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Magdalena Niedziałkowska, Julia Kończak, Sylwia Czarnomska & Bogumiła Jędrzejewska

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Species diversity and abundance of small mammals in relation to forest productivity in northeast Poland¹

Magdalena NIEDZIAŁKOWSKA², Mammal Research Institute, Polish Academy of Sciences,
17-230 Białowieża, Poland, e-mail: mniedz@zbs.bialowieza.pl

Julia KOŃCZAK, Mammal Research Institute, Polish Academy of Sciences, 17-230 Białowieża,
Poland, and Faculty of Forestry, Poznań University of Life Sciences, Wojska Polskiego 28,
60-637 Poznań, Poland.

Sylwia CZARNOMSKA & Bogumiła JĘDRZEJEWSKA, Mammal Research Institute,
Polish Academy of Sciences, 17-230 Białowieża, Poland.

Abstract: We studied factors shaping the diversity and abundance of small mammals in temperate woodlands in northeastern Poland at local (within the forests) and regional (among the forests) scales. We compared diversity and abundance of rodents and insectivores in habitats covering the widest possible range of forest productivity in Central Europe, from dry coniferous to wet deciduous forests. Small mammals were live-trapped during summer (2004-2006) on 206 circular plots. On the regional scale, the number of small mammal (rodent and shrew) species positively correlated with the proportion of deciduous stands in the woodland's area. In all forests, the bank vole (*Myodes glareolus*) and the yellow-necked mouse (*Apodemus flavicollis*) dominated, and their joint proportion in the community increased with share of deciduous forest habitats. On the local scale, the number of species increased significantly with productivity of both capture site and the whole woodland. Variation in rodent abundance was influenced mainly by forest productivity at the capture site, productivity of the whole woodland, and month of capture. Only a minor part of the variation in shrew abundance was explained by habitat productivity. The relationship between forest productivity and small mammal diversity was linear and positive on both local and regional scales. The different responses of rodents and insectivores to increasing productivity could be due to a wider ecological niche of shrews and their competition for space with rodents.

Keywords: biodiversity, dominant species, insectivores, productivity–diversity relationship, rodents, woodlands.

Résumé : Nous avons étudié les facteurs qui façonnent la diversité et l'abondance des petits mammifères dans des zones forestières tempérées du nord-est de la Pologne aux échelles locale (au sein des forêts) et régionale (entre les forêts). Nous avons comparé la diversité et l'abondance des rongeurs et des insectivores dans des habitats représentatifs de la plus grande étendue possible de productivité forestière en Europe centrale : des forêts sèches de conifères aux forêts humides feuillues. Des petits mammifères ont été capturés vivants durant l'été (2004-2006) dans 206 parcelles circulaires. À l'échelle régionale, le nombre d'espèces de petits mammifères (rongeurs et musaraignes) était corrélé de façon positive avec la proportion de peuplements feuillus dans la zone boisée. Dans toutes les forêts, le campagnol roussâtre *Myodes glareolus* et le mulot à collier *Apodemus flavicollis* étaient dominants et leur proportion combinée dans la communauté augmentait avec celle des habitats forestiers feuillus. À l'échelle locale, le nombre d'espèces augmentait significativement avec la productivité autant du site de capture que de l'ensemble de la zone boisée. La variation dans l'abondance des rongeurs était influencée principalement par la productivité forestière du site de capture, celle de l'ensemble de la zone boisée ainsi que par le mois de capture. Seule une faible partie de la variation dans l'abondance des musaraignes était expliquée par la productivité de l'habitat. La relation entre la productivité forestière et la diversité des petits mammifères était linéaire et positive tant à l'échelle locale que régionale. Les réponses différentes des rongeurs et des insectivores à l'augmentation de la productivité pourraient être dues à la niche écologique plus étendue des musaraignes et à leur compétition pour l'espace avec les rongeurs.

Mots-clés : biodiversité, espèces dominantes, insectivores, relation diversité-productivité, rongeurs, zones boisées.

Nomenclature: Mitchell-Jones *et al.*, 1999; White, White & Walters, 2005; Wilson & Reeder, 2005; Seneta & Dolatowski, 2006.

Introduction

There is an ongoing debate about the factors that shape species diversity at different spatial scales (Currie, 1991; Kay *et al.*, 1997; Hawkins *et al.*, 2003; Hawkins & Diniz, 2004; Field *et al.*, 2009); some of these include: climate,

climate variability, habitat heterogeneity, history of the colonization and evolution, available energy, competition, predation, and disturbance (Currie, 1991). Of these factors, 91 to 97% of the variability in regional species richness of birds, mammals, amphibians, and reptiles is explained solely by the physical conditions of the environment (Currie, 1991). However, different factors impact species diversity at large (Currie 1991; Hawkins *et al.*, 2003) and small spatial scales (Kay *et al.*, 1997; Andrews & O'Brien, 2000), causing

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²Author for correspondence.

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species richness to vary with energy in different ways at different spatial scales (Currie, 1991). In many studies the rate of energy flow to a system is described by its productivity, measured directly (e.g., by annual biomass accumulation) or indirectly (e.g., by rainfall, evapotranspiration) (Mittelbach *et al.*, 2001).

