Diversity and Distributions, A Journal of Conservation Biogeography

Diversity and Distributions, (Diversity Distrib.) (2015) **21**, 631–642

BIODIVERSITY RESEARCH

Habitat type shapes long-term plant biodiversity budgets in two densely populated regions in north-western Europe

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ABSTRACT

Aim At a global scale, biodiversity changes are mainly driven by extinction, resulting in an overall decrease in species richness. At regional and local scales, although immigration often (over)compensates for local extinction, biodiversity changes have no clear trends. We tested the hypotheses that (1) at both regional and local scales, biodiversity changes result from the differential dynamics of local extinction and immigration, ultimately leading to increases in biodiversity following periods of transient surplus or deficit and (2) habitats are differentially affected by human activities, resulting in contrasting trends and dynamics that together shape the regional biodiversity budget.

Location Northern France and Belgian Flanders, north-western Europe.

Methods We analysed changes in plant species richness over one century in two adjacent and densely populated regions. Because local to regional changes are expected to be driven by species–environment interactions, and because species ecology and environmental change are largely embodied by the habitat, we assessed biodiversity budgets according to the type of habitat.

Results We observed major changes in species composition at the regional scale with about one of every five to six species becoming regionally extinct or newly naturalized. Immigration offset or exceeded losses, with local extinctions generally preceding gains. Overall, regional dynamics were driven by contrasting changes in a few habitat types, with either local extinction or immigration predominating. Transient biodiversity surpluses or deficits were observed at the regional scale and in certain habitat types.

Main conclusions Including habitat types bridges the gap between regional and local studies and provides a more accurate assessment of the biodiversity budget: integrating habitat type into regional analyses or meta-analyses can lead future research towards the understanding of the determinisms of biodiversity change across spatial scales.

Keywords

Biodiversity change across scales, global change, habitat type, local extinction and immigration, long-term monitoring, plant species.

INTRODUCTION

More than three-quarters of the Earth's ice-free land has been extensively modified by human activities, causing a dramatic reduction in natural habitats, habitat degradation and fragmentation due to changes in land use, anthropogenic climate change and the introduction of alien species (Ellis & Ramankutty, 2008). As a result, biodiversity loss has occurred on the

DOI: 10.1111/ddi.12287
http://wileyonlinelibrary.com/journal/ddi

global scale (Pimm *et al.*, 1995). In contrast, at the regional scale ('the broad set of areas that are intermediate in extent between the entire globe and small study plots of less than a few dozen hectares', Sax & Gaines, 2003), there is often a net gain of species observed, resulting mainly from the arrival of alien species in urban settings (Sax & Gaines, 2003; Jackson & Sax, 2010). At the local scale ('small study plots of less than a few dozen hectares', Sax & Gaines, 2003), there are either species gains or losses, depending on the type of habitat. The elaboration of efficient policies in favour of biodiversity and the design of relevant 'biodiversity–ecosystem functioning' experiments (Cardinale *et al.*, 2012) require a better understanding of the mechanisms that govern these contrasting trends at different spatial scales (Sax & Gaines, 2003).

The different patterns of changes in species richness are probably driven by scale-dependent, distinct processes (Sax & Gaines, 2003; Ellis *et al.*, 2012; Fig. 1). At a global scale, extinction and speciation drive changes in species richness; extinction occurs at a greater rate, and the number of species is declining. At regional and local scales (*sensu* Sax & Gaines, 2003), additional mechanisms are also at work, namely local extinction and immigration (i.e. local arrival of new species, either natural or human-assisted). Immigration, mainly involving cosmopolitan species, tends to increase regional species richness and often offsets or even overcompensates losses (Sax & Gaines, 2003). At the local scale, all three possible trends have been reported: stability, decrease or increase in species richness (Sax & Gaines, 2003). At this scale, the processes driving these patterns still need to be identified. A better knowledge of processes at work at different spatial scales is thus essential to our understanding of the effects of global change on biodiversity (Fig. 1).

Time-scale is also of prime importance in shaping the observed dynamics, which in turn determine the biodiversity budgets assessed at a given point in time (Jackson & Sax, 2010). For example, local extinction and immigration usually do not occur immediately after human disturbance, nor do they occur simultaneously. Jackson & Sax (2010) suggest that the consecutive extinction debt and immigration credit can generate transient biodiversity surpluses or deficits, depending on when the biodiversity survey is taken. Long-term monitoring is therefore necessary, but knowledge is currently insufficient to determine a minimum length of time for such studies. Unfortunately, few long-term studies have been conducted at local scales at a significant number of sites (Sax & Gaines, 2003) because old records of species are rare.

