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Ecological niche shifts of understorey plants along a latitudinal gradient of temperate forests in north-western Europe

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ABSTRACT

Aim In response to environmental changes and to avoid extinction, species may either track suitable environmental conditions or adapt to the modified environment. However, whether and how species adapt to environmental changes remains unclear. By focusing on the realized niche (i.e. the actual space that a species inhabits and the resources it can access as a result of limiting biotic factors present in its habitat), we here examine shifts in the realized-niche width (i.e. ecological amplitude) and position (i.e. ecological optimum) of 26 common and widespread forest understorey plants across their distributional ranges.

Location Temperate forests along a ca. 1800-km-long latitudinal gradient from northern France to central Sweden and Estonia.

Methods We derived species' realized-niche width from a β -diversity metric, which increases if the focal species co-occurs with more species. Based on the concept that species' scores in a detrended correspondence analysis (DCA) represent the locations of their realized-niche positions, we developed a novel approach to run species-specific DCAs allowing the focal species to shift its realized-niche position along the studied latitudinal gradient while the realized-niche positions of other species were held constant.

Results None of the 26 species maintained both their realized-niche width and position along the latitudinal gradient. Few species (9 of 26: 35%) shifted their realized-niche width, but all shifted their realized-niche position. With increasing latitude, most species (22 of 26: 85%) shifted their realized-niche position for soil nutrients and pH towards nutrient-poorer and more acidic soils.

Main conclusions Forest understorey plants shifted their realized niche along the latitudinal gradient, suggesting local adaptation and/or plasticity. This macroecological pattern casts doubt on the idea that the realized niche is stable in space and time, which is a key assumption of species distribution models used to predict the future of biodiversity, hence raising concern about predicted extinction rates.

Keywords

Beta diversity, climate change, detrended correspondence analyses, Ellenberg indicator values, forest understorey plant species, niche optimum, niche width, plant community, realized niche.

INTRODUCTION

Global environmental changes are projected to be a major threat to biodiversity by enhancing species extinction rates throughout the 21st century (Sala *et al.*, 2000). In order to avoid extinction, species may either: (1) track suitable environmental conditions in space (i.e. distribution changes) or time (adjustments in the timing of species' life cycle events), or (2) adapt to the modified environment through acclimation (altered patterns of gene expression) or microevolutionary processes (ecotype differentiation) (Bellard *et al.*, 2012). In short, if increased temperature associated with climate change exceeds species' thermal tolerances, species need to track or adapt to changing environmental conditions to avoid extinction.

Distribution changes (i.e. shifts in geographical space) usually lead to local extinction. In contrast, adjustments in the timing of life cycle events (shifts in phenological space) and adaptive responses through acclimation and microevolution (shifts in ecological space) can prevent local extinction (Gienapp *et al.*, 2008). Numerous recent studies have documented altitudinal or latitudinal shifts in the geographical distributions of many species (Parmesan & Yohe, 2003; Lenoir *et al.*, 2008) as well as advances or delays in phenological events (e.g. Parmesan & Yohe, 2003), suggesting globally coherent fingerprints of contemporary climate change impacts on ecosystems. However, studies focusing on potential adaptive responses to changes in the environment are still scarce (but see Nicotra *et al.*, 2010). And yet, the existence of lags and mismatches between observed distributional or phenological shifts and what would be expected so as to perfectly match contemporary climate change (Visser & Both, 2005; Bertrand *et al.*, 2011) suggests that other processes including adaptive responses are at play. Determining which species are able to adapt to a new set of environmental conditions in the context of environmental changes is crucial for developing biological conservation strategies.

The niche can be viewed as the 'hyper-volume' in a multidimensional space defined by environmental variables and within which an organism is able to survive and reproduce or the combination of all abiotic and biotic conditions in which populations of a species maintain a positive growth rate (Hutchinson, 1957). Hutchinson (1957) defined the fundamental niche as the potential hyper-volume that a species can occupy in the absence of competitors, hence being genetically and physiologically determined (Pearman *et al.*, 2008). The realized niche consists only of those portions of the fundamental niche actually occupied by the species in presence of other species. While the fundamental niche is believed to be conserved over long evolutionary time-scales (Wiens & Graham, 2005), changes in the realized niche of species across space are still debated (Diekmann & Lawesson, 1999; Coudun & Gégout, 2005). However, most studies focused on restricted geographical extents, generally comparing two distant regions (but see Diekmann & Lawesson, 1999). Here, we test shifts in the realized niche (*sensu* Hutchinson, 1957) of species in several regions at a continental scale.

Shifts in the realized niche of a species within its distributional range may concern the values of two synthetic parameters: the realized-niche width (i.e. ecological amplitude or species' range of environmental conditions in which it can thrive) and the realized-niche position (i.e. ecological optimum or species' maximum probability of presence within its realized niche) (Coudun & Gégout, 2005). Given the conservation of the fundamental niche, two processes may cause a change in the realized niche (Diekmann & Lawesson, 1999): (1) biotic processes, which may result in expansion, contraction or shift of a species' realized niche beyond (e.g. facilitation) or within (e.g. competition) the range of its fundamental niche (Coudun & Gégout, 2005), or (2) habitat compensation processes, which may result in a species expanding, contracting or shifting its realized niche along at least one single axis of the ecological space while keeping its realized niche unchanged along the other axes of the ecological space (Walter & Walter, 1953).