One of the most discussed issues is the relationship between productivity and biodiversity at global, regional, and local scales (Mittelbach *et al.*, 2001; Chase & Leibold, 2002; Mittelbach, Scheiner & Steiner, 2003; Whittaker & Heegaard, 2003; Gillman & Wright, 2006; Orland & Kelt, 2007; Field *et al.*, 2009). A large number of papers show that a hump-shaped (where diversity peaks at intermediate productivity) or linear positive relationship most frequently occurs between productivity and species richness (Mittelbach *et al.*, 2001; 2003; Whittaker & Heegaard, 2003; Gillman & Wright, 2006). However, there is no universal pattern, and the relationship is dependent on study scale and taxon (Chase & Leibold, 2002; Whittaker & Heegaard, 2003). The results of various studies on the productivity–species diversity relationship are also very difficult to compare because of different scale treatment, productivity variables, and potential bias in the statistical procedures when meta-analysis is performed (Whittaker & Heegaard, 2003). Most productivity–diversity studies have been conducted on a small scale where local interactions (e.g., competition) occurred. These interactions could cause the decrease seen in the number of species at a fine scale, which is explained often as a cause of the hump-shaped interaction (Mittelbach *et al.*, 2001; Whittaker & Heegaard, 2003). Chase and Leibold (2002) claim that the relationship is hump-shaped when the productivity–diversity pattern is studied on a local scale and positively linear when the same data are viewed on a regional scale. At a larger scale, dissimilarity in composition of local species increased with productivity, e.g., ponds within watersheds of low productivity shared mostly the same species, but ponds within watersheds of high productivity differed in species composition (Chase & Leibold, 2002). This could be caused by higher heterogeneity of environmental factors in regions of higher productivity (Chase & Leibold, 2002). Mittelbach *et al.* (2001) reviewed 177 published papers on the productivity–diversity relationship and found that in vascular plants, the hump-shaped pattern occurred most often at geographical scales smaller than continents, whereas positive and hump-shaped relationships co-dominated at the continental scale. Gilman and Wright (2006) found that the positive relationship between productivity and plant species richness dominated at continental to global scale. However, for animals, no single pattern predominated: positive, negative, and hump-shaped patterns were common at most geographical scales (Mittelbach *et al.*, 2001).

Several studies have examined factors that shape species diversity of animals at different scales. Kay *et al.* (1997) investigated the relationship between plant productivity and local richness of Neotropical primates in South America. Chase and Leibold (2002) surveyed producer and animal richness in ponds at local and regional scales and revealed that the response of species richness to increasing productivity is scale-dependent. Wang *et al.* (2001) studied

the relationship between species richness of small mammals and plant primary productivity in the Inner Mongolian steppes and concluded that primary productivity was not always a good predictor of small mammal diversity on a local scale. In general, however, more rodent species occurred in habitats with more plant species (Wang *et al.*, 2001). Responses of the rodent community to changes in availability of food resources on local and regional scales were also studied by Orland and Kelt (2007) in California.

The aim of our study was to identify the factors that shape the diversity and abundance of small forest-dwelling mammals (rodents and insectivores) in temperate woodlands of northeastern Poland at local (within woodlands) and regional (among woodlands) scales. We considered factors such as productivity and area of the whole woodland, productivity at the trapping site, and mean age of forest stands. We predicted that the abundance and diversity of small mammals would increase with higher productivity in both the whole woodland and the sample sites.

Methods

STUDY AREA

The study was conducted in 7 large woodlands located in the lowlands of northeastern Poland: Augustów (Aug), Białowieża (Bial), Borki (Bor), Knyszyn (Knys), Mielnik (Miel), Pisz (Pisz), and Rominta (Rom) Forests in Warmia-Mazury and Podlasie regions (53° 56' – 54° 36' N, 21° 04' – 23° 94' E) (Figure 1). The landscape of the region has been shaped by glaciations (mainly the Riss, 310 000 to 130 000 y BP, and the Würm, 70 000 to 10 000 y BP). It is mostly a plain, with some belts of frontal and moraine hills and numerous postglacial lakes. The altitude is between 25 and 312 m asl. Forest cover is slightly higher (29.9%) than the mean for the country (28.7%) (Statistical Yearbook of the Republic of Poland, 2005). The climate is transitional between continental and Atlantic types. Mean temperature in January is –4 °C, and mean temperature in July is 17–18 °C. Annual precipitation is 550–700 mm. Snow cover lasts for 76–90 d·y^{–1}, and the growing season lasts for 180–200 d (Kondracki, 1972). The 7 studied woodlands spanned a maximum distance of 230 km in the S–N direction and 180 km in the E–W (Figure 1). They were mainly managed forests administrated by the Olsztyn and Białystok Regional Forest Directorates. Minor parts of Białowieża and Augustów Forests are protected as national parks, and from 2 to 24 smaller nature reserves are located in each forest. The Knyszyn and Rominta Forests are also protected as Landscape Parks.

The woodlands differed in size (from 126 to 1600 km²), productivity, and mean age of tree stands (Appendix I). The dominant tree species were Scots pine (*Pinus silvestris*), Norway spruce (*Picea abies*), common oak (*Quercus robur*), silver birch (*Betula pendula*), white birch (*B. pubescens*), and common alder (*Alnus glutinosa*). The percentage area of deciduous forest habitat ranged from 28.5 to 83.4%. However, the actual proportion of deciduous tree stands had been reduced to 11.6–47.6% (Appendix I). The difference between the potential and actual proportion of deciduous tree stands in all forests results from a longstanding

promotion of fast-growing coniferous species (mainly Scots pine) in commercial forests (see Jędrzejewska *et al.*, 1994). Pine monocultures have been widely planted not only on potential coniferous sites, but also on potential deciduous sites (Jędrzejewska *et al.*, 1994). The mean age of trees stands was highest in Białowieża Forest (80 y, and in its protected part, Białowieża National Park, 130 y) and lowest in Mielnik Forest (47 y) (Appendix I). The Białowieża Forest is the oldest and the best preserved woodland in the whole study area.

TRAPPING OF SMALL MAMMALS

Small mammals were trapped every year in the 7 woodlands from mid June until early September for 2004–2006. Each year, we trapped in different parts of the forests, and the sequence of surveying the woodlands was different, so that we trapped in each woodland at the beginning, in the middle, and at the end of the season. In each woodland we set traps in 8 to 11 new sites spanning 5 to 20 km. None of the circular sites were re-sampled during the study. The radius of trapping sites was 4–5 m for the traps placed on the ground and 15–20 m for the traps placed above ground (see below). This kind of sampling design, covering a larger

area and range of habitats, is recommended for species inventories at large (landscape) scales (Conard *et al.*, 2008). To avoid variation in species composition and numbers related to the successional stage of the tree stand (see Wołk & Wołk, 1982), we located our trapping sites in mature tree stands (age classes > 80 y).