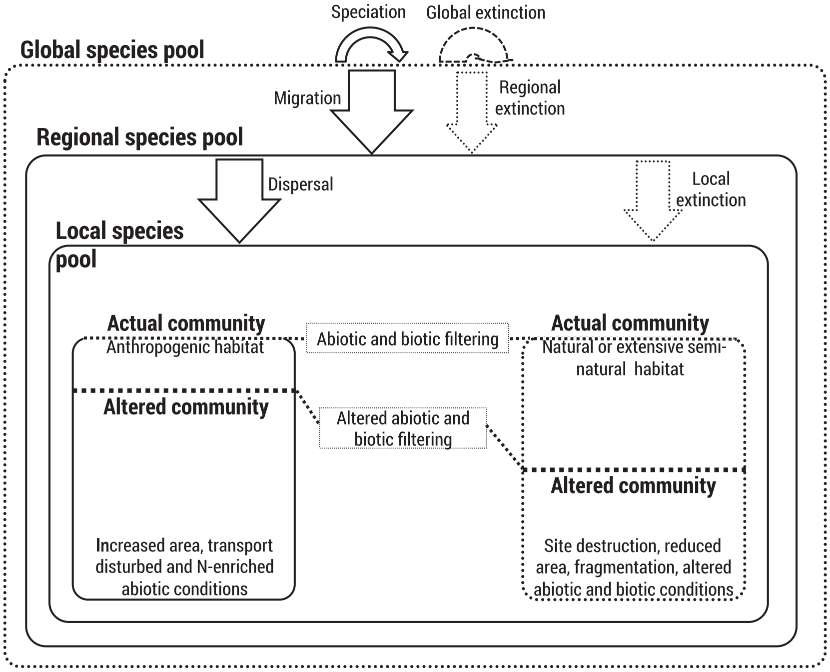

Figure 1 Assembly rules and their underlying processes in a context of global change (adapted from Götzenberger *et al.*, 2012). The global species pool is shaped by migration and speciation. From the global species pool, migration and regional extinction shape the regional species pool (phylogeographic assembly). The local species pool contains regional species that are able to disperse (dispersal assembly). Habitat filtering and biotic interactions (ecological assembly) will shape the actual local community, and local extinction is therefore possible, reducing the local species pool. Dotted lines represent decreasing biodiversity budgets. The global species pool decreases because extinction rates are higher than speciation. At the local scale, in vulnerable habitats and under strong human impact on biotic and abiotic conditions, losses due to local extinctions can exceed gains following immigration, which is lowered due to habitat fragmentation. The opposite happens in anthropogenic, highly modified or less vulnerable habitats. At the regional scale, biodiversity budgets depend on the dominance of each type of habitat: in about two-thirds of the global map, local extinctions are (over) compensated by immigration of alien species (Sax & Gaines, 2003; Ellis *et al.*, 2012).

Other important ecological organizational levels have to be considered to understand the diversity of regional and local patterns of change (Jackson & Sax, 2010). In particular, the effect of habitat has, to our knowledge, never been addressed in the global-decrease/local-increase body of research (Sax & Gaines, 2003). At a local scale, interactions between species, on the one hand, and between species and their physical environment, on the other hand, are of prime importance in determining diversity (Sax & Gaines, 2003). A large number of environmental variables and forcing events (*sensu* Jackson & Sax, 2010), as well as a large part of species ecological requirements, are embodied in the habitat; therefore, habitat type may be of major interest for understanding changes in species richness. Habitats may indeed be differentially affected in various ways by human activities. For instance, aquatic ecosystems are often drained and polluted by agricultural and industrial discharge, whereas forests are typically fragmented or more intensively managed, and grasslands suffer from increasing eutrophication. Moreover, over the last few decades, human societies have started protecting and managing the last local sites of rarefying habitats to maintain local biodiversity and promote the return of locally extinct species. Furthermore, the consequences of human activities will partly depend on past management (Dupouey *et al.*, 2002) or site connectivity (Hylander & Ehrlén, 2013). The interaction between human activities and habitat is thus likely to result in diverse local dynamics, which consequently affect regional dynamics. Lastly, the consequences of forcing events will also vary from one habitat to another according to species traits, for example ecological requirements or life history traits (Lindborg, 2007; Storkey *et al.*, 2012). Therefore, monitoring changes in species richness over time according to habitat type can provide new insights on these processes and facilitate our understanding of the local to regional patterns of biodiversity dynamics.

Here, we analyse the changes in plant species richness in two adjacent regions: northern France (Nord-Pas-de-Calais) and Belgian Flanders (Fig. 2). These regions have been strongly altered by human activities: they are densely inhabited, highly urbanized and industrialized, with, respectively, 70% and 50% of the land currently in agricultural use, and are areas of particularly intensive farming (Christians, 1998; Nationaal Instituut voor de Statistiek, 2011; French Ministry for Ecology, 2012). However, naturalists have been active over more than a century in these two regions, providing exhaustive long-term distributional data on vascular flora.

Here, we demonstrate that long-term studies that take habitat type into account are necessary to understand the patterns of change in local and regional species richness. First, we analyse the regional pattern of changes in the richness of the plant species pool over one century in these two densely populated regions, to test the hypothesis that, at a regional scale, biodiversity changes result from differential dynamics of local extinction and immigration, ultimately leading to increases in biodiversity following periods of transient surplus or deficit. Second, we test the hypothesis that habitat types are differentially affected by human activities, resulting in contrasting trends and dynamics that together shape the regional biodiversity budget. To do so, we tracked changes in species richness of plants associated with the 18

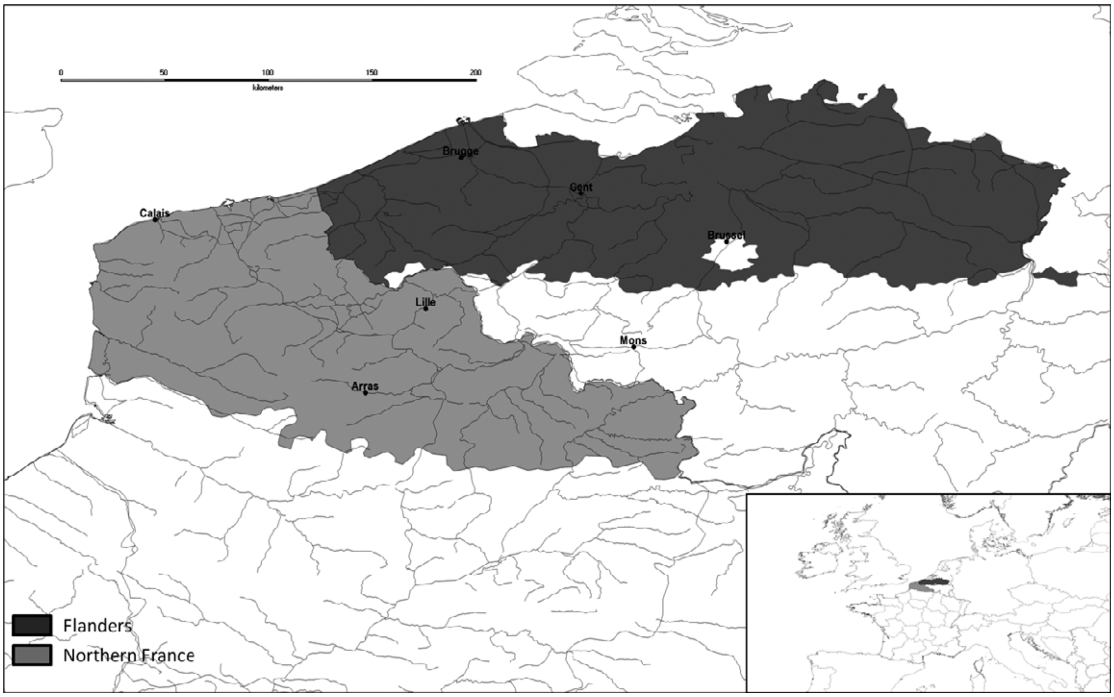

Figure 2 Map of north-western Europe displaying location and delineation of the study regions.

major habitat types that are present in the two regions. Instead of tracking changes in individual patches of habitats – which would drastically reduce the data set –,we investigated changes in the regional pool of species that are representative of each habitat type.

