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Influence of the size and density of *Carpinus betulus* on the spatial distribution and rate of deletion of forest-floor species in thermophilous oak forest

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Abstract

The change in the species richness following a gradual invasion of *Carpinus betulus* in the patch of oak forest (*Potentillo albae-Quercetum*) in Białowieża was studied between years 1980 and 1994. Species richness and species deletion were compared to the spatial variation in the density and size of *C. betulus* individuals. The study showed that, in a microscale, (1) the rate of deletion of heliophilous species was similar to that of shade-tolerant ones and was c. 2 species per 4 m^2 per 10 years, (2) species richness was negatively correlated with the density and size of *C. betulus* saplings recruited to the shrub layer, (3) species deletion was positively correlated with the number of saplings in the shrub layer. The results support the hypothesis that the invasion of *C. betulus* is a proximate cause of the decline of *Potentillo albae-Quercetum*, and in a microscale, it has three stages: (a) initial colonisation of the ground layer by the seedlings, (b) recruitment of juveniles to the shrub layer, deterioration of light conditions and rapid deletion of species, and (c) closure of the canopy and deletion of remaining heliophilous species and vulnerable shade-tolerant species.

Nomenclature: follows Ehrendorfer (1973) and Matuszkiewicz (1981).

Introduction

Forest communities from the order of *Quercetalia pubescentis* occur mostly in the sub-Mediterranean zone. In Poland, thermophilous oak forests are represented only by the phytocoenoses of *Potentillo albae-Quercetum* Libb. 1933. They occupy specific habitats: tops and south-facing slopes of moraine and kame mounds with gravel interbedding, which are relatively fertile and seasonally dry. The phytocoenoses are the richest climax communities in Poland and are characterized by a specific combination of otherwise ecologically different species. These include character and differential species of various syntaxa of meadows, pastures, and forests. The species belong to four major ecological groups with respect to the habitat preferences: (1) sunny and warm habitats with medium calcium content (*Quercetalia pubescentis*, *Festuco-Brometea*, *Trifolio-Geranietea*), (2) sunny acidic habitats (*Vaccinio-Piceetea*), (3) open habitats of seasonally wet meadows (*Molinio-Arrhenatheretea*), and (4) shady and mesotrophic habitats (*Querco-Fagetea*, *Fagetalia*).

The oak forest represents the only natural thermophilous vegetation in the Białowieża Forest. The communities occur close to the northern limit of the range of *Potentillo albae-Quercetum* and were once exceptionally rich in species (Matuszkiewicz & Kozłowska 1991): more than a hundred per 100 m^2 was found, including many rare and endangered ones (Kwiatkowska 1972, 1994). Unfortunately, for last 30 years, these phytocoenoses have been declining with respect to the number and the area of the patches (Faliński 1986). At present, there are no patches with a natural tree stand and a rich and diversified ground layer. The causes of the decline include the disturbance of the species composition and the age structure of the tree stand due to natural factors and to the human intervention. The proximate cause seems to be an invasion of hornbeam or *Carpinus betulus* (Faliński 1986, Kwiatkowska & Wyszomirski 1988, 1990). An increased abundance of hornbeam in the phytocoenoses of thermophilous oak forest has been a widespread phenomenon in Poland (Jakubowska-Gabara 1991).

The colonisation of oak forest habitat by *C. betulus* is gradual and progresses from the margins to the centre of the patch. It brings about a change in microclimatic conditions in the ground layer (Kwiatkowska 1993) which affects the abundance of thermophilous and heliophilous species. The frequency of most species decreases and some of them disappear from the patch, while the proportion of species with random dispersion pattern increases. At the same time, the number of statistically significant associations between species and the values of Shannon diversity and equitability indices decrease (Kwiatkowska 1994 a, b). Effectively, individual patches decrease in area and lose species, becoming more and more similar to the surrounding lime-hornbeam forest *Tilio-Carpinetum* (Kwiatkowska 1986; Kwiatkowska & Solińska-Górnicka 1993). Removal of hornbeam reverts the process and many heliophilous species return to the patch (Kwiatkowska & Wyszomirski 1990); the effect is however temporary.

The influence of *C. betulus* on the ground layer may be different depending on the size of the individuals. Juvenile hornbeams compete for space and resources with the perennials of the forest floor. As growing juveniles are recruited to the shrub layer, they start to shade the surrounding ground. The aim of this paper is therefore to analyse in a microscale the process of hornbeam invasion to the oak forest, and in particular, to assess the effect of size and density of *C. betulus* on the species richness and species deletion in the ground layer.