Because one of the aims of our study was to compare species diversity of small mammals among the forest habitats and woodlands, we tried to catch as many species as possible. Because the effectiveness of trap designs depends on the species of small mammals trapped, choice of trap type has an impact on trapping success (Pucek, 1969). Therefore, at each site, 3 types of live-traps were placed: small wooden traps (16.5 × 9.5 × 8 cm) for rodents, large wooden boxes (11 × 11 × 24.5 cm) for dormice, and metal pitfalls (15 × 25 cm) for shrews. Six small traps were placed on the ground, 5 large boxes were located on shelves stuck by sticky tape to tree trunks at a height of about 2 m, and 4 pitfalls were dug into the ground. The pitfalls had roofs made from plastic plates above them to protect the animals from rain. The small traps were baited with carrot and oats, the large ones were baited with hazelnuts, apple, and jam, and the pitfalls were baited with minced meat. Traps were checked twice—once in the morning and once in the evening—for 6–7 d. Trapping for 4–8 nights was regarded as appropriate for assessing small mammal diversity (Conard *et al.*, 2008).

In total, from 2004 to 2006, 206 trapping sites were monitored, from 25 to 31 in each of the 7 woodlands. Trapped animals were weighed and identified to species, sex, and age class (on the basis of body mass and appearance of genitals they were classified as young or adults). Since the end of the tail (1–2 mm) was cut for genetic analyses (results to be reported elsewhere), we were able to recognize the recaptured from new animals. All animals were released at the place of capture.

PROXIES OF FOREST PRODUCTIVITY OF ENTIRE WOODLANDS AND THE TRAPPING SITES

The proportion of deciduous forest habitat and actual deciduous tree stands in the 7 woodlands (data from Forest Inventory and Management Plans) were used as a proxy of productivity of the entire woodland. Forest habitats and their productivity (Appendix II) are assessed by the Regional Bureau for Forest Inventory. During field inventories done at 10-y intervals the entire woodlands are surveyed with a spatial resolution of about 400 m² with respect to geomorphology, water condition, soil type, structure and botanic inventory of the forest herb level, undergrowth, and tree stand, and age and structure of the tree stand. Data obtained from the field surveys are then used to produce detailed numerical maps of forest habitats, which form a part of the Forest Inventory and Management Plans (FIMP) of the respective forest districts.

We assessed the productivity of forest habitat at each trapping site based on tree, shrub, and herbaceous plant species, with special attention paid to dominant and indicator species. The same classification of forests into 9 types reflecting an increasing gradient of soil fertility and humidity used in FIMPs was applied in this study (see

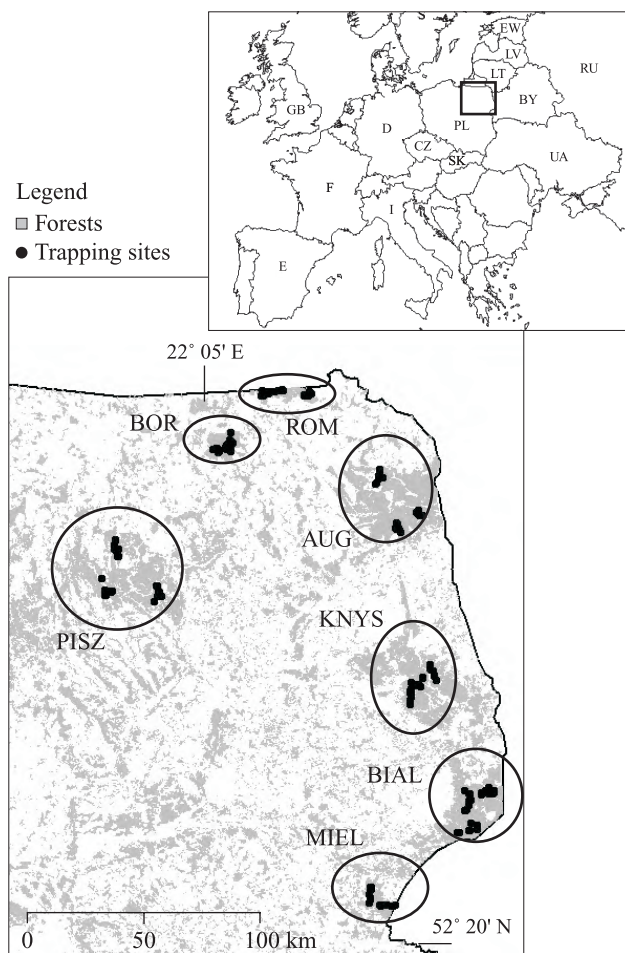


FIGURE 1. Schematic map of the study area consisting of 7 forests in northeastern Poland: Aug = Augustów, Pisz = Pisz, Knys = Knyszyn, Miel = Mielnik, Bial = Białowieża, Bor = Borki, Rom = Rominta forests.

Appendix II). Ranks of habitats (from 1 to 9) were used in data analyses of small mammal diversity and abundance. For some analyses, the 9 types of habitats were grouped into 3 main groups: coniferous and mixed coniferous (ranks 1–3), mixed deciduous (4–6), and deciduous forests (7–9).