METHODS

Study area

The study regions, northern France and Belgian Flanders (Fig. 2), are two bordering regions of comparable surface area (12.414 km^2 and 13.522 km^2, respectively), densely populated (324 inhabitants/km^2 and 462 inhabitants/km^2, respectively).

Data set

Data were obtained from two botanical databases: Digitale II (Conservatoire Botanique National de Bailleul, 1994–2011) and Florabank (Van Landuyt *et al.*, 2012). Both compile geolocalized data from systematic floristic surveys, botanical literature and herbaria by professional and non-professional botanists from the 19th century to the present. Only native or naturalized species were included in this study, excluding species that do not form self-replacing populations, namely casual alien species (*sensu* Richardson *et al.*, 2000). Complex taxonomic groups (*e.g. Rubus*, *Taraxacum*, *Salix* spp.), hybrids and subspecies were also removed, because taxonomic ambiguity can produce artefactual discontinuities in time series data (Tingley & Beissinger, 2009). The final data set included 1622 native or naturalized plant species whose taxonomic status was clearly defined, of which 1416 species in northern France and 1371 species in Flanders.

We converted data (primarily recorded by county or within designated grid squares) into presence–absence data per species, region and period (Table S1). This allowed the inclusion of data from 1900 to 1958, which were basically species lists without any specification of the number of investigated sites. Moreover, this data conversion approach reduced the bias of having different census protocols among periods, and at the regional scale, it reduced the risk of non-detection and geographical inaccuracies: two significant risks associated with historical records of species occurrence (Tingley & Beissinger, 2009). Suspicious absences (*e.g.* a one-decade absence of a species that was otherwise stable) were corrected if sites were known to be stable. These corrections represented 5.97% of the data set for northern France and 0.64% for Flanders. Other temporarily absent species were considered as having successfully re-established after a local extinction (hereafter called 'returns').

Species occurrence data were available for northern France and Flanders from the beginning of the 20th century to the present. Time series were divided into seven periods to provide an optimal inventory of each region for each period. The length of each period was defined so as to take into account variation in sampling effort over time (Fig. S1) and the chronology of known anthropogenic changes (climate and agricultural practices) in the studied region. Periods were defined as follows:

1. P1 (1900–1940): 22,051 species occurrence records in northern France and 244,759 grid-square records in Flanders before conversion into presence–absence data by region and by period. Census protocols were generally non-standardized (data from herbaria and botanical literature validated by experts), but rare species were intensively searched for. In 1939, an IFBL grid for systematic floristic surveys was created by the Belgium-Luxemburg Institute of Floristics (IFBL).
2. P2 (1941–1958): 40,830 and 242,866 records for northern France and Flanders, respectively, before conversion. Data had been centralized and published in newsletters (creation in 1947 of the Botanical Society of Northern France, which collected data from northern France and Belgium). Sampling effort remained limited in space and time. Intensive agricultural practices started to develop.
3. In the subsequent periods (P3 to P7), census protocols had been standardized. In 1973, the French-Belgian Institute of Floristics was founded. The chosen periods were decadal to reduce the risk of false absence, but may vary by more or less one year to adjust time series to sampling effort (number of records: P3 (1959–1968): 128,577 and 241,092 in northern France and Flanders, respectively; P4 (1969–1978): 95,365 and 279,329; P5 (1979–1989): 69,032 and 211,153; P6 (1990–1998): 369,102 and 230,488; and P7 (1999–2009): 553,502 and 251,781).

Species habitat preferences were obtained from phytosociological affiliations and published floras otherwise (Bournérias, 1979; Rameau *et al.*, 1993; Lambinon *et al.*, 2004). We allocated species to one of 18 distinct habitats (Table S1). These habitats were derived from the EUNIS classification (http://eunis.eea.europa.eu/habitats-code-browser.jsp; Davies *et al.*, 2004), modified to take into account trophic levels, water requirements, light and pH requirements (Table S2). Artificial habitats were grouped with agricultural habitats, except segetal communities, that is plant species found in harvested fields (wheat, flax, maize, etc.), due to the high level of intensification and shared species.

Data analyses

All analyses were performed with R 2.15.3.

Intensity of changes

To assess patterns of temporal difference in assemblage composition (i.e. temporal beta diversity) between P1 and P7, as well as species turnover (species replacement) and species nestedness (species loss or gain) – two components of beta diversity –, we compared the lists of species in P1 vs. P7 and measured the intensity of changes in species composition using the Jaccard index (Jaccard, 1912), as well as its components of turnover (βjtu), nestedness (βjne) and βratio = βjne / βjac, according to Baselga (2010, package ‘betapart’, R 2.15.3).

We quantified the current regional species richness (or anthropogenic species richness: ASR) as

$$\mathrm{ASR} = N - \mathrm{ASL} + \mathrm{ASI}$$

where N is ‘native’ (following Ellis *et al.*, 2012) or ‘incumbent’ species richness (following Jackson & Sax 2010). More specifically, N is the species richness in P1. Because at P1 resident species include numerous formerly naturalized species, we will hereafter follow the terminology of Jackson & Sax (2010), that is ‘incumbent’ species richness; ASL (anthropogenic) loss of incumbent species; ASI (anthropogenic) species increase by immigration and naturalization. Both were calculated from observed losses and gains. We also quantified ratios of anthropogenic-to-incumbent species richness and of immigration plus local extinction-to-incumbent species richness as

$$\mathrm{ASR}/N \text{ and } (\mathrm{ASI} + \mathrm{ASL})/N$$

following Ellis *et al.* (2012).

Temporal change in plant species richness: biodiversity budgets at regional scale

We assessed biodiversity budgets for each region, that is for each period from P1 to P7 (1) ASR: total species richness (SR per period, SR1 to 7), (2) ASI: cumulative number of immigrant species (naturalized species recorded after P1), (3) N-ASL: number of incumbent species that were still present at each period (the difference between P1 and Pi is the number of local extinctions) and (4) cumulative number of returns.

