

Landscape disturbance causes small-scale functional homogenization, but limited taxonomic homogenization, in plant communities

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Summary

1. Biotic homogenization (BH), a dominant process shaping the response of natural communities to human disturbance, reflects both the expansion of exotic species at large scales and other mechanisms that often operate at smaller scales.

2. Here, we examined the relationship between BH in plant communities and spatio-temporal landscape disturbance (habitat fragmentation and surrounding habitat conversion) at a local scale (1 km²), using data from a standardized monitoring programme in France. We quantified BH using both a spatial partitioning of taxonomic diversity and the average habitat specialization of communities, which informs on functional BH.

3. We observed a positive relationship between local taxonomic diversity and landscape fragmentation or instability. This increase in local taxonomic diversity was, however, paralleled by a decrease in average community specialization in more fragmented landscapes and in more unstable landscapes around forest sites. The decrease in average community specialization suggests that landscape disturbance causes functional BH, but there was limited evidence for concurrent taxonomic BH.

4. *Synthesis.* Our results show that landscape disturbance is partly responsible for functional BH at small scales via the extirpation of specialist species, with possible consequences for ecosystem functioning. However, this change in community composition is not systematically associated with taxonomic BH. This has direct relevance in designing biodiversity indicators: metrics incorporating species sensitivity to disturbance (such as species specialization to habitat) appear much more reliable than taxonomic diversity for documenting the response of communities to disturbance.

Key-words: common species, determinants of plant community diversity and structure, habitat conversion, habitat fragmentation, habitat specialization, human disturbance, land use history, monitoring scheme

Introduction

Conservation biology and ecological monitoring should be concerned with common species and the 'unreserved matrix' in which they live (Franklin 1993), in addition to the rare species and protected areas that are usually targeted. Quantitatively, common species play a key role in ecosystems and the most abundant species even contribute disproportionately to spatial patterns of species richness (Gaston & Fuller 2008). Variation in the abundance of a few common species may therefore have important consequences on ecosystems across large geographical areas, because common species are also typically widespread. Yet, declines in the abundance of common species

often remain undetected due to their wide distribution – widespread species can experience numerous local extinctions but still be observed at larger scales (Leon-Cortes, Cowley & Thomas 1999). Cases where data is available are rare, but changing abundances of common species are documented in several taxonomic groups (e.g. insects, Conrad *et al.* 2006; birds, Donald, Green & Heath 2001; amphibians, Carrier & Beebee 2003; or plants, Rooney *et al.* 2004), suggesting that even these species suffer substantial declines in response to human disturbance, such as habitat modification and destruction, overexploitation or climate change. The consequences of human disturbance on species abundance are generally not random; some species tend to decline consistently ('loser' species), whereas others ('winner' species) benefit from disturbance. This widespread phenomenon results in biotic homogenization (BH),

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i.e. a temporal increase in community similarity (McKinney & Lockwood 1999), which can be measured as a similarity of gene pools (genetic BH), taxonomic identities (taxonomic BH) or functional traits (functional BH) of species across biota (Clavel, Julliard & Devictor 2011).

Several ecological studies have documented taxonomic or functional BH in a variety of taxa (e.g. vertebrates – birds, Devictor *et al.* 2008; fish, Marchetti, Lockwood & Light 2006; or plants, Kuhn & Klotz 2006) but the underlying mechanisms are not fully understood. Although it is generally admitted that BH results from human activities, the relative effects of, for instance, species addition or expansion versus species extirpation remain unclear and may be scale dependent (McKinney 2008). Most studies were conducted at large spatial scales (up to continental levels), where the expansion of introduced species seems to be a widespread cause of BH (Qian & Ricklefs 2006). Fewer studies have investigated BH at a finer scale (landscape to regional level, e.g. Smart *et al.* 2006 for plants), where it may be driven mostly by declines of native species (Rogers *et al.* 2008).

To identify mechanisms underlying BH, one can examine the characteristics of winner versus loser species. This was done in several groups, showing that declining species can be characterized in terms of dispersal mode, sensitivity to herbivory or growth form in plants (Wiegmann & Waller 2006), breeding habits (Clergeau *et al.* 2006) and habitat specialization (Devictor *et al.* 2008) in birds or body size (Cardillo *et al.* 2005) in mammals. However, changes in community trait composition (functional BH) were seldom compared directly with taxonomic BH and it is not clear whether functional BH is systematically associated with taxonomic BH (as e.g. in Smart *et al.* 2006), which has direct relevance in choosing indicators of biodiversity change. In addition, the approach comparing the attribute of loser versus winner species should be combined with a study of the relationship between BH and the intensity of disturbance for a proper elucidation of the origin of BH. These two approaches have rarely been combined to examine functional BH (but see Devictor *et al.* 2008), especially in plants, although functional BH of plant communities has obvious consequences for ecosystem functioning.

