clay illuviation horizon and are classified as Albeluvisols or Luvisols (IUSS Working Group WRB [2006](#page-11-0); Dondeyne et al. [2012](#page-11-0)). These soils can be covered by a beech-dominated forest vegetation (Fagion sylvaticae) or by a mixed oak-hornbeam forest vegetation (Carpinion betuli) (Table [1](#page-3-0)). Alluvial soils without profile development are classified as Gleysols or Fluvisols and peat soils as Histosols (IUSS Working Group WRB [2006;](#page-11-0) Dondeyne et al. [2012\)](#page-11-0). The former can be suitable for an alluvial forest vegetation with black alder and European ash (Alno-Padion), whereas waterlogged soils and peat soils can be covered by black alder carr vegetation (Alnion glutinosae) (Table [1](#page-3-0)). Forests amounted to 11 % of the surface area in 2000. A more recent forest map is not available but according to the delivered permissions, forest changes were low after 2000 (Bos + 2012).

Methodological outline

We calculated ecological landscape indices on five forest maps, with and without specification for potential forest habitat type. Four maps represented forests at time slices between 1775 and 2000, and one map indicated forest continuity (FC) of forest patches in 2000. A first step was the digitization of forests displayed by historical maps (Fig. [2](#page-4-0)). The oldest available map, drawn at the end of the eighteenth century, was selected for digitization to maximize the

Table 1 Five forest habitat types (Roman numerals) of Flanders (northern Belgium), with the area potentially occupied (in ha and as a proportion of the area of Flanders), the soil

types of the Belgian soil map that determine the site classification, and the potential forest vegetation that can develop when sites are converted to forest

Soil names between brackets refer to the World Reference Base typology (IUSS Working Group WRB [2006\)](#page-11-0) corresponding with the Belgian soil typology (Dondeyne et al. [2012\)](#page-11-0). The taxonomical units between brackets refer to De Keersmaeker et al. ([2013\)](#page-11-0)

studied time period. The map drawn in the midnineteenth century was included as case studies indicated that several forests were cleared at that time (Verheyen et al. [1999](#page-12-0); Verheyen and Hermy [2001](#page-12-0)). The third selected historical map offered the possibility to apply a semi-automatic vectorization of forest patches by means of image classification. The most recent forest map was derived from the digital forest reference layer (AGIV [2001\)](#page-11-0). The overlay of the digital forest maps at four time slices resulted into a FC map (Fig. [2](#page-4-0)). This FC map indicates at which time interval a forest polygon originated and remained continuously present until 2000. As the FC map is affected by errors, we selected polygons of the FC map with a high accuracy, for further analysis (Fig. [2\)](#page-4-0). A map of potential forest habitat was used in five GIS overlays with the digital maps of the forests at four separate times and with the selected polygons of the FC map (Fig. [2\)](#page-4-0). By doing so, the historical areas of potential forest habitat types were reconstructed and the continuity and connectivity of potential forest habitat types in 2000 could be assessed.

Digitization of the forests at four times

Forests were digitized on three historical maps: the cabinet maps drawn by de Ferraris in 1775, the topographical maps drawn by Philippe Vandermaelen in 1850, and the military topographical maps edited by Dépôt de la Guerre between 1904 and 1931. Additional metadata of the studied historical maps can be found in Appendix 1 (supplementary material). Forests on the 1775 and 1850 maps were digitized by manual interpretation to moderate the positional errors. We scanned a 1:25,000 reproduction of the 1750 and 1850 maps at 600 dpi and reprinted it at 1:10,000 for this purpose. Forests on the 1:10,000 prints were located by means of topographical maps printed at the same scale on transparency film. When located, forest perimeters were delineated on an empty film that was attached to the transparency film on which the topographical map was printed. When all forests of a topographical map sheet were drawn, the film with the forest perimeters was scanned and georeferenced, using the marked edge points of the topographical map sheet. Finally, the forest perimeters on the georeferenced raster image were vectorized by auto tracing. Forests at the third time slice (1904–1931) were digitized by means of a semiautomatic procedure. The map sheets were first scanned and georeferenced. Pixels in forest patches, colored green, were selected by a supervised image classification. After a cleanup, the grid file was converted to a vector file. A post processing procedure was applied to obtain uniform criteria for polygons of the four time slices. Paths and small roads with a width Fig. 2 Flowchart of the methodological outline for assessing forest habitat loss and fragmentation caused by spatio-temporal forest changes between 1775 and 2000. Source data are seven historical maps and the digital forest layer 2000 (Appendix 1 in supplementary material), the systematically sampled plots of the forest inventory of Flanders (Waterinckx and Roelandt [2001\)](#page-12-0), and a map of five potential forest habitat types (see Table [1](#page-3-0))

 \leq 10 m that separate forest polygons, were removed by a closing procedure (buffer $+5$ m; dissolve; buffer -5 m). Polygons with an area below 0.5 ha were removed, as this was the threshold value for digitization of the forest reference layer (AGIV [2001](#page-11-0)). Digitization of forests on historical maps was performed between 1998 and 2001 in ArcInfo 7, for the spatial analyses on the resulting polygon maps, explained in the following sections, we used ArcInfo 9.3.

