

Niches of temperate tree species converge towards nutrient-rich conditions over ontogeny

Romain Bertrand, Jean-Claude Gégout and Jean-Daniel Bontemps

R. Bertrand (*romain.bertrand@engref.agroparistech.fr*), J.-C. Gégout and J.-D. Bontemps, *AgroParisTech, ENGREF, UMR1092 Laboratoire d'Étude des Ressources Forêt-Bois (LERFoB), 14 rue Girardet, FR-54000 Nancy, France, and: INRA, Centre de Nancy, UMR1092 Laboratoire d'Étude des Ressources Forêt-Bois (LERFoB), FR-54280 Champenoux, France.*

Niche changes during a species' lifespan are known as ontogenetic niche shifts. These shifts reflect changes in resource availability, requirements, organisms' foraging ability and/or size-dependent biotic interactions. In the plant kingdom, however, this issue remains poorly covered.

We investigated nutritional niche shifts over the ontogeny of 23 temperate tree species (among nine phylogenetic families) by a synchronic approach. We used 1963 temporary phytoecological surveys conducted throughout metropolitan French forests. The realised niches of three life-history stages (seedling: < 0.5 m; sapling: > 0.5 m and < 8 m; tree: > 8 m) in each tree species were modelled on the basis of presence/absence data and the main factors of species distribution (energy, water and nutritional resources). We computed the nutritional optima and amplitudes by bootstrapping partial response curves for the C:N ratio and base saturation rate. We assessed changes in these niche parameters over ontogeny and also evaluated the relative importance of ontogenetic shifts in the differentiation of nutritional niche among the selected tree species.

The tree stage was found to occur mainly at higher nutrient availability than the seedling (+16.3% on the nutritional gradient) or sapling (+11.1%) stages. In addition, nutritional niches of tree species exhibited, successively, a niche enlargement in eutrophic conditions and a niche restriction in oligotrophic conditions during growth. These global nutritional niche shifts observed over the species' lifespan contributed moderately but significantly to the niche separation in temperate tree communities (up to 4.5%).

We interpreted niche shifts as a response to an increase in nutritional requirements over ontogeny, leading to an intra-specific selection where individuals established in eutrophic soils have the maximal fitness. Biotic interactions and temporal changes in the environment may secondarily enhance or counteract the process. The importance of ontogenetic niche shifts requires consideration in the study of species autecology and plant community organisation.

The ecological niche is a fundamental concept, defined as an *n*-dimensional hypervolume characterising the set of ecological conditions required for a species to develop (Hutchinson 1957). In plant ecology, following the assumptions that (1) all life stages respond similarly to environmental gradients, or (2) the adult response is stronger than the juvenile, studies have focused mostly on either the adult stage or all life stages simultaneously (Clark et al. 1998, Collins and Carson 2004). Although this simplification allows us to deliver a global picture of species response, its application in population dynamics is less justified. Indeed, organisms' requirements and sensitivity to environmental factors change during their lifecycle (Grubb 1977). Grubb (1977) and Young et al. (2005) suggested analysing ecological niches according to critical life-history stages of species (e.g. reproduction, dispersal, growth). Ontogenetic niche shifts are therefore a crucial issue (Werner and Gilliam 1984, Miriti 2006).

In animal ecology, ontogenetic niche shifts are amply documented. Changes in resource availability and requirements (Hou et al. 2008), organisms' foraging ability (Hjelm et al. 2001), and/or a size-dependent change in risk of predation

and other biotic interactions (Claessen and Dieckmann 2002, Jones et al. 2003) result in niche shifts. This process can have real impacts on community structure and dynamics (Schreiber and Rudolf 2008). In particular, ontogenetic niche shifts affect energy transfer between ecosystems (Regester et al. 2006) and functional connectivity in landscapes, and lead to a high level of ecosystem complexity (Schreiber and Rudolf 2008).

In vegetation ecology, ontogenetic niche shifts remain a largely unexplored concept (Young et al. 2005). Habitat is imposed on plants by seed dispersal and the environmental conditions in which germination occurs (Schupp 1995). Niche changes over a lifecycle, therefore, are the result of mortality/survivorship due to changes in resource requirements, tolerance/resistance to biotic and abiotic environments, and/or environmental conditions (Eriksson 2002, Boege et al. 2007, Lenoir et al. 2009). Some studies have reported ecological niche shifts in relation to ontogeny among herbaceous (Parrish and Bazzaz 1985), shrub (Miriti 2006), and tree species (Stohlgren et al. 1998). Ontogenetic niche convergence towards better nutrient, water and/or

light availability, driven mainly by an increase in species requirements during growth, has also been described (Parrish and Bazzaz 1985, Quero et al. 2008). High dependence on parental reproduction and propagule dispersion (Moore and Elmendorf 2006), great susceptibility to environmental stress (Anderson et al. 2009), and the importance of functional trait definition (Poorter 2007) make the regeneration niche a crucial life-history stage in determining a species' niche and distribution (Grubb 1977, Young et al. 2005). However, few species and life-history stages have been analysed in previous studies. In addition, most existing studies have been conducted experimentally or at small geographical scales. A general assessment of ontogenetic niche shifts in plant populations developing in the natural environment remains to be conducted (Miriti 2006, Poorter 2007).