Here, we studied local scale taxonomic and functional BH in plant communities in relation to human disturbance by jointly examining (i) the relationship between BH and landscape disturbance, a major type of human threat, and (ii) the characteristics of winner versus loser species with respect to habitat specialization. We focused on habitat specialization, a proxy for niche width, because a widespread pattern of BH in both animal and plant communities is that loser species are generally habitat-specialist species (Rooney *et al.* 2004; Devictor *et al.* 2008), thus leading to functional BH. Using data from a common plant monitoring survey in France, as well as GIS-derived indices of landscape disturbance in space (habitat fragmentation) and time (habitat conversion), we specifically addressed the following questions: (i) Does landscape disturbance influence the average specialization of plant communities, with more generalist communities in

more disturbed landscapes? (ii) Is this change in community composition associated with taxonomic homogenization of plant communities?

Materials and methods

STUDY AREA AND HUMAN DISTURBANCE INDICES

We collected all data in Île-de-France, a region of 12 072 km² in northern-central France including the city of Paris (Fig. 1a), which is

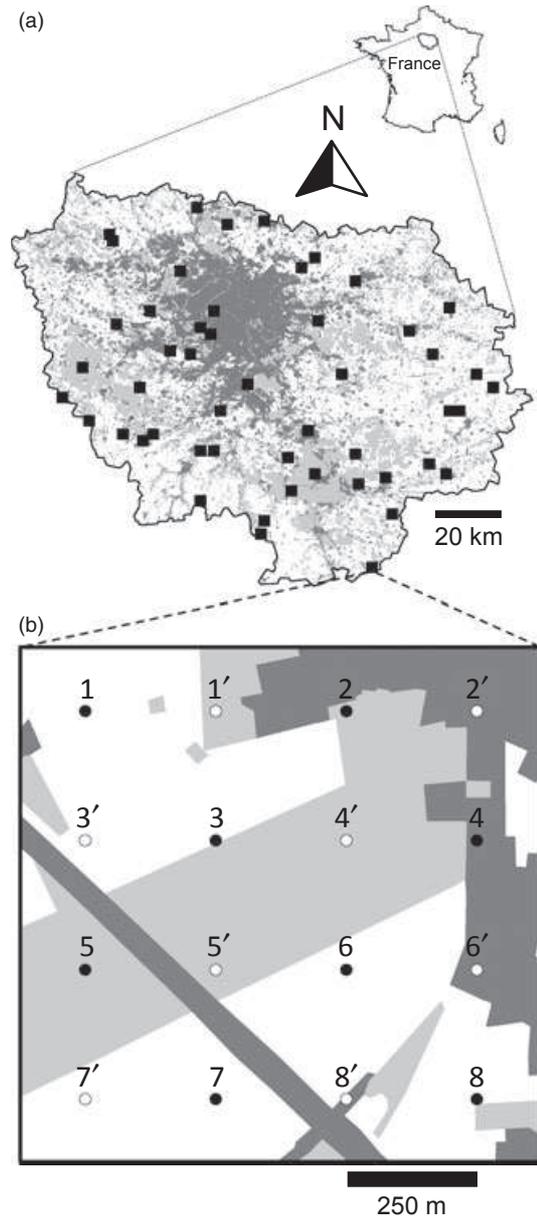


Fig. 1. The plant monitoring scheme in Île-de-France. (a) Map of the study area (copyright IAURIF), where urban and artificial areas appear in dark grey, forests and semi-natural habitats (i.e. rivers, grasslands) in pale grey and agricultural areas in white. Black squares represent the fifty 1-km² survey squares (enlarged by a factor 2 for a better view). (b) Detail of a survey square showing the sampling scheme. Eight permanent 10-m² plots were evenly distributed (black dots numbered from 1 to 8) together with eight replacement plots (white dots numbered from 1' to 8') in case the former were not accessible.

one of the most highly human impacted regions in France. A major feature of this region is the high population density of 922 people km⁻², which is associated with a dense road network (3.13 vs. 1.62 km km⁻² on average in France) indicating a high degree of fragmentation. We estimated the intensity of human disturbance in the survey sites, which consisted of fifty 1-km² squares randomly distributed in the area (Fig. 1a and see below), by measuring landscape heterogeneity in space (habitat fragmentation) and time (habitat conversion).

Habitat fragmentation

To quantify habitat fragmentation, we used the 2003 Land Use Pattern (LUP) of Île-de-France (Institute for Urban Planning of Île-de-France, IAURIF). We classified habitats according to the European CORINE Land Cover habitat classification and subsequently aggregated them into three categories: forests, urban areas and agricultural landscapes (Fig. 1a). In each survey square, we calculated edge density as a measure of landscape fragmentation, i.e. the sum of all polygon perimeters within a square (excluding the square perimeter), divided by square area (1 km²).