DATA ANALYSIS

As the aim of our study was to compare the relative abundance (and not the population densities) of small mammals among the sampling sites and the woodlands, the number of individuals of each species captured in a sample site per 100 trap-nights was used as an index of small mammal abundance. Species diversity of the small mammal community in each woodland and at all sampling sites was calculated using the Shannon–Wiener index:

$$H' = -\sum_{i=1}^S (p_i)(\log_2 p_i) \quad [1]$$

where H' is the index of species diversity, S is the number of species, and p_i is the share of species i in the sample of all captured species. For the sample sites where no animals were captured or only 1 species was recorded, we assumed H' value = 0.

To compare the evenness of the shares of species in the small mammal community in each woodland and at all sampling sites we used the evenness index:

$$E = H' / H'_{\max} \quad [2]$$

and

$$H'_{\max} = \log_2 S \quad [3]$$

where H' is the index of species diversity, and S is the number of species.

We performed multiple regression analyses to explain the variation in the number of recorded species and captured small mammals (in 3 categories: all small mammals,

rodents, and insectivores). The independent variables were year of capture (1–3), month of capture (June–September: 6–9), habitat productivity rank in the trapping site (1–9), percentage area of deciduous tree stands in the whole woodland, percentage area of deciduous forest habitats in the whole woodland, and size (area) of the woodland. The regression equation explaining the number of species in 7 woodlands was then standardized for the same woodland size (1000 km²) to avoid the bias caused by the increase in the number of species with increasing forest area. We also performed linear regression analysis to check how the proportion of dominant rodents (bank vole and yellow-necked mouse) and insectivores (common and pygmy shrews) in the small mammal community varied with increasing percentage area of deciduous forest habitats in the 7 studied woodlands. Kruskal–Wallis ANOVAs were used to check for significant differences between capture sites located in the 3 major classes of forest habitats in mean number of individuals captured per 100 trap-nights, number of species recorded, index of species diversity H' , and evenness index. We also performed Mann–Whitney U -tests to check if there were differences in the abundance of rodents between the first (June–15 July) and the second (16 July–September) part of the summer season in 3 groups of forest habitats: coniferous and mixed coniferous (ranks 1–3), mixed deciduous (4–6), and deciduous forest (7–9). All statistical analyses were performed in STATISTICA 7.1. (StatSoft, 2005).

Results

SPECIES DIVERSITY OF SMALL MAMMALS IN RELATION TO WOODLAND SIZE AND PRODUCTIVITY

We captured 1739 mammals belonging to 9 species over 18 332 trap-nights. The total number of small mammal species recorded varied from 5 in Pisz Forest to 9 in Białowieża Forest (Table I). The total number of species (N_{sp}) recorded during the study in the 7 woodlands

TABLE I. Species composition of small mammal community (numbers are percentages of all captured individuals), total number of recorded species, indices of species diversity H' , and evenness indices in 7 woodlands in northeast Poland. Abbreviations of woodland names as in Figure 1.

Species/variable	Woodland						
	Aug	Pisz	Knys	Miel	Bial	Bor	Rom
Bank vole (<i>Myodes glareolus</i>)	49	66.2	49.5	64.1	40.8	66.4	57.5
Yellow-necked mouse (<i>Apodemus flavicollis</i>)	16.8	16	32.4	23.1	45	22.6	31.1
Striped field mouse (<i>A. agrarius</i>)	-	-	-	-	-	-	0.3
Voles (<i>Microtus</i> sp.)	0.4	2.6	-	-	1.6	-	0.7
Northern birch mouse (<i>Sicista betulina</i>)	-	-	0.5	0.4	-	0.3	-
Harvest mouse (<i>Micromys minutus</i>)	-	-	-	-	-	0.3	-
Fat dormouse (<i>Glis glis</i>)	-	-	-	-	1.6	-	-
Forest dormouse (<i>Dryomys nitedula</i>)	-	-	0.9	1.8	0.4	-	-
Common dormouse (<i>Muscardinus avellanarius</i>)	-	-	-	3.1	-	0.3	-
Common shrew (<i>Sorex araneus</i>)	23.1	10.6	11	6.2	5.7	6.8	6.6
Pygmy shrew (<i>S. minutus</i>)	8.9	4.6	4.8	1.3	2.9	2.2	3.6
Water shrew (<i>Neomys fodiens</i>)	1.8	-	0.9	-	1.2	1.1	-
Miller's water shrew (<i>N. anomalus</i>)	-	-	-	-	0.8	-	-
Total number of species caught	6	5	7	7	9	8	6
Species diversity index H'	1.89	1.5	1.75	1.52	1.76	1.38	1.49
Evenness index	0.73	0.65	0.62	0.54	0.56	0.46	0.58
Total number of captured animals	268	151	210	225	245	354	286
Total number of trap-nights	2646.5	2705.5	2704	2144.5	2586	2773	2772.5
No. of animals per 100 trap-nights	10.1	5.6	7.8	10.5	9.5	12.8	10.3

positively correlated with the share of actual deciduous forests (DF) and the woodland size (WS) ($N_{sp} = 3.783 + 0.0838DF + 0.0007 WS$, $R^2 = 0.717$, $n = 7$, $P = 0.08$). The proportion of deciduous forests was more important (semipartial correlation squared, Tabachnick and Fidell [1983], $sr^2 = 0.574$, $P = 0.03$) than the woodland size ($sr^2 = 0.071$, $P = 0.32$). Figure 2 shows this relationship for the standardized area of 1000 km².

In all forests, the dominant species were the bank vole (*Myodes glareolus*) and the yellow-necked mouse (*Apodemus flavicollis*) (Table I). They constituted from 65.8% (both species pooled) in Augustów Forest to 89% in Borki Forest of all captured individuals, and their joint proportion in the small mammal community increased with the proportion of deciduous forest habitats in the 7 woodlands (Figure 2). The relative contribution of 2 species of shrews (common shrew [*Sorex araneus*] and pygmy shrew [*S. minutus*] pooled) to the small mammal community declined with increasing productivity of the woodland (Figure 2). All other species were rare, and their proportion in the community was not related to forest productivity.