Biodiversity budget per habitat

To classify habitats by their pattern of temporal change in species pool richness, we constructed one heat map for each region, for species pool richness by habitat type and period (weighted by the average richness in the habitat type, hereafter called ‘relative species pool richness’). A heat map is a colour-coded graphical representation of a matrix that reorders rows and columns according to hierarchical clustering. Distances among periods and among habitats were obtained from a correspondence analysis (CoA; northern France: axis 1 = 87.96%, axis 2 = 6.32% and axis 3 = 4.33%; Flanders: axis 1 = 77.93%, axis 2 = 15.82% and axis 3 = 3.08%; package ade4) and were used to build two hierarchical clustering trees (dendrograms) (1) between periods and (2) between habitats (chi-square distances, Ward’s method of agglomeration, package ‘heatmap.plus’). Variation in species pool richness was represented by a colour gradient to create a heat map that represented the relative species pool richness by period for each habitat type, from light (fewer species) to dark (more species).

Lastly, we assessed biodiversity budgets for each habitat type within each region, grouped according to the hierarchical clustering of overall biodiversity change determined for the heat maps.

RESULTS

Intensity of changes and biodiversity budgets at regional scale

Between P1 (1900–1940) and P7 (1999–2009), Jaccard indices were 19% for northern France and 16% for Flanders. Values of βratios revealed a dominant component of turnover in northern France (βratio = 0.003) and a combination of turnover and nestedness in Flanders (βratio = 0.36).

In P1, species richness (SR1) was 1276 plant species in northern France and 1206 in Flanders. The number of regionally extinct species from northern France and Flanders between P1 and P7 was 135 and 64 species, respectively. There were 134 newly naturalized species in northern France and 149 in Flanders. In addition, 21 and 36 species, respectively, have become locally extinct and successfully re-established later on, while 6 and 16 newly naturalized species (after P1) later went locally extinct. Across all periods, 1120 and 1106 species were observed. Therefore, species losses were offset in northern France (SR7 = 1275) and overcompensated in Flanders (SR7 = 1291) (Fig. 3). Continuous local

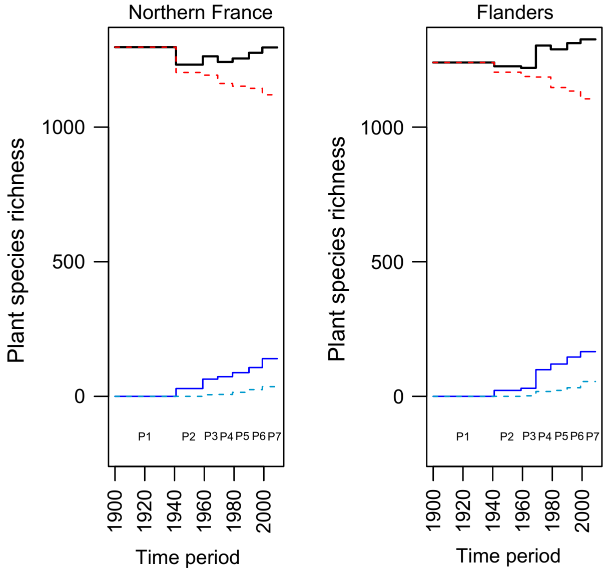

Figure 3 Biodiversity budgets, time series showing biodiversity change in northern France and Flanders. Dashed red line = number of incumbent species (resident species in P1; a decrease represents regional extinctions); solid blue line = number of immigrant species (i.e. naturalized after P1); dashed light blue line = returns, that is number of species that successfully re-established after local extinction; and black line = total species richness. Periods: P1 = 1900–1940; P2 = 1941–1958; P3 = 1959–1968; P4 = 1969–1978; P5 = 1979–1989; P6 = 1990–1998; and P7 = 1999–2009.

extinction was observed in both regions. Immigration was also continuous in northern France, and it accelerated after P3 in Flanders. Losses were higher than gains in the first three periods and immigration became predominant thereafter (Fig. 3).

Between P1 and P7, ratios of anthropogenic-to-incumbent species richness were 0.98 for northern France and 1.02 for Flanders. The ratios of immigration plus local extinction-to-incumbent species richness were 0.237 and 0.243, respectively.

Biodiversity budgets according to habitat type

Changes in species composition of habitats were continuous in time, resulting in a chronological pattern in the period dendrogram (i.e. on columns) for both regions (Fig. 4). In northern France, the first period (P1) was highly dissimilar from all other periods, which were grouped into two clusters (Fig. 4a). In Flanders, the first four periods were clustered in one group; the last three periods formed a second group of similarity (Fig. 4b). In both regions, habitat types (row dendrograms) were clustered into three main groups of biodiversity change: losses, gains and intermediate change in species pool richness (Fig. 4). The first group included the same habitat types ('segetal/stricto', 'oligo freshwater', 'heath') for both regions. Losses occurred between P1 and P2 in northern France and later (after P4) in Flanders. Species immigration was almost absent in these habitat types (Figs 4 & 5a). The second group included habitat types, that is 'anthropogenic', 'hydro fringe' and 'scrub' in both regions, displaying constant species gains (Fig. 4). In these habitats, local extinction was virtually absent (Fig. 5b). The last group included habitats showing intermediate change in species pool richness (Fig. 4) that is 'acid grassland', 'bog/fen', 'fringe', 'segetal/lato', 'calci grassland' and 'wet meadow' in both regions, mainly with a tendency for moderate loss, but also with strong but relatively constant losses in northern France, that is 'bog/fen', 'segetal/lato' and 'calci grassland'.

Clustering of habitats depending on their pattern of change in species pool richness was relatively consistent among regions, but some differences were also found. 'Forest', 'alluvial/riparian', 'aquatic/amphibious', 'coastal', 'meso freshwater' and 'dry meadow' were in the 'gains' group in Flanders, but in the 'intermediate change' group in northern France (Fig. 4). 'forest', 'alluvial/riparian', 'aquatic/amphibious', 'coastal', 'meso freshwater' and 'dry meadow' showed local extinction and immigration at the same time (Fig. 5). Few returns were observed, and of those, most were detected in Flanders ('heath', 'segetal/stricto', 'segetal/lato', 'calci grassland', 'wet meadow', 'coastal', 'anthropogenic', compared to 'anthropogenic' and 'oligo freshwater' in northern France).