Methods

The study was carried out in the best preserved patch of the oak forest which constitutes a permanent plot of the Białowieża Geobotanical Station of Warsaw University and has been a subject of extensive research (Matuszkiewicz 1977, Faliński 1986, Kwiatkowska 1972, 1986, 1993, 1994a, b; Kwiatkowska & Wyszomirski 1988; 1990; Kwiatkowska & Solińska-Górnicka 1993). In the 1970s, the phytocoenosis covered c. 1 ha; the dominant tree species was *Quercus robur* and the density of the canopy was 60%. The density of shrub layer was variable and was greater in the margins of the patch reaching 30–40%: the dominant species was *C. betulus* accompanied by *Picea abies, Quercus robur*, *Tilia cordata,* and *Malus sylvestris*. The ground layer was dense (c. 80%), lush, multi-layered and rich in species.

The research plot was situated in the centre of the patch. It measured 40 m $\times$ 40 m and was divided into a grid of 2 m $\times$ 2 m quadrats.

In order to analyse the effect of the invasion of *C. betulus* on the species richness, all species of vascular plants were recorded for every quadrat in the peak of the growing season (July-August) in years 1980, 1984, 1988 and 1994. Then, for each quadrat, the total number of species (T), and the numbers of heliophilous species (H: character and differential species of *Quercetalia pubescentis*, *Trifolio-Geranietea*, *Festuco-Brometea*, *Mollinio-Arrhenatheretea*, and *Vaccinio-Piceetea*), shade-tolerant species (S: character species of *Fagetalia* and *Querco-Fagetea*), and the remaining species (R) were calculated. Additionally, for each quadrat, the species deletion or the number of species which disappeared between years 1980 and 1994 was calculated. In 1994, the number of *C. betulus* juveniles (to 50 cm in height), saplings (to 5 m in height), and trees was recorded for each quadrat, and the diameter and girth of all saplings and trees were measured at the height of 50 cm.

The data based on 4 m^2 grid served to draw distribution maps only. Since the effect of hornbeam saplings and trees on the species richness might extend beyond the quadrat in which they were recorded, the data used in the other analyses were recalculated based on 16 m^2 grid, i.e. the mean of four adjacent quadrats was used. This size was chosen based on the average space captured by a young tree. The relationships between the parameters of the hornbeam population and the species richness and species deletion were investigated with Spearman correlation coefficients and regression equations calculated with CSS: Statistica (1991), the latter using logarithmic transformation of the data. Additionally, in order to test the hypotheses on the causal relationships among the variables, a path model was analysed using SEPATH of Statistica for Windows 5.0 (Steiger 1995).

Results

Gradual invasion of *C. betulus* caused notable reduction in the number of species (Fig. 1). Between 1980 and 1984, the mean number of all species, H-species, S-species, and R-species per quadrat decreased by 25%, 44%, 18%, and 16%, respectively. Fifteen years after the beginning of the research, the value for H-species dropped by 83% while that for S-species and for R-species by 36% and 55%, respectively. On average, the total number of species per quadrat decreased by half. The rate of deletion of heliophilous species was similar to that of shade tolerant plants and was equal to c. 2 species per quadrat per 10 years, but the initial values were different and the proportion of H-species to S-species rapidly decreased from c. 0.5 to 0.1. Finally, the quadrats almost entirely lost their thermophilous character and the heliophilous species ceased to play significant role in the patch.

The rate of species deletion varied depending on the position of the quadrat. The ‘island’ of rich vegetation, including quadrats with the highest total number of species, was situated south-east from the centre of the plot and was also characterized by the highest number of heliophilous species (Figure 2). In 1980, c. 70% quadrats had no less than 20 species; in 1984, the area of the ‘island’ decreased to 30%, in 1988 to 20%, and finally in 1994 to 10% of the plot. This process affected more the H-species than the S-species, and effectively the ‘island’ no longer constituted a habitat of thermophilous vegetation but only a relatively more rich patch dominated by shade-tolerant plants.

The plot may be divided into three zones with respect to the size and density of hornbeam individuals (Figure 3). In the first zone, encompassing the north-eastern part, the density of juvenile hornbeams in the ground layer and the density of saplings in the shrub layer was rather low (one individual per 4 m^2) but the saplings were relatively thick (6–10 cm). The western part was characterized by higher density of both hornbeam juveniles and undergrowth (to 5 per 4 m^2) and lower trunk diameter (2–5 cm). The youngest undergrowth (to 1 cm in diameter) dominated in the central and southern part of the plot, and the density of juveniles often exceeded 10 individuals per 4 m^2. The trunk diameter is correlated with the size and age of the individuals: the zones may therefore reflect the stages of *C. betulus* invasion.

The number of species per quadrat is apparently related to the age of the hornbeam undergrowth. In the first zone, occupied by the oldest saplings, the mean number of species per quadrat in 1994 was rather low (to 10) and H-species were practically absent. The second zone was also species-poor but the heliophilous plants were still occasionally found (one species per 4 m^2). In the third zone, characterized by the youngest undergrowth, more than 16 species per 4 m^2 occurred, including 2–3 or more heliophilous species. The maps of the species richness, particularly the map of the distribution of H-species, are almost ‘negatives’ of that of the variation in trunk diameter.