The index of species diversity (H') ranged from 1.38 in Borki to 1.89 in Augustów Forest (Table I). There was no significant relationship between H' index and the proportion of deciduous forest habitats or actual deciduous tree stands ($P = 0.236$ and $P = 0.487$, respectively). However, the evenness index decreased significantly with the proportion of deciduous forest habitats ($R^2 = 0.726$, $P = 0.015$) and with the actual proportion of deciduous tree stands ($R^2 = 0.624$, $P = 0.03$) in the 7 woodlands.

SPECIES DIVERSITY AND ABUNDANCE OF SMALL MAMMALS IN RELATION TO PRODUCTIVITY OF CAPTURE SITE

The number of small mammal species captured per trapping site increased with increased productivity of forest habitat from 0–4 (on average 1.73) in coniferous and mixed coniferous stands to 0–7 (on average 2.35) in deciduous stands (Table II). Also, the number of small mammals per trapping site increased with productivity of trapping sites in the 3 classes of forest types (Table II). The largest differences between forest habitats were found in the 2 dominant species of rodents: bank vole and yellow-necked mouse. A slight increase with productivity was also recorded for the number of common, pygmy, and water shrews (Table II). In effect, the total number of captured animals increased from an average of 6.16 per 100 trap-nights in coniferous and mixed coniferous forests to 10.43 in deciduous forests (Table II).

The index of species diversity (H') was significantly lower in the coniferous and mixed coniferous forest than in the more fertile deciduous and mixed deciduous forests (Table II). The evenness index tended to be lower in coniferous than in other kinds of forests, but the differences were not statistically significant (Table II).

For all small mammals trapped, as well as for the 2 main taxonomic groups (rodents and insectivores), we performed multiple regression analyses to determine the entire set of environmental variables that best explained the observed variation in their abundance. The most important

factors for all small mammals were the month of capture, the productivity of the trapping site, and the proportion of actual deciduous tree stands (Table III). The model containing these 3 variables explained 29% of variation in the number of captured small mammals (Table III). The abundance of animals increased with increasing productivity of forest habitat (Figure 3) and with season (from June to September). Semipartial correlations squared (sr^2) showed that month of capture and habitat rank of the trapping site were the most important factors (Table III).

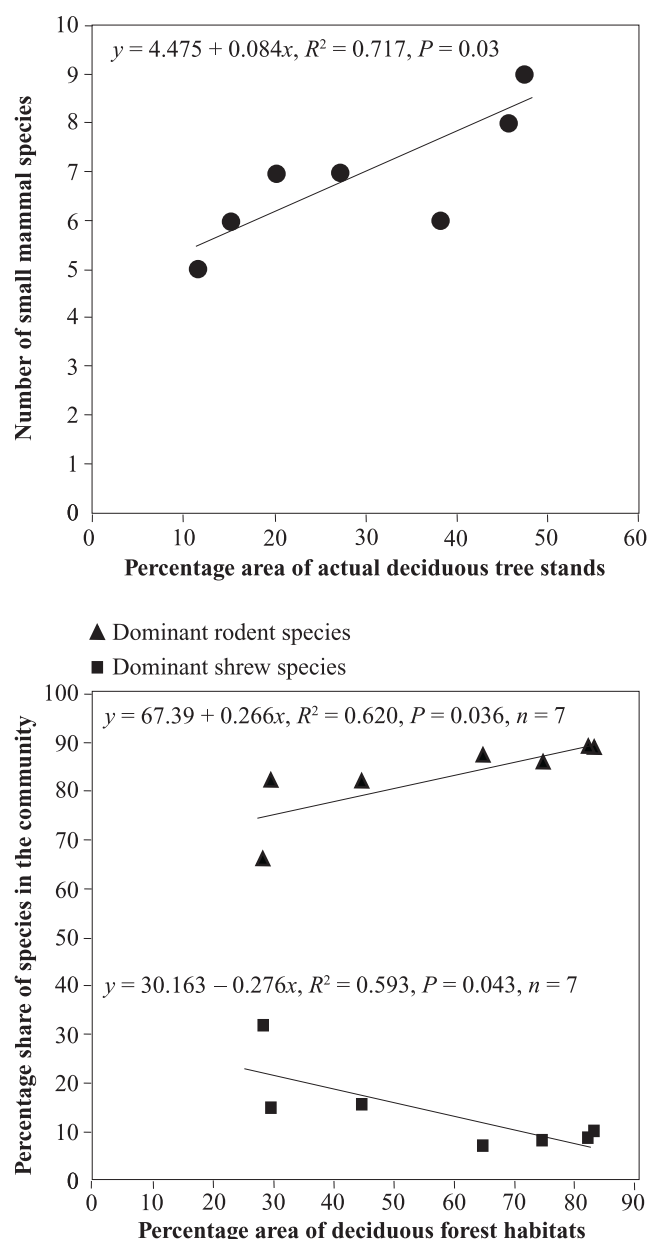


FIGURE 2. Upper panel: Number of small mammal species in relation to the percentage area of deciduous tree stands in 7 woodlands of north-eastern Poland. The regression line and equation shows the relationship for the standardized area (1000 km²) of woodlands. Lower panel: Percentage shares of the abundance of dominant rodent species (bank vole and yellow-necked mouse) and dominant insectivores (common and pygmy shrews) in the communities of small mammals in relation to productivity of the woodlands. Data shown in Tables I and III.

TABLE II. Mean \pm SE number of individuals captured per 100 trap-nights, number of species recorded, index of species diversity H' , and evenness index in one capture site located in the 3 major classes of forest habitats. Statistical differences among the 3 forest classes were calculated using Kruskal-Wallis ANOVA; df in all cases = 2.