Except for the experimental work of Parrish and Bazzaz (1985) on six annual plant species, all studies to date have focused on light and water gradients, but not on soil nutritional availability. Nevertheless, forest ecosystems in which tree species develop are mainly nutrient-constrained (Tamm 1990), and nutrient resources are an important dimension in the ecological niches of tree species (Bigelow and Canham 2002). For these reasons, we focused on niche shifts along soil nutrient resources (i.e. nutritional niche shifts). Following the exploration of Parrish and Bazzaz (1985), we hypothesised that niche shifts along a nutrient gradient also occur during the development of perennial tree species, and that later life-history stages actually tend to be more nutrient-demanding than early stages. In the present study, we investigated ontogenetic shifts in the realised nutritional niche within temperate tree species, by monitoring changes in optimum and amplitude (Fig. 1) computed from a comparison of complete ecological niche models (integrating energy, water, and nutritional dimensions). To track a general pattern of ontogenetic shifts in nutritional niche, we analysed the niches of 23 species belonging to nine phylogenetic families over a large study area (French territory) along two nutritional gradients (C:N ratio and base saturation rate). We analysed ontogeny according to three life-history stages (seedling, sapling, and tree). We addressed the following questions: (1) Do ontogenetic shifts in the realised nutritional niche occur among temperate tree species? (2) What is the nature of these shifts: expansion, contraction, or change in niche position (Fig. 1)? (3) Do the nutritional niche shifts highlight a general pattern? (4) Are these shifts important in the niche differentiation of tree species?

Material and methods

Data description

To study nutritional niche shifts over ontogeny, we modelled the probability of presence of each species for each life stage as a function of environmental indicators (realised niche model) and compared the resulting response curves along the nutrient gradient. We used the EcoPlant database (Gégout et al. 2005), which contains more than 6400 georeferenced floristic surveys coupled with soil analyses, distributed throughout metropolitan French forests. Most of the plots had an area of 400 m². The plots were prospected during the growing period of vegetation, and a complete

species list (coded by presence/absence), coupled with vegetation layer information, was compiled. To exclude the early stages of forest succession, which depend highly on land use or pasture abandonment, and to limit the local environmental change due to stand maturation, we selected sites having a tree layer (size > 8 m). The surveys sampled did not undergo sudden disturbance (e.g. fire, storm) which could cause apparent ontogenetic niche shifts. We analysed a total of 1963 plots sampled between 1970 and 2003 (Fig. 2).

Because the plots are temporary, we could not monitor species populations over the total lifespan. Rather, we performed a synchronic analysis of ontogenetic niche shifts, based on the niche comparison at different life-history stages. In agreement with Grubb (1977) and Quero et al. (2008), we chose to analyse niche evolution in a broad range of successive life stages. Three life stages based on size thresholds documented in the database were distinguished: the seedling stage

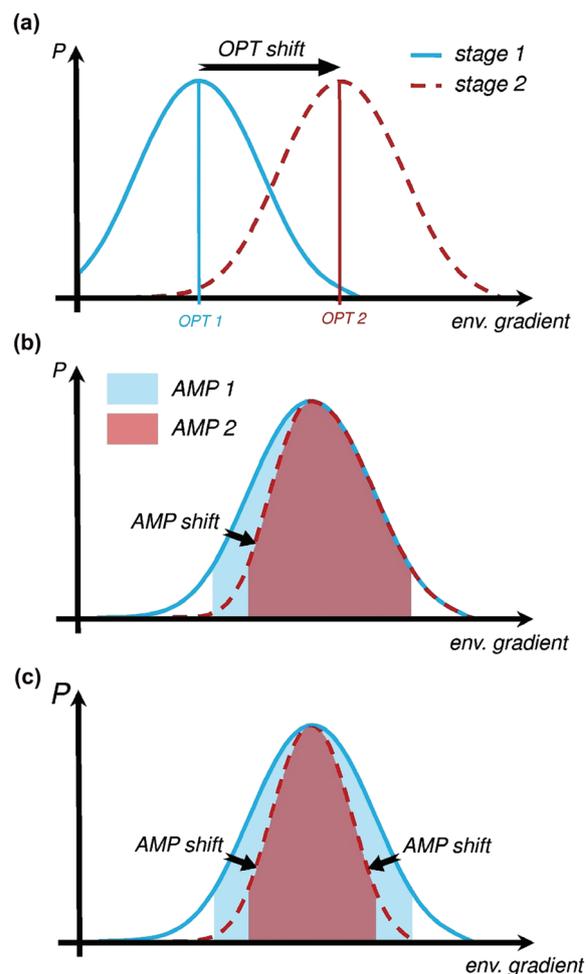


Figure 1. Three theoretical examples of niche shifts measured in the present study. (a) Optimum (OPT) shift: observed when high constraints (e.g. competition and requirements) tend to separate niches along the environmental gradient. (b) Asymmetric shift in amplitude (AMP): affects a niche when constraints act on one part (or several parts) of the gradient, leading to asymmetric niche contraction (shown here) or expansion. (c) Symmetric shift in amplitude: affects a niche when two opposite and globally equal pressures act along the environmental gradient, leading to symmetric niche contraction (shown here) or expansion. Niche shifts can be mixed. P = probability of presence. *env. gradient* = environmental gradient.

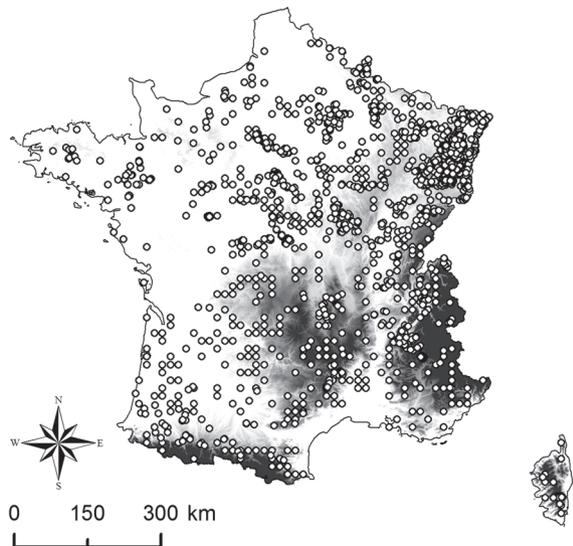


Figure 2. Spatial distribution of the 1963 sites investigated on a gray-scale topographic map of France.