Forest continuity

The digital forest maps of four time slices each contained binary information (forest or no forest) that was combined into an overlay map. This resulted into 15 classes of polygons with a unique forest history (Appendices 2 and 3 in supplementary material). The eight classes for sites that were still forested in 2000 were recoded to four classes of FC. Each class of this FC map represented forest patches in 2000 that originated in the same time period and never were deforested thereafter (Appendices 2 and 3 in supplementary material). By convention, AF in Flanders is forest that was already present on the 1775 map and that was continuously present since that time (Hermy et al. [1999](#page-11-0)).

Accuracy analysis and sliver elimination

The FC map is affected by two types of errors. A first error type is the result of positional errors of the included historical maps. These positional errors are propagated in the overlay and influence landscapes indices calculated on it (Leyk et al. [2005;](#page-12-0) De Clercq et al. [2009;](#page-11-0) Burnicki [2012](#page-11-0)). A second error type results from undetected land-use changes. As the interval between the four map series included into the FC map

amounted to approximately 75 years (Fig. [2\)](#page-4-0), sites indicated as forest on two successive time slices could have been temporarily cleared in between both. The amount of error of the FC map was quantified by comparison with an accurate assessment of forest continuity, based on 1,238 forest inventory sample points. The forest inventory sample points are located on the intersections of a 1×1 km grid and are covered by forest according to a desk-top interpretation of orthophotographs. All points covered by forest were visited during a field survey, between 1997 and 1999 (Waterinckx and Roelandt [2001\)](#page-12-0). The forest inventory points were carefully located and land use was determined on all eight map series listed in Appendix 1 (supplementary material), independently from the FC map and working back in time from 2000 to 1775. We assumed that this point-based assessment of FC was less affected by positional errors and by errors that originate from missed land-use conversions, than the FC map. The point-based assessment of FC can result into eight classes (based on eight maps) but this information was reduced to four classes that cover the same time intervals as the four FC map classes, and used as a reference for comparison with the FC map classes in an error matrix. If the pointbased assessment indicated that a sample point was converted to open land for some time, whereas the FC map indicated a continuous presence of forest for the same time interval, or vice versa, there was disagreement between both assessments. The counts of sample points with agreement are listed on the diagonal of the error matrix, whereas counts of disagreement are listed elsewhere in the error matrix. As the forest inventory points are systematically sampled, the counts represent a proportion of the forest area in 2000.

The probability of agreement between forest continuity based on four maps (FC map) versus forest continuity independently assessed on forest inventory points only, using eight maps, was modeled using a logistic regression in R (R Core Team [2014](#page-12-0)). The probability of agreement was explained by the shape of the FC map polygons and by the FC map classes. High values of the perimeter to area ratio (PAR) of FC map polygons could indicate slivers, i.e. narrow polygons along the border of forest patches that result from the propagation of positional errors of the four maps included into the FC map (see Appendices 2 and 3 in supplementary material).We used the Epi package (Carstensen et al. 2013) in R to fit a receiver operating characteristic (ROC) curve (Metz [1978\)](#page-12-0) to this model. The ROC curve was used to obtain optimal threshold values for the PAR values of FC map polygons. The selection of polygons based on these threshold values results into a high sensitivity while maintaining a high specificity, meaning that accuracy of the FC map increased by the removal of polygons that contain wrong information (e.g. slivers) without losing too much information as a result of the removal of polygons with correct information.

Habitat typology and map

The reconstruction of historical forest habitat is complicated by the fact that systematically collected historical inventories on forest species composition seem to be missing in Europe, as opposed to North America (Batek et al. [1999](#page-11-0); Hall et al. [2002;](#page-11-0) Bolliger et al. [2004\)](#page-11-0) and Australia (Fensham and Fairfax [1997](#page-11-0)). Instead, a map of Potential Natural Vegetation can be used for habitat typology (Wulf and Rujner [2011](#page-12-0)). We used the potential natural vegetation (PNV) map of Flanders (De Keersmaeker et al. [2013](#page-11-0)) for this purpose, depicting five forest habitat types that can develop when sites are covered by forest (Table [1\)](#page-3-0). The five habitat types are the result of significant relationships between forest vegetation and soil types that are based on slowly changing, morphogenetic soil characteristics (Table [1](#page-3-0)). However, it should be kept in mind that the applied map is a site classification that does not give information on the species composition of present-day or historical forest vegetation. The map of potential forest habitat represents the most mature herbaceous forest vegetation that can develop on a specific site, if it is covered by forest and if all conditions (landscape factors, habitat quality, forest management) are favorable. Approximately 20 % of the total study area is not classified, comprising water bodies, built-up areas, disturbed soils (Technosols), military areas, and marine polders and dunes (Table [1](#page-3-0)).

Ecological landscape indices

Following indices were calculated: the total forest area at four time slices, the patch size and perimeter to area ratio (PAR) at four time slices, the proportion of AF versus RF calculated on the forest map in 2000, and the proportion of RF in physical contact with AF in 2000. The forest patch size and the PAR of forest patches were determined without specification of forest habitat types. The overlay of the forest maps with the map of potential forest habitat was used to calculate the potential areas of forest habitat types at the four time slices.

