

Article

Is There Any Difference?—Carabid Beetle Assemblages (Coleoptera: Carabidae) in Managed Coniferous and Deciduous Forests and Their Relevance for Sustainable Forest Management

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Abstract

Unsustainable forest management in the past and current climate change are altering the species composition and spatial structure of forest vegetation. As a result of these transformations affecting the entire forest ecosystem, both the quality and quantity of animal communities are also being modified. Insects are especially sensitive to environmental changes, and among them, carabid beetles (Carabidae) are widely regarded as model organisms. The aim of this study was to examine alterations in the structure of carabid beetle assemblages found in coniferous (CON) and deciduous (DEC) forests. The study was carried out in north-eastern Poland in four forest habitat types: deciduous fresh forest (Df), deciduous mixed fresh forest (DMf), coniferous mixed fresh forest (CMf), and coniferous fresh forest (Cf). Carabid beetles were captured using pitfall traps from May to October in 2013 and 2014. A total of 20,125 individuals representing 79 Carabidae species were collected. The recorded carabid beetles showed high ecological plasticity. Most species were distributed across both forest types despite differences in structure and environment, including vegetation characteristics and microclimatic conditions. No significant differences were observed between coniferous and deciduous forest assemblages in terms of carabid beetle abundance, species richness, or diversity. The differences observed between deciduous and coniferous forests were primarily related to species composition and the ecological structure of Carabidae. Unexpectedly, most of the distinguished ecological groups differed from the established pattern found in the literature, which states that deciduous forest communities are the primary refuge for forest carabid beetles. The similar species richness and diversity levels observed in both groups, together with the balanced distribution of predatory, winged and open-habitat carabid beetles across forest types, suggest the presence of detrimental ecological processes. Forest management is known to homogenize the qualitative, quantitative, and spatial structure of vegetation, which, along with climate change, may result in negative transformations reflected in carabid beetle assemblages. Therefore, maintaining structurally diverse forest stands and supporting habitat continuity may be important for biodiversity conservation, and incorporating biodiversity indicators such as carabid beetles into forest monitoring may support the long-term sustainability and resilience of forest ecosystems.

Keywords: carabid beetles; diversity; life traits; coniferous forest; deciduous forest; sustainable forest management



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1. Introduction

Human activity has caused two global crises: the mass extinction of species and climate change [1,2]. These crises are partly interconnected. Climate change contributes to species extinction and drives rapid biodiversity loss. Consequently, climate-driven environmental change leads to substantial shifts in species' geographic distributions, as well as in their phenology, behavior and foraging patterns. This results in changes to species composition, species interactions, and the functioning of entire ecosystems, both terrestrial and aquatic [3–5].

Forests possess the highest levels of biodiversity among terrestrial ecosystems and cover 31% of the Earth's land surface. While deciduous tree species generally dominate forests worldwide [6], conifers are more prevalent in European forests [7]. This is partly because in Europe conifers were considered the most useful for timber production. Additionally, their ecological characteristics allow conifers to thrive in a variety of forest habitats [8,9]. Maintaining forest biodiversity while ensuring the sustainable provision of ecosystem services has therefore become one of the major challenges of contemporary forest management. However, due to ongoing climate change, a marked increase in the area of deciduous forests is projected across Europe, accompanied by a simultaneous decrease in the area of coniferous forests [4]. It is believed that in several decades, deciduous species, particularly oaks (*Quercus robur* and *Q. petraea*), beech (*Fagus sylvatica*), and ash (*Fraxinus excelsior*), will form forest communities in Europe [4], while the projected substitution of coniferous species by broadleaved species will affect half of the forest area in this region [7].

Shifts in tree species composition are likely to have important consequences for forest biodiversity, although their magnitude and direction remain uncertain. It has been suggested that the presence of deciduous tree species in coniferous forests diversifies vegetation structure, stabilizes the microclimate, and improves soil physicochemical properties [9,10]. As a result, a wider variety of animal species may be able to find suitable habitats than in coniferous monocultures. For instance, the thick layer of organic matter from deciduous trees provides more shelter and breeding sites than conifer needles [9,11,12]. However, not all previous studies have confirmed the beneficial effect of deciduous tree species on animal diversity or species richness [13,14]. Therefore, more research on this important issue is needed.

Insects are a particularly important component of forest faunal diversity. This is partly due to their widespread occurrence, as they account for about 70% of all animal species worldwide [15]. Insects are also a group of animals that are especially vulnerable to the aforementioned changes in the species composition of forest stands [16,17]. It is important to note that for many insect species, their taxonomy, ecology, and responses to emerging changes are well understood [18,19]. Therefore, these insects can serve as an effective tool for predicting future changes in forest biodiversity.