(<0.5 m; coded H), the sapling stage (from 0.5 m to 8 m; coded S) and the tree stage (>8 m; coded T). This thus made it possible to distinguish between two phases in ontogeny: growth (i.e. the transition from H to S and from S to T) and recruitment (i.e. the transition from T to H, characterised by reproduction, dispersion, and seedling establishment).

To derive acceptable ecological niche models, we examined species that met a presence criterion of more than 30 occurrences in at least two life stages (mean species occurrence [standard deviation] = 194 [182]). We focused on 23 temperate tree species belonging to nine phylogenetic families, including angiosperms and gymnosperms: *Aceraceae* (*Acer campestre*, *A. platanoides* and *A. pseudoplatanus*), *Betulaceae* (*Betula pendula*, *B. pubescens* and *Carpinus betulus*), *Fagaceae* (*Fagus sylvatica*, *Castanea sativa*, *Quercus humilis*, *Q. petraea*, and *Q. robur*), *Oleaceae* (*Fraxinus excelsior*), *Pinaceae* (*Abies alba*, *Picea abies* and *Pinus sylvestris*), *Rosaceae* (*Prunus avium*, *Sorbus aria*, *S. aucuparia* and *S. torminalis*), *Salicaceae* (*Populus tremula*), *Tiliaceae* (*Tilia cordata* and *T. platyphyllos*), and *Ulmaceae* (*Ulmus minor*).

Environmental variables included in niche models

To avoid the potential confounding effects of niche dimensions other than the nutritional one, the environmental variables were selected to cover the main factors of plant species distribution (energy, water and nutritional resources; Coudun et al. 2006). The available energy was represented by the mean temperature of the growing season, taken as April–September ($Tm49$). The available water was represented by the summer climatic water balance (CWBs; precipitation – potential evapotranspiration, based on the work of Turc (1961), summed from July to August). Mean monthly temperature and water balance data for the period 1961–1990 were extracted from the meteorological model AURELHY spatialised at a 1-km² resolution (Bénichou and Le Breton 1987).

The C:N ratio and base saturation rate (BS) were used to characterise the nutritional resources available to tree species. The C:N ratio is an index of microbial activity and

nitrogen availability (Aber et al. 1998): $C:N = [C]/[N]$. Here, C:N values vary from 10 to 40. Low C:N values are found on favourable sites with high microbial activity and nitrogen supply (Andrianarisoa et al. 2009). The BS is the relative abundance of base nutrients in the exchange complex: $BS = 100 \times ([Ca] + [Mg] + [K])/([Ca] + [Mg] + [K] + [Al] + [H])$. The BS has a gradient from close to 0 for sites with high Al content and/or low base nutrient supply to 100% for favourable sites with high availability of base nutrient cations and without Al toxicity (Cronan and Grigal 1995). Each variable was measured in the laboratory from the upper organo-mineral A layer of sample soils. Soil samples were air-dried and sieved at 2 mm. Exchangeable Ca, K, Mg and Al were extracted at the soil pH and identified by spectrometry. Protons were identified by titration. The total carbon and nitrogen contents were determined by the Anne (chromic acid digestion) and Kjeldahl methods, respectively (Kjeldahl 1883, Anne 1945). The correlation between C:N ratio and BS was very low over the sample ($R^2 = 0.175$).

Modelling method

Generalised additive models (GAM; Hastie and Tibshirani 1990) with binomial likelihoods were used to model the environmental dependence of the presence/absence of each species at the three different life-history stages considered. GAMs do not require any assumption regarding the shape of the response curves to environmental factors (Oksanen and Minchin 2002). We fitted all niche models through the equation $g(P_{species, stage}) = s_1(Tm49) + s_2(CWBs) + s_3(C:N) + s_4(BS)$, where g is the logistic link function, $P_{species, stage}$ is the probability of presence, conditional to the environmental state, estimated for one species and life-history stage, and s_x are smoothing functions for environmental indicators, estimated non-parametrically with local cubic splines. We limited the degrees of freedom of the smoothness to four. We assessed the effect of the explanatory variables in the niche model by an analysis of deviance (Hastie and Tibshirani 1990). We also computed D^2 values for each model: $D^2 = 100 \times (null\ deviance - deviance\ model)/null\ deviance$. D^2 represents the percentage of deviance explained by the model and was used to assess the performance of the fitted models (Yee and Mitchell 1991).

Estimation of niche parameters with bootstrap simulations

We estimated the niche parameter values from the partial response curves for the C:N ratio and BS, extracted from the niche models. Using partial response curves allowed us to demonstrate the effect of the nutrient variables on the species occurrence, once the other environmental variables were taken into account. For accurate estimation of niche parameters, we used a bootstrap approach. For each species, life-history stage, and nutrient gradient, we estimated the empirical bootstrap distribution of the niche parameters from n bootstrapped niche models and computed the mean value as the best estimator of the niche parameters.

Two parameters were used to summarise the niche characteristics (ter Braak and Looman 1986): the ecological optimum (OPT) and the ecological amplitude (AMP). OPT is

the ecological gradient value for which the probability of presence is maximal. AMP is the ecological gradient range in which the presence conditions are optimal. It was computed as the range containing 80% of the distribution of probability of presence (Gégout and Pierrat 1998). This way of measuring the amplitude allows a clear numerical comparison between regions and is applicable to any response shape (symmetric and asymmetric). We computed the OPT and AMP values from 5000 bootstrapped niche models (Fig. 3).

