Ann. Bot. Fennici 48: 120–128 ISSN 0003-3847 (print) ISSN 1797-2442 (online)
Helsinki 29 April 2011

Forest inventory data reveal stand history from 115 years ago

Michał Żmihorski

Museum and Institute of Zoology, Polish Academy of Sciences, Wilcza 64, PL-00-679 Warsaw, Poland (e-mail: zmihorski@miiz.waw.pl)

Received 19 Feb 2010, revised version received 3 Nov. 2010, accepted 23 Nov. 2010

Żmihorski, M. 2011: Forest inventory data reveal stand history from 115 years ago. — *Ann. Bot. Fennici* 48: 120–128.

The relationship between the present distribution of some vascular plants in managed forests and forest history was investigated in western Poland. A forest inventory report was used as the source of data for plant distribution in the 211 subcompartments of the forest, and archive maps for the stand history assessment. The "history" of a sub-compartment (ancient *vs*. recent) increases the parsimony of the models, as assessed with AIC, explaining understory plant species occurrence. Occurrences of *Vaccinium myrtillus* and *Pteridium aquilinum* appeared to be most reliable predictors of forest history. Among the 110 sub-compartments where the two species were recorded, 103 were covered by ancient forest. The two plant species selected as reliable predictors of ancient forest continuity also appeared to be significant predictors of forest history in the nearby control area. The use of indicator species described in the reports may be an attractive source of knowledge on the ecosystem.

Introduction

Some of the changes in a habitat's structure and its spatial configuration in the landscape may have a lagged impact on the distribution of species found there. As a result, the temporal aspects of habitat–organism interaction have to be considered (Helm *et al*. 2006) to answer the two most fundamental questions in ecology: why is a species present in a particular area and why do so many specimens of the species occur in a given area (Krebs 1994). In the case of temperate zone forest ecosystems, the lagged reaction of forest organisms to changes in forest cover can be driven by two main processes: delayed extinction and delayed colonization — independently of the fact that species' colonization capacities can be limited by the poor habitat quality in recent forests (Baeten *et al*. 2009). First, dispersal abilities of many forest-dwelling organisms are low (e.g. Dzwonko 2001, Verheyen & Hermy 2001, Hedin *et al*. 2008). Therefore, newly created patches of habitat cannot be colonized immediately by plants and animals limited by weak dispersion. This problem affects biodiversity of recent forests, which may remain species-poor despite suitable habitat conditions (Hermy & Verheyen 2007, Fritz *et al*. 2008). For this reason, the continuity of forest habitat is crucial for sustaining poorly dispersing species (Mazgajski *et al*. 2010). Second, some organisms are found not to experience the population decline expected as a result of the rate of their habitat decrease (Hanski & Ovaskainen 2002, Cousins 2009). As a consequence, the species richness of recently and quickly reduced forest patches may be higher than expected given the amount of available habitat (e.g. Vellend *et al.* 2006). Historical habitat distribution can therefore be useful in predicting the current distribution of some species because of lagged colonization as well as lagged extinction.

On the other hand, these lagged dynamics may be considerably disturbed by additional factors, e.g. those related to human activity, such as harvesting or changes in ownership structure, etc. (Wesołowski 2005, Mazgajski *et al.* 2010, Żmihorski *et al.* 2010). One might expect that the considerable and permanent ecosystem transformations taking place in managed forests could weaken the importance of forest history for current species distribution (Bradshaw 2004, Svenning *et al.* 2009). Using a forest for timber production clearly results in reduction of the stand mean age as compared with that in natural stands (Wesołowski 2005). Moreover, some tree species are preferred (e.g. pine) in managed stands, while the importance of others is reduced (e.g. hornbeam), and some non-native species are introduced (e.g. robinia, red oak). As a consequence, managed stands may be weakly related to the local features of a site. Additionally, some timber harvesting and artificial regeneration practices (e.g. deep-soil ploughing) are commonly used to this day.

In light of the facts presented above, an important question arises: can the history of a stand later managed for timber production still provide an explanation for its current species composition? In the present paper, I address the importance of forest history for the present distribution of some vascular plants in managed forests and make an attempt to use indicator species to make predictions about the land-use history.