Carabid beetles have been used in numerous studies on forest biodiversity [20–23]. As other authors of previous articles indicate, several elements of the forest environment determine the qualitative and quantitative composition of carabid beetle assemblages. The composition and spatial structure of the stand, as well as the herb-layer species composition, are considered key factors [24,25]. This is because they affect, among other things, the quality and quantity of dead organic matter. Organic matter derived from deciduous trees is particularly important because it decomposes more quickly than needles [26], thereby enriching the soil and enhancing vegetation structure [27]. Moreover, a thick layer of broadleaved organic matter positively affects the richness of carabid beetle food resources, including earthworms and springtails, as well as the heterogeneity of their ecological niches [13,24,28,29].

Another important factor affecting carabid beetle biodiversity is microclimatic conditions. A high degree of shading on the forest floor, especially in deciduous forests compared with coniferous ones, significantly affects the physicochemical properties of soil and air. Other authors have stated that deciduous forests, compared to coniferous forests, provide cooler, more humid microclimatic conditions. In addition, these parameters, i.e., humidity and temperature, show smaller fluctuations over time, both seasonally and diurnally [24,25,30].

Depending on the species, carabid beetles differ in their requirements or preferences regarding the forest environmental conditions described above. Forest assemblages of Carabidae include species with high ecological plasticity. Carabid beetles have flexible environmental requirements and use a variety of food sources depending on their location and the time of year. As a result, these species are widely distributed throughout the forest ecosystem [20]. At the same time, species with a high degree of specialization are also present. These carabid beetles occur in specific places within the forest ecosystem and use particular resources. An example is moist dead wood, in which they overwinter [14,31].

The environmental requirements of carabid beetles also reflect their association with different ecological groups. Habitat and trophic preferences, as well as body size, breeding type and movement mode, are traits of each Carabidae species that determine its distribution [32,33]. For example, large predatory species with an autumn breeding pattern are generally characterized by a long larval development period and a high demand for animal prey. Forest soil rich in dead organic matter provides them with shelter, food and a stable breeding site [34,35]. These environmental conditions are characteristic of deciduous forests [24].

Coniferous forests, in turn, tend to favor the presence of macropterous carabid beetles of open habitats and many eurytopic species with a spring breeding pattern. These carabid beetles poorly tolerate shading and prefer moderately moist to dry, warm soils [36,37]. Due to their ability to fly, they can actively search for favorable environmental conditions. Macropterous carabid beetles may even colonize small patches of exposed forest ground, for example, following windthrow events [20,38]. Therefore, depending on environmental conditions across the forest ecosystem and on the requirements of carabid beetles, the richness, diversity, species composition and ecological structure of their assemblages vary in space and time [20,22,39].

Despite there being a large body of literature dedicated to carabid beetle assemblages in forest ecosystems, many gaps remain unresolved. Only a few studies have presented a broad assessment of forest carabid beetle assemblages [33]. Moreover, previous comparisons of carabid beetle assemblages have produced inconclusive results, as in the case of forests differing in tree species composition. According to Finch [40], deciduous stands are characterized by higher richness, abundance and diversity of carabid beetles than their coniferous counterparts. In the study by Jung and Lee [41], this pattern was observed only for species number, whereas Fuller et al. [24] reported this relationship only for carabid beetle abundance. Taboada et al. [27], who studied older stands in unmanaged forest communities, recorded a similar number of carabid beetle species in deciduous and coniferous communities; however, the latter were more diverse.

Moreover, the ecological structure of carabid beetle assemblages has been analyzed relatively rarely, or analyses have focused only on selected ecological traits, omitting important characteristics such as flight ability, developmental type or trophic preferences [14,24,27,40,41]. It should be noted that in previous studies, carabid beetles were often collected using a small number of traps and/or over a short period [14,40], which may be associated with relatively small sample sizes. Therefore, there remains a need for studies based on larger numbers of species and individuals collected, allowing for more accurate

inference. Such knowledge is also essential for developing sustainable forest management strategies that reconcile timber production with the conservation of biodiversity and the long-term resilience of forest ecosystems.