The aim of our study was to assess shifts in the realized-niche width and position of 26 widespread forest understorey plant species along a latitudinal gradient covering most of the temperate deciduous forest biome in north-western Europe. We hypothesized that niche expansions towards the north are mainly due to competitive release from other forest understorey plants, as plant diversity decreases towards the poles (cf. MacArthur, 1972; Normand *et al.*, 2009). With respect to the realized-niche position, we assumed potential shifts to be consistent with directional changes in environmental conditions along the latitudinal gradient (cf. local adaptation hypothesis, Leimu & Fischer, 2008). This hypothesis suggests that local populations of a species are better adapted to their home environments compared with foreign populations.

MATERIALS AND METHODS

Study area and sampling design

An identical sampling design was carried out across seven regions located along a ca. 1800-km-long latitudinal gradient from northern France to central Sweden and Estonia via Belgium, western and eastern Germany, and southern Sweden (Fig. 1). This latitudinal gradient encompasses most of the temperate deciduous forest biome in north-western Europe and spans a large range of mean annual temperature conditions, from 5 to 10 °C between the northernmost (Stockholm, Sweden; Tartu, Estonia) and southernmost (Amiens, France) regions (Tables 1, FAO, 2005).

Within each of these seven regions, we sampled two 5 × 5 km landscape windows, containing a representative set of deciduous forest patches. All 14 windows shared similar landscape features in terms of patch morphology and of the relative proportion of meadows, agricultural land and forests (see Appendix S1 in Supporting Information). Additionally, we assessed patch-size variability within each window by computing the range (maximum–minimum) of patch-size values. Most of our forest patches are small (median: 10,980 m²), with 61% (360 out of 594) being smaller than 15,000 m². We also used generalized

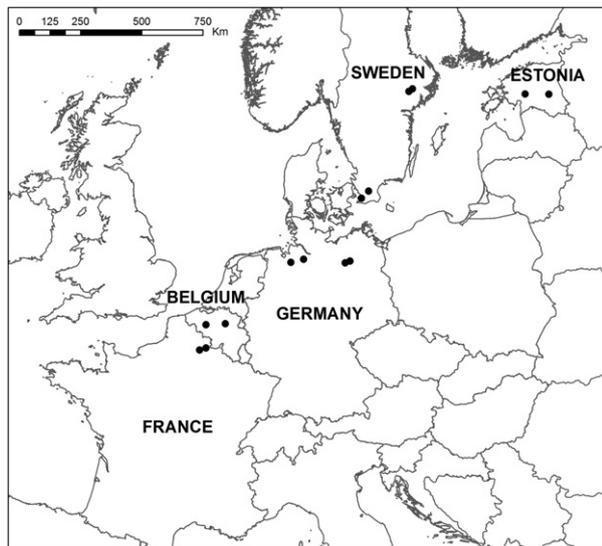


Figure 1 Study regions along the latitudinal gradient in north-western Europe. In each region, two 5×5 km landscape windows were surveyed.

linear models (GLMs) to detect any differences in patch-size variability among studied windows (see Appendix S2 for the model-selection strategy). Patch-size variability was comparable across all 14 windows since we found no significant changes (P -value = 0.8) in the range of patch-size values along the studied latitudinal gradient. Within each landscape window, all deciduous forest patches were intensively surveyed for all (in 9 out of 14 windows) or a subset of vascular plants (in 5 out of 14 windows). In the five windows lacking an exhaustive survey (i.e. both windows in Belgium and in western Germany and one window in southern Sweden), only typical forest understorey plants were recorded.

Species pool and studied species

In order to assess shifts in the realized niche of species along the latitudinal gradient, we focused on a subset of widespread understorey plant species that belong to the species pools of all seven regions (cf. Zobel, 1997). A total of 48 species met this criterion, of which 26 were sufficiently frequent to be retained for statistical analysis (i.e. occurring within at least 10 out of the 14 windows; see Appendix S3 for the list of studied species).

Using the nine landscape windows for which we had an exhaustive survey of all vascular plants occurring in each forest patch, we tested the representativeness of this set of 26 selected species relative to the entire patch's plant community observed in the field following the approach proposed by Vellend *et al.* (2008) (see Appendix S4 for more information on the method). We found strong correlations for species richness and species composition measured from the full list of forest plant species observed in the field and species richness measured from our subset of 26 focal species (see Appendix S4).

Environmental conditions and environmental heterogeneity

We assessed environmental conditions as well as environmental heterogeneity within and across landscape windows to assess whether these are comparable between landscape windows. Indeed, strong variations in environmental conditions or environmental heterogeneity across regions may also drive shifts in either the realized-niche width or position of species throughout changes in environmental availability (Soberón & Peterson, 2011; Broennimann *et al.*, 2012).