Material and methods

Study area

The research was conducted in a large (14 000 ha) forest complex located in western Poland (52.8°N, 14.3°E). Before World War II, this region was a part of Germany and was characterized by a higher human population density and less forest cover than today. After the war, a considerable proportion of agricultural land was afforested (Fig. 1).

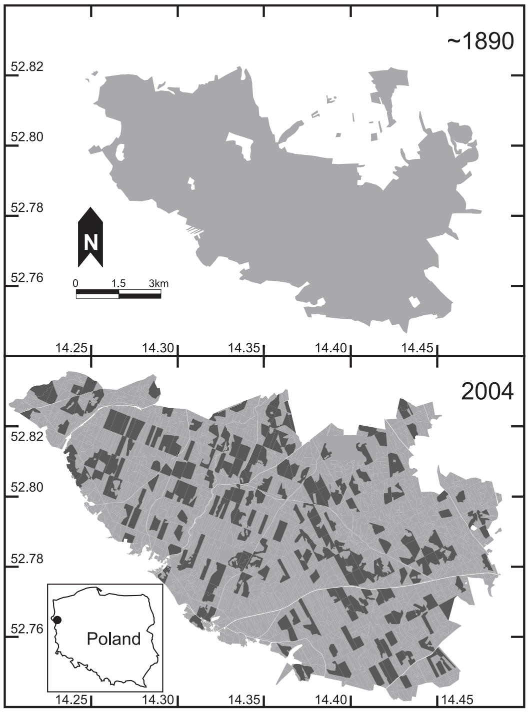

Fig. 1. Distribution of the wooded area (pale grey) in the two periods compared (1890 and 2004) in western Poland. Selected sub-compartments (n = 211) used for the analysis are marked in dark grey in the lower subplot; geographical coordinates are given along the picture borders. Note that both subplots are presented in the same scale.

The forest is dominated by poor, fresh habitats with an acidophilous oak forest (*Fago-Quercetum petraeae*) as the potential vegetation type (Matuszkiewicz 2001). Sand and sandy boulder clay prevail in the area. This has led to the formation of podsols and poor brown soils. Most of the forest area is flat, ca. 30–50 m a.s.l.; however, some parts of the forest complex are located on the overgrown slopes of the Odra river valley. The region is characterized by a relatively mild climate, with a mean annual January temperature of approximately –1.2 °C and a mean July temperature of 18.2 °C. The total annual precipitation is 550 mm and the growing season lasts 220 days (Matuszkiewicz 2001, Kondracki 2002).

During the period analysed (1890–2004), the stand was managed for timber production and is managed in this way to date. The tree stand is dominated by pine (*Pinus sylvestris*) and oak (*Quercus* spp.), with a considerably smaller proportion of the latter. Clear cutting is used as the timber harvesting method, so that open areas are present within tree stands. New stands re-grow as the result of artificial replanting.

Data on understorey plants

Forest inventory data were used as the source of data for understorey plant distribution in the forest complex. I used an official document created as the result of a detailed forest inventory conducted in 2004. During an inventory, every sub-compartment (i.e. forest patch homogenous in term of structure) is visited by an experienced observer who describes many forest characteristics in detail, such as: stand composition, age, mean diameter at breast height for every tree species, timber volume, tree height, forest compactness index and site classification. The observer also notes understorey plants, since this vegetation characteristic can provide important information on soil features, which in turn affect the potential stand composition, its quality, optimal management methods, timber harvesting, etc. According to the standard methodology, the observer notes occurrences of most abundant understory plants.

It seems that there is one possible source of error when analysing relationships between understorey plant distribution and habitat features on the basis of forest inventory data. Plants sparsely distributed in the forest may not be present in the smallest sub-compartments despite the existence of suitable habitat features for them. Therefore, for the analysis I used data from the largest sub-compartments only. Among all the sub-compartments in the forest complex (over 3000), I selected all exceeding 10 ha (n = 211, 14.4 ± 0.29 ha (mean ± SD), range 10.001–31.786). Further analysis presented in this work is based on the 211 sub-compartments only.