Species/variable	Mean \pm SE number of species and individuals captured in one site located in a given forest habitat class			Kruskal-Wallis ANOVA	
	Coniferous and mixed coniferous	Mixed deciduous	Deciduous	H	P
Number of species trapped	1.73 \pm 0.12	2.18 \pm 0.15	2.35 \pm 0.13	9.55	0.009
Bank vole	3.73 \pm 0.53	4.74 \pm 0.56	5.66 \pm 0.52	9.66	0.008
Yellow-necked mouse	1.32 \pm 0.30	2.36 \pm 0.42	3.06 \pm 0.46	11.42	0.003
Other rodents	0.19 \pm 0.06	0.06 \pm 0.03	0.22 \pm 0.06	2.52	0.283
Common shrew	0.62 \pm 0.14	0.92 \pm 0.26	0.96 \pm 0.21	1.95	0.377
Pygmy shrew	0.29 \pm 0.07	0.34 \pm 0.10	0.37 \pm 0.10	0.14	0.934
Water shrews	0.03 \pm 0.02	0.04 \pm 0.03	0.16 \pm 0.05	5.08	0.079
Total small mammals	6.16 \pm 0.63	8.46 \pm 0.77	10.43 \pm 0.66	21.65	< 0.0001
Index of species diversity H'	0.57 \pm 0.07	0.79 \pm 0.08	0.79 \pm 0.06	6.14	0.046
Evenness index	0.45 \pm 0.05	0.58 \pm 0.05	0.57 \pm 0.04	2.60	0.273
Total number of capture sites	73	50	83	-	-
Total number of captured animals	441	432	865	-	-
Total number of trap-nights	6461.5	4435.5	7435	-	-

TABLE III. Results of the multiple regression analyses: relationships among the abundance indices (all captured mammals, rodents, insectivores; $\ln([N/100 \text{ trap-nights}] + 1)$) and environmental factors; sr^2 = semipartial correlations squared, showing the relative contributions of each independent variable to the total variation explained (Tabachnick & Fidell, 1983); *** P < 0.0001, ** P < 0.01, * P < 0.05.

Independent variable	All small mammals		Rodents		Insectivores	
	Parameter	sr^2	Parameter	sr^2	Parameter	sr^2
Intercept	-1.643	-	-2.230	-	0.586	-
Month of capture	0.368***	0.108	0.417***	0.14	-	-
Habitat rank (1–9)	0.124***	0.116	0.120***	0.11	0.080**	0.047
Actual deciduous forests (% area)	0.013**	0.041	0.016***	0.06	-	-
Deciduous forest habitats (% area)	-	-	-	-	-0.006*	0.019
R^2 of regression model	0.29		0.34		0.054	
Statistical significance of the regression model	P < 0.000001		P < 0.000001		P < 0.00376	

Variation in rodent abundance was affected mainly by month of capture, habitat productivity of the capture site, and productivity of the whole woodland (expressed as percentage area of actual deciduous tree stands). The model with these 3 variables explained 34% of the variation in the number of trapped rodents (Table III). The number of rodents increased with increasing habitat productivity at both capture-site scale and whole-woodland scale, and both capture-site productivity and whole-woodland productivity contributed to the variation explained by the model (sr^2 = 0.110 and 0.060, respectively). However, month of capture was the most important factor in the model (Table III).

In the case of insectivores, only a small proportion of the observed variation in abundance (5%) was explained by the model including habitat productivity of the capture site and productivity of the whole woodland (Table III). The number of shrews increased slightly with increasing productivity of trapping site and was negatively correlated with the productivity of the whole woodland.

The positive relationship between productivity of capture site and captured animals, found in all analyses, is shown in Figure 3. Season also influenced the number of rodents captured (Figure 3). In the most fertile deciduous forests (ranked 7–9) rodents reached their highest numbers in June–July

and remained at the same level until September. In the least productive coniferous forests (ranked 1–3), populations of rodents remained low in the first half of summer and attained their seasonal peaks in August–September (Figure 3). The differences between the abundance of rodents in the first (June–mid July) and the second part (end of July–September) of the summer season were statistically significant only in the least productive coniferous and mixed coniferous forest habitats (ranked 1–3) (Mann–Whitney test, Z = -3.900, P = 0.000065).

Discussion

HABITAT PRODUCTIVITY AND NUMBER OF MAMMAL SPECIES

The relationship between productivity and number of species was linear and positive on both local and regional scales. Our trapping sites covered the whole range of forest productivity gradient typical for European lowland temperate forests (Matuszkiewicz, 1978). Thus, it is not possible that this relationship is only part of a unimodal pattern and would become hump-shaped if areas of still higher productivity were investigated (Abrams, 1995).

Groner and Novoplansky (2003) suggested that study of diversity–productivity patterns should be based on direct productivity estimates, e.g., production of mass ($\text{g}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$), energy ($\text{J}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$), or community standing biomass ($\text{g}\cdot\text{m}^{-2}$),