For this assessment, we used Ellenberg indicator values (EIVs, Ellenberg *et al.*, 1999). Ellenberg *et al.* (1999) ranked most of the central European vascular plant species along ordinal scales ranging from 1 to 9 (or 12) according to the position of their optimum along the main ecological gradients for light (L), soil nutrients (N), soil pH (R), soil moisture (F), temperature (T) and continentality (K). The applicability and usefulness of using EIVs outside their area of origin have been shown by several studies reporting an accurate correlation between mean indicator values and corresponding measurements of environmental variables in the field (Schaffers & Sýkora, 2000; Diekmann, 2003). In spite of being criticized by many authors (e.g. Zelený & Schaffers, 2012), the applicability and usefulness of EIVs have been confirmed in several European countries (Lawesson, 2000; Dzwonko, 2001). First, we calculated the mean EIVs to estimate local environmental conditions for L, N, R and F within each forest patch across all landscape windows, using the 48 species of the common species pool. We did not focus on the mean EIVs for T and K since climatic conditions were not comparable between the seven studied regions (Table 1). Besides, very few of the 48 forest species had indicator values for T and K, leading to unreliable estimates of mean EIVs in these cases. Then, we computed the median and the range (maximum–minimum) of values for the mean EIVs for L, N, R and F to represent environmental conditions and environmental heterogeneity within a given landscape window, respectively. Finally, in order to detect any significant change in either environmental conditions or environmental heterogeneity along the studied latitudinal gradient, we used GLMs (see Appendix S2).

Data analysis

To assess potential shifts in the realized niche of each of the 26 species along the latitudinal gradient, we distinguished shifts in the realized-niche width from shifts in the realized-niche position.

Realized-niche width

To quantify the realized-niche width of each of the 26 species, we used the co-occurrence-based metric developed by Fridley *et al.* (2007). This biotic approach is based on the concept that the realized-niche width increases if the focal species co-occurs with more species. Fridley *et al.* (2007) quantified the realized-niche width of species by using a continuous metric (θ) derived from

Table 1 Location, climatic characterization and number of patches of the two landscape windows within each of the seven study regions.

Country or region	Latitude (°N)	Longitude (°E)	MAT (°C)	MTC (°C)	MTW (°C)	MAP (mm)	NP
Northern France	49.9	3.9	9.8	2.2	17.9	737	62
	49.8	3.6	10.3	2.7	17.5	760	29
Belgium	50.8	3.8	9.85	2.7	17.2	756	58
	50.9	4.9	9.4	2	17	824	71
Eastern Germany	53.2	11.9	8.3	-0.5	17.3	576	28
	53.3	12.3	8.2	-0.5	16.5	572	17
Western Germany	53.2	8.7	8.6	0.7	17.2	744	49
	53.3	9.4	8.5	0.4	16.6	743	44
Southern Sweden	55.8	13.6	8.1	-0.2	17	644	57
	55.5	13.1	8.3	0	16.9	662	16
Estonia	58.6	24.9	5.7	-5.6	17	623	27
	58.4	26.6	5.2	-6.6	17.3	581	14
Central Sweden	59.3	16.9	6.0	-3.8	16.6	542	66
	59.4	17.2	6.0	-3.9	16.6	540	56

MAT, mean (1961–1990) annual temperature; MTC, mean temperature of the coldest month; MTW, mean temperature of the warmest month; MAP, mean annual precipitation (FAO, 2005); NP, number of patches.

a β -diversity measure. Thus, a species that co-occurs with many different species in the different forest patches of a given landscape window will have a relatively high rate of species turnover, hence a high θ value, indicating a relatively wide realized niche.

In the first step, we determined the most suitable measure of β -diversity to compute the θ metric. In the original method, Fridley *et al.* (2007) used an additive partitioning approach to quantify β -diversity, but multiplicative turnover indices were found to be more robust against variation in species pool size along environmental gradients and against variation in species frequency (Zelený, 2008; Manthey & Fridley, 2009). Here, we used the multiple Simpson's dissimilarity index, which provided performances similar to null modelling approaches (data not shown), such as the probabilistic Raup & Crick index (Vellend *et al.*, 2007) and its recently modified version (Chase *et al.*, 2011).

Additionally, species differ widely among each other in frequency of occurrence within a given dataset not only due to their differing realized-niche width, but also due to survey designs that are biased towards collection of certain habitats or species (Fridley *et al.*, 2007). To remove the effect of survey design, Fridley *et al.* (2007) proposed a randomization technique to randomly choose for all studied species a fixed number of sites containing a focal species before calculating β . In our study, it was crucial to remove the signature of differences in frequencies of a focal species between landscape windows by choosing a fixed number of randomly selected forest patches containing this species across all landscape windows. The choice of this number of randomly selected forest patches containing a focal species should represent a compromise between choosing a high number, which excludes the species with few occurrences, and choosing a low number, which would increase variance due to sample size effects. We here chose a minimum frequency of 5 for all species and across