For each sub-compartment, I used data on the occurrence (presence *vs.* absence) of all understorey plant species from the forest inventory report. In total, I collected data on the distribution of 33 plant species or groups of species (not all plants were identified to species during the inventory). However, most of the species were characterized by low frequency in the plots, so for further statistics I used data for species whose frequencies exceeding 20% (n = 8 species) in the sub-compartments. The species or groups of species were: (1) *Rubus idaeus*, (2) *Rubus* spp. other than *R. idaeus*, (3) fern *Dryopteris carthusiana*, (4) grass *Calamagrostis epigejos*, (5) moss *Pleurozium schreberi*, (6) fern *Pteridium aquilinum*, (7) bilberry *Vaccinium myrtillus*, (8) grass *Deschampsia flexuosa*.

Explanatory variables

I used four habitat characteristics to describe the current distribution of the plants. First, I used the stand age in each sub-compartment (57.53 ± 1.67 years), since age influences the light conditions on the forest floor. One may expect that more light is available for understorey plants in older forests where stand density is lower (e.g. Gaudio *et al.* 2008). Moreover, stand age indicates the time elapsed since the last timber harvest and artificial replanting, which considerably reduces the understorey vegetation (Godefroid *et al.* 2005). Second, I used the stand type. Because of the high level of habitat homogeneity in the forest complex, only two stand types were recorded: deciduous mixed forest (n = 55 sub-compartments) or coniferous mixed forest (n = 156). One may expect that the stand type influences particular plant species according to their ecological requirements. Third, I checked for the presence of forest at the end of 19th century in the locality of every sub-compartment. For this purpose, I used German maps available for this area (Messtischblätter series). The maps present the landscape configuration in 1890 at a scale of 1:25 000 and were compared in a GIS environment with the current forest distribution. In the case of sub-compartments whose areas were only partially afforested in the past, I adopted the result for the larger part of the sub-compartment. As a result, I obtained binary information on history of each sub-compartment (present or absent forest in the past). As the fourth variable, I used the sub-compartment area, which may be related to the sampling effort of the observers during the forest inventory.

Statistical analysis

I used the Redundancy Analysis (RDA) implemented in the CANOCO software (Lepš & Šmilauer 2003) in order to visualize the relationship between species distribution in the sub-compartment in relation to the three explanatory variables (forest age, habitat type and forest history). The fourth variable — sub-compartment area — was used as a covariate in order to exclude the possible effect of these characteristics. I applied the Monte-Carlo test (Lepš & Šmilauer 2003) with 5000 permutations to check the significance of the general pattern and the relationship between plant distribution and the three variables.

To check the importance of the stand history for the current distribution of 8 selected plant species, I used a logistic regression implemented in the SPSS 15.0 software. For each species, I built three logistic models explaining the occurrence of a given species. The three models used stand type, patch area and stand age as explanatory variables. Next, I checked whether inclusion of stand history as an additional explanatory variable in each of the three models, improved their fit to the data of species occurrences. For this purpose, I computed Akaike's information criterion scores (AIC; Johnson & Omland 2004) for models with and without stand history as an explanatory variable (e.g. AIC for model with stand type *vs*. AIC for model with stand type and stand history). In this way, it was possible to check whether stand history contributed to explaining the occurrences of plants.

As a next step, I used the data on the understorey plant distribution to build a model explaining forest history (ancient *vs*. recent). Here, I used the occurrence of selected plant species as explanatory variables and forest history as a response variable in the forward stepwise logistic regression.

Finally, I checked the usefulness of the plant species selected as indicators of forest history in another forest complex, used as a control. For this purpose, I used a nearby Warnice Forest complex, located ca. 10 km to the east of the study area. On the basis of forest inventory data available for the Warnice Forest, I selected all sub-compartments with the two species selected as reliable indicators of forest history (n = 47) and 47 randomly selected others. For each sub-compartment, I assessed the history of the forest habitat with the same method used for the Mieszkowice Forest. Then I checked if the species used as forest history indicators in Mieszkowice Forest were still significant predictors of forest history in the Warnice Forest.

