3.3 Forest-specific diversity of vascular plants, bryophytes, and lichens

Wolf-Ulrich Kriebitzsch, Helga Bültmann, Goddert von Oheimb, Marcus Schmidt, Hjalmar Thiel and Jörg Ewald

In temperate forests, a great diversity of vascular plants, bryophytes, and lichens exists

These organisms make up the different forest strata (the tree, shrub, herb, and moss layer) and can be classified according to the substrate they live on as epigeic (in/on the soil), epiphytic (on another living plant), epixylic (on deadwood), or epilithic (on rock surfaces). The tree layer makes up the forest's structure, constitutes most of the biomass in the forest, and controls many important ecosystem functions and services. Furthermore, the structure, composition, and diversity of the overstorey exert substantial influence on the understorey and epiphytes by determining light availability, soil conditions, bark pH, microclimate, and forest floor quality (Braun-Blanquet 1964, Ellenberg and Leuschner 2010).

The understorey, and most notably the herb layer, hosts the greatest diversity of vascular plants, both in terms of species richness and phenological, structural, and functional differentiation (Gilliam 2007). Understorey vegetation also contributes to energy flow and element cycling and offers habitat and food for many organisms. Juvenile woody plants (seedlings, sprouts and saplings) are a transient part of the herb layer, whence they either grow into higher strata or die off. Understorey dynamics may therefore exert an important influence on forest regeneration and dynamics.

Epiphytic and epixylic bryophytes and lichens represent another highly significant component of overall forest diversity, whose richness outnumbers that of vascular plants in many forest types

Instead of rooting in soil, epiphytes obtain moisture and nutrients from the atmosphere. This enables them to grow on otherwise uninhabitable surfaces and to use a wide range of habitat conditions that can be very different from those of the forest floor (Rose and

Coppins 2002). Due to low growth rates epiphytes depend on perennial plant structures such as the bark of stem bases, trunks, branches, and, rarely, leaves of evergreen trees. The surface areas of these structures normally exceed the ground area of forests, greatly extending the space colonisable by plants. Dead and decaying wood provides substrate for epixylic bryophytes and lichens. Its quality changes with ongoing decay. This process is driven by fungi, insects, and other animals and is accompanied by a succession of epixylic vegetation. Coarse woody debris and the dead parts of old living trees are especially important in providing a particularly suitable physical and chemical environment for numerous epixylics.

Many vascular plants, bryophytes, and lichens in forests occupy highly specific realized ecological niches along certain environmental gradients. These species therefore lend themselves as indicator plants for resource availability or old-growth forest sites

Forest plant diversity is highly variable across climatic, geographic, topographic, edaphic, and light gradients (Ellenberg and Leuschner 2010). Besides these factors, diversity may be affected by historical land use and current forest management (Verheyen et al. 2003), dispersal limitation, herbivory, and chronic resource alterations caused by global change (e.g. nitrogen deposition, climate change). Epiphytic, epixylic, and epilithic cryptogams are particularly responsive to microclimatic as well as physical and chemical substrate properties, which directly depend on tree age and diameter, bark texture, or decay stages of deadwood (Rose and Coppins 2002). In addition, ubiquitous plant species and even species from open habitats such as grasslands occur in forests, which may result in high species richness of disturbed forests. Therefore, in evaluating diversity, completeness, typical development, and naturalness, it is necessary to distinguish forest plant species according to how closely they are associated with forests. The most promising approach for this is an extensive expert system based on a consistent methodology.

Vascular plants have the lowest and lichens the highest proportion of extinct and threatened species in Central Europe

For vascular plants and bryophytes, the larger share of red-listed species is typical for open land, whereas the reverse is true for lichens, of which the majority of threatened species depend on forest habitats (Hauck et al. 2013, Schmidt et al. 2011). Thus, with 58 % threatened and 33 % extinct or threatened by extinction, epiphytic lichens are top-runners on red lists. Many red-listed epiphytic forest bryophytes and lichens have not fully recovered from heavy air pollution (smoke damage by SO_2 and NO_x caused by unfiltered burning of fossil fuels), which has been largely controlled since the 1990s (Bobbink et al. 1998).