Landscape indices calculated on land-use change maps are affected by positional errors (Burnicki [2012\)](#page-11-0) and therefore patch size and PAR were not calculated on the FC map. The areas of the four FC classes, also specified for the five potential habitat types, were calculated on the selection of polygons with a high accuracy according to the ROC analysis.

The recovery potential of recent forest (RF), being all FC classes together except AF, was qualified based on the connectivity with AF. We discerned two connectivity levels, assuming that RF in physical contact with AF has a higher potential for vegetation recovery than RF separated from AF by open land (as demonstrated by e.g. Peterken and Game [1984\)](#page-12-0). This categorization is also supported by the traits of AF plants, that are mostly stress-tolerant (i.e. shadetolerant) species that rely on short-distance dispersal modes and can be excluded by competitive or ruderal species outside forests (Hermy et al. [1999\)](#page-11-0). RF of a specific habitat type was connected with AF if the adjacent AF was of the same habitat type.

Results

Forests at four time slices

Total forest area remained low since 1775, ranging between 9.7 % of the total study area in 1850 and 12.2 % in 1904–1931 (Table 2). In 1775 forests were mainly located in the west and south and these areas were gradually deforested afterwards. By contrast, in 1775 forest was scarce in the northeast, but this area was gradually afforested (Fig. [3](#page-7-0)).

Approximately 50 % of the forest area in 1775 was classified to habitat types III and IV, but in 2000 a similar proportion of the forest area was classified to habitat type V. There was a strong decline of forest classified to habitat types III (minus 45 %) and IV (minus 71 %), whereas the areas of forest classified to habitat types I and V increased and were four and two times higher in 2000 than in 1775, respectively (Table 2). As a result, more than 30 and 20 % of the area that is suitable for habitat types I and V, respectively, are forests in 2000. By contrast, the proportion of forest on sites suitable for habitat types III and IV only amounted to approximately 5 % in 2000. The total forest area of habitat type II did not change as much as other habitat types and approximately 14 % of the total area suitable for this habitat type were forests in 2000.

Although the total forest area in 2000 was of a similar magnitude as in 1775 (Table 2), the total number of forest patches increased from approximately 12000 in 1775 to 19000 in 2000. The decline of the median patch size and the increase of the PAR indicate a progressive forest fragmentation between 1775 and 2000 (Fig. [4\)](#page-8-0). The median patch size, between 1.5 and 2.0 ha, was low at all four time slices (Fig. [4](#page-8-0)).

Forest continuity and recovery potential

According to the error matrix 71 % of the FC map area was classified correctly (Table [3](#page-8-0)). Accuracy was relatively high for the FC classes representing AF

Table 2 Forest area in Flanders at four time slices, subdivided over five forest habitat types (Roman numerals) and expressed as a surface area (ha) and as a proportion of the potential area suitable for that forest habitat type $(\%)$

Habitat type	1775		1850		1904-1931		2000	
	(ha)	$(\%)$	(ha)	$(\%)$	(ha)	$(\%)$	(ha)	(%)
I	1,789	6.6	1,659	6.2	3,394	12.6	8,154	30.3
П	18,920	14.0	14,901	11.0	13,126	9.7	19,487	14.4
Ш	17,291	10.0	10,464	6.1	9,090	5.3	9,502	5.5
IV	59,629	16.4	40,884	11.2	23,885	6.6	17,486	4.8
V	37,324	10.5	48,488	13.6	87,296	24.5	72,991	20.5
Not classified	11,700	3.9	14,614	4.9	27,707	9.4	15,172	5.1
Total	146,653	10.8	131,010	9.7	164,499	12.2	143,711	10.6

Habitat types and the potential areas are listed in Table [1](#page-3-0)

Fig. 3 Maps of forests on four time slices between 1775 and 2000, a map with the location of selected ancient forests $(N = 463$, see Appendix 5 in supplementary material), and a

and sites that were afforested after 1904–1931, but very low (33 %) for the FC class representing sites afforested between 1775 and 1850 (Table [3\)](#page-8-0).

The accuracy of the FC map increased from 71 % to 82 % by selecting polygons with PAR values below threshold values listed in Appendix 5 (supplementary material). The total area of selected polygons amounted to 66.7 % of the total forest area in 2000. Accuracy of the FC class that represents AF increased from 76 % to 86 % by selecting 463 polygons with a low PAR (Appendix 5 in supplementary material). None of the polygons of FC class 2 was selected, a consequence of the low accuracy of this FC class (see Table [3\)](#page-8-0).

map of five potential forest habitat types in Flanders (northern Belgium), explained in Table [1](#page-3-0)

The proportion of the total forest area that is AF was 14.9 % on the overlay of maps (Table [4\)](#page-8-0). The accurate calculation using the forest inventory sample points, resulted into a value of 16.2 % (Table [3\)](#page-8-0). AF is not evenly distributed but concentrated in the west, south, and center of Flanders (Fig. 3). AF is scarce in the southeast and in the northeast, where approximately 60 % of the total forest area in 2000 is located.