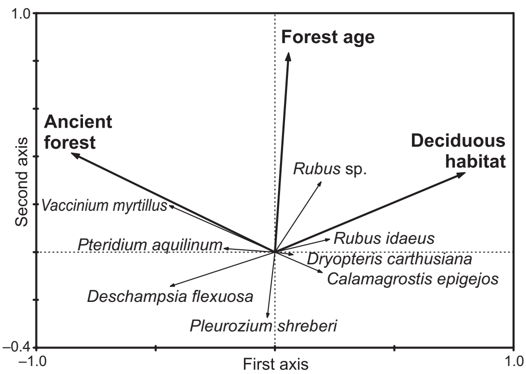

Fig. 2. Ordination diagram of the Redundancy Analysis with the distribution of 8 understorey plant species in 211 forest sub-compartments explained by the three habitat characteristics: stand age, stand type and forest history. The sub-compartment area was used as a covariate to exclude its effect from the general pattern.

Results

The redundancy analysis, controlled for the sub-compartment area, revealed correlations between the occurrence of particular species and the three habitat variables (Fig. 2). The three habitat variables seem to be uncorrelated. Among the eight plant species, *Vaccinium myrtillus* and *Pteridium aquilinum* showed positive relation to ancient forests, whereas *Dryopteris carthusiana* and *Calamagrostis epigejos* showed a different tendency. *Rubus idaeus* and *Deschampsia flexuosa* seem to be most strongly related (although reversely) to stand type, whereas *Pleurozium* seems to prefer younger stands (Fig. 2). The distribution of the plant species in relation to the canonical axes extracted by RDA was not random (Monte Carlo test: trace = 0.108, F-ratio = 8.39, p = 0.0002).

The occurrence of most of the investigated species was affected by the history of a given sub-compartment. In 19 out of 24 model-pairs, AIC scores for the model with history included as an explanatory variable were considerably lower than for models without this variable, and in 15 out of 19 cases, the difference (i.e. ΔAIC) exceeded 3 (Table 1). This tendency did not hold only in the case of *Rubus* sp. and *Dryopteris carthusiana*; however, the differences in AIC scores between the with-history and without-history models were not great (and ΔAIC did not exceed 3). This indicates that the history variable increases the parsimony of the models explaining the understorey plant species occurrence.

Among the eight plant species, five appeared to be significant predictors of patch history (forward stepwise logistic regression). However, on the basis of model fitting criteria (Table 2), I selected *Vaccinium myrtillus* and *Pteridium aquilinum* for further analyses. This selection based on the fact that the two species were the strongest predictors (in the statistical sense). Moreover, inclusion of *Pteridium aquilinum* significantly increased parsimony of the model (AIC reduced by 15.26, BIC reduced by 11.91), however inclusion of another species, *Rubus idaeus*, did not increase parsimony significantly (AIC reduced by 5.59, BIC reduced by 2.24), and the increase of R^2 was not large (Table 2). Additionally, significant co-occurrence of *Pteridium aquilinum* and *Rubus idaeus* across the 211 subcompartments (χ^2 = 7.49, df = 1, p = 0.006) lowered the reliability of this set of three species as indicators and supported the rejection of *Rubus idaeus* from further analyses. Finally, since the group of indicator species should not be numerous to guarantee usefulness of the indicator-species approach, selection of only *Vaccinium myrtillus* and *Pteridium aquilinum* seems to be justified.

Occurrences of the two species, *Vaccinium myrtillus* and *Pteridium aquilinum*, appeared to be significant predictors of forest history (*see* Table 3: Mieszkowice Forest). Among the 110 sub-compartments where *Pteridium aquilinum* or *Vaccinium myrtillus* were recorded, 103 were covered by ancient forest (93.64%), whereas among the 18 sub-compartments where both species were present, all (100%) were ancient.

Table 1. Comparisons of the logistic regression models explaining the occurrence of the eight understorey plants in 211 sub-compartments in a managed forest of western Poland. For each cell, differences between AIC scores computed for the two models presented in the first column are given. Negative values indicate that the model including history as an explanatory variable is more parsimonious then the model without this variable. The absolute values > 3 are set in boldface. Ple sch = *Pleurozium shreberi*, Rub ida = *Rubus idaeus*, Cal epi = *Calamagrostis epigejos*, Rub sp. = *Rubus* sp., Dry car = *Dryopteris carthusiana*, Des fle = *Deschampsia flexuosa*, Vac myr = *Vaccinium myrtillus*, Pte aqu = *Pteridium aquilinum*.