all landscape windows in order to introduce all 26 studied species that have variable frequencies between landscape windows. For each of the 26 species, this randomization was applied 100 times and the average β -value, being the θ metric, was used in further analyses. For each focal species and each landscape window, θ was calculated with respect to the 48 species belonging to the common species pool. In order to detect any significant change in the realized-niche width along the studied latitudinal gradient we used GLMs (see Appendix S2). Although we focused on the 26 most widespread species belonging to the common species pool, the θ metric might still be affected by variation in the actual species richness in a given landscape window (γ -diversity) (Manthey *et al.*, 2011). In order to assess to which extent the measure of θ for each of the 26 studied species is affected by γ -diversity, we calculated the actual species richness within a given landscape window (γ -diversity) as the total number of species from the common species pool of 48 species that co-occur with the focal species and analysed the relationship between this focal value of γ -diversity against latitude using GLMs (see Appendix S2). We found that the latitudinal trends in the observed changes in the realized-niche width (θ) for the 26 species under investigation were independent from γ -diversity (Table 2).

Realized-niche position

We assessed shifts in the species' realized-niche position using two different approaches: a species-indicator-based approach, namely EIVs (Ellenberg *et al.*, 1999), and an indirect gradient analysis approach based on detrended correspondence analysis (DCA) (Hill & Gauch, 1980). While the ordination approach is solely based on similarities in species composition, the EIV approach is based on values derived from an independent source and gives environmental interpretation of the data (Diekmann

Table 2 Latitudinal trends in the observed changes in the realized-niche width (θ) and position (species scores along the first axis of species-specific DCA) along the studied latitudinal gradient for 26 forest understorey plant species. SR shows the relationships between latitude and the species richness of the community hosting the focal species. Group shows species groups according to latitudinal changes in θ : A (invariant: i.e. conserved niche width), B (positive linear relationship), C (U-shape relationship) and D (\cap -shape relationship) with the latitude.

Species	Group	θ	DCAs	SR
<i>Anemone nemorosa</i>	A	n.s.	/***	\cap ***
<i>Milium effusum</i>	A	n.s.	/***	\cap ***
<i>Paris quadrifolia</i>	A	n.s.	/***	*
<i>Poa nemoralis</i>	A	n.s.	/***	\cap *
<i>Scrophularia nodosa</i>	A	n.s.	/***	\cap *
<i>Polygonatum multiflorum</i>	A	n.s.	/***	\cap ***
<i>Stachys sylvatica</i>	A	n.s.	/***	\cap **
<i>Adoxa moschatellina</i>	A	n.s.	/***	n.s.
<i>Circaea lutetiana</i>	A	n.s.	\cap *	n.s.
<i>Deschampsia flexuosa</i>	A	n.s.	/***	\cap ***
<i>Dryopteris carthusiana</i>	A	n.s.	/***	\cap ***
<i>Dryopteris filix-mas</i>	A	n.s.	/***	\cap **
<i>Maianthemum bifolium</i>	A	n.s.	U**	\cap ***
<i>Moehringia trinervia</i>	A	n.s.	/***	\cap *
<i>Stellaria holostea</i>	A	n.s.	/***	**
<i>Vaccinium myrtillus</i>	A	n.s.	/***	n.s.
<i>Festuca gigantea</i>	A	n.s.	U*	\cap ***
<i>Luzula pilosa</i>	B	/**	/***	n.s.
<i>Oxalis acetosella</i>	B	/**	/***	\cap ***
<i>Athyrium filix-femina</i>	B	/*	/***	\cap ***
<i>Convallaria majalis</i>	B	/***	/***	\cap *
<i>Equisetum sylvaticum</i>	B	/***	/***	\cap *
<i>Brachypodium sylvaticum</i>	C	U**	\cap *	n.s.
<i>Carex sylvatica</i>	C	U**	/***	n.s.
<i>Lamium galeobdolon</i>	C	U**	/***	n.s.
<i>Epipactis helleborine</i>	D	\cap **	/***	n.s.

Symbols are as follows: / and \ indicate positive and negative linear relationships with latitude, respectively; U and \cap indicate concave and convex relationships, respectively. Levels of significance are: * $0.01 < P < 0.05$; ** $0.001 < P < 0.01$; *** $P < 0.001$. DCA, detrended correspondence analysis; n.s. means not significant.

& Lawesson, 1999). Because both approaches led approximately to the same results and conclusions regarding shifts in the realized-niche position of species, we decided to report results from the ordination approach solely (see Appendix S5 for explanations, results and interpretations regarding the EIV approach).

Species scores along DCA axes represent the centroids of the species' response curves or the locations of their maximum abundance (optima) (Jongman *et al.*, 1995). For this reason, species scores along DCA axes are particularly well suited to track changes in species' realized-niche position. We developed a novel approach to run species-specific DCAs allowing the focal species to shift its realized-niche position along the studied latitudinal gradient while holding the realized-niche position of