The conclusion that the number of species depends mainly on the size and density of hornbeam undergrowth has been also confirmed by multiple regression analysis. The number of species was significantly correlated with the trunk diameter and the number of saplings ($R = 0.57$, $P < 0.00001$, partial correlation coefficients $r = -0.43$ and $r = -0.36$, respectively) while the contribution of the number of seedlings was insignificant. Interestingly, when computed separately, the trunk diameter explained 30% of the variation in the species number ($P < 0.00001$; Figure 4) while the correlation with the number of saplings was not significant.

The number of juveniles in the ground layer was also correlated with both the trunk diameter and the number of saplings ($R = 0.50$, $P < 0.001$, partial correlation coefficients $r = -0.25$ and $r = 0.30$, respectively). When computed separately, the best predictor of the number of juveniles is the average trunk diameter (Spearman correlation coefficient $r = -0.66$, $P < 0.00001$; Figure 4).

The null hypothesis that the path model perfectly fits the data has been rejected at $P < 0.02$ although some noncentrality-based indices were more favourable, for instance McDonald’s index amounted to 0.977 (confidence interval 0.920–0.998). The model has confirmed that mean trunk diameter is the main factor determining both the number of species and the number of hornbeam seedlings per quadrat (Figure 5).

Contrary to the species richness, the species deletion was significantly correlated only with the number of saplings ($R = 0.41$, $P < 0.01$; partial correlation $r = 0.40$; Figure 6) while the regression weights for the trunk diameter and the number of juveniles were insignificant. This particularly concerned the values for the first period, between years 1980 and 1988. The species deletion between years 1988 and 1994 was not significantly correlated with any of the investigated variables.