Competing models	Ple sch	Rub ida	Cal epi	Rub sp.	Dry car	Des fle	Vac myr	Pte aqu
Habitat *vs.* Habitat + History	**–6.418**	**–4.410**	**–6.553**	1.847	0.676	–0.808	**–28.995**	**–13.512**
Area *vs.* Area + History	–1.008	**–8.133**	**–8.635**	1.216	0.463	**–13.093**	**–44.879**	**–14.235**
Age *vs.* Age + History	–0.064	**–9.650**	**–8.480**	–0.267	0.310	**–14.950**	**–42.070**	**–15.974**

Table 2. Model fitting criteria for the five forward stepwise logistic regression models explaining stand history (ancient *vs.* recent) on the basis of plant species occurences. For each model, Akaike information criterion (AIC), Bayesian information criterion (BIC), and Cox and Snell pseudo R^2 values are given. *See* Table 1 for abbreviations.

Model	AIC	BIC	R^2
Vac myr	202.30	219.06	0.20
Vac myr + Pte aqu	187.04	207.15	0.27
Vac myr + Pte aqu + Rub ida	181.45	204.91	0.30
Vac myr + Pte aqu + Rub ida + Ple sch	178.74	205.55	0.31
Vac myr + Pte aqu + Rub ida + Ple sch + Des fle	176.00	206.16	0.34

Vaccinium myrtillus and *Pteridium aquilinum*, selected as reliable predictors of ancient forest, also appeared to be significant predictors of forest history in the Warnice Forest (Table 3). Usefulness of the two species' distributions as predictors of forest history was similar in both areas: 95% confidence intervals for the odds ratio of the two species computed for the Mieszkowice and Warnice forests overlapped. Among the 47 sub-compartments in the Warnice Forest where *Pteridium aquilinum* or *Vaccinium myrtillus* were recorded, 42 were classified as ancient forest (89.36%). However, no sub-compartment with both species present was recorded.

Discussion

The concept of indicator species related to habitat history has received much attention in recent decades (Høiland & Bendiksen 1996, Lindblad 1998, Sverdrup-Thygeson & Lindenmayer 2003, Liira & Sepp 2009, Thomas *et al*. 2009), including several critical papers (Norden & Appelqvist 2001, Rolstad *et al*. 2002). Rolstad and colleagues pointed out several problems with the reliability of indicator species in correctly determining habitat history. Therefore, data on the distribution of species related to habitat history should be treated with caution and, if possible, supplemented with direct measurements of forest structures with the help of dendrological or paleoecological techniques (e.g. Groven *et al*. 2002).

The results presented in this paper show that forest history is important for the current distribution of the main understorey plants in an ecosystem. This close dependence might not have been expected since long-term forest management provides many occasions for, or even forces, dispersion from ancient to recent tree stands. Transportation of harvested timber, saplings for afforestation and workers, as well as automotive traffic lasting for decades may be efficient ways for plants to colonize unsettled forest patches (Zwaenepoel *et al*. 2006). Also endo- and exozoochory are known as important ways of plant movement in forested habitats (Servigne & Detrain 2008, Jaroszewicz *et al*. 2008). Every patch of the Mieszkowice Forest was logged at least once (i.e. the stand layer was removed) and then afforested (with the use of deep soil ploughing). Despite the high spatio-temporal dynamic of the forest habitat, the clear separation of ancient and recent woods is still visible and forest history explains the current distribution of many understorey plant species, which is consistent with results of the previous studies of this topic (Bradshaw 2004, Hermy & Verheyen 2007, Fritz *et al*. 2008, Svenning *et al*. 2009).