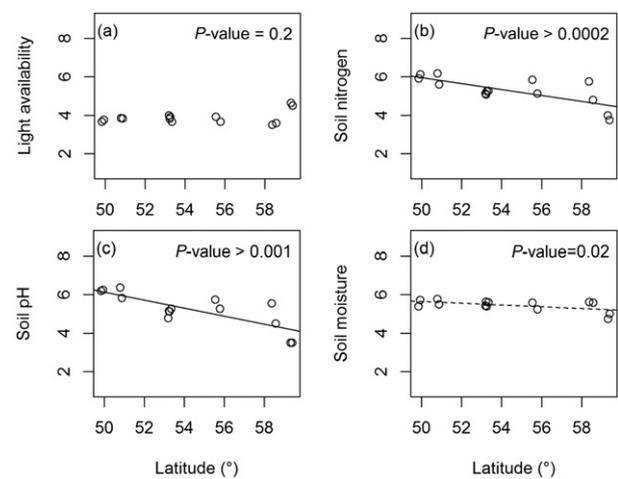


Figure 2 Latitudinal variation in environmental conditions across landscape windows estimated from vegetation data and calculated as the median value for the mean Ellenberg indicator values for: (a) light availability, (b) soil nutrients, (c) soil pH, and (d) soil moisture. Plain and dashed lines describe strong and limited latitudinal variation in environmental conditions, respectively, when moving towards north.

other species constant. To achieve this, we first used the full patch-by-species matrix (594×48) and split the column containing presence/absence information of the focal species into 14 sub-columns: one sub-column for each landscape window. Each of these 14 sub-columns contained presence/absence information of the focal species for the focal landscape window and zero elsewhere. We then performed a DCA on this newly obtained patch-by-species matrix (594×61) and extracted the scores of the focal species for each of the 14 windows along the first DCA axis. Finally, we used GLMs (see Appendix S2) to fit the scores of the focal species against the latitudinal position of the 14 windows and to assess any shift in the realized-niche position of the focal species. We decided to focus on the first DCA axis solely since it contains most of the variation, ranging from 38 to 44%. To interpret the ecological meaning of the first DCA axis for the focal species, we computed the correlation coefficients (using Spearman method) between patch scores along the first DCA axis and the corresponding mean EIVs for L, N, R and F. Note that mean EIVs were computed from the list of species co-occurring in forest patches where the focal species was present, the latter being deleted from the calculation to avoid circularity. This procedure was repeated for each of the 26 studied species separately.

All statistical analyses were run in R 2.14.1 (R Development Core Team, 2011).

RESULTS

Ellenberg soil nutrient and pH values decreased with increasing latitude (Fig. 2b,c). Latitudinal variation in light (Fig. 2a) and soil moisture (Fig. 2d) conditions was very limited (i.e. less than 1 unit between the maximum and minimum values), though

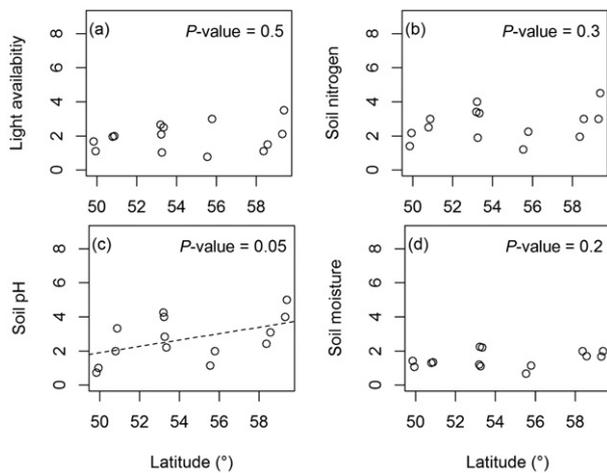


Figure 3 Latitudinal variation in environmental heterogeneity across landscape windows estimated from vegetation data and calculated as the range of values for the mean Ellenberg indicator values for: (a) light availability, (b) soil nutrients, (c) soil pH, and (d) soil moisture. Plain and dashed lines describe strong and limited latitudinal variation in environmental heterogeneity, respectively, when moving towards north.

there were significant latitudinal changes for soil moisture. We did not find any significant variation in environmental heterogeneity across landscape windows for light, soil nutrients and soil moisture (Fig. 3). As latitude increased, environmental heterogeneity in soil pH increased, though only marginally significantly (Fig. 3).

Latitudinal changes in the realized-niche width and position differed between species (Table 2). While a majority of species (17 out of 26) conserved a similar realized-niche width along the studied latitudinal gradient (i.e. θ was invariant; group A: e.g. *Anemone nemorosa*, *Circaea lutetiana*, *Stachys sylvatica*), some species showed positive linear (group B: *Athyrium filix-femina*, *Convallaria majalis*, *Equisetum sylvaticum*, *Luzula pilosa*, *Oxalis acetosella*), U-shaped (group C: *Brachypodium sylvaticum*, *Carex sylvatica*, *Lamium galeobdolon*) or \cap -shaped (group D: *Epipactis helleborine*) relationships with latitude.