We postulated that ontogenetic niche shifts, in addition to OPT (Fig. 1a) and symmetric AMP shifts (Fig. 1c), may affect the shape of the ecological response curves. Asymmetric shifts may also affect AMP, through expansion or restriction in one part of the niche (Fig. 1b). For this reason, we defined and compared the partial amplitudes of successive life-history stages in both the oligotrophic (AMPo) and eutrophic (AMPe) parts of the nutritional gradient. Oligotrophic and eutrophic conditions were separated by the OPT position. We assessed AMPo and AMPe as described above, i.e. as the range containing 80% of the distribution of probability of presence on each part of the gradient. To avoid any bias in the comparison of partial amplitudes between life-history stages, we compared them along an equal nutrient gradient range (defined as the minimum gradient range where the probabilities of presence of both life stages were higher than 0) and between life stages undergoing an OPT shift of less than 10% of the ecological gradient.

To standardise the range and sense of variation in nutritional variables, we expressed them as percentages. The C:N ratio values were reversed, so that the standardised gradient exhibits an increasing nutrient supply. First, we compared the OPT, AMP, AMPo, and AMPe values over the three life stages. Ecological niche shifts (S) were identified by niche parameter differences between successive life-history stages: $S_{(species, stage 2, stage 1)} = np_{(species, stage 2)} - np_{(species, stage 1)}$, where np are the niche parameter values of both life-history stages (stages 2 and 1 are the last and early stages in the ontogeny phase, respectively). To determine the general pattern among temperate species, we analysed the niche shifts by considering the 23 species simultaneously (species were not

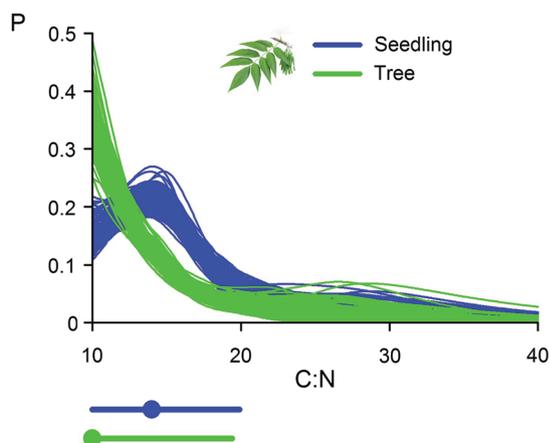


Figure 3. C:N ecological response curves ($n = 100$ bootstraps) of *Fraxinus excelsior* in the seedling (H) and tree (T) stages. Optima positions and niche amplitudes computed from the 100 fitted curves are shown by points and lines, respectively, below the figure. P = probability of presence.

analysed individually). The nutritional niche shifts were tested by non-parametric tests (the Kruskal–Wallis rank sum test [KWt] and Wilcoxon signed-rank test [Wt]). In order to assess the relative importance of ontogenetic shifts in the nutritional niche separation of the 23 temperate tree species, we evaluated the respective weights of both ontogenetic stage and interspecific differences in the variation of niche parameters (only OPT and AMP were tested), using an analysis of variance (ANOVA). The importance of ontogenetic niche shifts was measured using the decomposition of variation: $100 \times (SS_{ont}/SS_{tot})$, where SS represents the ontogenetic portion (ont) and the total (tot) of the sum of the squares. All computations were performed in the R environment (R Development Core Team 2010). We used the GAM package (Hastie 2010) to derive the ecological niche models.

Results

All ecological niche models computed from the 5000 bootstraps were significant (comparison to null model by analysis of deviance: $p < 0.05$). The environmental factors used to model the ecological niches were better predictors in the older than early life stages (see the increase in D^2 values over ontogeny in Table 1). The nutritional dimensions were significant in more than 85% of the bootstrapped niche models (Table 1). This percentage did not differ significantly over ontogeny (KWt: $DF = 2$, $p = 0.38$).

Niche optimum shifts

The positions of optima (OPTs) changed over ontogeny (KWt: $DF = 2$, $p = 0.011$) (Fig. 4). We reported that tree stage mainly occurred in higher nutritional conditions than early life stages: +15.3% [SD = 22.6] and 5.2 units [SD = 5.3] along the BS and the C:N ratio gradient on average, respectively (Fig. 3, 4). We observed this pattern in 88.9% of cases. During growth, the OPT shifts were significant and were sharper from sapling to tree stage (mean shift [SD] = +11.1% [16.8] of nutritional supply, paired Wt: $p < 0.001$) than from seedling to sapling stage (mean shift [SD] = +4.8% [23.1], paired Wt: $p = 0.031$). The recruitment phase (transition from T to H) displayed high and significant OPT shifts towards nutritional supplies lower than those in the adult stage (mean shift [SD] = -16.3% [20] of nutritional supply, paired Wt: $p < 0.001$, Fig. 4).

We found that both ontogeny (ANOVA: $DF = 2$, $p < 0.05$) and interspecific differences (ANOVA: $DF = 22$, $p < 0.001$) contributed significantly to the separation of nutritional optima among the 23 temperate tree species. Ontogeny-related and interspecific differences explained 4.5% and 60.6% of the variation of nutritional optima positions, respectively.