Habitats with transient biodiversity surplus ('meso freshwater' in Flanders) and transient deficits ('coastal' and 'segetal/lato' in Flanders, 'forest' in northern France) were also observed (Fig. 5).

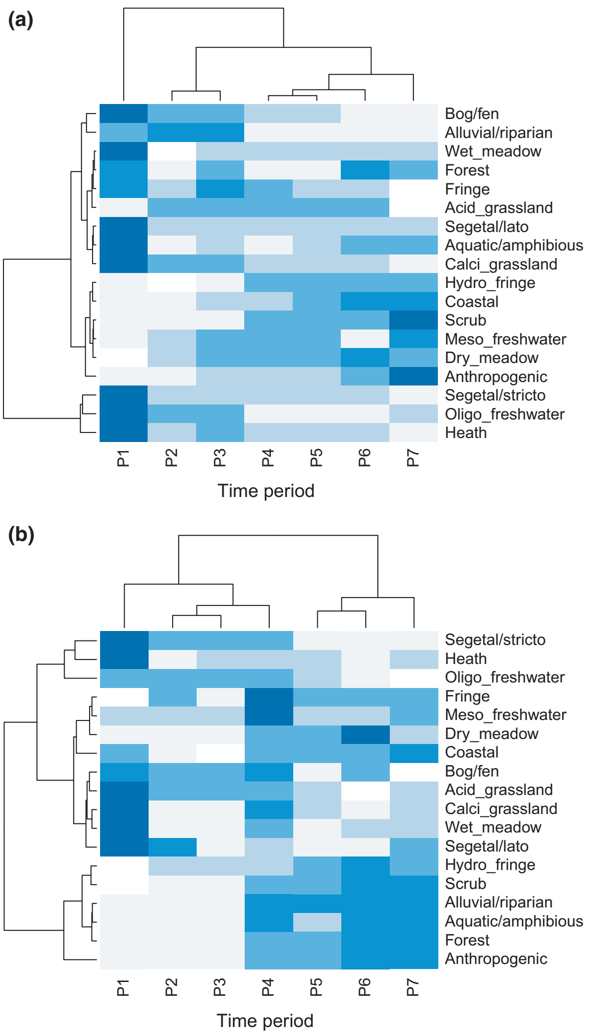

Figure 4 Heat map of species pool richness according to habitat type and period. (a) Northern France (b) Flanders. See text for details on clustering method. Dark cells represent the highest species pool richness for the considered habitat, light cells the lowest. Habitat abbreviations (see also Table S2 for habitat descriptions): aquatic/amphibious = aquatic to amphibious short perennial vegetation, meso- to eutrophic, alluvial/riparian = alluvial and riparian woods, acid grasslands = semi-dry siliceous grasslands, anthropogenic =anthropogenic habitats (urban, slag heap, roadsides, intensive fields at the exclusion of harvested fields of wheat, barley, maize and flax), bogs/fens = mires, bogs and fens, calci grasslands = neutro-alkaline or calcareous grasslands, coastal=coastal and littoral habitats, dry meadows = dry to mesic meadows, forests =woodland and forests, fringes =seam and forest and woodland herb fringe, heaths = wet and dry heathland, hydro fringes = tall herb fringes along watercourses, meso freshwater = euhydrophyte communities of meso- to eutrophic freshwaters, oligo freshwater = euhydrophyte communities of oligotrophic freshwaters, scrub = hedgerows and early-stage woodlands, segetal/lato = segetal communities *lato sensu* (communities of arable weeds, fallow fields and other habitats), segetal/stricto = segetal communities *stricto sensu* (flora of extensively cultivated cereals) and wet meadows = grasslands and meadows on wet soils. Periods: see Fig. 3 and text.