The proportion of AF is high for forest of habitat types III and IV (63 and 36 %, respectively), and low for forest of habitat types II, V and I (10, 8, and 1 %, respectively) (Table [4\)](#page-8-0). More than 80 % of the forests of habitat types I and II originated after 1904–1931. The proportion of the forests of habitat Fig. 4 Boxplots that represent the log_{10} transformed values of size (ha) and the perimeter to area ratio (PAR) of forest patches at four time slices illustrate the increased forest fragmentation between 1775 and 2000

Table 3 Error matrix on 1,238 forest inventory sample points, confronting forest continuity (FC) as represented by the FC map, with FC assessed on forest inventory sample points

The four capitals refer to the time period at which a sample point was converted to forest and never deforested ever since: before 1775 (ancient forest: A), between 1775 and 1850 (B), between 1850 and 1904–1931 (C), after 1904–1931 (D)

type V that originated between 1850 and 1904–1931, is of a similar order of magnitude (approximately 45 %) as the proportion that originated after that time (Table 4).

Forests in 2000 consisted for 86 % of RF that is not connected to AF, meaning that it is separated from AF by open land (Table [5\)](#page-9-0). Connectivity is very low for RF of habitat types I and II (3.4 and 9.8 %, respectively), and relatively high for RF of habitat types III and IV (21.9 and 18.9 %, respectively).

Table 4 Areas potentially suitable for forest habitat types (Roman numerals) in 2000, subdivided over three forest continuity (FC) classes (capitals)

Habitat type	FC classes						
	A		C		D		
	(ha)	$(\%)$	(ha)	$(\%)$	(ha)	$(\%)$	
I	85	1.3	583	9.2	5,699	89.5	
П	1.310	10.4	953	7.5	10.358	82.1	
Ш	4.485	63.0	377	5.3	2,255	31.7	
IV	3.805	35.8	1,741	16.4	5,078	47.8	
V	4,032	8.3	23.031	47.2	21.718	44.5	
Not classified	612	5.9	1.531	14.7	8.253	79.4	
Total	14.329	14.9	28.217	29.5	53.362	55.6	

Habitat types are explained in Table [1,](#page-3-0) FC classes (capital letters) in Table 3. FC class B was not retained by the ROC analysis (see Appendix 5 in supplementary material)

Discussion

Forest area changes and forest continuity

Forest area changes since the eighteenth century have been studied in NE America (Foster [1992](#page-11-0); Hall et al. [2002;](#page-11-0) Matlack [2005\)](#page-12-0) and in central and western Europe (Sereda and Lukana [2009](#page-12-0); Wulf et al. [2010](#page-12-0); Skalos et al. [2012\)](#page-12-0). Most of these studies registered a decline of forests in the nineteenth century, as we did for our

ϵ ¹							
Habitat type	Connected		Not connected				
	(ha)	$(\%)$	(ha)	$(\%)$			
I	212	3.4	6,070	96.6			
H	1,107	9.8	10,204	90.2			
Ш	577	21.9	2,055	78.1			
IV	1,287	18.9	5,532	81.1			
V	6,596	14.7	38,153	85.3			
Total	9,778	13.6	62,015	86.4			

Table 5 Connectivity of recent forest in 2000 (classes C and D in Tables [4](#page-8-0) and 5) with ancient forest (class A in Tables [4](#page-8-0) and 5), specified for five habitat types (Roman numerals explained by Table [1](#page-3-0))

Connected recent forest is included into a forest patch with ancient forest of the same habitat type

study area. In spite of this decline in the nineteenth century, the total forest area in Flanders did not change much between 1775 and 2000. However, the low variability of the total forest area masks very high spatio-temporal changes and as a result forest continuity in Flanders is low as compared to other areas studied for a similar time period. In central Bohemia the total forest area ranged between 12 and 18 % between 1780 and 2007, but 53 % of the total forest area was continuously present (Skalos et al. [2012](#page-12-0)), as opposed to 16 % in Flanders. The total forest area of the Prignitz region (Germany) amounts to 23, 35 % of which is AF (Wulf and Gross [2004\)](#page-12-0). The total forest area is low in England and Wales (8 %), but 34 % of it is qualified as AF, being forest that was continuously present since 1600. Approximately 7 % of the AF area in England and Wales was cleared for other land-use in the past 50 years (Spencer and Kirby [1992\)](#page-12-0). In Flanders, 37 % of the forest that was continuously present between 1775 and 1904–1931 (totaling almost 30,000 ha), was cleared after that time period.