Niche amplitude shifts

We observed no significant change in niche amplitude (AMP) over the entire lifespan of the species (KWt: $DF = 2$, $p = 0.68$). However, significant opposite shifts were reported over the growth phase (paired Wt: $p = 0.039$): niche enlargement from seedling to sapling stage (mean shift

Table 1. Comparison of ecological niche models derived for each tree species and life-history stage. Results were computed from 5000 bootstrapped niche models. D^2 is the mean value of the percentage of deviance explained by the model (standard deviations are in parentheses). BS (for base saturation rate) and C:N (for C:N ratio) represent the percentage of bootstraps within the nutrient variables that are significant (analysis of deviance: $p < 0.05$). H = seedling stage; S = sapling stage; T = tree stage.

Species	D^2 (%)			BS (%)			C:N (%)		
	H	S	T	H	S	T	H	S	T
<i>Abies alba</i>	27.8 (1.9)	34 (1.9)	45.4 (2.1)	81.5	82.4	76.4	100	99.9	100
<i>Acer campestre</i>	24.9 (2.2)	29.6 (1.9)	34.8 (2.2)	100	100	100	99.9	98.3	82.1
<i>Acer platanoides</i>		18.8 (2.8)	24.4 (3.9)		99.9	92.4		84.6	77.8
<i>Acer pseudoplatanus</i>	14.5 (1.6)	19 (1.8)	26.4 (2)	98	100	100	96.2	100	100
<i>Betula pendula</i>	27.5 (4.7)	19.9 (2.8)	18.9 (1.9)	99.7	99.5	100	17	99.4	39.3
<i>Betula pubescens</i>		35.5 (5.2)	29.1 (4.1)		73	89.7		86.8	75.2
<i>Carpinus betulus</i>	20.4 (2)	24.8 (1.6)	29.1 (1.6)	96.9	99.9	100	100	100	100
<i>Castanea sativa</i>	21.2 (2.6)	22.9 (2.3)	23.4 (2.2)	99.1	100	100	55.1	96.3	98.6
<i>Fagus sylvatica</i>	11.4 (1.2)	14.9 (1.3)	18.9 (1.4)	17.8	99.6	97.2	100	100	100
<i>Fraxinus excelsior</i>	19.3 (1.6)	19 (1.7)	31.2 (2)	100	100	100	100	100	100
<i>Picea abies</i>	32 (2.9)	30.8 (2.2)	31.7 (2.1)	99.8	56	34.8	85.1	99.7	89
<i>Pinus sylvestris</i>	27.6 (5)	29.2 (3.5)	16.3 (2)	96.8	52.1	81.6	97.3	100	100
<i>Populus tremula</i>	22 (3.1)	20.6 (2.7)	17.9 (2.2)	99.9	99.6	97.4	31.2	48.8	55.6
<i>Prunus avium</i>	15.9 (2)	16.1 (1.7)	17.4 (1.7)	79.3	99.9	99.8	100	100	100
<i>Quercus humilis</i>	41.1 (5.2)	38.6 (3.9)	36.9 (2.9)	99.9	100	100	89.2	87.7	97.6
<i>Quercus petraea</i>	12.9 (1.8)	16.9 (1.9)	25.5 (1.6)	82.5	99.5	96.7	99.9	100	100
<i>Quercus robur</i>	14 (2)	21 (2.5)	23.7 (1.5)	75.4	93.6	38.8	69.2	32.9	100
<i>Sorbus aria</i>	23.8 (4)	20 (2.1)	24.9 (2.5)	99.9	100	100	97.2	100	93.1
<i>Sorbus aucuparia</i>	27.7 (2.6)	22.1 (1.9)	30.2 (3.7)	90	67.9	10.5	94.5	83.9	19.3
<i>Sorbus torminalis</i>	21.1 (2.3)	22.5 (2)	20.7 (2)	93.3	98.5	100	99.2	100	99.6
<i>Tilia cordata</i>		22.3 (2.9)	25.7 (3)		69.1	68.8		100	87.7
<i>Tilia platyphyllos</i>		28.4 (4)	41.4 (4.5)		100	100		76	51.1
<i>Ulmus minor</i>		34.3 (3.7)	40.9 (3.3)		100	100		91.4	97.6
All species	22.5 (7.9)	24 (7)	27 (8.2)	89.4	91.2	85.8	85	91	86.3

[SD] = +4.5% [11.6]), followed by niche restriction from sapling to tree stage (mean shift [SD] = -3.5% [14.05]).

The niche amplitude over ontogeny evolved differently in oligotrophic and eutrophic conditions (Fig. 5). During tree growth, the nutritional niche enlarged significantly in nutrient-rich conditions from seedling to tree stage (mean shift [SD] = +3.6% [6.1]) (Fig. 5). In contrast, significant niche restriction occurred in nutrient-poor conditions from sapling to tree stage (mean shift [SD] = -2.6% [11.5]) (Fig. 5). Conversely, recruitment led to a significant niche restriction under high resource availability (mean shift [SD] = -8.5% [7.3]) and to significant niche expansion under low resource availability (mean shift [SD] = +2.8% [12.9]) (Fig. 5).

We found no significant contribution of ontogenetic niche shifts to the differences in nutritional amplitude among the 23 temperate tree species (ANOVA: DF = 2, $p = 0.71$). Only the effect of species explained the differences in the nutritional amplitude (ANOVA: DF = 22, $p < 0.001$).

Discussion

The effects of ontogeny on the ecological niche of plant species – long-lived tree species in particular – remain largely unknown. Because the forest ecosystems in which tree species develop are mainly nutrient-constrained (Tamm 1990), we postulated that shifts in nutritional niche occur over the species' lifespan, and that later life-history stages tend to be more nutrient-demanding. Using an appropriate

methodology to carefully control the effects of other water and energy factors on the probability of presence of species, we investigated shifts in the realised niche over ontogeny along the nutritional gradients for 23 temperate tree species. A working assumption was that true ontogenetic shifts in the fundamental niche of species, if they exist, result in a selection process of species individuals, and can be attested in the realised niche, assessed from presence/absence data.