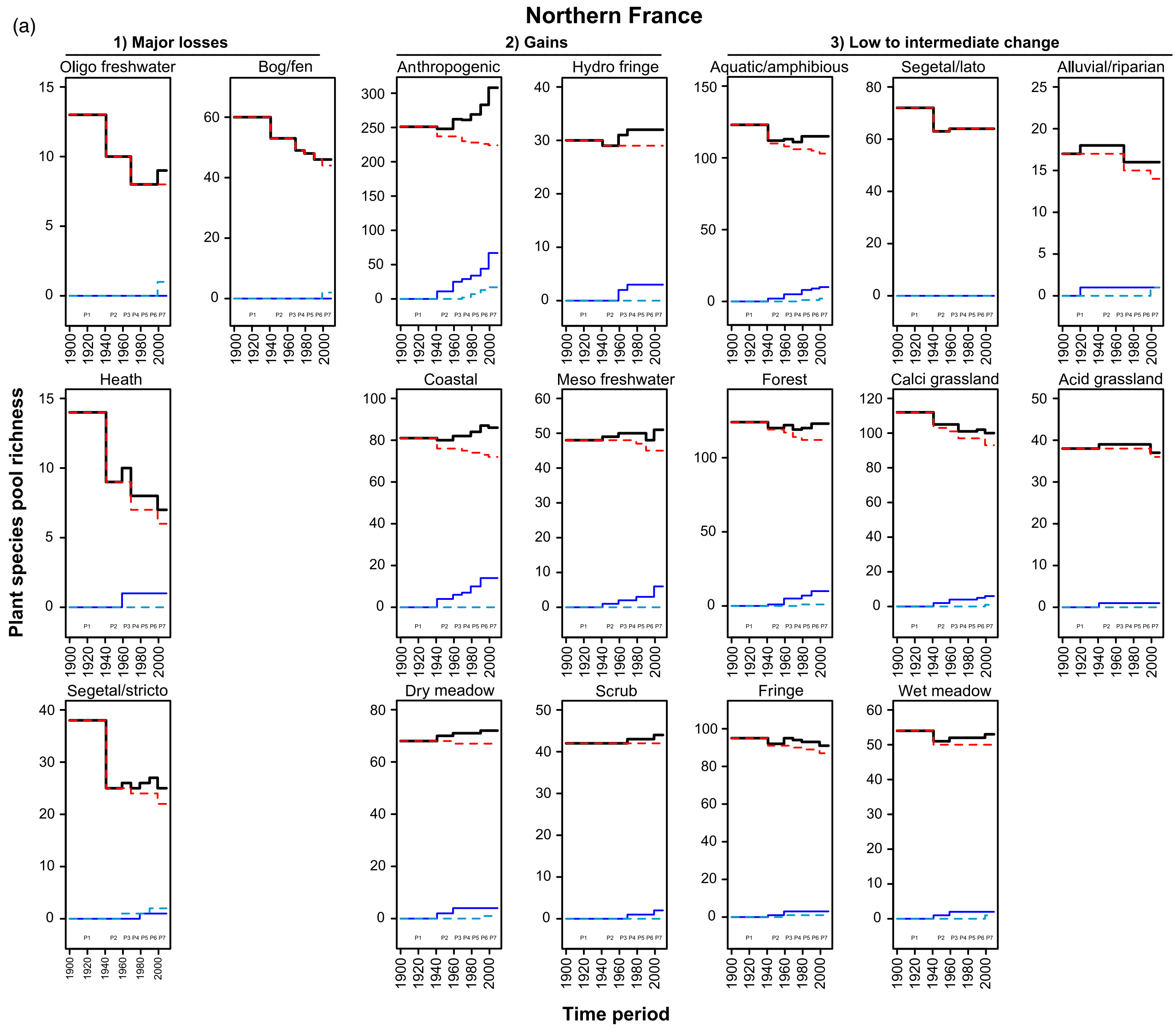

Figure 5 Time series showing biodiversity dynamics for each habitat type in northern France and Flanders. Habitat types are grouped in three trends of biodiversity change (major losses, gains and intermediate change) according to heat map clusters (Fig. 4) at the exception of bog/fen in northern France (see Discussion) (a) northern France (b) Flanders. Dashed red line = number of incumbent species (resident species in P1; a decrease represents regional extinctions); solid blue line = number of immigrant species (i.e. naturalized after P1); dashed light blue line = returns, that is number of species that successfully re-established after local extinction; and solid black line = total species pool richness. Period and habitat type abbreviations: see Figs 3 & 4.

DISCUSSION

Major biodiversity changes at the regional scale

We observed major changes in species composition at the regional scale, with about one of every six species (Flanders) to one of every five species (northern France) being regionally extinct or newly naturalized over the last century, resulting in a high rate of species turnover.

Ratios of anthropogenic species richness-to-incumbent species richness and of immigration plus local extinction-to-incumbent species richness were similar to the values reported by Ellis *et al.* (2012) for rural, pastoral or cultivated regions. Immigration offset (northern France) or overcompensated local extinction (Flanders), confirming previous results by Sax & Gaines (2003) and Ellis *et al.* (2012). Our study takes these results further. We observed a clear trend in which losses precede gains over a period of 100 years. These recent floristic changes have occurred in areas of traditional anthropogenic and altered environments, thereby exemplifying the last steps of a continuous process.

Comparing patterns of biodiversity change among regions

Both regions are intensively cultivated and densely inhabited. As expected, and despite some differences in regional sampling effort, we observed quite similar patterns of change in