Methodological aspects

Land-use changes can be mapped with a high accuracy over a long time period when small areas are studied (Foster [1992](#page-11-0); Verheyen et al. [1999;](#page-12-0) Cousins [2001](#page-11-0)). Spatial or temporal resolution often are relatively low for large study areas (Iverson [1988](#page-11-0); Hall et al. [2002](#page-11-0); Wickham et al. [2007](#page-12-0)). Achieving a high resolution over a long time period and for a large area is complicated by the relative inaccuracy of old maps. Several authors applied a rubber sheeting to reduce the positional errors of old maps (Cousins [2001;](#page-11-0) Wulf et al. [2010;](#page-12-0) Andrieu et al. [2011](#page-11-0); Skalos et al. [2012](#page-12-0)). We applied for this purpose a manual interpretation using a slide, as Lindbladh et al. ([2007](#page-12-0)) did. In spite of this correction, the FC map was affected by error propagation. As a result of error propagation, a high proportion of the area of such an overlay can be false land-use change (slivers) and the area that continuously remained forest, can be underestimated (De Clercq et al. [2009](#page-11-0)). The proportion of the total area that is misclassified, is positively correlated with the positional error of the included maps and with the level of fragmentation (De Clercq et al. [2009](#page-11-0)), but is also reduced by a high temporal change of land-use (Burnicki [2012](#page-11-0)).

The error analysis indicated that we achieved a high accuracy for three out of four FC classes. Land-use of the forest inventory sample points, used for the error analysis, was carefully interpreted on all eight available historical maps series. By doing so, the error analysis evaluated the slivers in the overlay, but also the errors that originate from the use of a reduced number of historical maps. The assessment of land-use history on forest inventory sample points can be highly useful for an accuracy assessment, as it is much less time-consuming than the digitization of forest patches.

Indications of habitat loss and fragmentation for forest plant species

As a result of the high rate of spatio-temporal forest changes, forest continuity is low in Flanders. A high rate of land-use changes, exceeding species colonization rates, can result into a loss of forest biodiversity (see e.g. Matlack [2005](#page-12-0)). As our map of potential forest habitat was based on herbaceous forest vegetation, we will focus on the potential effects for herbaceous forest plants, in particular AF plant species.

AF plant species are mostly slow colonizers associated with AF, that can exhibit colonization rates below 1 m year⁻¹ in RF (De Keersmaeker et al. [2011;](#page-11-0) Brunet et al. [2012](#page-11-0)). The recovery of vegetation of RF is lagging behind reforestation for a considerable time and the magnitude of the AF loss determines the recovery potential (Vellend [2003;](#page-12-0) Matlack [2005\)](#page-12-0). Our analysis indicated that only 16 % of the forest area in Flanders is AF and that the total forest area remained low (maximum 12 %) and highly fragmented, with a median patch size between 1.5 and 2 ha, throughout the studied time period.

Peterken [\(2000](#page-12-0)) demonstrated that new forest patches are mostly isolated from old forests if the total forest area is lower than 30 %. This is confirmed by our results as only 14 % of the RF in Flanders was located adjacent to AF. The recovery level of vegetation of RF is higher in landscapes with a high connectivity between forest patches (Honnay et al. [2002;](#page-11-0) Verheyen et al. [2006\)](#page-12-0). RF in physical contact with AF is richer in forest plant species than isolated RF (Peterken and Game [1984;](#page-12-0) Jacquemyn et al. [2003](#page-11-0)).

Spatio-temporal forest changes were specific for the discerned sites of forest habitat types. Similar changes, albeit not related to a habitat typology, were also observed in other regions. Forests also increased since the nineteenth century on aeolian sand soils in Prussia (Wulf et al. [2010](#page-12-0)) and on waterlogged soils in central Bohemia (Skalos et al. [2012](#page-12-0)) that had a marginal value for intensifying agriculture. Reforestation of fields in central New England (MA, USA) since the middle of the nineteenth century, started at poorly drained sites (Foster [1992](#page-11-0)). In contrast, forests on land with a good nutrient and water supply were cleared (Wulf et al. [2010;](#page-12-0) Skalos et al. [2012](#page-12-0)). Slowcolonizing AF plants, e.g. Anemone nemorosa, Hyacinthoides non-scripta, Lamium galeobdolon, and Primula elatior, are mostly found in forests on soils that have an intermediate humidity, nutrient availability, and acidity (Hermy et al. [1999\)](#page-11-0). Sites with a potential for forest habitat types II and III were severely affected by loss of forest area, and by temporal disruption and fragmentation of the forests. These sites have the highest potential for forest vegetation with a high number of AF plant species (De Keersmaeker et al. [2013\)](#page-11-0). Forest on sites with a potential for habitat types I and V, on waterlogged and acid sand soils, increased but on these sites AF is scarce and connectivity of RF is low. Furthermore, the sites of habitat types I and V are suitable for only a few AF plant species (Hermy et al. [1999](#page-11-0); De Keersmaeker et al. [2013](#page-11-0)).

The spatial analysis using ecological landscape indicators thus indicated that the potential habitat of slow-colonizing forest plants was highly affected by area loss, and by temporal and spatial disruption. Yet, the Red list of vascular plants in Flanders (Van Landuyt et al. [2006\)](#page-12-0), determined on grid-based species inventories collected between 1939 and 2004, did not register a significant decline for any of the 44 AF plant species listed by Cornelis et al. [\(2009](#page-11-0)). Possible

explanations could be: the spatial resolution of the grid used for the Red list is coarse (4 \times 4 km) as compared to our spatial explicit data; the data of the Red list comprised only 65 years as opposed to 225 years by our study; AF plants show a slow response that can result into an extinction debt, meaning that species populations continue to decline for some time after habitat loss and fragmentation have stopped (Vellend et al. [2006](#page-12-0)).