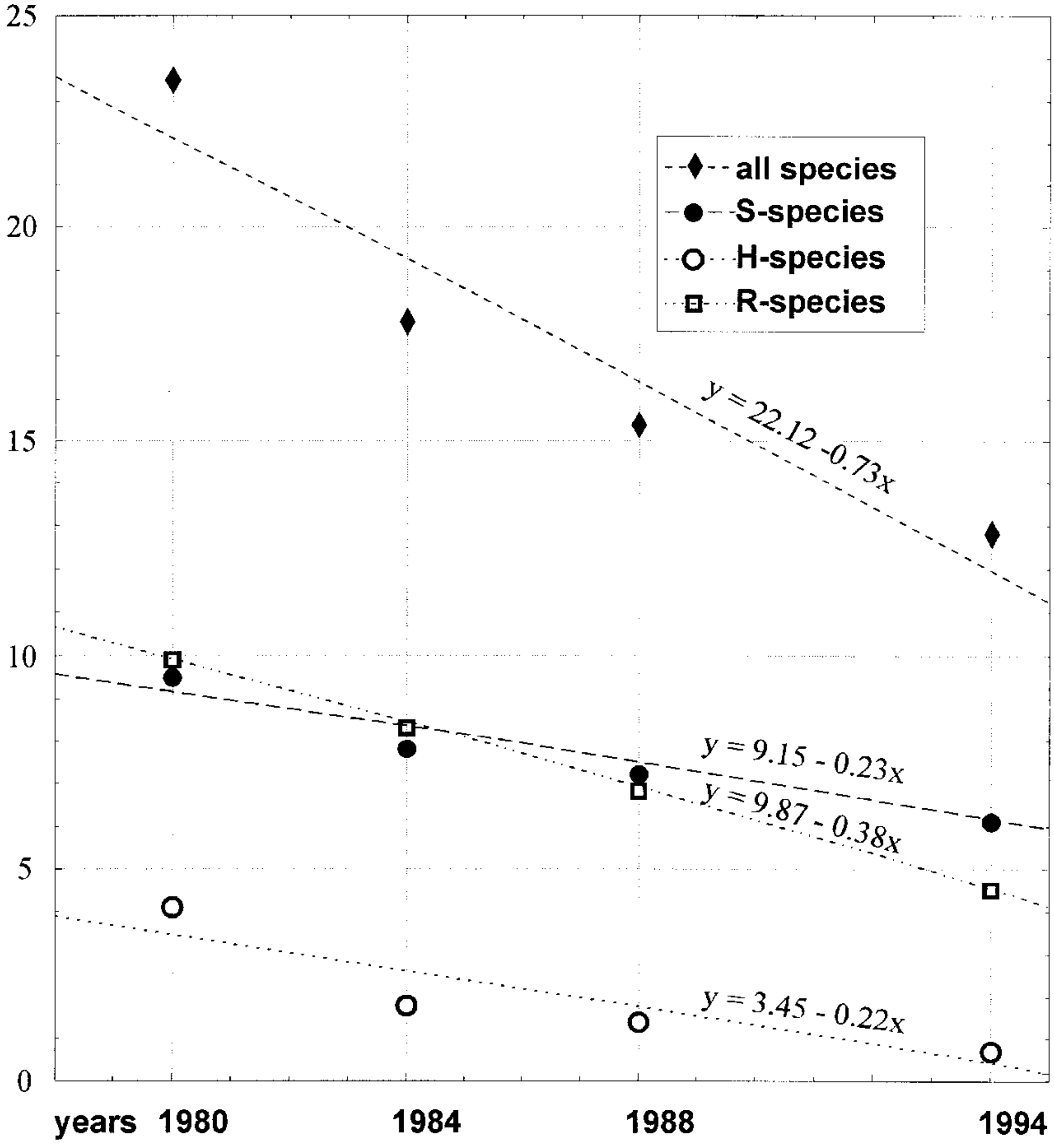

Figure 1. Changes in the mean number of species per quadrat of 4 m^2 following the invasion of *Carpinus betulus*.

Discussion

The rate of species extinction is at present thousand times greater than in previous geological eras (Wilson 1988). Effectively, the biodiversity decreases locally and globally with respect to the number of species and ecosystems. Białowieża Forest represents the best preserved ecosystem of European lowland climax forests but it has also been affected by this process. At the beginning of the 20th century, the communities

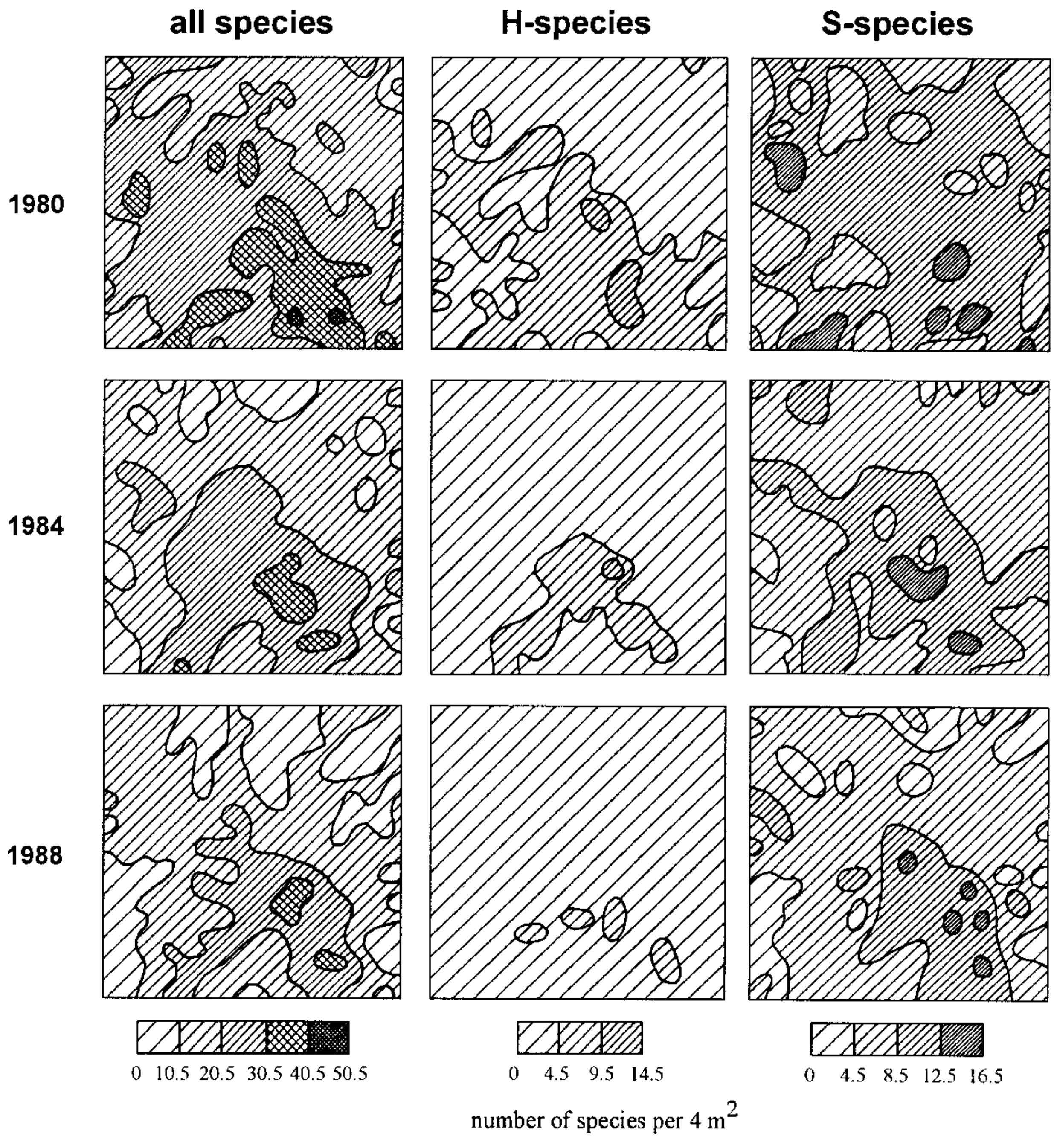

Figure 2. Spatial variation in the number of all, shade-tolerant (S) and heliophilous (H) species per quadrat of 4 m^2 in the research plot between years 1980 and 1988.