> *Lichens, which comprise a large number of old-growth and deadwood specialists, are particularly sensitive to human intervention*

Plant species are threatened through a range of factors, the most important being habitat fragmentation and destruction, change of management practices, eutrophication, amelioration, and drainage (Verheyen et al. 2003). The largest group of threatened forest vascular plants and bryophytes, as well as soil-dwelling reindeer lichens, requires a combination of oligotrophic soils and open canopies as found in pine and oak forests. These stress-tolerant strategists, which also include several rare tree species, are easily overgrown by nitrophytic and shade-tolerant competitors. Broad-scale nutrient enrichment tends to level out species composition to the disadvantage of rare and threatened species, resulting in homogenized landscapes (Bobbink et al. 1998). Once widespread in pre-industrial multiple-use woodlands and natural oligotrophic early successional forest stages, stress-tolerant strategists survive in forest openings and fringes, often remnants of coppicing and forest pasture, but decline due to nitrogen emissions, self-amelioration, and canopy closure.

> *While continuous cover forestry is obviously detrimental to stress-tolerant plants, it is doubtful whether intensification of modern timber harvesting alone can benefit this species group without simultaneously favouring ubiquitous ruderals and even invasive plants*

In Central Europe, oligotrophic habitats are naturally bound to early stages of successions on immature, skeletal, and sandy soils, as induced by morphodynamics such as river (sandbanks, gravel plains, undercut slopes), slope (rockfalls, landslides) and wind erosion (dunes), and peat bogs fed by rainwater (Figure 49). Such habitats have been largely destroyed by regulation, amelioration, and draining. Many normal forest sites were degraded by exporting biomass through fuel extraction, forest pasture, and litter raking in pre-modern times, creating secondary oligotrophic habitats (Ellenberg and Leuschner 2010).

Under modern emission regimes, driven by agriculture and combustion, restoration of oligotrophic sites requires profound disruptions of the nitrogen cycle such as topsoil removal, which are unusual in forests. Thus, the survival of these species depends on continued or reinstalled historic uses and primary succession after soil removal, as may occur in abandoned sandpits or quarries (Flinn and Vellend 2005).

Box 28. A comprehensive list of forest species of vascular plants, bryophytes, and lichens for Germany

For the first time, Schmidt et al. (2011) provided a comprehensive list of forest species of vascular plants, bryophytes, and lichens for Germany. As an extension of the concept of fidelity, lists of forest species categorize plants according to their affinity to forest vs. open land habitats. Regional differences in species behaviour are accounted for by separate evaluation within three major physiographic regions of Germany ((1) Northern Lowlands, (2) Hillsides and Low Mountains, and (3) Alps). The list of forest plants is differentiated into four groups of species that depend on forest habitats.

Fidelity classes:

1 restricted to forest habitats
- 1.1 largely restricted to closed forest
- 1.2 prefers forest edges and clearings

2 occurring in forest and open land
- 2.1 occurs in forests as well as in open land
- 2.2 may occur in forests, but prefers open land

The lists for bryophytes and lichens mention the substrates on which the species regularly dwell regardless of physiographic region. While some bryophytes and lichens are restricted to one single substrate (Ellenberg et alal. 2001), many have a broader ecological amplitude and are found on several substrate types (Figure 47).

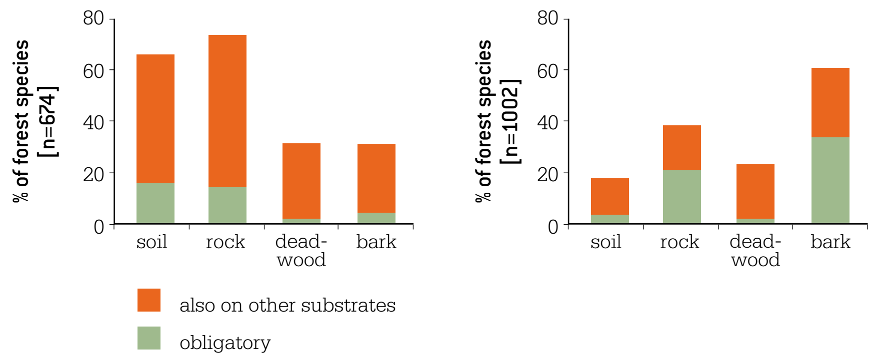

Figure 47. Forest bryophytes (left) and lichens (right) and their substrates: an analysis of the list of forest plants shows that a high proportion of bryophytes and lichens is confined to bark, deadwood, and rocks. Species growing on these substrates require specific conservation measures. Their assessment should complement monitoring of soil vegetation.