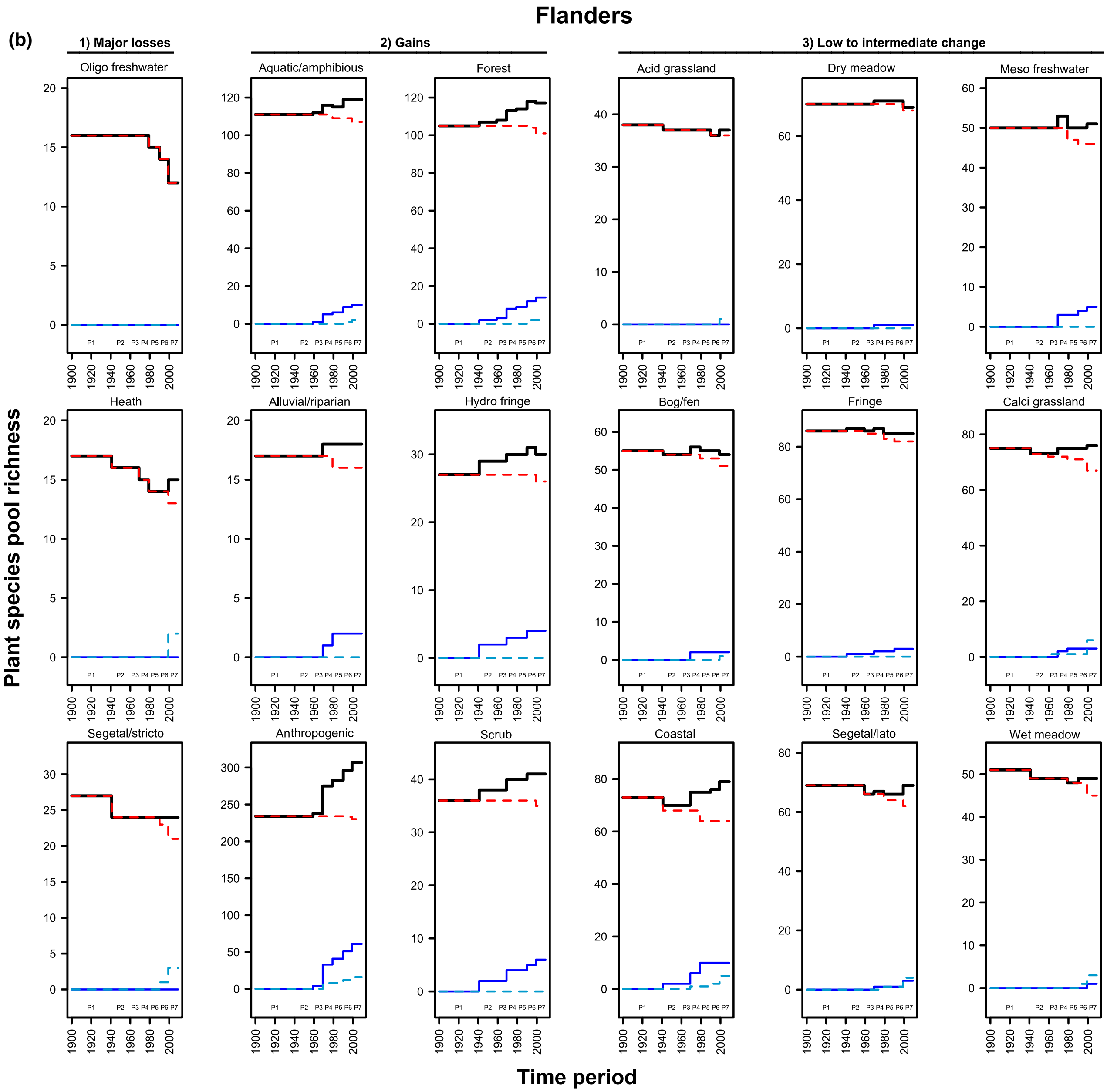

Figure 5 (Continued)

species richness. There were, however, some noteworthy differences. In particular, in terms of species richness, the first time period (P1) was very different from other periods in northern France, while changes were greater between the first four and the last three periods in Flanders. This difference was discernible despite the lower sampling effort in P1 in northern France, which may have underestimated the actual difference between P1 and, for example, P3, due to potential false absences of rare species in P1. Moreover, the chronological continuity between periods in the heat map, the highly diverging patterns among habitat types and their congruence across regions attest to the robustness of the observed patterns in the light of the potential bias due to lower sampling effort in northern France. The contrasting dynamics between regions were also evident in oligotrophic freshwaters, segetal communities and heaths. Although these habitats showed intense species loss, timing differed between regions. Both countries are now bound by EU directives, but past policies and country-specific implementation of these directives have resulted in different agricultural landscapes, for example average farm size is larger in northern France (42–51 ha) than in Flanders (15.6 ha, INSEE, 2001), while specialization is higher and has increased since the 1960s in Flanders, but not in northern France (Bowler, 1986; Christians, 1998). We are not aware of any long-term analysis of agricultural policies in these regions, but they were clearly different and may have contributed to the contrasting chronological patterns observed here.

Contrasting patterns among habitats

Major losses in habitats altered by agricultural intensification and increased eutrophication

We observed early major species losses (40–75% of the incumbent species in northern France) in habitats that are highly sensitive to eutrophication and to changes in farming practices, that is segetal communities, oligotrophic freshwater and heaths. Although in a lower proportion (27%) and also more continuously, substantial losses were observed in bogs and fens too, as well as in neutro-alkaline and calcareous grasslands in northern France. These habitats have all been dramatically altered or have disappeared locally due to drainage and farm inputs (Pykälä, 2000; Robinson & Sutherland, 2002; Tamis *et al.*, 2005), abandonment of traditional agro-pastoral practices (Poschlod & WallisDeVries, 2002; Robinson & Sutherland, 2002) or conversion to crops (Piessens & Hermy, 2006). Habitats that are now often protected have been significantly affected by changes in human activities in the past, especially wetlands, calcareous grasslands, bogs and fens and heaths (formerly related to extensive shepherding, Piessens & Hermy, 2006; Pärtel *et al.*, 2007).

Major species losses also occurred by the early 20th century in segetal communities. These habitats are not protected *stricto sensu* but are the targets of agri-environment schemes (management of conservation headlands). However, no clear impact on plant biodiversity has been observed thus far (Kleijn & Sutherland, 2003).

Furthermore, losses may even be underestimated. Because we defined species pools first by their regional occurrence and then by their preferential habitat types, the loss of one species from all sites of its preferential habitat type would not be apparent if the species was still present in, or migrated to, a secondary habitat.

Returns were rare (occurring mainly in segetal communities or heaths in Flanders, oligotrophic freshwater in northern France), which is expected in an altered landscape (Vellend, 2003). Species may return following reintroduction programmes, agri-environmental schemes and connectivity restoration. In the present study, returns were also rare in habitats that were part of conservation programmes, for example bogs and fens. This can be attributed to inappropriate measures and high immigration credit in fragmented landscapes, or to low success rates of plant reintroduction programmes (Godefroid *et al.*, 2011), which are moreover few and recent.

Some habitat types with increased species pool richness

Arrival of new species was observed in the anthropogenic habitat (supporting Ellis *et al.*, 2012). This observation corroborates previous studies that show increasing species richness associated with nutrient-rich environments, rocky ground (as are colliery waste heaps) (Tamis *et al.*, 2005) or high human population densities (McKinney, 2002).

Habitat types with increased species pool richness are also highly connected by human activities and rich in cosmopolitan species, that is coastal and anthropogenic habitat types. Shoreline and roadside engineering as well as transport systems connect many habitats and facilitate immigration (Hulme, 2009; Penone *et al.*, 2012). As a result, global taxonomic homogenization (Olden *et al.*, 2004) increases with human pressure (*e.g.* in urban areas, Lososová *et al.*, 2012), which is regionally or locally detected through immigration.

Immigration was a strong component of biodiversity change in forests in Flanders. Similarly, species richness has been maintained and the proportion of non-native species has increased in British forests (Keith *et al.*, 2009).

Two hypotheses may partly explain these gains. First, as expected according to a species–area relationship, gains may be linked to the increase in the total area of the anthropogenic habitat type due to urban development. However, the modification of biotic and abiotic conditions may also contribute: regional species richness has increased in Flanders, suggesting that disturbance and other environmental changes favour, at least in part, immigration.

Many habitats with relatively constant species pool richness

Nine habitats of 18 showed low to substantial change in species pool richness. This can result from different dynamics: (1) rare local extinctions and arrivals, which was the case in bogs and fens in Flanders, perhaps because they were less altered and rarefied than in northern France; (2) simultaneous local extinction and immigration, for example in meso- to eutrophic freshwater habitats or (3) local extinction preceded immigration, for example aquatic and amphibious short perennial vegetation and forests in northern France, coastal habitats or meso- to eutrophic freshwaters in Flanders. In such habitats, dynamics should be considered in greater detail.