This study aimed to examine differences between carabid beetle assemblages in deciduous and coniferous stands. As changes in forest composition are commonly discussed in the context of nature conservation and sustainable forest management, we see that understanding these differences may be of great importance for future management decisions. In this study, we tested the following hypotheses and predictions: H1—deciduous forests, compared with coniferous forests, exhibit distinct qualitative and quantitative features of carabid beetle assemblages. Specifically, we predict that deciduous forests support higher species richness (P1.1), greater abundance (P1.2), and higher assemblage diversity—increased values of the Shannon diversity index (H') and Pielou's evenness index (J') (P1.3). The second hypothesis (H2) assumes that the ecological characteristics of carabid beetles differ between forest types. We expect (P2.1) that deciduous forests harbor predatory, wingless species with an autumn breeding pattern, whereas coniferous forests are expected to support winged, omnivorous and phytophagous species with a spring breeding pattern. Furthermore, we predict that carabid beetle assemblages in deciduous forests are dominated by moisture-preferring, large-bodied, forest-associated species. In contrast, we expect that carabid beetle assemblages in coniferous forests are dominated by eurytopic and open area species with small and medium body sizes (P2.2).

2. Materials and Methods

2.1. Study Area

Our data were collected in the Wipsowo and Jedwabno forest districts, located in Northeastern Poland (Figure 1). Both forest districts are characterized by similar climate conditions—a lake-land climate with transitional features between continental and maritime climates. The average annual temperature is 7.0–7.7 °C, and the average annual rainfall reaches 630 mm. The growing season lasts from 190 to 200 days [42,43].

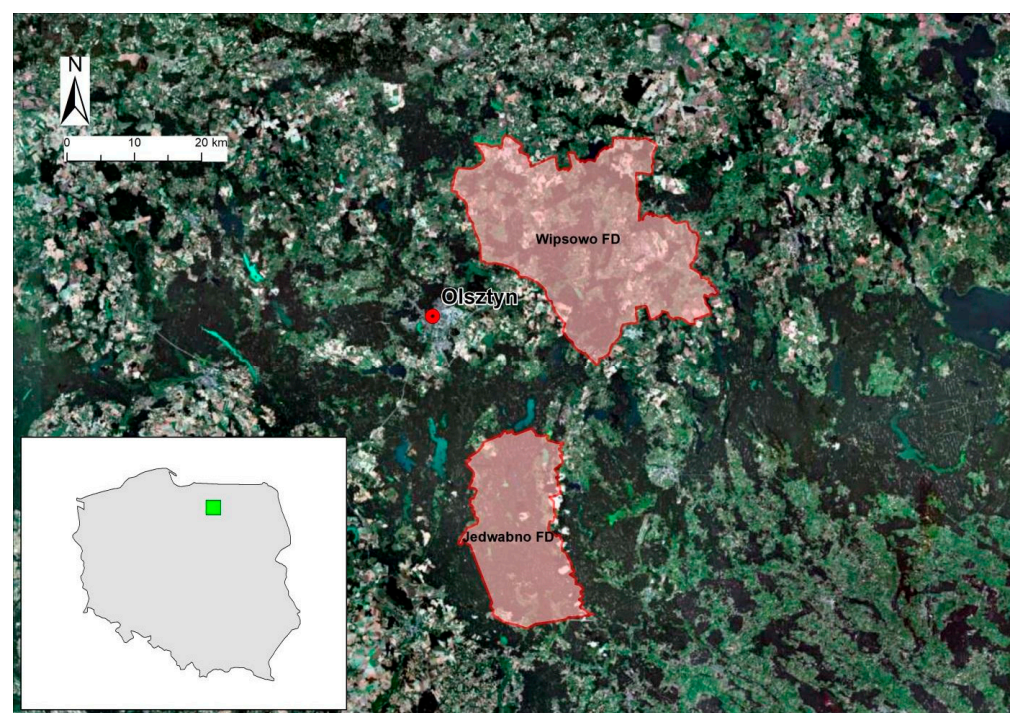


Figure 1. Location of the study areas: Wipsowo and Jedwabno forest districts. Green square—location of the study area in Poland.

The Wipsowo forest area covers 23,600 hectares. To classify the forest site types, we followed the classification used by the State Forests in Poland. Deciduous forest site types, including fresh forest (Df) and mixed fresh forest (DMf), make up 68% of the total forest area. Coniferous forest site types account for 22% of the forest, with coniferous mixed forest (CMf) being the predominant type at 18% of the total forest area. The major tree species in the Wipsowo forest are Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*), which together comprise 65% of the total forest area. However, there is a noticeable increase in the area occupied by deciduous tree species, particularly silver birch (*Betula pendula*), pedunculate oak (*Quercus robur*), black alder (*Alnus glutinosa*), and beech (*Fagus sylvatica*). The topography of the Wipsowo area is slightly undulating, with elevations ranging from 100 to 220 m above sea level. It features typical young-glacial relief, characterized by numerous lakes and ponds.