Conversion of surrounding habitats

We quantified habitat conversion around a site, a measure of landscape stability, using data from the LUP updates (1982, 1987, 1990, 1994, 1999 and 2003). For each square, we considered a rate of change in land-use among the three habitat categories, calculated as the total number of polygon changes (i.e. habitat conversion) during the last 20 years, divided by the total number of polygons in a square. This yielded an index of habitat conversion, ranging between 0, when all polygons within a square had remained in the same habitat class, and 1, when all polygons within a square were modified at least once in 20 years.

We performed all calculations using the Geographical Information System ArcView 3.2 (Economic and Social Research Institute (ESRI) (2000) with the Patch Analyst extension (Elkie, Rempel & Carr 1999) and R 2.10.1 (R Development Core Team 2004). We checked that habitat fragmentation and conversion were uncorrelated. We also ruled out a possible effect of geographical clustering by checking the absence of spatial autocorrelation in square fragmentation and surrounding habitat conversion using the global Moran's *I* statistic in the *spdep* R package: Moran's *I* = 0.073 (*P* = 0.12) for habitat fragmentation and -0.035 (*P* = 0.247) for habitat conversion.

PLANT SAMPLING AND SPECIES CHARACTERISTICS

We used data collected in 2006 from the French common plant monitoring programme (<http://www.vigie-flore.fr>), which is currently in its pilot phase. This monitoring programme uses a two-stage standardized sampling scheme, described below. We randomly selected fifty 1-km² squares in the study area (Fig. 1a) to provide an accurate picture of the different habitat types. Within each square, eight permanent plots were evenly distributed together with eight replacement plots in case the former were not accessible (Fig. 1b). The permanent plots were circular areas of 10 m², in which a single observer recorded all vascular plants twice a year, in spring and summer, with 8–10 weeks between two consecutive visits. We measured the percentage cover of each species using the Braun–Blanquet cover–abundance scale. Finally, we collected information on habitat considering the four following types: forests, arable fields, cities and ruderal habitats (i.e. interstitial vegetation, wastelands or set-asides). We pooled the

data collected during the two visits to obtain species lists within each plot. For each species, we retained the maximum percentage cover of the two visits. We estimated species abundance within plots using the median of the Braun–Blanquet classes. Due to limited accessibility of privately owned land (e.g. gardens and building roofs), we could not survey 48 plots, which resulted in under-representation of urban habitats (10% of plots surveyed vs. 20% land cover in the study area). We observed 330 species in the 352 plots sampled.

Species specialization

We computed species specialization from a large, independent floristic data set provided by the National Botanical Conservatory of the Parisian Basin (<http://cbnbp.mnhn.fr/cbnbp/>). This floristic data set consisted of species presence data collected between 2001 and 2005 for 1329 species in 8930 sites throughout Île-de-France. To quantify species habitat specialization we chose to work with Fridley *et al.*'s (2007) index of specialization developed for forest plant communities on the basis of species co-occurrence. Assuming that a given generalist species tends to occur in several habitat types, it is expected to co-occur with numerous species throughout its range. In contrast, a specialist species tends to be confined to a limited number of habitat types and should co-occur with relatively few species. Thus, species turnover among plots, θ , can be used to quantify species specialization as follows:

$$\theta = \gamma - \mu(\alpha)$$

where γ is the mean number of species co-occurrences among plots and $\mu(\alpha)$ is mean plot species richness. Note that specialist species are thus characterized by small values of θ .

Following Fridley *et al.* (2007), we used a randomization technique whereby we randomly chose 20 plots containing a focal species before calculating species turnover, which avoided bias due to differences in abundance among species. This implies that we did not calculate θ for rare species occurring in less than 20 plots, although we did not discard these species for calculations of co-occurrences. We measured species specialization (or niche width) as the average θ value over 100 randomizations, which we could compute for most species observed in the common plant monitoring scheme (304 of 330 species). The 26 species without θ were rare both in the large data set and the common plant monitoring scheme (all observed in fewer than seven plots) and discarding them should not influence the indices of community specialization much, because species are weighted by their abundance (see below). In the following, we refer to θ as species (or community) specialization, for the sake of consistency, but note that small values of θ correspond to high specialization.

IMPACT OF HUMAN DISTURBANCE ON BIOTIC HOMOGENIZATION AND COMMUNITY SPECIALIZATION

Spatial partition of taxonomic diversity

We investigated the effect of human disturbance on the spatial distribution of total diversity in a given square (γ -diversity), using multiplicative partitioning of diversity within plots (α -diversity) and between plots (β -diversity). Following the recommendations of Jost (2007), we measured taxonomic diversity using the 'true diversity' Shannon index, $\exp[-\sum p_i \ln(p_i)]$, where p_i is the abundance of species *i*. We preferred this index to species richness because accounting for species abundance is crucial to the study of community similarity (Lambdon, Lloret & Hulme 2008). We then used the *vegan* R package (Oksanen *et al.* 2010) to partition γ -taxonomic diversity in each square into

within-plot and between-plot diversity for each 1-km² square ($\gamma = \alpha\beta$), after discarding six squares with missing data in more than three permanent plots. We performed this partitioning on the whole data set, but also on the subset of plots sharing the same habitat within a square. This allowed us to examine β -diversity within habitat types without the inflating effect of habitat differences within squares. As before, we discarded squares with less than five permanent plots, which left us with a total of 29 squares for this second partitioning of diversity.