Implications for forest policy and landscape planning

Forest fragmentation is an indicator of the Montreal Process for assessing sustainable forest management in 12 countries outside Europe (Montréal Process Criteria and Indicators for the Conservation and Sustainable Management of Temperate and Boreal Forests [2009](#page-12-0)). The fragmentation indicator of the Montréal process is quantified at forest type level, to increase relevance of the statistics for forest biodiversity conservation (Riitters et al. [2003](#page-12-0)). Forest area is a quantitative indicator used for the protection of forests in Europe that should be classified for vegetation type, if appropriate (Ministerial Conference on the Protection of Forests in Europe [1998](#page-12-0)). Our results indicate that it is also recommended to assess forest continuity in combination with a forest habitat typology, for areas with a land-use that is rapidly changing in time. If only the total area and fragmentation of forests would be used as indicators, there was more or less a status quo in Flanders since 1775.

By contrast, spatio-temporal forest changes since that time resulted in a low proportion of AF in Flanders. This finding emphasizes that the conservation of AF should be a priority in areas with a dynamic forest area. A similar conclusion was drawn by Peterken and Game [\(1984](#page-12-0)), Spencer and Kirby [\(1992](#page-12-0)), Wulf [\(2003](#page-12-0)), and De Frenne et al. ([2011](#page-11-0)). Most of the forests in Flanders are established on open land after 1775 and have a low potential for the recovery of a vegetation with a high number of slowcolonizing AF plant species. The conversion of open land on suitable sites to forest could increase the connectivity between RF and AF, which is in agreement with the pan-European guidelines 11 and 24 for afforestation and reforestation (Ministerial Conference on the Protection of Forests in Europe [2009](#page-12-0)). Based on the EU forest policy documents, Wulf ([2003\)](#page-12-0) made a similar recommendation. We demonstrated that a GIS analysis could provide qualitative and quantitative, spatially explicit information that can be used for these purposes.

Acknowledgments We would like to thank Marc Esprit who accomplished most of the laborious digitization work, and the Nature and Forest Agency who put the forest inventory sample points to our disposal. This research was the result of project VLINA/C97/06b, funded by the Flemish Community.