We tried to avoid confounding factors (water and energy resources, for which we used the summer water balance and mean temperature of the growing season) in the assessment of ecological niches. We also tried to avoid arbitrary mathematical formulations of the response curves, since asymmetric shifts should be allowed. Therefore, we used non-parametric generalized additive models (GAM). GAMs are sensitive to border effects and multi-modal response curves (Oksanen and Minchin 2002). For these reasons, we derived niche models with strong smoothing and computed the niche parameters by bootstrapping (Heikkinen and Makipaa 2010). Our life-history stage classification was based on three classes of tree size (Methods). Using size rather than age as a proxy for developmental stage is consistent with the size-dependence of tree growth and most functional processes (West et al. 2001, Peñuelas 2005).

In the 23 species studied, we have shown significant shifts in the nutritional dimension of the niche over life stages. We first highlighted a general pattern (representative of 88.9% of cases studied), which is especially marked from sapling to tree stage, in which the

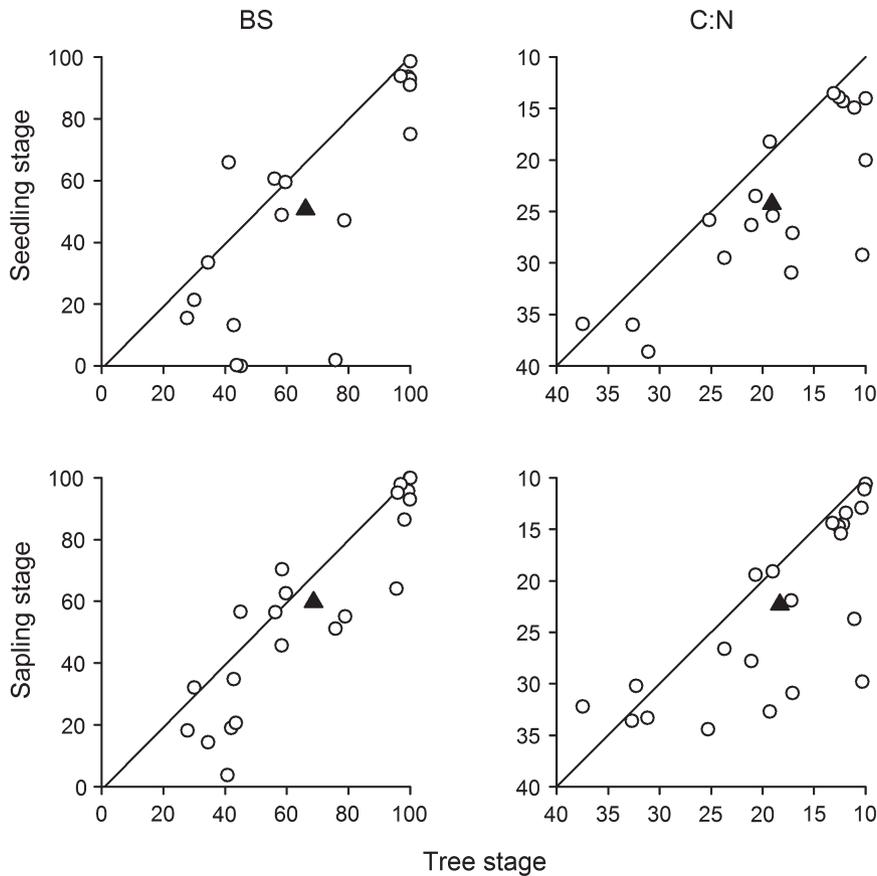


Figure 4. Optima positions of the tree species on the BS (expressed in percent) and C:N gradients for the three life-history stages. Tree species plotted are those for which an ecological response curve was derived. Points indicate species optima positions. Black triangles represent the scatter plot barycentre. Optima positions below the straight line ($y = x$) indicate a better nutritional resource supply in the tree stage than in earlier stages. To maintain the same optimum shift signification between nutrient gradients, the C:N values appear in decreasing order on the axes (because low C:N values indicate the best N-availability). BS and C:N values are not standardised.

nutritional niche converged towards conditions of nutrient-richer supply (Fig. 6). Second, successive asymmetric shifts affected nutritional niche amplitude over ontogeny, leading to niche restriction (from sapling to tree stage) and niche expansion (from seedling to sapling stage and

from sapling to tree stage) in oligotrophic and eutrophic conditions, respectively, during tree growth (Fig. 6). Conversely, niche contraction in nutrient-rich conditions and both niche expansion and an optimum shift towards nutrient-poorer conditions led to seedling development

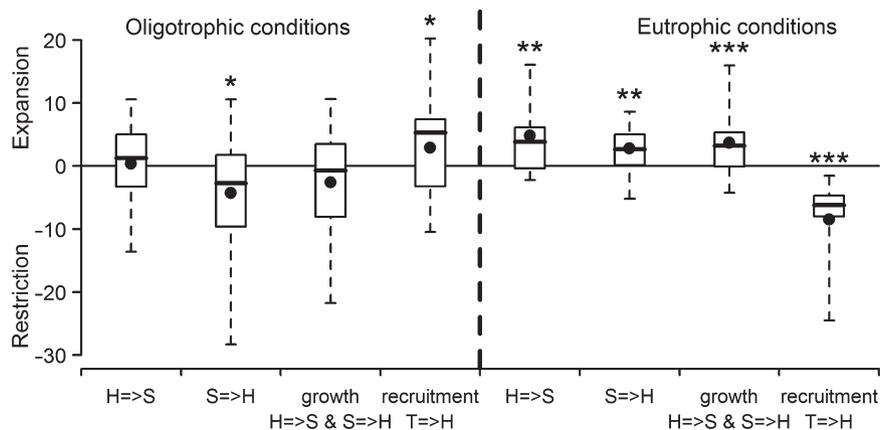


Figure 5. Niche amplitude shifts over ontogeny in both oligotrophic and eutrophic conditions in quasi optimum stability conditions (OPT shift <10% of gradient). Developmental transitions are indicated by arrows (" $=>$ " = towards; H = seedling; S = sapling; T = tree). Boxes represent the inter-quantile range (25th to 75th percentile; median as horizontal segments; mean as points), and whiskers indicate the 5th and 95th percentiles. Significant shifts are highlighted by non-parametric paired-sample Wilcoxon signed rank tests (one-sided difference; significance: * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$).