Along the latitudinal gradient, the DCA scores of 22 out of 26 species increased towards the north (Table 2). For these 22 species, the first DCA axis was negatively correlated with both soil N and pH (Table 3), meaning that their realized-niche position shifted towards nutrient-poorer and more acidic soils when moving northwards. For *B. sylvaticum* and *C. lutetiana*, which showed a convex \cap -shape relationship with latitude, the first DCA axis was negatively correlated with both soil nutrients and pH. For *Festuca gigantea* and *Maianthemum bifolium*, which showed a U-shape (concave) relationship with latitude, the first DCA axis was either positively (*F. gigantea*) or negatively (*M. bifolium*) correlated with these soil properties. This means that while *B. sylvaticum*, *C. lutetiana* and *F. gigantea* shifted the position of their realized niche towards nutrient-richer and less acidic soils, *M. bifolium* shifted its

Table 3 Spearman's correlation coefficients between the mean Ellenberg indicator values for light (L), soil nutrients (N), soil pH (R), and soil moisture (F), as calculated from the list of species co-occurring in forest patches where the focal species was present (excluding the focal species from calculations to avoid circularity) and the scores of these patches along the first axis of species-specific DCA.

Species	L	N	R	F
<i>Adoxa moschatellina</i>	-0.07	-0.82	-0.87	-0.34
<i>Anemone nemorosa</i>	0.60	-0.90	-0.94	-0.76
<i>Athyrium filix-femina</i>	-0.07	-0.81	-0.88	-0.38
<i>Brachypodium sylvaticum</i>	-0.34	-0.77	-0.83	-0.03
<i>Carex sylvatica</i>	-0.43	-0.78	-0.81	-0.10
<i>Circaea lutetiana</i>	-0.12	-0.80	-0.86	-0.09
<i>Convallaria majalis</i>	0.78	-0.85	-0.90	-0.84
<i>Deschampsia flexuosa</i>	0.67	-0.78	-0.87	-0.74
<i>Dryopteris carthusiana</i>	-0.02	-0.70	-0.85	-0.29
<i>Dryopteris filix-mas</i>	0.34	-0.83	-0.90	-0.60
<i>Epipactis helleborine</i>	-0.14	-0.77	-0.90	-0.19
<i>Equisetum sylvaticum</i>	0.32	-0.89	-0.92	-0.62
<i>Festuca gigantea</i>	0.28	0.80	0.85	0.50
<i>Lamium galeobdolon</i>	-0.29	-0.82	-0.90	-0.48
<i>Luzula pilosa</i>	0.47	-0.92	-0.95	-0.72
<i>Maianthemum bifolium</i>	0.17	-0.6	-0.81	-0.32
<i>Milium effusum</i>	0.18	-0.79	-0.84	-0.43
<i>Moehringia trinervia</i>	0.20	-0.79	-0.85	-0.50
<i>Oxalis acetosella</i>	0.05	-0.72	-0.88	-0.56
<i>Paris quadrifolia</i>	-0.16	-0.66	-0.76	-0.23
<i>Poa nemoralis</i>	0.61	-0.86	-0.86	-0.70
<i>Polygonatum multiflorum</i>	-0.11	-0.82	-0.87	-0.44
<i>Scrophularia nodosa</i>	0.04	-0.79	-0.81	-0.60
<i>Stachys sylvatica</i>	-0.3	-0.74	-0.85	-0.23
<i>Stellaria holostea</i>	-0.11	-0.8	-0.88	-0.39
<i>Vaccinium myrtillus</i>	0.71	-0.84	-0.91	-0.83

DCA, detrended correspondence analysis.

realized-niche position towards nutrient-poorer and more acidic soils when moving northwards or southwards from mid-latitudes.

DISCUSSION

We found strong evidence of changes within species' realized-niche position across space when analysing 26 widespread forest understorey plant species along a latitudinal gradient at a continental scale and using various complementary approaches to assess both species' realized-niche width and position. However, few species (9 out of 26) exhibited a change in their realized-niche width across latitude. Although many studies have compared the realized niche of several forest understorey plant species between different regions in Europe (Diekmann & Lawesson, 1999; Coudun & Gégout, 2005; Prinzing *et al.*, 2008), we here provide the first large-scale assessment that represents a gradient covering most of the temperate forest biome

in north-western Europe. Below we discuss how species shifted their realized niche along the latitudinal gradient before concluding on the relevance of our results for global-change ecology.

A stable niche width across space does not necessarily imply niche conservatism

Although the majority of our study species (17 out of 26: 65%) exhibited no change in their realized-niche width, the realized-niche position of these species shifted along the studied latitudinal gradient. All these species shifted their realized-niche positions towards nutrient-poorer and more acidic soils with increasing latitude, except for three species (*C. lutetiana*, *F. gigantea* and *M. bifolium*). Interestingly, soil nutrient and soil pH conditions decreased when moving northwards (Fig. 2b,c), suggesting that these species adapt the position of their realized niche to the local environmental conditions along the latitudinal gradient. This result is consistent with a former study detecting shifts in the realized-niche position of eight forest plant species between Germany and Sweden (Diekmann & Lawesson, 1999). To the contrary, a more recent study focusing on a much smaller spatial extent (northern France) found a relative stability in the realized-niche position of 46 herbaceous forest species (Coudun & Gégout, 2005). Hence, the size (i.e. extent) of the studied geographical region appears to be a key factor to detect shifts in species' realized-niche position.