References

- AGIV (2001) Digital forest reference layer 2000. Flemish Geographical Information Agency and the Nature and Forest Agency of the Flemish Community. [http://metadata.](http://metadata.agiv.be/Details.aspx?fileIdentifier=63D62DD2-E800-4406-BF59-74DF33D109E1) [agiv.be/Details.aspx?fileIdentifier=63D62DD2-E800-4406-](http://metadata.agiv.be/Details.aspx?fileIdentifier=63D62DD2-E800-4406-BF59-74DF33D109E1) [BF59-74DF33D109E1](http://metadata.agiv.be/Details.aspx?fileIdentifier=63D62DD2-E800-4406-BF59-74DF33D109E1). Accessed Feb 2013
- Andrieu E, Ladet S, Heintz W, Deconchat M (2011) History and spatial complexity of deforestation and logging in small private forests. Landsc Urban Plan 103:109–117
- Assmann T (1999) The ground beetle fauna of ancient and recent woodlands in the lowlands of north-west Germany (Coleoptera, Carabidae). Biodivers Conserv 8:1499–1517
- Batek MJ, Rebertus AJ, Schroeder WA, Haithcoat TL, Compas E, Guyette RP (1999) Reconstruction of early nineteenth century vegetation and fire regimes in the Missouri Ozarks. J Biogeogr 26:397–412
- Bolliger J, Schulte LA, Burrows SN, Sickley TA, Mladenhoff DJ (2004) Assessing ecological restoration potentials of Wisconsin (USA) using historical landscape reconstructions. Restor Ecol 12(1):124–142
- Bos+ (2012) Bosbarometer 2012: waar blijven de daden? Bos+, Melle. [http://www.bosplus.be/images/stories/kenniscentrum/](http://www.bosplus.be/images/stories/kenniscentrum/bosbeleid/bosbarometer/) [bosbeleid/bosbarometer/](http://www.bosplus.be/images/stories/kenniscentrum/bosbeleid/bosbarometer/). Accessed Jan 2013
- Brunet J, De Frenne P, Holmström E, LajosMayr M (2012) Lifehistory traits explain rapid colonization of young postagricultural forests by understory herbs. For Ecol Manag 278:55–62
- Burnicki AC (2012) Impact of error on landscape pattern analyses performed on land-cover change maps. Landscape Ecol 27:713–729
- Carstensen B, Plummer M, Laara E, Hills M (2013) Epi: A Package for Statistical Analysis in Epidemiology. R package version 1.1.49. [http://CRAN.R-project.org/](http://CRAN.R-project.org/package=Epi) [package=Epi](http://CRAN.R-project.org/package=Epi) Accessed May 2014
- Cornelis J, Hermy M, Roelandt B, De Keersmaeker L, Vandekerkhove K (2009) Bosplantengemeenschappen in Vlaanderen, een typologie van bossen gebaseerd op de kruidlaag. Agentschap voor Natuur en Bos en Instituut voor Natuur- en Bosonderzoek, Brussels
- Cousins SA (2001) Analysis of land cover transitions based on 17th and 19th century cadastral maps and aerial photographs. Landscape Ecol 16:41–54
- De Clercq EM, Clement L, De Wulf RR (2009) Monte Carlo simulation of false change in the overlay of misregistered forest vector maps. Landsc Urban Plan 91:36–45
- De Frenne P, Baeten L, Graae BJ, Brunet J, Wulf M, Orczewska A, Kolb A, Jansen I, Jamoneau A, Jacquemyn H, Hermy M, Diekmann M, De Schrijver A, De Sanctis M, Decocq G, Cousins SA, Verheyen K (2011) Interregional variation in the floristic recovery of post-agricultural forests. J Ecol 99:600–609
- De Keersmaeker L, Vandekerkhove K, Verstraeten A, Baeten L, Verschelde P, Thomaes A, Hermy M, Verheyen K (2011) Clear-felling effects on colonization rates of shade tolerant forest herbs into a post-agricultural forest adjacent to ancient forest. Appl Veg Sci 14:75–83
- De Keersmaeker L, Rogiers N, Vandekerkhove K, De Vos B, Roelandt B, Cornelis J, De Schrijver A, Onkelinx T, Thomaes A, Hermy M, Verheyen K (2013) Application of the ancient forest concept to Potential Natural Vegetation mapping in Flanders, a strongly altered landscape in Northern Belgium. Folia Geobotanica 48:137–162
- Desender K, Ervynck A, Tack G (1999) Beetle diversity and historical ecology of woodlands in Flanders. Belg J Zool 129:139–156
- Dondeyne S, Van Ranst E, Deckers J (2012) Converting the legend of the soil map of Belgium into the World Reference Base for soil resources. KU Leuven and UGent, Leuven
- Fensham RJ, Fairfax RJ (1997) The use of the land survey record to reconstruct pre-European vegetation patterns in the Darling Downs, Queensland, Australia. J Biogeogr 24:827–836
- Foster DR (1992) Land-use history (1730-1990) and vegetation dynamics in central New England, USA. J Ecol 80:753–771
- Fritz Ö, Gustafsson L, Larsson K (2008) Does forest continuity matter in conservation?—A study of epiphytic lichens and bryophytes in beech forests of southern Sweden. Biol Conserv 141:655–668
- Hall B, Motzkin G, Foster DR, Syfert M, Burk J (2002) Three hundred years of forest and land-use change in Massachusetts, USA. J Biogeogr 29:1319–1335
- Hermy M, Honnay O, Firbank L, Grashof-Bokdam C, Lawesson JE (1999) An ecological comparison between ancient and other forest plant species of Europe, and the implications for forest conservation. Biol Conserv 91:9–22
- Honnay O, Verheyen K, Butaye J, Jacquemyn H, Bossuyt B, Hermy M (2002) Possible effects of habitat fragmentation and climate change on the range of forest plant species. Ecol Lett 5:525–530
- IUSS Working Group WRB (2006) World reference base for soil resources 2006. A framework for international classification, correlation and communication. World soil resources report 103, FAO, Rome
- Iverson LR (1988) Land-use changes in Illinois, USA: the influence of landscape attributes on current and historic land use. Landscape Ecol 2:45–61
- Jacquemyn H, Butaye J, Hermy M (2001) Forest plant species richness in small, fragmented mixed deciduous forest patches: the role of area, time and dispersal limitation. J Biogeogr 28:801–812
- Jacquemyn H, Butaye J, Hermy M (2003) Impacts of restored patch density and distance from natural forests on colonization success. Restor Ecol 11:417–423
- Leyk S, Boesch R, Weibel R (2005) A conceptual framework for uncertainty investigation in map-based land cover change modeling. Trans GIS 9:291–322