in oligotrophic conditions during recruitment (Fig. 6). The coherence between optimum shifts and asymmetric amplitude shifts over the species' lifespan (observed when optimum shifts were small) suggested a sequential response of nutritional niches to increased nutritional constraints: when such constraints are minor, only niche amplitude is affected (Fig. 1b–c). Shifts in the optimum are observed with increasingly severe constraints (Fig. 1a).

Increase in nutritional requirements over tree species' lifespan

The observed shifts were identified by comparing the average response of species populations documented in the EcoPlant database and partitioned according to life-history stages. The ecological niche of the seedling stage is an instantaneous picture of conditions required for tree species establishment. In contrast, the realised niche of the adult stage integrates all the variations in environmental conditions experienced over the lifespan. Hence, in addition to true ontogenetic effects, global or local temporal changes in the environment may cause these apparent shifts (Lenoir et al. 2009).

Over the last century, temperate forest ecosystems have undergone global nitrogen enrichment due to atmospheric deposition, which has caused both eutrophication and base cation depletion through soil acidification (Vitousek et al. 1997, Erisman and de Vries 2000, Lövblad et al. 2004). In France, nitrogen enrichment has remained moderate over the last decade at levels of deposition not exceeding $0.0015 \text{ kg m}^{-2} \text{ year}^{-1}$ (Croisé et al. 2005). Were the long-term anthropogenic soil changes to account for the apparent niche shifts reported, older stages would be expected to occur mainly under conditions of both richer N and poorer base cation availability, as observed by Thimonier et al. (1994) in northeastern France. Here, the temporal niche changes observed over species' lifespan are consistent with

eutrophication but not with acidification and base cation depletion hypothesis. According to this and because increasing nitrogen concentration contributes greatly to soil acidification (Vitousek et al. 1997, Erisman and de Vries 2000), the atmospheric deposition seems unconvincing as the single cause of apparent niche shifts towards higher N-availability.

Local changes in soil conditions related to ecosystem maturation or changes in species composition (plant–soil interactions) may also play a role in these apparent niche shifts. While such interactions are acknowledged in tree species, they however appear in contradiction with our finding. In general (except e.g. nitrogen-fixing species), tree species tend to depress the nutritional status of forest soils, and participate to soil acidification (Binkley and Richter 1987, Van Breemen and Finzi 1998, Ehrenfeld et al. 2005). This relies on several mechanisms including: (1) an increase in the nutrient demand as trees grow, implying increased nutrient uptake and sequestration in the living biomass (Binkley and Richter 1987), (1) a net flux of protons in soils, resulting from root uptake exchanges (Binkley and Richter 1987, Ehrenfeld et al. 2005), and (3) the fall of low-quality litters, of high lignin content, favouring carbon accumulation and the release of organic acids in forest soils (Binkley and Richter 1987, Binkley and Giardina 1998, Ehrenfeld et al. 2005). Soil acidification has been evidenced specifically in several genus, e.g. *Picea* (Binkley and Giardina 1998), *Pinus* (Ehrenfeld et al. 2005), *Fagus* (Finzi et al. 1998, Godefroid et al. 2005) and *Quercus* (Finzi et al. 1998). Conversely, we found that the tree stage of these genus occurred in better nutritional conditions than early stages (*Picea abies*: +45%; *Pinus sylvestris*: +12%; *Fagus sylvatica*: +8.6%; *Quercus humilis*: +8.5% on average along the BS gradient). Moreover, nutritional niches were derived from vegetation plots sampled in mature forest stands (mean tree canopy cover = 69% [computed from 858 plots for which information was available]) and not along forest succession stages involving soil