We subsequently tested the effect of landscape disturbance indicators on mean α -, β - and γ -taxonomic diversity, using simple linear models in which α -, β - or γ -taxonomic diversity was a function of habitat fragmentation, habitat conversion and an interaction between these two variables. All residuals were normally distributed. Note that we also considered a linear mixed model including a random effect of square to examine the relationship between within-site α -diversity and landscape variables while accounting for the nestedness of our sampling design (see below for average specialization). We only present results on average α -diversity at the square level because both models yielded the same results.

Average community specialization

We addressed the influence of human disturbance on functional BH by examining mean community specialization. We quantified the latter by calculating an average community specialization (θ_c) in each plot, as the abundance-weighted average of species specialization θ . We subsequently examined the relationship between mean community specialization and landscape disturbance indicators using a mixed linear model where variation in community specialization was a function of habitat type, habitat fragmentation, habitat conversion and all pair-wise interactions between these three variables. The model also included a random effect of survey squares, which accounted for the spatial structure of our sampling scheme, where survey plots are nested within squares and are therefore not independent replicates.

Individual species response

To explore the relationship between human disturbance and community specialization in more detail, we finally examined how disturbance indices affected individual species. To this end, we tested whether the impact of disturbance on species abundance depended on species specialization θ as follows. First, we regressed species abundance against landscape fragmentation (respectively surrounding habitat conversion) index and habitat type, for each species observed in at least five squares in the plant monitoring scheme (52 species). From this, we collected the slope of the regression of abundance on

disturbance (negative if a species suffers from the disturbance, positive if a species benefits from the disturbance). We then examined the relationship between these 52 slopes and species specialization θ .

Results

RELATIONSHIP BETWEEN HUMAN DISTURBANCE AND TAXONOMIC OR FUNCTIONAL DIVERSITY

Both α -diversity within squares and γ -diversity increased with habitat fragmentation and surrounding habitat conversion (Table 1, Fig. 2). The effects of both landscape variables were of comparable magnitude and independent of each other (non-significant interaction, Table 1). The resulting β -diversity was unrelated to landscape disturbance variables when all habitat types within a square were considered (Table 1, Fig. 2). However, β -diversity within habitat types (i.e. the differentiation between plots of a same habitat) tended to decrease with increasing habitat fragmentation ($F_{1,26} = 4.24$, $P = 0.05$, Fig. 3), but not with increasing habitat conversion (Fig. 3, $F_{1,26} = 0.26$, $P = 0.62$).

RELATIONSHIP BETWEEN HUMAN DISTURBANCE AND AVERAGE COMMUNITY SPECIALIZATION

The specialization index θ of species observed in the common plant survey ranged from 262.9 for the most specialist species (*Rubia peregrina*) to 488.5 for the most generalist species (*Centaureium erythraea*). At the community level, mean community specialization depended strongly on habitat type (Fig. 4, $F_{3,243} = 17.9$, $P < 0.001$): forests and ruderal habitats exhibited the highest and lowest mean community specialization, respectively, and cities and agricultural fields appeared to support communities of intermediate specialization.

In addition to this strong habitat effect, mean community specialization decreased with habitat fragmentation (Fig. 5, $F_{1,46} = 17.0$, $P < 0.001$), but not surrounding habitat conversion (Fig. 5, $F_{1,46} = 2.74$, $P = 0.11$). The relationship between mean community specialization and surrounding habitat conversion, however, depended on habitat type (significant interaction between habitat type and habitat conversion, $F_{3,243} = 4.44$, $P = 0.005$). There was a significant negative relationship between community specialization and surround-

Table 1. Effects of landscape fragmentation and habitat conversion on Shannon taxonomic diversity indices in plant communities across spatial scales. α -, β - and γ -diversity refer to true Shannon diversity within 10-m² plots, between plots and at the 1-km² square level, respectively. The direction of significant relationships is indicated in parentheses after the P -value

	d.f.	α -diversity		β -diversity		γ -diversity	
		F	P	F	P	F	P
Disturbance variables							
Fragmentation	1	8.41	0.006 ⁽⁺⁾	0.17	0.68	5.43	0.02 ⁽⁺⁾
Conversion	1	8.58	0.006 ⁽⁺⁾	3.27	0.08	9.65	0.003 ⁽⁺⁾
Interaction	1	2.38	0.13	0.02	0.88	1.03	0.32
Residuals	40						
Multiple R-squared		0.40		0.10		0.36	