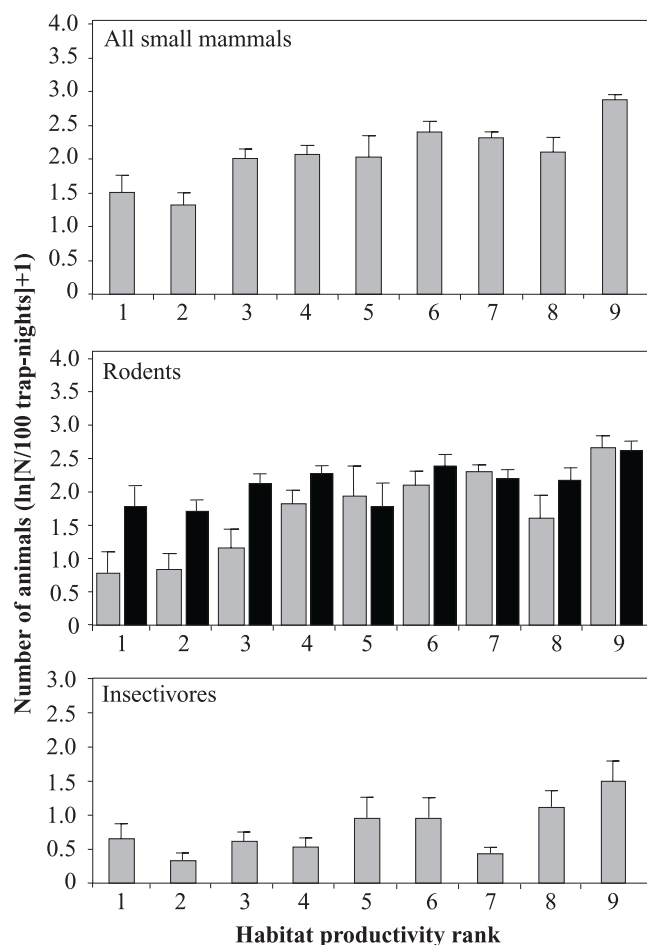


FIGURE 3. Mean (\pm SE) abundance of captured animals in relation to the rank of forest productivity of a trapping site. Rodents: grey bars = the first half of summer (June–15 July); black bars = the second half of the summer (16 July–September). See Appendix II for description of forest habitats ranked 1–9.

especially when meta-analyses of communities of different trophic levels are performed. However, in many studies, indirect estimates of available energy are used, *e.g.*, latitude, altitude, actual evapotranspiration, average annual temperature of the studied ecosystems (Mittelbach *et al.*, 2001; Groner & Novoplansky, 2003). Hawkins *et al.* (2003) postulated that the global diversity of animals and plants is driven by direct or indirect (via plant productivity) interactions between water and energy and therefore that understanding water–energy dynamics is critical to future biodiversity research. Also, Field *et al.* (2009) noticed that climate and productivity play an important role in explaining species richness at large scales. However, local ecological communities are mainly driven by regional-scale influences, including evolutionary and biogeographic processes (*e.g.*, latitudinal richness pattern, differential dispersal among geographic regions, rates of diversification) (Harrison & Cornell, 2008). Although we did not assess productivity directly (*e.g.*, estimating standing biomass), the productivity gradient used reflected well both water–energy dynamics and smaller-scale processes such as forest management.

In northeast Poland, forest productivity was the most important factor explaining the number of species at the

regional (among forests) and local (within forests) scales. The highest number of species occurred in woodlands with the highest proportion of deciduous forests and in deciduous habitats. European deciduous and mixed forests provide major food resources (green, herbaceous vegetation on the forest floor and seeds from trees) for forest rodents, and their dynamics often depend on mast years of deciduous trees, *e.g.*, oak and hornbeam (Pucek *et al.*, 1993; Hansson, Jędrzejewska & Jędrzejewski, 2000). Similar species diversity–habitat productivity relationships have been found elsewhere (Kay *et al.*, 1997; Orland & Kelt, 2007).

Plant species diversity, one of the factors that could influence vertebrate richness, has been studied by Currie (1991), Andrews and O’Brien (2000), Boone and Krohn (2000), and Hawkins and Pausas (2004). However, in most of these studies, climatic variables explained vertebrate richness better than primary productivity or plant species richness (Currie, 1991; Boone & Krohn, 2000; Hawkins & Pausas, 2004).

In contrast, in studies conducted in the Inner Mongolian steppes in China, the relationship between small mammal species richness and aboveground biomass of plants was linear and negative at the local scale due to seasonal movements and use of different habitats during the year by some of the small mammals (Wang *et al.*, 2001). However, at a larger spatial scale the relationship was unimodal (Wang *et al.*, 1999) because local movement of small mammals did not affect species richness at such a scale (Wang *et al.*, 2001).

HABITAT PRODUCTIVITY AND SPECIES DIVERSITY INDICES: THE ROLE OF DOMINANTS

We found a negative impact of increasing abundance of dominant species on the species diversity index (Shannon–Wiener index). Similar results have been reported by Orland and Kelt (2007), Brady and Slade (2001), and Gliwicz and Jancewicz (2004): in years with peak population numbers, the dominant species monopolized food resources or competed for space with other species in the community. One of the reasons for decreasing species diversity at higher productivity levels is an increase in interactions among species, *e.g.*, competition or predation (Abramsky & Rosenzweig, 1984; Abrams, 1995; Huston, 1999; Groner & Novoplansky, 2003). In our study, despite an increasing number of small mammals with increasing forest productivity, there was no significant relationship between species diversity index H' and productivity, and the evenness index decreased with productivity. However, at the local scale (in 3 classes of productivity of sample sites) the situation was different: there was a slight increase of species diversity with productivity, and the differences in evenness were not significant. The share of the 2 dominant species in the community grew as forest productivity increased. When the number of individuals of the dominant species increases, they probably out-compete other small mammal species in optimal habitats, although the pressure of dominants is not always evident (Aulak, 1970; Fasola & Canova, 2000; Huitu, Norrdahl & Korpimäki, 2004; Rychlik & Zwolak, 2005; Żmihorski, Balčiauskienė & Romanowski, 2008).

Brady and Slade (2001) used long-term data to investigate how the 2 dominant species, prairie vole (*Microtus*

ochrogaster) and hispid cotton rat (*Sigmodon hispidus*), influenced the local diversity of a grassland rodent community. They found that the vole as a dominant species did not influence the diversity of other species in the community. However, the cotton rat had a negative influence on the total community diversity, but only during a short, 2-y period (Brady & Slade, 2001). The impact of the dominant species on the diversity of the entire community can be different at both spatial and temporal scales and depends on the abundance of the dominant species.