The forest in Jedwabno covers 28,900 ha. Coniferous forest site types, including mixed fresh forest (CMf) and fresh forest (Cf), make up 64% of the total forest area. Deciduous forest site types, mainly mixed fresh forest (DMf), account for 20% of the total forest area. The predominant tree species in this forest is Scots pine, which comprises 85% of the total forest area. The remaining area is primarily occupied by deciduous species such as silver birch, black alder, and pedunculate oak. The northern part of Jedwabno features a varied topography characterized by moraines and is interspersed with numerous lakes and swamps. In contrast, the southern region is characterized by an outwash plain.

2.2. Sampling Design

We chose four locations in Northeastern Poland: two in Wipsowo (W1, W2) and two in Jedwabno (J1, J2). The first (W1) was within a deciduous fresh forest site type (Df) with multi-storied 50–120 year-old tree cover (53°59′06″ N 20°36′21″ E). The most frequent tree species were beech, pedunculate oak, hornbeam (*Carpinus betulus*), silver birch, and Norway spruce. There was moderate to loose horizontal tree cover. The forest floor was covered with herbaceous plants and sod. The second (W2) was in deciduous fresh (Df) and deciduous mixed wet (DMw) forest site types (53°53′20″ N 20°37′23″ E). There was a 70–100 year-old tree cover with beech and hornbeam as the dominant tree species. Locally (species occurrence in the stand <5%), there were also Scots pine, pedunculate oak, Norway spruce and silver birch. There was loose, intermittent or moderate horizontal tree cover present. The third (J1) was located within DMf and CMf forest site types with 47–108 year-old Scots pine as the dominant tree species (53°21′58″ N 20°38′12″ E). Rowan (*Sorbus aucuparia*), silver birch, pedunculate oak, and hazel (*Corylus avellana*) formed the understory layer. There was intermittent or moderate horizontal tree cover. The soil cover was sodded or heavily weeded. The fourth (J2) was within CMf and Cf forest site types (53°30′21″ N 20°43′58″ E) with 47–96 year-old Scots pine as the dominant tree species. The understory layer consisted of trees and shrubs: silver birch, bird cherry (*Padus avium*), alder buckthorn (*Frangula alnus*), rowan, Norway spruce, beech, juniper (*Juniperus communis*) and pedunculate oak. The tree stand featured intermittent to moderate horizontal cover. The soil cover was sodded or moss-tufted.

Three sampling plots were selected at each location—six in deciduous forests (2 × 3) and six in coniferous forests (2 × 3). Sampling plots were separated by at least 200 m. At each sampling plot, we arranged pitfall traps in 200 m transects, set perpendicular to the forest edge. To provide stable interior forest conditions, as potential edge effects extend approximately 20–30 m from the forest edge [44–46], each trap line began at 20 m from the forest edge (first trap). Then, to ensure statistically independent samples and true replicates [20,40], we installed the next traps along the transect at 20 m intervals up to

200 m from the forest edge (each trap line consisted of 10 pitfall traps in total). This resulted in a total of 120 traps: 60 in deciduous and 60 in coniferous forests.

2.3. Carabid Beetle Sampling

Carabid beetles were collected using pitfall traps. We used plastic cups with a 100 mm diameter and 140 mm depth, partially filled (150–200 mL) with 70% ethylene glycol as a killing–preservation solution and a few drops of detergent to break the surface tension of the liquid. The pitfall traps were then installed in the dug holes and covered with bark roofs, placed 3–5 cm above the traps to protect them from litter and rain. Our trapping season began in early May and continued through late October in 2013 and 2014. We made every effort to ensure that our activities had the minimal possible impact on the functioning of the ecosystems under study. The capture of carabid beetles was conducted in a manner minimizing the risk of trapping animals that were not the target of our research. The pitfall traps were inspected regularly and replenished with a killing–preserving solution containing detergent, which helped reduce the risk of prolonged suffering and delayed death of the insects. Pitfall traps were emptied fortnightly.

We used the Hůrka [47] key to identify the carabid beetles. The systematic arrangement and nomenclature of the carabid beetles occurring in the study area were based on the division proposed in the Catalogue of Palaearctic Coleoptera [48].