Additionally, such shifts in species' realized-niche position are highly consistent with recent studies detecting lags between changes in environmental conditions and the expected biotic response (Lenoir *et al.*, 2008; Bertrand *et al.*, 2011). This supports the local adaptation hypothesis (Leimu & Fischer, 2008) claiming that populations are generally adapted to their home environments. Indeed, our results suggest that most forest understorey plant species adapt the position of their realized niche to the local environmental conditions along the latitudinal gradient. However, based on these results, it is impossible to say whether such adaptive responses resulted from acclimatization effects, microevolutionary processes, changes in biotic interactions, or habitat compensations. For plants, there is increasing evidence for microevolutionary processes, at least when they grow in large populations (Leimu & Fischer, 2008). For instance, using reciprocal transplant experiments along the studied latitudinal gradient, adaptation to local environmental conditions has been shown for *A. nemorosa* and *Milium effusum* (De Frenne *et al.*, 2011), which is coherent with the results of the present study. However, shifts in the realized-niche position may also be linked to the latitudinal variation in environmental conditions between landscape windows (Soberón & Peterson, 2011). For instance, low environmental heterogeneity within each landscape window combined with significant changes in environmental conditions between windows would be likely to: (1) truncate a species' realized niche within each window due to limited environmental availability, and (2) change a species' realized-niche position between windows due to different environmental conditions.

Such changes in the realized-niche position of species would therefore be likely to mimic directional changes in environmental conditions between windows. However, this cannot explain the directional shifts in species' realized-niche position in our case, as both soil nutrient and soil pH conditions showed sufficient environmental heterogeneity within each landscape window, thus providing available habitats for forest species. Furthermore, the marginally increasing trend in environmental heterogeneity for soil pH towards the north suggests that more habitats are available for species regarding soil pH conditions. And yet, almost all species showed similar shifts in their realized-niche position towards more acidic soils, suggesting adaptation to local environmental conditions.

The realized-niche positions of *C. lutetiana*, *F. gigantea* and *M. bifolium* also changed along the latitudinal gradient. While *C. lutetiana* and *F. gigantea* shifted the position of their realized-niche positions towards nutrient-richer and less acidic soils, *M. bifolium* shifted its realized-niche position towards nutrient-poorer and more acidic soils at both extremes of the studied latitudinal gradient. Interestingly, *C. lutetiana* and *F. gigantea* are typically found on nutrient-rich and neutral soils, whereas *M. bifolium* is typically found on nutrient-poor and acidic soils (Rameau *et al.*, 2003). This indicates that these species are found within their most suitable habitats in terms of soil characteristics, at both extremes of the latitudinal gradient, whereas at mid-latitudes, the same species shift their realized-niche position towards less suitable habitats. This is particularly consistent with the fact that almost all of the 48 species belonging to the common species pool co-occur at mid-latitudes (see Appendix S6), thus increasing the risk that plant–plant competition induces shifts in the realized-niche position of a species within its fundamental niche.

Evidence for niche width changes

Among the few species exhibiting significant changes in their realized-niche width across latitudes (9 out of 26: 35%), five species coexisted with an increasing number of species along the latitudinal gradient, hence showing a more generalistic behaviour towards the north. All five species had their realized-niche positions following the general decreasing trend in soil nutrient and soil pH towards northern latitudes. Taken together, these results stress that these five species both expand their realized-niche width and shift their realized-niche position with increasing latitude, suggesting adaptation to the local environment. We see two explanations for these changes. First, this may result from an increased tolerance to one or more environmental factors (i.e. expansion of both the fundamental and realized niches due to microevolutionary processes). Second, this may be caused by competitive release since γ -diversity (i.e. total vascular plant species richness across all forest patches occurring within a landscape window) decreases towards northern latitudes. Hence, the discrepancy between the fundamental and the realized niches is likely to decrease towards the poles, or, in other words, species are shifting their realized niche by filling their fundamental niche (Pearman *et al.*, 2008; Normand *et al.*, 2009)

through competitive release. This relates to MacArthur's theory (MacArthur, 1972), which claims that the restriction of species' realized-niche width by competition increases with regional diversity. However, Manthey *et al.* (2011) showed that there was no such effect of the size of the species pool (i.e. plant–plant competition) on the restriction of the species' realized-niche width and that plant species are more constrained by environmental conditions than by competition.

Three species exhibited a U-shaped relationship between their realized-niche width (θ) and latitude (*B. sylvaticum*, *C. sylvatica* and *L. galeobdolon*), indicating that they are generalists at both extremes of the latitudinal gradient, but specialists at mid-latitudes. Remarkably, while γ -diversity followed a bell-shaped relationship with latitude, the focal γ -diversity of these three species' recipient communities (i.e. total species richness across the subset of forest patches hosting the focal species within a landscape window) did not vary significantly, being inconsistent with MacArthur's hypothesis. However, intraspecific competition, likely to be more important at the centre of a species' distribution (Brown, 1984), may also be responsible for the discrepancy between the fundamental and the realized niche. Besides, this U-shape relationship between θ and latitude may also result from an increased tolerance to one or more environmental factors towards their range limit. Indeed, populations at the periphery of the range are usually genetically different from populations in the centre of the distribution range (Eckert *et al.*, 2008) and may exhibit larger tolerances and phenotypic plasticity to environmental heterogeneity (Ghalambor *et al.*, 2006), thus potentially increasing the width of both their fundamental and realized niches.