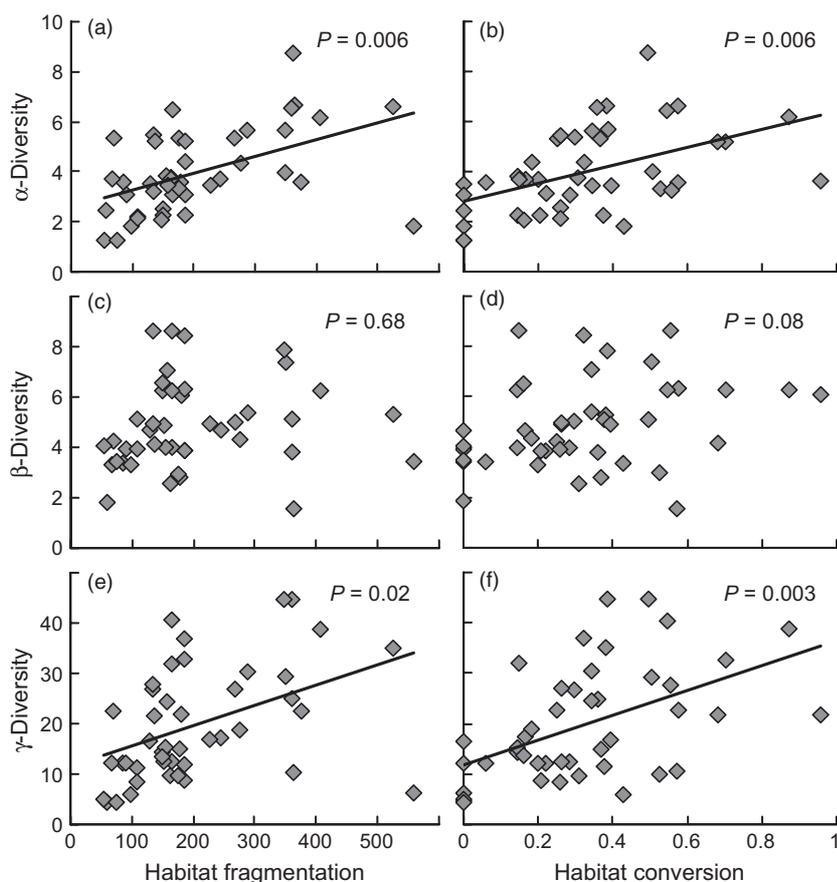


Fig. 2. Relationship between different levels of plant taxonomic diversity and spatial (a, c, e) and temporal (b, d, f) landscape disturbance. (a, b) α -Diversity is the average Shannon diversity within 10-m² plots; (c, d) β -diversity is the average Shannon diversity between plots; (e, f) γ -diversity is the total Shannon diversity at the 1-km²-square level. *P*-values indicate the statistical significance of the effects of landscape disturbance variables, obtained from a linear model.

ing habitat conversion in forest sites (mixed-model ANOVA on community specialization θ_c , effect of habitat conversion, $F_{1,20} = 5.15$, $P = 0.03$), but no significant association in other habitat types. All other interactions were non-significant and the results remained unchanged after removing two outliers with high average community specialization (low θ_c , Fig. 5).

RELATIONSHIP BETWEEN HUMAN DISTURBANCE AND INDIVIDUAL SPECIES RESPONSE

At the species level, we observed no significant relationship between individual species specialization θ and species response to landscape disturbance, when considering the 52 most widespread species (linear model on 48 d.f.: $t = -1.21$, $P = 0.23$ for habitat fragmentation; $t = -0.49$, $P = 0.62$ for surrounding habitat conversion; $R^2 = 0.03$).

Discussion

HUMAN DISTURBANCE AFFECTS THE LOCAL TAXONOMIC AND FUNCTIONAL COMPOSITION OF PLANT COMMUNITIES

Influence of human disturbance on local taxonomic diversity (α -diversity)

At a local scale, we observed a strong positive correlation between landscape fragmentation and α -taxonomic diversity.

This is consistent with the dispersal assembly view (Hubbell 2001): in a highly fragmented and heterogeneous landscape, species richness and diversity within a given habitat is sometimes increased by immigration from neighbouring habitats. The observed effect of habitat fragmentation on local species diversity may, however, also be attributable to other environmental variables that are known to covary with fragmentation. For example, fragmentation in our study area is associated with the degree of urbanization and cities often exhibit high local floristic richness (Kuhn, Brandl & Klotz 2004). Similarly, fragmentation in the study area is also associated with a dense transport network that can enhance species diversity by (i) promoting the introduction of alien species (Hansen & Cleverger 2005) and (ii) creating favourable habitats (e.g. road verges that can act as refuges for wild flora) in an otherwise hostile context of intensive agriculture.