In their present form, the lists of forest species for the whole of Germany enumerate 1,216 vascular plants, 674 bryophytes, and 1,002 lichens. The list of vascular plants contains 76 trees, 4 epiphytes, 116 shrubs, and 1,020 herbaceous species.

In total, the three lists comprise 41 % of the vascular plant species, 58 % of the bryophyte species, and 51 % of the lichen species listed in the respective reference lists for Germany. Thanks to the higher ecological heterogeneity, forest species pools of the hillside and low mountain region are distinctly larger than those of the Northern Lowlands. Considering the small surface area, the pools of forest species in the Alps are also remarkable.

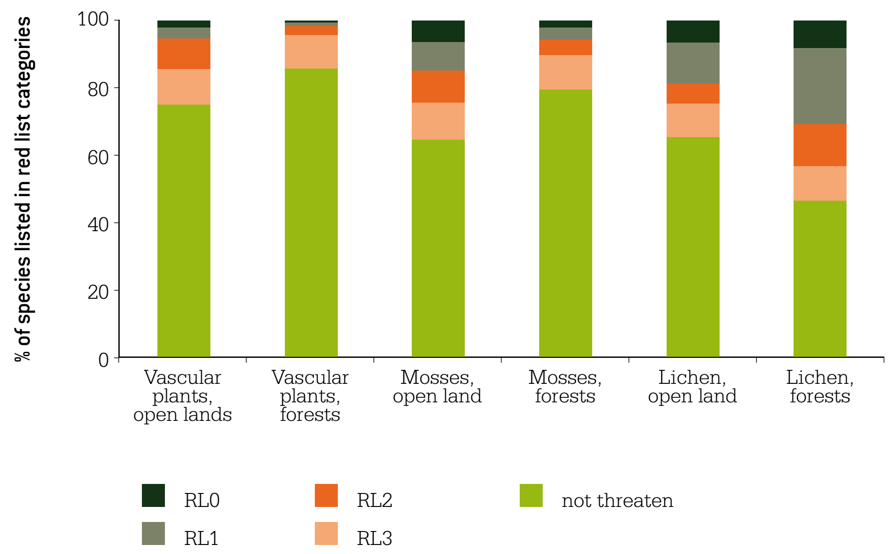

Figure 48. Comparison of red list status of forest plant species (categories 1.1, 1.2 and 2.1) and species of the open land (categories 2.2 and 0) in Germany. RL0: extinct or possibly extinct; RL1: critically endangered; RL2: endangered; RL3: vulnerable. Category "not threatened" subsumes unlisted species as well as all other red list categories.

Draining of wetlands and damming of floodplains have exerted broad-scale effects on forest sites, often leading to improved production, but severe habitat loss for specialised plants

Figure 49. Recurrent morphodynamics of wild alpine rivers initiate primary successions with oligotrophic sites and semi-open successional forests. Photo by J. Ewald.

Figure 50. Oligotrophic Scots pine forest on a raised bog in Upper Bavaria. Photo by J. Ewald.

Another important part of endangered vascular plants and bryophytes depend on wet forest habitats. Forest wetland plants are highly diversified according to nutrient supply, including oligotrophic raised bogs (Figure 50), minerotrophic fens, and alluvial forests. As long as the hydrology is left intact and adapted harvesting technology is employed, sustainable forestry and wetland conservation are compatible or even synergistic (i.e. by favouring oaks and rare tree species). Allowing and re-initialising natural geomorphodynamics may also restore oligotrophic sites in river floodplains, steep mountain slopes, and along coasts.

Epiphytic and epixylic diversity of forest plants in Central Europe has declined in the past 100–150 years due to removal of old trees and deadwood from managed forests

Old, crooked, damaged, and dead trees offer a wealth of microhabitats. Their removal results in a decline of biodiversity. Specialist species depend on such trees (Figure 51; Liira and Sepp 2009). Thus, certain lichen communities require deep furrows of thick, water-retaining bark and other cavities that are sheltered from rain. Bark chemistry on old and damaged trees is often more variable. Stemflow from rot holes in old beech trees raises bark pH locally and thereby supports epiphyte diversity and rare species. Many extinct or red-listed epiphytic bryophytes and lichens are sensitive to air pollution, especially sulphur dioxide and nitrogen oxides (Bobbink et al. 1998, Hauck et al. 2013). Air quality has improved during the last decades, but sensitive species are returning extremely slowly due to dispersal limitation.