Finally, one single species exhibited a \cap -shaped relationship between its realized-niche width and latitude (*E. helleborine*), indicating that it is a specialist at both extremes of the latitudinal gradient, but a generalist at mid-latitudes. *E. helleborine* is an orchid usually occurring on calcareous and nutrient-rich soils (Rameau *et al.*, 2003). These are soil conditions that become rarer towards the north (Pärtel, 2002), as confirmed by the general trends of soil nutrient and soil pH conditions in our study area. Its frequency was insufficient in the northern part of the studied gradient (present in less than five patches) for inclusion in our first analysis. Hence, we could not determine the behaviour of this species along the entire latitudinal gradient.

The pros and cons of co-occurrence-based approaches to measure species' realized-niche shifts

The co-occurrence-based metrics we used allow estimating potential shifts in species' realized niche from a more biotic (i.e. focus on the community) perspective without the need of extensive field measurements of the main environmental variables that putatively matter for the actual species distribution. Contrary to traditional approaches focusing on a single dimension (i.e. environmental gradient) of the realized niche (e.g. Coudun & Gégout, 2005), co-occurrence-based metrics account for the multidimensionality of the ecological space by incorporating

not only the abiotic but also the biotic dimensions (Fridley *et al.*, 2007; Manthey *et al.*, 2011). Hence, from this point of view, such metrics are useful descriptors to detect shifts in species' realized-niche shifts. However, these co-occurrence-based metrics are relying on community data solely without any independent measurements of (classical) niche dimensions. From this point of view, such metrics may put too much emphasis on the biotic components and underestimate the abiotic components of the realized niche. For instance, it has been made very clear by Zelený & Schaffers (2012) that an important fraction of the information in mean EIVs is independent from the actual indicator values but instead is connected to the species composition, for example, the pattern that remains when replacing the 'true' indicator values with random numbers. For this reason, it is not surprising that both the EIV approach and the indirect gradient analysis approach based on DCA reveal very similar results regarding shifts in the realized-niche position of species since both approaches are based on the same species composition data. This can be taken as an indication that species might have also changed their optimum position along major environmental gradients but independent measurements are needed to confirm this assumption.

CONCLUSIONS AND IMPLICATIONS

The potential adaptation of many forest understorey plant species to global change within their current habitats will likely be a key feature for their short- and long-term persistence. Not only shifts in both geographical and phenological space are to be expected under new environmental conditions, but also shifts in ecological space (Bellard *et al.*, 2012). Therefore, assessing both realized and fundamental niche shifts across environmental gradients is crucial for global-change biology. Widely distributed species may perform well in a wide range of environmental conditions (Joshi *et al.*, 2001), but the capacity of individual genotypes to perform well across the entire range of environmental conditions is thought to be limited (DeWitt *et al.*, 1998). Here, we provide evidence for realized-niche shifts in a majority of widely distributed understorey plant species along a latitudinal gradient in European temperate forests. Obviously, we cannot assume that species will respond to temporal changes in environmental conditions in the same way as they respond to spatial variability, because the observed spatial variation in species' realized niches likely results from adaptation of plant populations to their home environment (Leimu & Fischer, 2008; De Frenne *et al.*, 2011). This occurs over time-scales of multiple generations and is probably slower than the predicted pace of climate change (Jump & Peñuelas, 2005). However, by placing local populations close enough to a new phenotypic optimum for directional selection to act, adaptive plasticity may enhance fitness and facilitate adaptive evolution on ecological time-scales in new environments (Ghalambor *et al.*, 2007). Similarly, rapid evolution in response to environmental change has been proven in natural plant populations, based on genetic variation already present within the population (Jump *et al.*, 2009), reinforcing the importance of popu-

lation size in local adaptation to environmental change (Leimu & Fischer, 2008). Most importantly, the fact that the most common and widespread understorey plants shifted either the width or the position of their realized niche across space suggests that the realized niche is not completely stable in space and time, rising concern about predicted extinction rates from species distribution models which basically assume niche conservatism in space and time.

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SUPPORTING INFORMATION

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Appendix S1 Variation in landscape features among the 14 studied windows.

Appendix S2 Model-selection strategy.

Appendix S3 A list of forest understorey plant species belonging to the common species pool.

Appendix S4 Testing the representativeness of the 26 studied species relative to the entire plant community of each forest patch.

Appendix S5 Analysing shifts in the realized-niche position of species by means of Ellenberg indicator values.

Appendix S6 Latitudinal variation in actual species richness at the landscape-window level (γ -diversity: total number of species from the common species pool of 48 species).

BIOSKETCH

Safaa Wasof is a PhD student at the Jules Verne University of Picardie in France and is interested in plant community ecology and in how plant communities are affected by contemporary environmental changes. Data collection was done by the research group FLEUR (<http://www.fleur.ugent.be>), a European network of researchers interested in the dynamics of forest plant species in a changing environment and to which all of the authors belong.

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