A positive relationship was also observed between local species diversity and habitat conversion, with two possible explanations. First, landscape change generates a turnover of plant communities, which can lead to transient coexistence of species that are usually found in contrasting habitats. This phenomenon may result from time-delayed extinction of species following habitat destruction (extinction debt, Tilman *et al.* 1994). In plant communities, delayed extinctions can extend over several decades to several centuries (e.g. Rogers *et al.* 2009), so that it is likely to occur in our data set, where habitat turnover is measured on a shorter time-scale (20 years). Second, surrounding habitat conversion in the study region consists mostly of

Fig. 3. Relationship between within-habitat β -diversity and spatial (a) or temporal (b) landscape disturbance. β -diversity is the average Shannon diversity between plots located in identical habitats within a square. P -values indicate the statistical significance of the effects of landscape disturbance variables, obtained from a linear model.

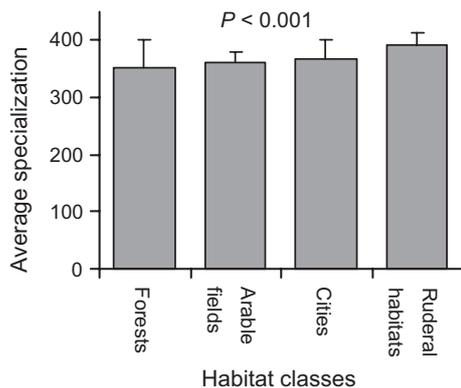
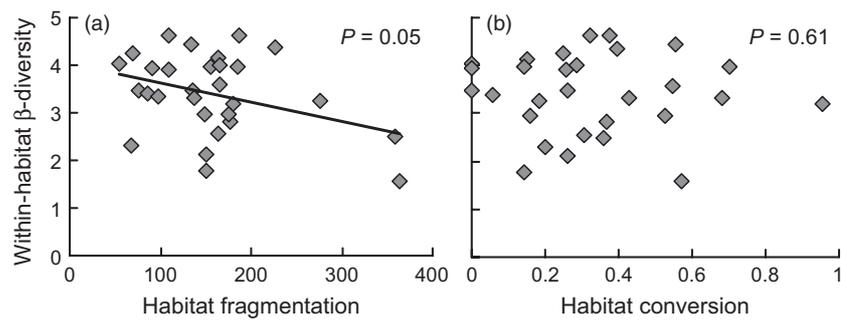


Fig. 4. Average plant community specialization θ_c across the four habitat classes. Error bars indicate standard deviations.

urbanization in former agricultural landscapes (a phenomenon that affected 560 km², *c.* 5%, in Île-de-France during the past 20 years). Thus, the observed larger species diversity in more disturbed landscapes may also result from the progressive replacement of agricultural plant communities by urban plant communities around a given site, because the latter are known to be more diverse than surrounding natural habitats (Wania, Kuhn & Klotz 2006).

Influence of landscape disturbance on the average specialization of plant communities

The local increase in plant taxonomic diversity with increasing landscape fragmentation was paralleled by a significant decrease in average community specialization. This suggests that generalist species progressively replace specialist species in

fragmented landscapes, which was already observed in bird communities (Devictor *et al.* 2008) and is predicted by niche theory. The viability of specialist species, which, by definition, are tolerant to a narrower range of environmental conditions, should decline in fragmented landscapes due to isolation and reduction in size of their habitat (Fridley *et al.* 2007). In contrast, generalist species, which can grow under a variety of environmental conditions and are not confined to small stands, should benefit from habitat fragmentation, which generates landscape heterogeneity (Marvier, Kareiva & Neubert 2004). Here, the replacement of specialist species by generalist species was, however, not supported by the species-centred approach; it showed no significant relationship between species specialization and the individual response of species to habitat fragmentation (or conversion), i.e. specialist species and generalist species were apparently equally affected by habitat fragmentation. This discrepancy between the species- and community-centred approaches may be due in part to low statistical power: the test assessing individual responses was based on 52 species only (vs. 352 plots for community specialization), because rare species, for which individual response to disturbance could not be assessed, were excluded.

Within sites, we also found a prominent effect of habitat type on the average community specialization (Fig. 4). Part of this is probably connected with habitat age and stability. Theory predicts that specialization should evolve in stable habitats, whereas a generalist strategy is considered a response to variable, unpredictable environments (Futuyma & Moreno 1988). Accordingly, specialist communities were observed in forests, a typical historical land use type in the study area, so that most forest sites have probably been stable over the last centuries. In contrast, highly generalist communities were found in ruderal habitats, which consist of interstitial vegetation (road verge,