of thermophilous oak forest were abundant (Faliński 1986) and included many thermo- and heliophilous species. In the 1920s, such relatively rare species as *Aquilegia vulgaris*, *Anthericum ramosum*, *Campanula glomerata*, *Cephalantera rubra*, *Digitalis grandiflora*, *Gladiolus imbricatus*, *Hypericum montanum*, *Lilium martagon*, *Lathyrus niger*, *L. laevigatus*, *Melittis melisophyllum*, *Polemonium coeruleum*, *Primula veris*, *Potentilla alba*, *Ranunculus polyanthemos*, *Trollius europaeus*, *Trifolium alpestre*, *T. lupinaster*,

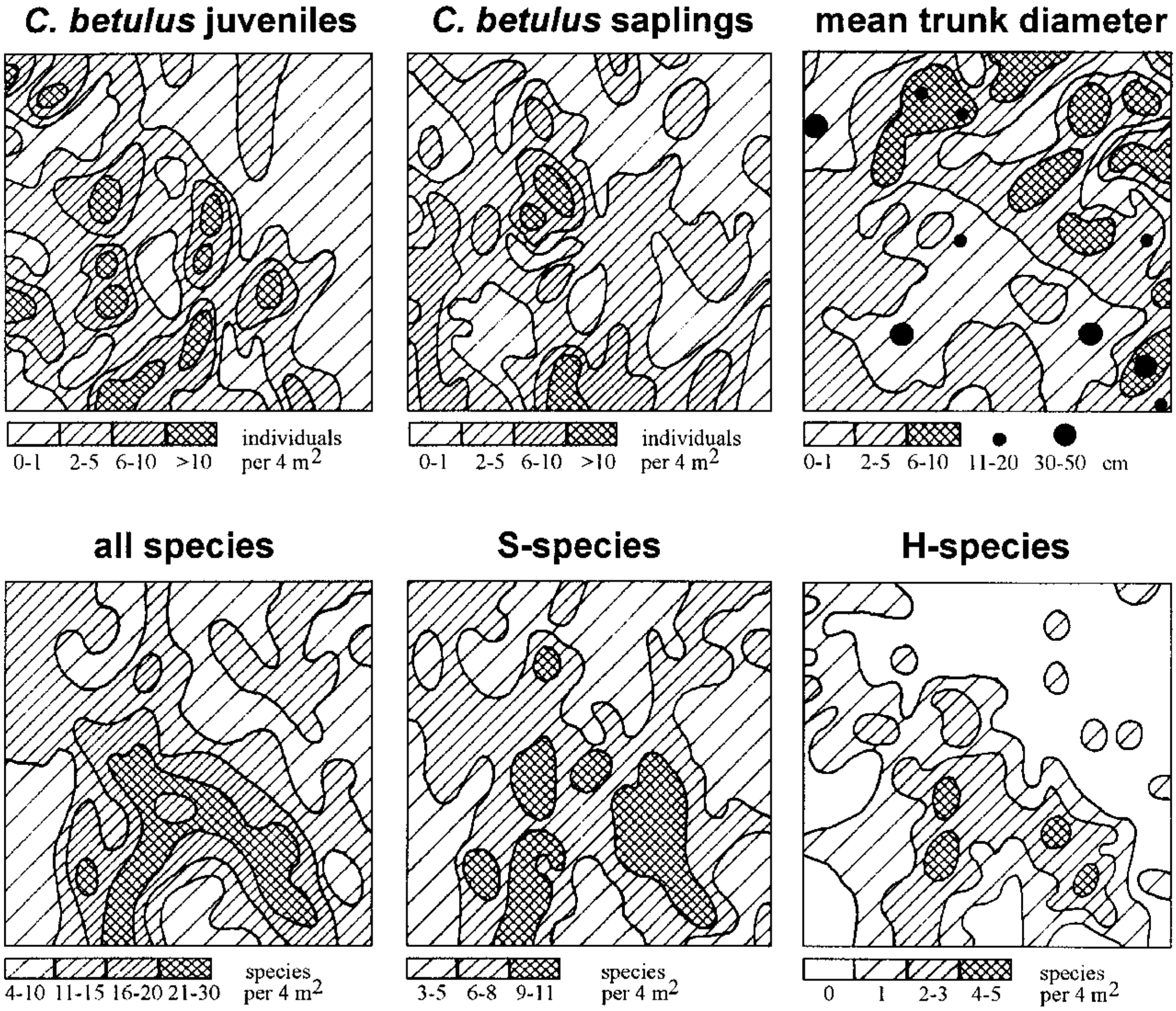

Figure 3. Spatial variation in the number of *Carpinus betulus* juveniles (height <50 cm), the number of saplings (height >50 cm), mean trunk diameter of the saplings and trees, the number of species, the number of shade-tolerant species (S-species), and the number of heliophilous species (H-species) per quadrat of 4 m^2 in 1994.