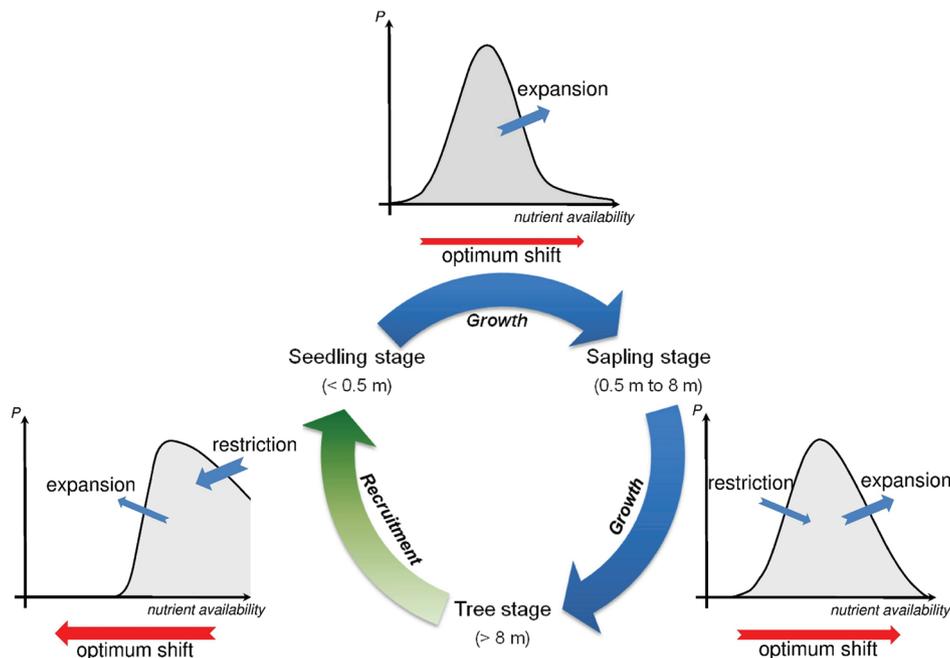


Figure 6. Main nutritional niche shifts over the ontogeny of temperate tree species. Arrows represent shifts leading to the nutritional niche in the next life-history stage. Arrow thickness varies with the intensity of the niche shift. P = probability of presence.

changes during stand maturation (Godefroid et al. 2005). The reported apparent shift towards higher soil nutritional status over ontogeny is thus in conflict with the plant–soil interaction hypothesis with respect to soil nutritional status.

Ontogenetic shifts in realised niche encompass changes in both abiotic requirements, but also biotic interactions during the species' lifespan (Young et al. 2005). Nutrient allocation studies performed over the complete tree lifespan have found that nutrient and biomass accumulation are very similar (Peri et al. 2006), suggesting that later life-history stages tend to be more nutrient-demanding. In the present study, both the higher mortality rate in nutrient-poor conditions and ontogenetic niche convergence towards nutrient-richer conditions are consistent with this hypothesis. This effect on niche shifts may also be strengthened by the high Al concentration in acidic soils (with low BS), leading to toxicity effects and higher mortality (Cronan and Grigal 1995). Under the competition hypothesis, we would expect that higher competitive ability of the tree stage may inhibit seedling and sapling growth and/or suppress individuals in oligotrophic conditions (Schwinning and Weiner 1998). Both niche restriction in the oligotrophic conditions and niche shift towards better nutrient supply during growth (Fig. 6) were found to be consistent with this hypothesis. However, belowground competition subsides with improved nutrient availability (Wilson and Tilman 1991, Coomes and Grubb 2000). Because the niche shifts were also observed between life-history stages in eutrophic conditions (Fig. 4), competition alone cannot drive the observed niche shifts.

Among the different drivers likely to change the nutritional realised niche in temperate tree species development, true ontogenetic niche shifts, including increases in growth requirements, appear to be the most plausible explanation. Biotic interactions and environmental changes may counteract (e.g. acidification, plant–soil interaction) or enhance (e.g. eutrophication, competition) ontogenetic niche shifts.

Importance of ontogenetic niche shifts

In contrast to mobile species, plants cannot actively seek environmental conditions that maximise survivorship and growth in each life-history stage. Considering this major constraint, ontogenetic niche shifts during growth can only result in species population mortality. Thus, the ontogenetic niche convergence towards nutrient-richer conditions (Fig. 6) implies that mortality occurs in oligotrophic conditions, following increased nutritional requirements during growth. Because these shifts were inferred from presence/absence data (which is less sensitive than abundance data), ontogenetic niche shifts appear strong enough to induce local extinction in the less favourable sites for species. Nevertheless, the successive asymmetric shifts in niche width highlighted the importance of species' tolerance faces biotic and abiotic constraints over ontogeny (Pearman et al. 2008). The observed ontogenetic niche shifts are therefore interpreted as a consequence of an intra-specific selection process where individuals established in eutrophic conditions have the maximal fitness. Consistent with this interpretation, several studies have shown that tree species undergo selection towards higher nutrient, light, water availability, and/or water-use efficiency (Parrish and Bazzaz 1985, Donovan

and Ehleringer 1991, Stohlgren et al. 1998, Cavender-Bares and Bazzaz 2000, Quero et al. 2008). That numerous species exhibit temporal niche shifts towards high nutrient, light and water availability may thus be interpreted as the first evidence of a general niche shift process towards better resource supplies during plant development.

A number of authors have suggested that the ecological niche of early life stages is the main factor defining the species' niche space and distribution (Grubb 1977). It has been demonstrated that the juvenile niche becomes important in stress/disturbance conditions (Anderson et al. 2009) and can have long-lasting effects on the form and shape of plant species (Poorter 2007). Both the highest environmental dependence of tree stage occurrence (Table 1) and the intra-specific selection towards higher nutritional conditions over ontogeny found in this study indicate that the mature life-history stage is crucial. Because seedling establishment is constrained by adult-stage location and reflects the original niche position (Anderson et al. 2009), both the juvenile and adult stages are important in determining the species' niche. In the actual context of environmental changes, the integration of ontogenetic variations into the niche concept (especially as they relate to the juvenile and adult life stages) should improve the accuracy of species distribution models. It should also make it easier to distinguish between environment- and ontogeny-driven distribution shifts with time.

In tree communities, niche separation and life-history tradeoff are known to play a significant role in species' coexistence and community organisation (Bigelow and Canham 2002, Silvertown 2004). The high inter-specific niche differentiation that we report underlines the importance of niche separation. However, species' development can interfere greatly with the main drivers of community organisation (Comita et al. 2007, Anderson et al. 2009): ontogenetic niche convergence towards high resource availability was shown to also contribute to niche differences in the temperate tree species (by up to 4.5%). It would be even higher if one-to-one comparisons of neighbouring species on the nutrient gradients were considered. The theories of both coexistence and community organisation should be expanded to consider ontogenetic niche shifts.

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