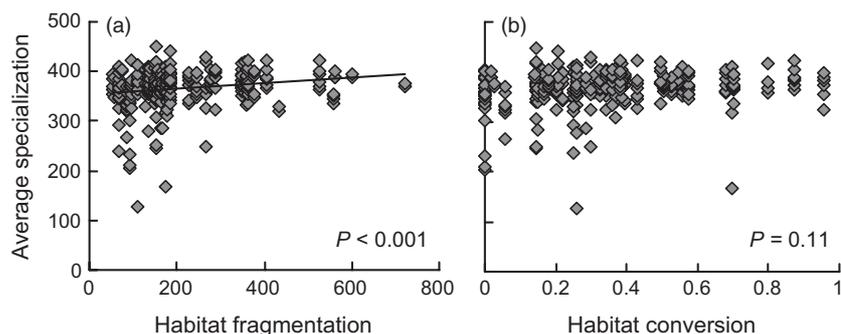


Fig. 5. Relationship between average community specialization (θ_c) in 10-m² plots and spatial (a) or temporal (b) landscape disturbance. P -values indicate the statistical significance of the effects of landscape disturbance variables, obtained from a linear mixed model.

field margins), urban wastelands or set-asides, all of which have high turnover. The two other main habitat classes are either relatively ancient but submitted to annual disturbance (farmlands) or more recent (cities) and exhibit intermediate specialization level species.

The relationship between community specialization and habitat stability was also found to a lesser extent at the landscape level. We examined how communities at a given site were affected by the temporal variation in the surrounding landscape, because plant communities are known to exhibit delayed responses to landscape disturbance (Piessens & Hermy 2006), so that landscapes with similar current structures, but contrasting histories, cannot be readily compared. Our results revealed a significant relationship between community specialization and surrounding habitat conversion in forests only, i.e. in the older habitat. This possible influence of surrounding landscape turnover on forest community composition is apparently not a mere by-product of habitat fragmentation; although fragmentation and conversion are positively correlated around forest sites, there is a marginally significant negative interaction of these two variables on community specialization ($F_{1,20} = 4.21$, $P = 0.05$), so that the effect of habitat conversion is even stronger in moderately fragmented landscapes. This suggests that past changes in landscape structure may influence forest community composition (notably average specialization) a few years or decades later. In contrast, man-made habitats (i.e. arable fields, ruderal habitats and cities) do not seem to be influenced by past surrounding landscape turnover, whose effects are probably overruled by high turnover in the habitat itself. The occurrence of periodic disturbance may be sufficient to explain community composition in each of these habitats: mostly weeds (i.e. annuals, R-strategists) in arable land and ruderal species (i.e. biennials or perennials, C-strategists) in ruderal habitats (Lososova *et al.* 2006). Nonetheless, we cannot exclude that this result in man-made habitats is also due to sampling bias, as our sample sizes could be too small to detect an existing relationship in under-represented habitat types (e.g. cities).

FUNCTIONAL CHANGE IN COMMUNITY COMPOSITION IS NOT SYSTEMATICALLY ASSOCIATED WITH TAXONOMIC BIOTIC HOMOGENIZATION

The local replacement of specialist by generalist species is a general pattern that is commonly interpreted as BH (see Clavel, Julliard & Devictor 2011 for a review), but there have been few attempts to compare BH and the functional composition of communities so far (Smart *et al.* 2006; Devictor *et al.* 2010b for a comparison of taxonomic and functional diversities in plants and birds respectively). Here, we observed a significant decrease in average community specialization with increasing landscape disturbance, but there was little sign of taxonomic BH associated with disturbance in our species assemblages. We did observe a significant negative relationship between habitat fragmentation and β -diversity among communities within a same habitat class (Fig. 3), but this pattern remained weak in comparison to what was observed in similar

studies of taxonomic BH in plants (Rooney *et al.* 2004; Kuhn & Klotz 2006; Wiegmann & Waller 2006; Vellend *et al.* 2007; Rogers *et al.* 2008). This discrepancy between our and previous studies may be related to scale issues that we discuss below.

Most former studies observing taxonomic homogenization were conducted at a large scale, from regional (McKinney 2004) to continental levels (Olden, Poff & McKinney 2006). At coarse-grained scales, BH was generally attributed to the expansion of a few non-native species – for example, exotic species tend to be distributed more randomly with respect to ecological conditions, but more widely than native species (Qian & Ricklefs 2006), so that distant communities are prone to share the same few exotic species, which can significantly increase community similarity (McKinney 2008). The present study was conducted at a smaller scale, at which change in community composition involved mechanisms other than expansion of exotic species. Naturalized species, although relatively frequent (observed in *c.* 25% of plots) in our data set, generally occurred at low abundance (e.g. *Veronica persica* or *Coryza canadensis* < 10% per plot on average) and our main results remained unchanged after discarding invasive species (not shown). This is consistent with the expectation that geographically close communities are less prone to the homogenization effect of introduced species, due to a relatively high spatial autocorrelation of native communities (La Sorte *et al.* 2008; Rogers *et al.* 2009).