T. montanum, and *Vincetoxicum hirundinaria* were common (Paczoski 1930). Most of them still occurred in the investigated patch in 1969 (Kwiatkowska 1972, 1993) but they are no longer present. During the first phases of hornbeam invasion, thermophilous plants disappeared rapidly (Kwiatkowska & Wyszomirski 1988; Kwiatkowska 1993) and the rate of deletion, in a macroscale, was 1.5 species per 100 m^2 per year (Kwiatkowska & Wyszomirski 1988). Later, the rates of deletion of remaining heliophilous species and shade-tolerant ones are similar, as shown in the present study.

The results of the study support the hitherto proposed hypothesis that the invasion of *C. betulus* is a proximate cause of species deletion in the patches of *Potentillo albae-Quercetum* (Faliński 1986; Kwiatkowska & Wyszomirski 1988, 1990). Every five years, an average quadrat loses one heliophilous species, one shade-tolerant species, and two species without a syntaxonomic affiliation. However, neither remaining shade-tolerant species increase in frequency nor another species take the place of the disappearing ones (Kwiatkowska 1994a).

Decline of species richness after woody species colonisation has been reported elsewhere (e.g. Specht & Morgan 1981; Hobbs & Mooney 1986; Richardson et al. 1989, Rejmánek & Rosén 1992) although most of

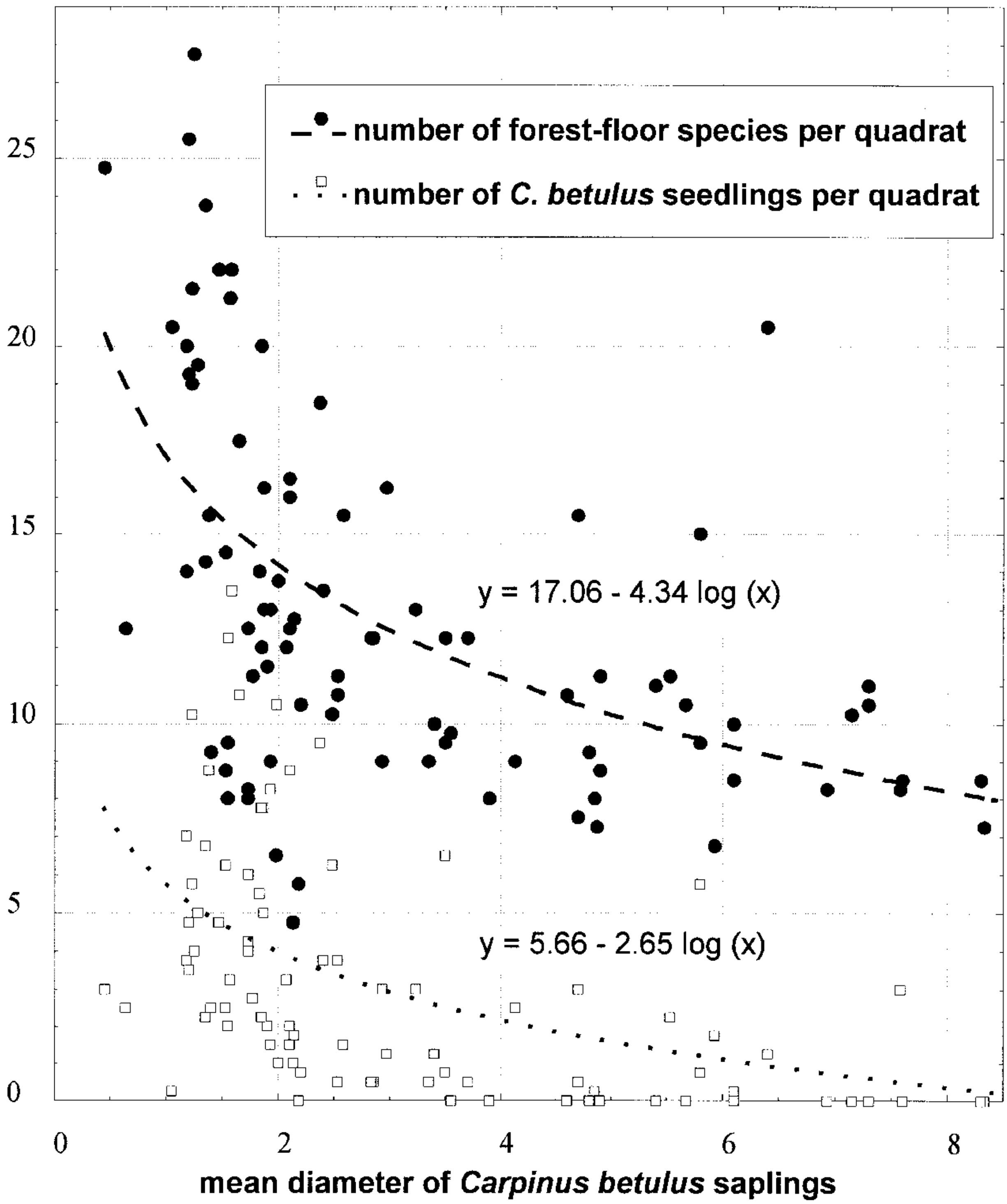

Figure 4. The relationship between the mean trunk diameter of *Carpinus betulus* saplings and trees and the number of species and the number of *C. betulus* juveniles per quadrat of 4 m^2 in 1994.