Figure 51. Specialist species are solely restricted to old, crooked, damaged, and dead trees. *Lobaria pulmonaria*, Vosges, France. Photo by H. Bültmann.

Figure 52. Rocks are refugia of endangered cryptogams in forested areas, Sauerland, North Rhine-Westphalia. Photo by H. Bültmann.

The hardness, structure, and chemistry of deadwood not only depend on tree species, but also on the size of the deadwood element. In particular, coarse woody debris can retain considerable amounts of water, providing a constantly moist substrate and sustaining a high diversity of epixylics. Species numbers, especially of liverworts, are often particularly high in a microclimate of constant high air humidity. In contrast to vascular plants, which usually profit from enhanced light levels, opening the tree canopy can reduce humidity, damage shade-tolerant species, and may result in a decline of epixylic growth (Rose and Coppins 2002).

A considerable proportion of threatened forest vascular plants, bryophytes, and lichens are bound to special habitats in forests

Biotopes such as springs, streamlets, fens, stones, rocks, or boulder slopes are a characteristic part of many forests (Figure 52). Such sites have ecological conditions that differ from those of the surrounding forest. Their vegetation is specific and adds disproportionally to the diversity of species. Although tree cover or location in a forest is not essential for their existence, these communities depend on shading and a microclimate typically found in forests. Bryophytes and lichens growing on rocks can serve as an example: According to the list of forest plants in Germany (Schmidt et al. 2011), 73 % of forest bryophytes and 39 % of forest lichens use this substrate (Figure 47). These special habitats are protected by law and must be respected by forestry. Shaded and exposed rocks can carry very different assemblages of rare bryophytes and lichens. Both may suffer from changes in meso- and microclimate, as induced by felling (shaded rocks) or dense coniferous thickets (open rocks). Sensitive special habitats require special protection, e.g. against depositing slash.

Figure 53. Ancient deciduous woodland site in the Northern Lowlands near Uelzen (Lower Saxony) with some ancient forest species such as *Anemone nemorosa* and *Melica uniflora*. Photo by M. Schmidt.

Land-use history and habitat continuity has substantial impacts on ecological processes and plant species composition in forest ecosystems

In many parts of Europe, forests have undergone cycles of deforestation and conversion to agricultural land followed by forest recovery, resulting in considerable differences in the composition of understory vegetation between ancient (Figure 53) and recent forests. Former agricultural use impacts species composition directly (local elimination of plants and propagules of forest species) or indirectly (altered environmental conditions, fertilization, and eutrophication, often persisting for centuries; Flinn and Vellend 2005). Because of the direct effects, recent forests have to be recolonised by forest plants. However, ancient forest species are mostly long-lived perennials with the capacity to reproduce clonally, but unfit for long-distance seed dispersal (Verheyen et al. 2003). Like vascular plants, epiphytic bryophytes and lichens differ widely in their ability to recolonise. Some slow dispersers are very specific indicators of forest continuity. Restoration of recent forests is therefore a question of time, spatial arrangement, and connectivity.

As forest cover and history differ between regions, the indicator value of ancient forest species requires accounting for regional differentiation

In the northwestern lowlands of Germany, overall forest cover is low (10 to 25 %), and only one quarter of these forests are classified as ancient (Figure 54). In contrast, the northeastern lowlands have ca. 50 %, and the mountain regions of Germany, where total forest cover is considerably higher than in the lowlands, have some 90 % of ancient forests.