HABITAT PRODUCTIVITY AND POPULATION ABUNDANCE OF RODENTS AND SHREWS

In the woodlands of northeast Poland, the abundance of small mammals increased with forest productivity at both the local and regional spatial scales, although productivity alone explained only a small proportion of the variability in the numbers of small mammals. Moreover, herbivorous (in a wide sense) rodents responded strongly, whereas predatory insectivores responded rather weakly to increasing productivity. This result shows that the productivity–diversity gradient is based on trophic relationships: more productive deciduous forests offer more abundant and diverse food resources (soft tissue plants in ground cover, seeds of trees and bushes), which support higher numbers of both rodent species and individuals. The dynamics of bank vole and yellow-necked mouse numbers with the crop years of deciduous tree species is well known (Pucek *et al.*, 1993; Hansson, Jędrzejewska & Jędrzejewski, 2000). The major role of trophic relationships is also corroborated by the fact that in the most productive deciduous forests rodents reached their seasonal peak in numbers 2–3 months earlier than in coniferous forests. The main reason for this may be the earlier seasonal (in spring and early summer) phenological development of forest floor plants in deciduous forests compared to mixed and coniferous forests (Falińska, 1973; Faliński, 1986).

The positive relationship between the productivity of ground vegetation (as indicator of food availability to rodents) and rodent abundance was reported earlier by Jędrzejewski and Jędrzejewska (1996) on a very large geographic scale in various biomes in the Palaearctic. Based on 30 data points placed in 7 biomes of the Palaearctic, they showed that mean (calculated from spring and autumn estimates) densities of rodents were lowest in tundra, desert, and forests (taiga, mixed and deciduous forests, steppe woodland) and highest in steppe (Jędrzejewska & Jędrzejewski, 1996). Among the different categories of forests, the highest rodent densities were recorded in the deciduous forest (Jędrzejewska & Jędrzejewski, 1996), which provided the highest amount of herbs during the summer season (Falińska, 1973; Faliński, 1986); together with seeds of the deciduous trees, these constituted the main food resources of the bank vole and yellow-necked mouse (Zemanek, 1972; Gębczyńska, 1976). Our study produced the same results at regional and local scales.

The lack of a direct relationship between number of shrews and forest productivity may result from the fact that the abundance of invertebrates does not vary along the same gradient as forest vegetation productivity. Studies

on the diet of *Sorex* and *Neomys* have shown that there is no strong competition for food resources among different insectivores and suggest that the availability of prey was not a limiting factor for these opportunistic predators, especially during summer (Churchfield, 1982; 1984; Churchfield & Rychlik, 2005). In Great Britain, prey resources for shrews were always abundant, and the seasonal changes in prey availability were weakly correlated with the diet of *Sorex araneus* (Churchfield, 1982). The lack of relationship between the abundance of shrews and forest vegetation productivity could also be a result of a wider habitat niche of shrew species compared to rodent species (Aulak, 1970). In Białowieża National Park, the second most preferred habitat of shrews (after oak–lime–hornbeam forest) was pine forest where the biomass of invertebrates was high (Aulak, 1970). Yet another reason for the different response of shrews to habitat productivity could be competition for space with rodents; there is some evidence for this possibility (Huitu, Norrdahl & Korpimäki, 2004).

In conclusion, the species diversity and abundance of small mammals in mature temperate lowland forests in Central Europe were markedly influenced by forest productivity, and this relationship was more strongly pronounced for herbivores (rodents) than for predatory species (insectivores). In addition, other factors such as woodland size and year of capture modified the productivity–diversity or productivity–abundance relationships in small mammals.

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APPENDIX I. Characteristics of 7 woodlands of northeast Poland. Data concerning size of the forests and share of potential and actual deciduous forests were taken from the current Forest Inventory and Management Plans of the respective forestry districts and Sokołowski (2006). The areas of Białowieża and Rominta forests are given for the whole woodlands, but the age of the tree stands and share of the potential and actual deciduous forests were calculated only for Polish parts of the woodlands as data for the Belarussian (Białowieża Forest) and Russian (Rominta Forest) parts were not available; Aug = Augustów, Pisz = Pisz, Knys = Knyszyn, Miel = Mielnik, Bial = Białowieża, Bor = Borki, Rom = Rominta forests (see Figure 1 for location of woodlands).

Woodland characteristic	Aug	Pisz	Knys	Woodland Miel	Bial	Bor	Rom
Area of contiguous forests (km ²)	1600	1050	1244	192	1500	126	390
Mean age of tree stands (y)	66	64	59	47	80	62	54
Deciduous forest habitats (% area)	28.5	29.7	44.8	65	74.9	82.4	83.4
Actual deciduous forests (% area)	15.3	11.6	20.2	27.2	47.6	45.8	38.3

APPENDIX II. Forest habitats identified in trapping sites, ranked in order of increasing soil fertility and humidity and their dominant tree species. The classification of the forest habitat follows (with slight modification) that used in forest management (Matuszkiewicz, 1978).

Rank	Forest habitat description	Dominant tree species
1	Dry coniferous forest	Scots pine (<i>Pinus silvestris</i>), Norway spruce (<i>Picea abies</i>)
2	Fresh coniferous forest	Scots pine, Norway spruce
3	Mixed coniferous forest	Scots pine, Norway spruce, common oak (<i>Quercus robur</i>), silver birch (<i>Betula pendula</i>), and white birch (<i>B. pubescens</i>)
4	Mixed deciduous forest	Common oak, common hornbeam (<i>Carpinus betulus</i>), Scots pine, Norway spruce
5	Bog alder wood/coniferous forest	Common alder (<i>Alnus glutinosa</i>), white birch, Norway spruce
6	Riparian deciduous/coniferous forest	Common alder, common ash (<i>Fraxinus excelsior</i>), Norway spruce
7	Mesic deciduous forest	Common oak, common hornbeam, small-leaved lime (<i>Tilia cordata</i>), Norway maple (<i>Acer platanoides</i>)
8	Bog alder wood	Common alder, white birch
9	Riparian deciduous forest	Common alder, common ash