Biodiversity dynamics

A direct comparison of the first with the last period – disregarding events that occurred in between – would suggest high species turnover at the regional scale. However, this direct comparison (*e.g.* due to an observational lag) would be an oversimplification, because local extinctions generally preceded net gains. In both regions, we observed a transient deficit in total plant species richness, as well as in some habitat types. Transient surplus was also observed in meso- to eutrophic freshwaters in Flanders. Similar patterns were predicted by Nagelkerke *et al.* (2002) and Jackson & Sax (2010) as a consequence of time-lags before species are locally extinct (resulting in extinction debt) and before alien species can immigrate (resulting in immigration credit) after a forcing event. In the present study, this trend was stronger when all habitats were considered altogether (*i.e.* biodiversity budgets at the regional scale), because major losses and major gains indeed occurred at different times in different habitat types. Similarly, Cousins & Vanhoenacker (2011) reported a higher extinction debt at the landscape scale than at the local scale, supposedly because habitats are more heterogeneous at broad spatial scales, suggesting that habitat heterogeneity has to be considered carefully.

Despite the implementation of measures to favour of biodiversity, local extinction has remained intense over the past few decades. The surface area of bogs and fens did not decrease between 1990 and 2000 nor between 2000 and 2006 in northern France (Corine Land Cover, 2006), but species pool richness has continued to decline, perhaps resulting from extinction lags and insufficient site protection strategies (Krauss *et al.*, 2010).

Forcing events can be rapid (*e.g.* conversion to intensive agricultural practices), in which case the combination of extinction debt and immigration credit could explain these patterns correctly, or they might also be gradual (*e.g.* progressive eutrophication of habitats or increasing fragmentation in a large area in relation to population growth or economic development). Continuous disturbance within and without sites and intensification of exchanges are indeed likely and may explain the progressive changes in biodiversity and, perhaps, the uncoupling of local extinction and immigration. Very few studies can rule out this hypothesis (as specified by Jackson & Sax, 2010). Integrating delays in budget balancing and timing of forcing events is a notable challenge for future theoretical and empirical research.

Consequences of the contrasting dynamics among habitat types on scale effects

Habitats showed contrasting biodiversity dynamics and budgets, from predominant local extinction resulting in decreased species pool richness to predominant immigration resulting in increased species pool richness. This result sheds new light on the understanding of recent local changes in biodiversity. Studies at the regional scale provide relatively consistent results in densely populated regions such as Europe (which generally show increasing species richness), but studies at the local scale show more variable results (Sax & Gaines, 2003; Ellis *et al.*, 2012). At the habitat level, for example, the proportion of non-native species has increased in urban woodland parks (DeCandido, 2004), whereas there have been net losses of butterfly species on calcareous grasslands (Polus *et al.*, 2007). These two examples of gain and loss are both consistent with our results in anthropogenic habitats, forests and calcareous grasslands. Similarly, Van Calster *et al.* (2008) reported, in an adjacent region, species losses in wetlands, grasslands and arable lands, but losses were higher and immigration was lower in woodlands, which is consistent with the more rural nature of this region.

Studies at the regional scale have also shown a variety of trends depending on the magnitude of human activities (Ellis *et al.*, 2012). McKinney (2002) reports a positive correlation between alien species establishments and human population density in the USA. This result fits perfectly with the dramatic net gains we observed in the anthropogenic habitat. The 'anthropogenic habitat type' of the early 21st century is different in terms of plant species composition from the one of the early 20th century, probably due to a combination of qualitative environmental change (*e.g.* urban densification, increased use of pesticides), increased total surface area and intensified introduction of new species. There is an underlying assumption in most regional or global studies that natural habitats (or of semi-natural habitats associated with traditional agricultural practices) are replaced by more intensively managed habitats (Ellis *et al.*, 2012). However, in the present study, habitat types themselves evolved.

As concluded by Ellis *et al.* (2012), we also observed that 'anthropogenic patterns of plant species richness still appear to strongly resemble native patterns' at the regional scale. Immigration has indeed offset or overcompensated for species losses, but this was mainly due to immigrant species typical of the anthropogenic habitat type, whereas regional extinctions mainly involved incumbent species representative of oligotrophic freshwater, segetal or heath habitat types. According to this pattern, floras will become phylogenetically and functionally more similar (Winter *et al.*, 2009) with potential implications for ecosystem functionality: locally extinct species are oligotrophic species, whereas immigrants are largely nitrophilous ruderals (Fig. S2).

CONCLUSION

Understanding the patterns of biodiversity change along geographical scales is a future challenge. More local and regional studies should be conducted with the inclusion of habitat type. The regional scale provides a very broad vision of biodiversity change, with its own advantages and disadvantages. At this scale, it is difficult to distinguish between extinction debt and continuous dynamics of extinction due to ongoing habitat changes, or between immigration credit and increasing exchanges. Distinguishing among these dynamics requires studies on small sites with accurate historical data on environmental change; however, local studies do not provide general patterns and are highly sensitive to small changes in community composition. Adding a habitat type level bridges the gap between regional and local studies: integrating the habitat type into regional analyses or meta-analyses can lead future research towards the understanding of determinisms of biodiversity change from sites to landscape, from the environmental engineering scale to intergovernmental policy scales.

ACKNOWLEDGEMENTS

This study was financially supported by the Nord-Pas de Calais Regional Council (ARCIR GIS Biodiversité BioImpact E000076R and Retroscen E000078R) and by Belspo (for digitising the IFBL flora checklists). We thank two anonymous referees and F. Essl for helpful comments.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 Sample-size-based rarefaction curves per period and region: species richness on sampling effort (occurrence records before conversion into presence-absence data and after correction for suspicious absences, replaced by one occurrence).

Figure S2 Change in the relative contribution of the different habitat types to total species richness across the time periods.

Table S1 Species occurrence per period and region, and their preferential habitats

Table S2 Habitat types adapted from the EUNIS classification for Northern France and Belgian Flanders.

BIOSKETCH

The general research interests of the group of authors lie in biological responses to global change, particularly with regard to conservation, communities and invasions.

Author contributions: NH and YP designed the study; BT and WVL obtained the data; LF, YP, BT, WVL and FVR prepared the databases; LF, NH and CL performed the analyses; NH led the writing; and all authors contributed to revisions.

Editor: Franz Essl