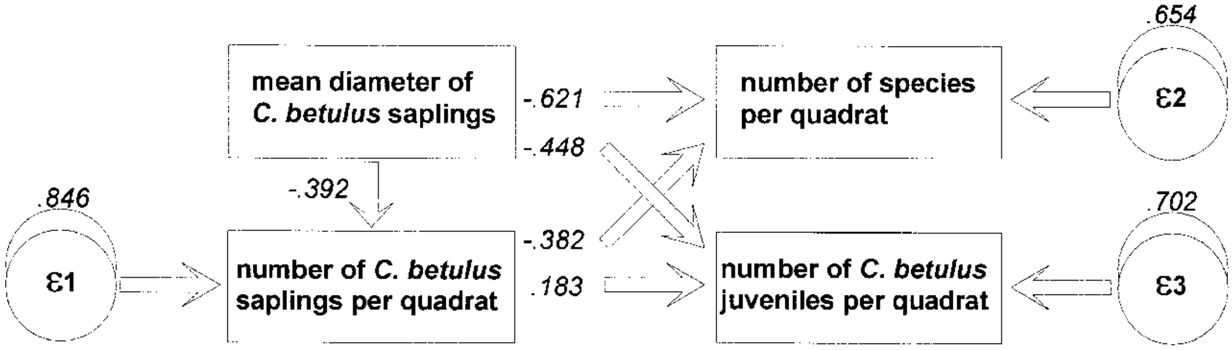

Figure 5. Path model illustrating the influence of mean trunk diameter of *Carpinus betulus* on the number of hornbeam saplings, number of juveniles and the number of species per quadrat of 4 m^2.

the studies concerned different succession stages rather than the decline of a climax community.

In a microscale, the invasion of *C. betulus* and the eventual changes in the composition of the ground layer have three phases: (1) initial colonisation of the ground layer by hornbeam seedlings, (2) recruitment of the juveniles to the shrub layer associated with a rapid drop in the species richness, (3) closure of the canopy of shrub layer and further deletion of the forest-floor species.

The first stage does not bring about a significant reduction in the species richness. So long as the yearly cohorts of hornbeam seedlings are suppressed in the ground layer, their effect on the species composition is negligible. Juveniles may remain to ten years in the ground layer and then, within one year, reach 1.5 m in height (Kwiatkowska, pers. obs.). When they manage to overgrow the surrounding herbs, they start to shade the ground layer and cause a dramatic drop in the number of species, both heliophilous and shade-tolerant. Later, due to self-thinning, as the saplings grow their density decreases but it does not accelerate the species deletion: the most vulnerable ones have already gone. This may explain why the rate of species deletion is significantly correlated only with the number of saplings but not with the mean trunk diameter. However, further growth of saplings and young trees continuously deteriorates light conditions in the ground layer and the actual number of species per quadrat is negatively correlated with the mean size and the number of hornbeams in the shrub layer. Apparently, shading also affects the abundance of *C. betulus* seedlings.

The rate of deletion of H-species and S-species is similar but the initial number of the first was lower and they soon disappeared, while shade-tolerant species have remained in the patch. The advanced stages of the regression of oak forest can be classified as mesophilous lime-hornbeam forest (Faliński 1986). They differ from the typical *Tilio-Carpinetum* in lower species richness, lower density of the ground layer and lower frequency of the species in the patch (Kwiatkowska & Wyszomirski 1990, Kwiatkowska 1993).

The question is what ultimate factors cause the decline of the thermophilous oak forest in Białowieża (Faliński 1986; Kwiatkowska 1986; Kwiatkowska & Wyszomirski 1988, 1990; Kwiatkowska 1994 a, b). The stability of an ecosystem depends both on its complexity and on the nature and intensity of disturbance (Pimm 1984). More complex plant communities are less stable and less likely to return to their state prior to perturbation (McNaughton 1977; Begon *et al.* 1986). Small and isolated ‘islands' of rich vegetation, as the phytocoenoses of *Potentillo albae-Quercetum*, are more likely to face accidental species extinction. It is not therefore surprising that the thermophilous oak forests are generally unstable and are declining in Poland (Jakubowska-Gabara 1991). However, the disturbing factors may be different and changing from place to place.