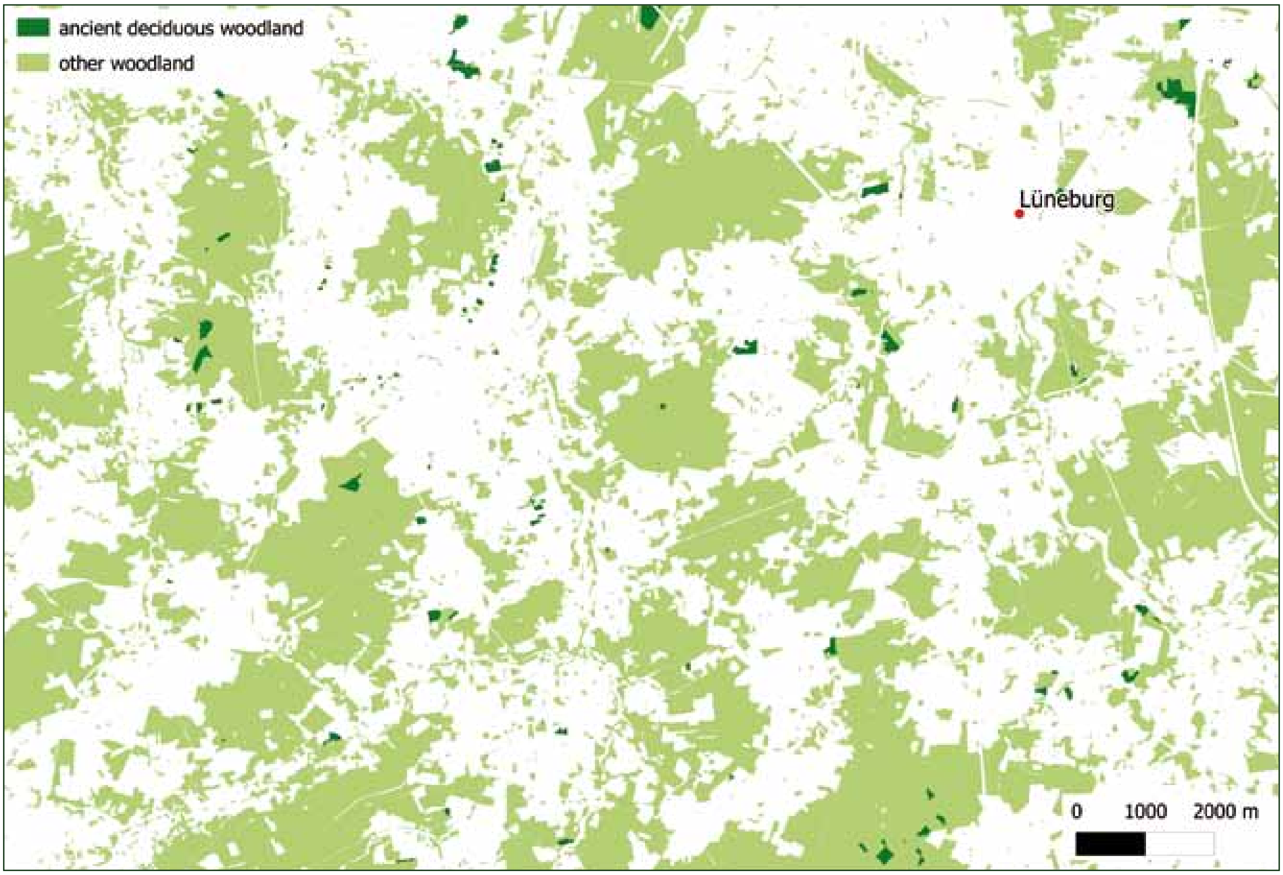

Figure 54. Example for the distribution of ancient deciduous woodland and other woodland in the Northern Lowlands.

Box 29. Recommendations for management

Managing for plant biodiversity must take account of the different requirements of this large number of forest plants. Considering the diversity of life forms and realized ecological niches, there cannot be a single recipe to protect all forest plants. Nevertheless, some general principles can be recommended:

1. Close-to-nature forestry

Forest management should prefer native tree species, and it should aim to retain and emulate elements of natural forest communities. Thus, naturally regenerating native tree species, both of site-specific climax stages and pioneer phases, should be allowed their place in managed forests. Game populations should allow regeneration of all native tree species. Roads and skidding lines should be spaced at distances that leave sufficient area of untouched forest floor for a typical understorey to develop.

2. Respect ecological gradients and habitat diversity

Natural gradients of moisture, pH, and nutrients, as depicted in site maps, offer niches for many different forest plants. Special habitats are protected by EU or regional law if they conform to the respective legal requirements. These special habitats often harbour a large number of rare or endangered species, and, thus, maintaining and restoring these sites has a disproportionally large effect on biodiversity. Special habitats and their surroundings should be excluded from commercial forestry use but managed under a conservation regime. Furthermore, all stages of forest development in proportions corresponding to the natural disturbance regime should be maintained. Thus, the continuous cover strategy may have to be supplemented by concepts to preserve all native tree species and forest community types.