- Lindbladh M, Brunet J, Hannon G, Niklasson M, Eliasson P, Eriksson G, Ekstrand A (2007) Forest history as a basis for ecosystem restoration—a multidisciplinary case study in a south Swedish temperate landscape. RestorEcol 15(2): 284–295
- Matlack GR (2005) Slow plants in a fast forest: local dispersal as a predictor of species frequencies in a dynamic landscape. J Ecol 93(1):50–59
- Metz CE (1978) Basic principles of ROC analysis. Semin Nucl Med 8:283–298
- Ministerial Conference on the Protection of Forests in Europe (1998) Annex 2 of the resolution L2, Pan-European Operational Level Guidelines for Sustainable Forest Management. Adopted at the Fifth Expert Level Preparatory Meeting of the Lisbon Conference on the Protection of Forests in Europe, 27–29 April 1998, Geneva, Switzerland. [http://www.foresteurope.org/docs/MC/MC_lisbon_resolu](http://www.foresteurope.org/docs/MC/MC_lisbon_resolution_annex2.pdf) [tion_annex2.pdf.](http://www.foresteurope.org/docs/MC/MC_lisbon_resolution_annex2.pdf) Accessed June 2013
- Ministerial Conference on the Protection of Forests in Europe (2009) Pan-European guidelines for afforestation and reforestation with a special focus on the provisions of the UNFCCC. Adopted by the MCPFE Expert Level Meeting on 12–13 November 2008 and by the PEBLDS Bureau on behalf of the PEBLDS Council on 4 November 2008.[http://](http://www.foresteurope.org/documentos/Pan-EuropeanAfforestationReforestationGuidelines.pdf) [www.foresteurope.org/documentos/Pan-EuropeanAfforesta](http://www.foresteurope.org/documentos/Pan-EuropeanAfforestationReforestationGuidelines.pdf) [tionReforestationGuidelines.pdf.](http://www.foresteurope.org/documentos/Pan-EuropeanAfforestationReforestationGuidelines.pdf) Accessed June 2013
- Montréal Process Criteria and Indicators for the Conservation and Sustainable Management of Temperate and Boreal Forests (2009) Technical notes on implementation of the Montréal Process criteria and indicators, criteria 1–7, third edition available from [http://www.montrealprocess.org/](http://www.montrealprocess.org/documents/publications/techreports/2009p_2.pdf) [documents/publications/techreports/2009p_2.pdf](http://www.montrealprocess.org/documents/publications/techreports/2009p_2.pdf). Accessed May 2014
- Nordén B, Appelqvist T (2001) Conceptual problems of ecological continuity and its bioindicators. Biodiversity Conserv 10:779–791
- Peterken G (2000) Rebuilding networks of forest habitats in lowland England. Landsc Res 25:291–303
- Peterken GF, Game M (1984) Historical factors affecting the number and distribution of vascular plant species in the woodlands of central Lincolnshire. J Ecol 72:155–182
- Ponge JF, Dubs F, Gillet S, Sousa JP, Lavelle P (2006) Decreased biodiversity in soil springtail communities: the importance of dispersal and landuse history in heterogeneous landscapes. Soil Biol Biochem 38:1158–1161
- Riitters KH, Coulston JW, Wickham JD (2003) Localizing national fragmentation statistics with forest type maps. J Forest 101:18–22
- Sereda S, Lukana M (2009) Assessment of changes in land-use development in the Magura and the Eastern Tatras in the years 1772–2003. Oecol Mont 18:1–13
- Skalos J, Engstova B, Trpakova I, Santruckova M, Podrazsky V (2012) Long-term changes in forest cover 1780–2007 in central Bohemia, Czech Republic. Eur J Forest Res 131:871–884
- Spencer JW, Kirby KJ (1992) An inventory of ancient woodland for England and Wales. Biol Conserv 62:77–93
- R Development Core Team (2014). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, [http://www.R-project.org/.](http://www.R-project.org/) Accessed May 2014
- Van Landuyt W, Hoste I, Vanhecke L, Van Den Bremt P, Vercruysse W, de Beer D (2006) Atlas van de flora van Vlaanderen en het Brussels Gewest. Flower, Research Institute for Nature and National Botanic Garden of Belgium, Brussels
- Vellend M (2003) Habitat loss inhibits recovery of plant diversity as forests regrow. Ecology 84:1158–1164
- Vellend M, Verheyen K, Jacquemyn H, Kolb A, Van Calster H, Peterken G, Hermy M (2006) Extinction debt of forest plants persists for more than a century following habitat fragmentation. Ecology 87:542–548
- Verheyen K, Hermy M (2001) The relative importance of dispersal limitation of vascular plants in secondary forest succession in Muizen Forest, Belgium. J Ecol 89:829–840
- Verheyen K, Bossuyt B, Hermy M, Tack G (1999) The land use history of a mixed hardwood forest in western Belgium and its relationships with chemical soil characteristics. J Biogeogr 26:1115–1128
- Verheyen K, Fastenaekels I, Vellend M, De Keersmaeker L, Hermy M (2006) Landscape factors and regional differences in recovery rates of herb layer richness in Flanders (Belgium). Landscape Ecol 21:1109–1118
- Waterinckx M, Roelandt B (2001) De bosinventaris van het Vlaamse Gewest. Ministerie van de Vlaamse Gemeenschap, afdeling Bos and Groen, Brussel
- Wickham JD, Riiters KH, Wade TG, Coulston JW (2007) Temporal change in forest fragmentation at multiple scales. Landscape Ecol 22:481–489
- Wulf M (2003) Forest policy in the EU and its influence on the plant diversity of woodlands. J Environ Manag 67:15–25
- Wulf M, Gross J (2004) Application of the historical Schmettau map (1767–1787) in landscape analysis. In: Verhandlungen der Gesellschaft für Okologie, Band 34, Giessen, 13–17 September 2004
- Wulf M, Rujner H (2011) A GIS-based method for the reconstruction of the late eighteenth century forest vegetation in the Prignitz region (NE Germany). Landscape Ecol 26:153–168
- Wulf M, Sommer M, Schmidt R (2010) Forest cover changes in the Prignitz region (NE Germany) between 1790 and 1960 in relation to soils and other driving forces. Landscape Ecol 25:299–313