It should be noted that I recorded dozens of sub-compartments covered by ancient stand (i.e. continuously wooded since 1890) where *Vaccinium myrtillus* and *Pteridium aquilinum* were not recorded. These unexpected absences of the species may reflect real gaps in their distribution (e.g. caused by unsuitable habitat, anthropogenic disturbances or forest history before 1890) or, inaccuracy of the inventory (e.g. the species may have been overlooked during the inventory,

Table 3. Results of the two logistic regression models explaining the history of sub-compartments (ancient *vs.* recent forests) on the basis of two understorey plant species (*Vaccinium myrtillus* and *Pteridium aquilinum*) occurring in the Mieszkowice and Warnice forests. The reference category of the dependent variable is 0.

Source	Mieszkowice Forest				Warnice Forest			
	B	Wald statistic	*p*	Odds ratio (95% CI)	*B*	Wald statistic	*p*	Odds ratio (95% CI)
Intercept	–0.14	0.52	0.471	0.866 (0.586–1.280)	–3.93	14.96	< 0.001	0.020 (0.003–0.144)
Pte aqu = 1	2.23	12.10	0.001	9.269 (2.643–32.510)	2.06	9.31	0.002	7.808 (2.085–29.241)
Pte aqu = 0	0*				0*			
Vac myr = 1	2.92	28.10	< 0.001	18.486 (6.287–54.354)	1.66	4.15	0.042	5.250 (1.064–25.897)
Vac myr = 0	0*				0*			

* Due to its redundancy, this parameter is set to 0.

and/or extremely small populations of the plants may not have been noted intentionally by the observer). Therefore, it seems that the absence of the two species cannot be treated as a reliable indicator of recent forests. In other words, the occurrence of *Pteridium aquilinum* and/or *Vaccinium myrtillus* seems to be an indicator in "one direction". In contrast, occurrences of the two species in a given sub-compartment were significant predictors of sub-compartment's history both in Mieszkowice Forest and in the Warnice Forest.

The relation between *Vaccinium* spp. distribution and forest history is not a novel finding and has been reported in several studies (summarized in Hermy *et al.* 1999). By contrast, it is interesting that *Pteridium aquilinum* appeared to indicate ancient forests. This species has been associated with more disturbed forests (Rutkowski 2004), where it can even inhibit tree regeneration (McDonald *et al.* 2008). As a fern, it would also seem to have high colonizing ability. Therefore, its association with ancient forests was unexpected. However, it seems that higher fertility of recent relative to ancient stands can drive the preferences of the fern to ancient forest. Irrespectively of the causes of the pattern obtained, the usefulness of forest inventory reports as a source of data on the distribution of this and other plant species is not well known. It should be kept in mind that data on plants summarized in forest inventory reports are not very precise and do not allow as detailed inferences to be made as the results of professional botanical studies (e.g. Verheyen & Hermy 2001, Svenning *et al.* 2009). They also provide much less information (only presence–absence data), not allowing for the detection of the more sophisticated responses of plant biology to the environmental factors being investigated (e.g. Nielsen *et al.* 2007). However, forest inventory reports have one great advantage over other techniques: they are ready and available for free for most of the wooded areas. For instance, in Poland, forest inventories are prepared for each forest district (over 400 in Poland) managed by the State Forests National Forest Holding every ten years using strictly the same methods. It is worth noting that state forests comprise nearly 80% of all forests in Poland (i.e. over 7 000 000 ha), and this share is similar for many other central European countries. However, maps used in this study for inferences on stand history (Messtischblätter series) are not available for the whole area of Poland, and their analysis is time consuming, requiring specific software and knowledge. Therefore, the use of indicator species described in the inventory reports may be an attractive source of knowledge on the ecosystem.

Inventories of natural resources are always expensive and time consuming, while their results are reliable only for a short period. On the other hand, precise data are necessary to effectively manage an ecosystem and preserve biodiversity. Therefore, indicator and surrogate species are used as alternatives or supplementary data sources, which, despite evident shortcomings, allow inventory procedures to be simplified and reduced in cost (Niemi & McDonald 2004). The need to reduce the time and costs of conducting inventories should also lead to the search for new data sources, alternatives to traditional inventories. Therefore, it seems justified to consider forest inventory reports, which can be helpful in assessing the natural resources of an ecosystem (e.g. Fernandes 2009). For example, these data were recently used to model the distribution of hazel grouse and middle-spotted woodpecker in managed stands (Åberg *et al.* 2003, Müller *et al.* 2009).