3. Respect old growth structures, deadwood, and groups of large trees with epiphytes

Management should leave and create niches for epiphytic and epixylic bryophytes and lichens that require old trees, deadwood, and certain key tree species. Shade and humidity should be maintained by selective logging and retention. As continuity of microclimate is important for bryophytes and many lichens, it is also essential to retain large groups of trees without harvesting.

4. Respect forest continuity and counteract fragmentation

In agricultural landscapes, especially in Central European lowlands, the value of forest islands for plant conservation depends on historical continuity. Here, conservation management should be focused on ancient forest remnants and their reconnection by habitat corridors. In regions with a low proportion of ancient forest sites, the remaining ancient deciduous forests should not be converted to coniferous or deciduous-coniferous forests for economic reasons.

5. Respect and continue traditional forest management

Traditional forest uses such as forest pasture, coppicing, and coppice-with-standards have almost become extinct in Central Europe and persist only in a few localized regions. Yet many of the older stands still bear legacy features of these practices that can be of high conservation value. Thus, wooded pastures are hotspots of threatened old-growth and deadwood specialists such as beetles and moths, cavity-breeding birds, and saproxylic fungi. Coppicing favours light-demanding organisms, such as rare tree and shrub species with high capacity to resprout, flowering plants, butterflies, and photophytic epiphytes.

High proportions of forest species in the total floras of the three plant groups underpin the great responsibility that forestry holds for preserving biodiversity in Central Europe

All members of the lists of forest species should be treated first and foremost as forest plants, even when they occur in, or even prefer, open land. In the practice of forest conservation, specialists restricted to forest habitats will often be the main focus. However, in the face of increasing pressures on open land habitats (land-use intensification, eutrophication, urbanization), forests are gaining importance as refuges for threatened plants of broader amplitude (Box 28, groups 2.1, 2.2).

References

Bobbink, R., Hornung, M. and Roelofs, J. G. M. 1998. *The effects of air-borne pollutants on species diversity in natural and semi-natural European vegetation. Journal of Ecology 86:717–738.*

Braun-Blanquet, J. 1964. *Pflanzensoziologie. Grundzüge der Vegetationskunde. 3. Aufl., Berlin, Wien, New York. 865 p.*

Ellenberg, H. and Leuschner, Ch. 2010. *Vegetation Mitteleuropas mit den Alpen. 6. Aufl., Ulmer-Verlag, Stuttgart. 1334 p.*

Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., Werner, W. and Paulissen, D. 2001. *Zeigerwerte von Pflanzen in Mitteleuropa. 3. Aufl. Scripta Geobotanica 18:1–262.*

Flinn, K.M. and Vellend, M. 2005. *Recovery of forest plant communities in post-agricultural landscapes. Frontier in Ecology and the Environment 3:243–250.*

Gilliam, F.S. 2007. *The ecological significance of the herbaceous layer in temperate forest ecosystems. BioScience 57:845–858.*

Hauck, M., de Bruyn, U. and Leuschner, Ch. 2013. *Dramatic diversity losses in epiphytic lichens in temperate broad-leaved forests during the last 150 years. Biological Conservation 157:136–145.*

Liira, J. and Sepp, T. 2009. *Indicators of structural and habitat natural quality in boreo-nemoral forests along the management gradient. Annales Botanici Fennici 46:308–325.*

Rose, F. and Coppins, A.M. 2002. *Site assessment of epiphytic habitats using lichen indices. In: Nimis, P.L., Scheidegger, C. and Wolseley, P.A. (eds.) Monitoring with Lichens – Monitoring Lichens. [NATO Science Series IV. Earth and Environmental Sciences Vol. 7]. Kluwer Academic Publishers, Dordrecht, Boston, London. Pp 343–348.*

Schmidt, M., Kriebitzsch, W.-U. and Ewald, J. (eds.) 2011. *Waldartenlisten der Farn- und Blütenpflanzen, Moose und Flechten Deutschlands. BfN-Skripten 299:1–111 p.*

Verheyen, K., Honnay, O., Motzkin, G., Hermy, M. and Foster, D.R. 2003. *Response of forest plant species to land-use change: a life-history trait-based approach. Journal of Ecology 91:563–577.*