Another scale issue that may arise in our study is that of landscape heterogeneity. Plant taxonomic BH was previously observed at regional scales comparable to that of our study, as a consequence of predation (herbivory, Rooney *et al.* 2004; Wiegmann & Waller 2006), urbanization (Kuhn & Klotz 2006), habitat turnover at a landscape scale (Vellend *et al.* 2007) or a combination of various human disturbance together with a strong effect of initial conditions (Smart *et al.* 2006). However, most of these studies considered taxonomic homogenization within a single habitat class (generally forest communities), whereas the fine-scale spatial heterogeneity of our study region led us to compare contrasting habitat types, as was probably also the case in the only other study examining taxonomic BH within 1-km² squares (Smart *et al.* 2006). Habitat heterogeneity inflates the measure of β -diversity and may explain why we observed a tendency for taxonomic BH with habitat fragmentation (Fig. 3) only when we restricted our analyses to a single habitat class.

Conclusions

Shannon diversity and community specialization, two indices that depend greatly on common species, correlate with human disturbance (e.g. habitat fragmentation and turnover). This confirms that common plant species are affected by human pressures and should be considered to document biodiversity (Gaston & Fuller 2008). However, most studies dealing with the effect of anthropogenic disturbance on wild flora often focus on rare and emblematic species or habitats, partly due to a bias in data collection and availability. For example, several studies that documented taxonomic homogenization in plant

communities focused on patterns of species richness (Smart *et al.* 2006; Vellend *et al.* 2007), most likely because no abundance data was available. Rare species contribute disproportionately to species richness and its spatial partitioning, so that the observed change in similarity across sites may be due to extinctions or invasions of species at low abundance, whereas substantial change in the abundance of common species, with potentially large effects on ecosystem functioning, may remain undetected (but see Canham & Thomas 2010). There is thus an urgent need for monitoring data of common plant species, including abundance variation. As of now, monitoring programmes targeting common species focus mostly on birds (Devictor *et al.* 2008, but see Weber, Hintermann & Zangger 2004 or Smart *et al.* 2006).

In addition, we confirmed that simple taxonomic indices that are widely used to document biodiversity changes, such as species richness (Helm, Hanski & Partel 2006), Shannon diversity index (this study) or changes in species commonness and rarity (Thompson & Jones 1999), may be misleading (Devictor & Robert 2009). For instance, human-induced disturbance resulted in larger species diversity both at a local and regional scale (Fig. 2), but was also associated with reduced average community specialization (Fig. 5), a pattern that can be interpreted as functional BH (Devictor *et al.* 2008). Similarly, although taxonomic BH is an unquestionable sign of biodiversity loss (McKinney & Lockwood 1999), the reverse is not true, because functional BH is not systematically associated with taxonomic BH.

Community specialization can thus be seen as an effective biodiversity indicator (Balmford, Green & Jenkins 2003), accounting for the widespread replacement of specialist species ('losers') by more tolerant, generalist species ('winners') (McKinney & Lockwood 1999), with potential consequences for ecosystem functioning. Effective implementation will however depend on (i) a proper assessment of the actual functional consequences of the spread of generalist species and (ii) an accurate quantification of species specialization. Until recently, loser and winner species were described on the basis of a small number of qualitative (sometimes quantitative) attributes, with the idea that, for example, small species are intuitively more sensitive to extinction (Duncan & Young 2000) or that biotically dispersed species should be more specialized on their habitat (Wiegmann & Waller 2006). These methods relying on a small number of functional traits may be useful to infer potential distributions via mechanistic models, but they often yield inconsistent results (e.g. species sensitivity to disturbance is highly dependent on the type of disturbance, Henle *et al.* 2004; Freville *et al.* 2007) and they are subject to observer bias (Futuyma & Moreno 1988). Recently, quantitative specialization indices were developed from the observed variation in species occurrence or abundance across habitat types (e.g. Herman *et al.* 1997; Rooney *et al.* 2004; Julliard *et al.* 2006) or from patterns of species co-occurrence across sites (Fridley *et al.* 2007); they provide promising tools to compute average community specialization easily from most biodiversity data bases and, in combination with more classical trait approaches, could help improve our

understanding of community responses to human disturbance (Devictor *et al.* 2010a).

Acknowledgements

The research was funded by Île-de-France region. E.P. was partly supported by a grant from the Agence Nationale de la Recherche (ANR Grant #2006-JCJC-0032) and the French common plant monitoring Vigie-flore by ANR Biodiversité Grant 2006 QDiv. We thank F. Perriat and S. Filoche for help in plant identification, the Conservatoire Botanique National du Bassin Parisien for access to their data base, V. Devictor and O. Filippi-Codaccioni for help in calculating landscape metrics, as well as two anonymous referees for helpful comments on an earlier version.

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Received 25 October 2010; accepted 10 May 2011

Handling Editor: Richard Bardgett