Acknowledgements

I am grateful to Katarzyna Barańska for a valuable discussion about the manuscript. Two anonymous referees provided helpful comments on the previous version of the text. The English was kindly verified by Barbara Przybylska. The study was partially supported by the Polish Ministry of Science and Higher Education (grant no. N N304 027034).

References

Åberg, J., Swenson, J. E. & Angelstam, P. 2003: The habitat requirements of hazel grouse (*Bonasa bonasia*) in managed boreal forest and applicability of forest stand descriptions as a tool to identify suitable patches. — *Forest Ecology and Management* 175: 437–444.

Baeten, L., Hermy, M. & Verheyen, K. 2009: Environmental limitation contributes to the differential colonization capacity of two forest herbs. — *Journal of Vegetation*

Science 20: 209–223.
Bradshaw, R. H. W. 2004: Past anthropogenic influence on European forests and some possible genetic consequences. — *Forest Ecology and Management* 197: 203–212.
Cousins, S. A. O. 2009: Extinction debt in fragmented grasslands: paid or not? — *Journal of Vegetation Sciences* 20: 3–7.
Dzwonko, Z. 2001: Effect of proximity to ancient deciduous woodland on restoration of the field layer vegetation in a pine plantation. — *Ecography* 24: 198–204.
Fernandes, P. M. 2009: Combining forest structure data and fuel modelling to classify fire hazard in Portugal. — *Annals of Forest Science* 66: art. 415.
Fritz, Ö., Gustafsson, L. & Larsson, K. 2008: Does forest continuity matter in conservation? — A study of epiphytic lichens and bryophytes in beech forests of southern Sweden. — *Biological Conservation* 141: 655–668.
Gaudio, N., Balandier, P. & Marquier, A. 2008: Light-dependent development of two competitive species (*Rubus idaeus*, *Cytisus scoparius*) colonizing gaps in temperate forest. — *Annals of Forest Science* 65: art. 104.
Godefroid, S., Rucquoij, S. & Koedam, N. 2005: To what extent do forest herbs recover after clearcutting in beech forest? — *Forest Ecology and Management* 210: 39–53.
Groven, R., Rolstad, J., Storaunet, K. O. & Rolstad, E. 2002: Using forest stand reconstructions to assess the role of structural continuity for late-successional species. — *Forest Ecology and Management* 164: 39–55.
Hanski, I. & Ovaskainen, O. 2002: Extinction debt at extinction threshold. — *Conservation Biology* 16: 666–673.
Hedin, J., Ranius, T., Nilsson, S. G. & Smith, H. G. 2008: Restricted dispersal in a flying beetle assessed by telemetry. — *Biodiversity and Conservation* 17: 675–684.
Helm, A., Hanski, I. & Partel, M. 2006: Slow response of plant species richness to habitat loss and fragmentation. — *Ecology Letters* 9: 72–77.
Hermy, M., Honnay, O., Firbank, L., Grashof-Bokdam, C. & Lawesson, J. E. 1999: An ecological comparison between ancient and other forest plant species of Europe, and the implications for forest conservation. — *Biological Conservation* 91: 9–22.
Hermy, M. & Verheyen, K. 2007: Legacies of the past in the present-day forest biodiversity: a review of past land-use effects on forest plant species composition and diversity. — *Ecological Research* 22: 361–371.
Høiland, K. & Bendiksen, E. 1996: Biodiversity of wood-inhabiting fungi in a boreal coniferous forest in Sor-Trondelag County, central Norway. — *Nordic Journal of Botany* 16: 643–659.
Jaroszewicz, B., Pirożnikow, E. & Sagehorn, R. 2008: The European bison as seed dispersers: the effect on the species composition of a disturbed pine forest community. — *Botany* 86: 475–484.
Johnson, J. B. & Omland, K. S. 2004: Model selection in ecology and evolution. — *Trends in Ecology and Evolution* 19: 101–108.
Kondracki, J. 2002: *Geografia regionalna Polski*. — Polish Scientific Publisher, Warszawa.