Contrary to acorns, light hornbeam seeds are not able to germinate in a thick oak-leaf litter while the seedlings cannot survive under a dense canopy of herbs (Kwiatkowska 1996). They can only thrive in places where the ground cover has been damaged either by humans or grazing animals. In Białowieża Forest, the invasion of hornbeam was presumably caused by an extensive pressure of herbivores, the number of which at the end of the 19th century much exceeded the carrying capacity of the ecosystem. The increased supply of germination microsites allowed the first colonisation of the oak-forest habitats by *C. betulus* thus beginning the invasion. A subsequent reduction of the population of

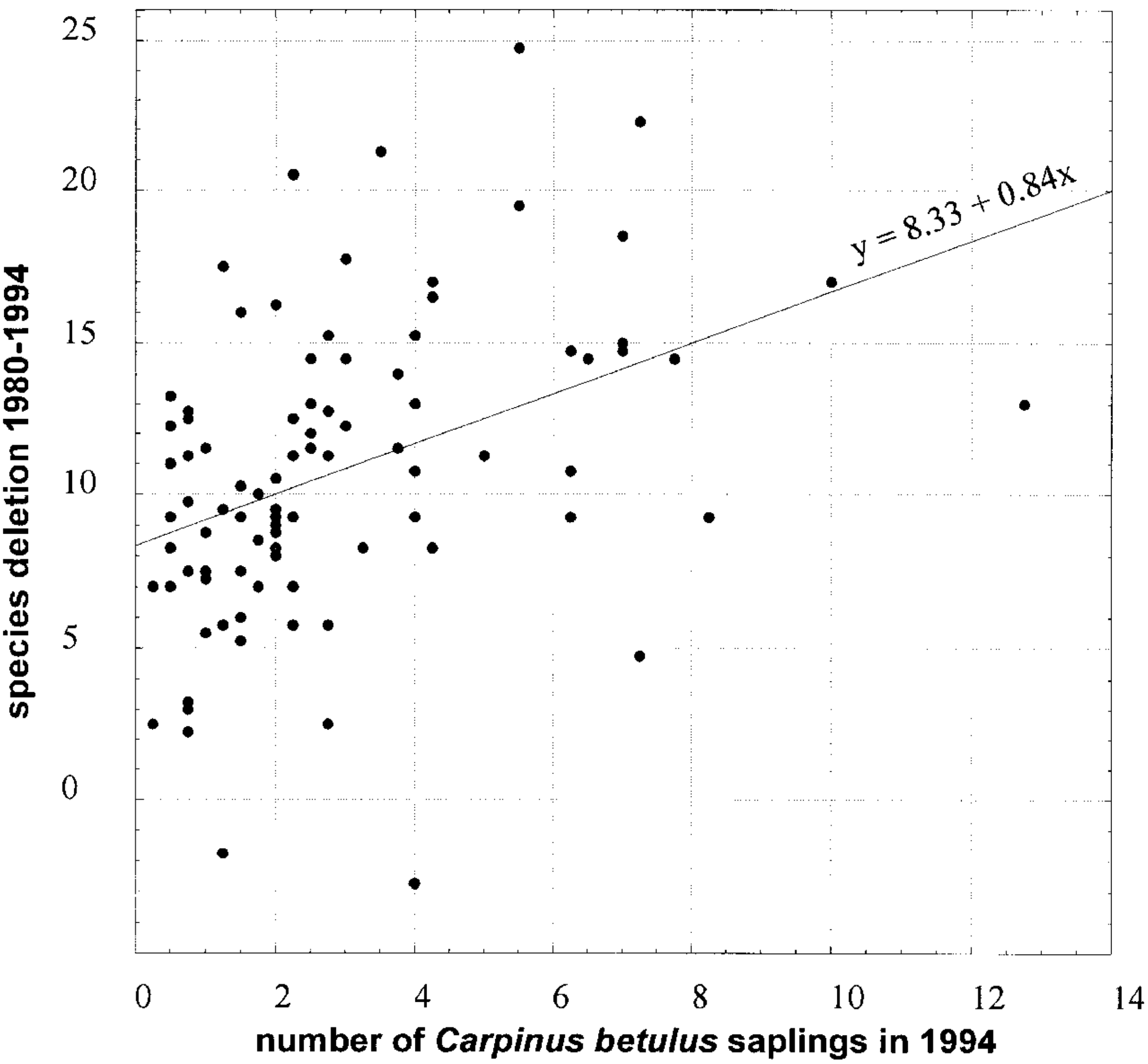

Figure 6. The relationship between the number of *Carpinus betulus* saplings in 1994 and the number of species which disappeared per 4 m^2 between the years 1980 and 1994.

red deer, 'tree-eaters' hitherto controlling the density of hornbeam seedlings and saplings, and the reintroduction of the European bison, a dominant 'herb-eater', may have accelerated the decline of *Potentillo albae-Quercetum* in Białowieża Forest.

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