Krebs, C. J. 1994: *Ecology. The experimental analysis of distribution and abundance*. — Harper-Collins College Publishers, New York.
Lepš, J. & Šmilauer, P. 2003: *Multivariate analysis of ecological data using CANOCO*. — Cambridge University Press, Cambridge.
Liira, J. & Sepp, T. 2009: Indicators of structural and habitat natural quality in boreo-nemoral forests along the management gradient. — *Annales Botanici Fennici* 46: 308–325.
Lindblad, I. 1998: Wood-inhabiting fungi on fallen logs of Norway spruce: relations to forest management and substrate quality. — *Nordic Journal of Botany* 18: 243–255.
Matuszkiewicz, W. 2001: *Zespoły leśne Polski*. — Polish Scientific Publisher, Warszawa.
Mazgajski, T. D., Żmihorski, M. & Abramowicz, K. 2010: Forest habitat loss and fragmentation in central Poland during the last 100 years. — *Silva Fennica* 44: 715–723.
McDonald, R. I., Motzkin, G. & Foster, D. R. 2008: The effect of logging on vegetation composition in Western Massachusetts. — *Forest Ecology and Management* 255: 4021–4031.
Müller, J., Pöllath, J., Moshammer, R. & Schröder, B. 2009: Predicting the occurrence of middle-spotted woodpecker *Dendrocopos medius* on a regional scale, using forest inventory data. — *Forest Ecology and Management* 257: 502–509.
Nielsen, A., Totland, Ø. & Ohlson, M. 2007: The effect of forest management operations on population performance of *Vaccinium myrtillus* on a landscape-scale. — *Basic and Applied Ecology* 8: 231–241.
Niemi, G. J. & McDonald, M. E. 2004: Application of ecological indicators. — *Annual Review in Ecology, Evolution and Systematics* 35: 89–111.
Nordén, B. & Appelqvist, T. 2001: Conceptual problems of ecological continuity and its bioindicators. — *Biodiversity and Conservation* 10: 779–791.
Rolstad, J., Gjerde, I., Gundersen, V. S. & Sætersdal, M. 2002: Use of indicator species to assess forest continuity: a critique. — *Conservation Biology* 16: 253–257.
Rutkowski, L. 2004: *Klucz do oznaczania roślin naczyniowych Polski niżowej*. — Polish Scientific Publisher, Warszawa.
Servigne, P. & Detrain, C. 2008: Ant-seed interactions: combined effects of ant and plant species on seed removal patterns. — *Insectes Socieaux* 55: 220–230.
Svenning, J. C., Baktoft, K. H. & Balslev, H. 2009: Land-use history affects understorey plant species distributions in a large temperate-forest complex, Denmark. — *Plant Ecology* 201: 221–234.
Sverdrup-Thygeson, A. & Lindenmayer, D. B. 2003: Ecological continuity and assumed indicator fungi in boreal forest: the importance of the landscape matrix. — *Forest Ecology and Management* 174: 353–363.
Thomas, S. L., Wagner, R. G. & Halteman, W. A. 2009: Influence of harvest gaps and coarse woody material on click beetles (Coleoptera: Elateridae) in Maine's Acadian forest. — *Biodiversity and Conservation* 18: 2405–2419.
Vellend, M., Verheyen, K., Jacquemyn, H., Kolb, A., Van Calster, H., Peterken, G. & Hermy, M. 2006: Extinction

debt of forest plants persists for more than a century following habitat fragmentation. — *Ecology* 87: 542–548.
Verheyen, K. & Hermy, M. 2001: The relative importance of dispersal limitation of vascular plants in secondary forest succession in Muizen Forest, Belgium. — *Journal of Ecology* 89: 829–840.
Wesołowski, T. 2005: Virtual conservation: how the European Union is turning a blind eye to its vanishing primeval forests. — *Conservation Biology* 19: 1349–1358.
Zwaenepoel, A., Roovers, P. & Hermy, M. 2006: Motor vehicles as vectors of plant species from road verges in a suburban environment. — *Basic and Applied Ecology* 7: 83–93.
Żmihorski, M., Chylarecki, P., Rejt, Ł. & Mazgajski, T. D. 2010: The effects of forest patch size and ownership structure on tree stand characteristics in a highly deforested landscape of central Poland. — *European Journal of Forest Research* 129: 393–400.