2.4. Carabid Beetle Life Traits

As some ecological classifications of life traits of carabid beetles may simplify the ecological variability of species, we conducted comprehensive literature review to obtain information on the biology and ecology of carabids [47,49–53]. Diet and habitat preferences, body size, breeding type and flight were used for the ecological division of the carabids. Trophic groups were as follows: herbivorous species (phytophages, feeding only on plants); omnivorous species (hemizoopages, feeding on plants and animals); and carnivores (zoophages, feeding predominantly on animals). The habitat division comprised forest, wetland, generalist (eurytopic, and open-area species). The division based on breeding type consisted of two groups: autumn breeders (reproducing in autumn and hibernating as larvae) and spring breeders (hibernating as adults and reproducing in spring). Depending on dispersal possibility, the carabids were divided into three groups: wingless (brachypterous), dimorphic (brachypterous and macropterous specimens) and winged (macropterous) species. Body size division distinguished small (body length below 5.0 mm), medium (body length 5.1–12.0 mm) and large (body length more than 12.0 mm) species. Body size is also used to calculate the Mean Individual Biomass (MIB), as its value reflects environmental conditions favorable to carabid beetles with high ecological requirements, e.g., breeding sites or food resources [24,54]. The MIB describes the relationship between the carabid body length and its biomass [55,56].

2.5. Data Analysis

Differences in mean values in the number of species and individuals, according to data distribution, were tested using Student's *t*-test (with normal data distribution) or the Mann–Whitney U test (with no normal data distribution). Non-metric multidimensional scaling (NMDS) was performed to assess differences in carabid beetle assemblages between deciduous and coniferous forests. We used ANOSIM with the Bray–Curtis coefficient and 10,000 data permutations to examine the significance of dissimilarities. Then, as significant differences emerged, we surveyed which species contributed most to them using SIMPER (similarity percentages) analysis [57]. The Indicator Value (IndVal) procedure [58] was conducted to determine which carabids may be considered characteristic species of deciduous or coniferous forests. The IndVal ranges from 0 to 1, with 0 indicating that the

species is least associated with a given forest type and 1 indicating it is most associated with that forest type. The NMDS, ANOSIM, SIMPER, and IndVal procedures were conducted in PAST (v. 4.17) and in R (v. 4.0.3). Student's *t* test and Mann–Whitney U test were performed using Statistica for Windows (v. 13.3).

We also used Detrended Correspondence Analysis (DCA) and Redundancy Analysis (RDA) to determine whether carabid beetle ecological groups were divided by forest stand type. The gradient length in DCA was initially analyzed. The largest gradient length was below 4.0 standard deviation units (1.709), suggesting that RDA was an appropriate tool for correlating carabid ecological groups with forest stand types [59]. We used Canoco (v. 4.5) for the analysis.

3. Results

We identified 79 species among 20,125 individuals captured in the study area. In deciduous forests, we found 54 species from 9056 individuals, while in coniferous forests, we recorded 62 species from 10,619 individuals. The most abundant species were *Pterostichus niger* in the deciduous forest, accounting for 26% of the total, and *Pterostichus oblongopunctatus* in the coniferous forest, accounting for 28% of the total (Table A1).

Contrary to P 1.1 and P 1.2, the Student *t* test and Mann–Whitney U test showed that neither the species number ($t = 1.32$; $p = 0.19$) nor the number of individuals ($Z = 1.49$; $p = 0.14$), respectively, was significantly different between coniferous and deciduous forests (Figure 2a,b). Additionally, the Shannon diversity index (H') and evenness index (J') values also did not differ significantly (H' : $t = 2.58$, $p = 0.06$; J' : $t = 1.439$, $p = 0.15$), and were similar between the two forest types ($H' = 1.02$ vs. 0.98 , $J' = 0.57$ vs. 0.57 in coniferous and deciduous forests, respectively) (Table A1). As a result, P1.1, P1.2 and P1.3 were all rejected. Although none of our predictions was accepted, the NMDS analysis showed significant differences in species and quantitative composition between carabid beetle assemblages from coniferous and deciduous forests (Figure 3). Furthermore, according to SIMPER analysis, the overall average dissimilarity between the two forest habitats was 66% (Table A2). IndVal analysis (Table A3) found that some species, e.g., *Carabus nemoralis*, *Pterostichus oblongopunctatus*, *Carabus arvensis*, *Carabus convexus* and *Pterostichus melanarius*, *Carabus hortensis*, *Pterostichus niger*, *Carabus granulatus*, *Limodromus assymilis* (collected in coniferous and deciduous forests, respectively) were recognized as species being distinctly associated with both forest types, and they contributed most significantly to the differentiation within them. Therefore, as important differences between coniferous and deciduous forests in the composition of carabid beetle assemblages occurred, we partially accepted H1.

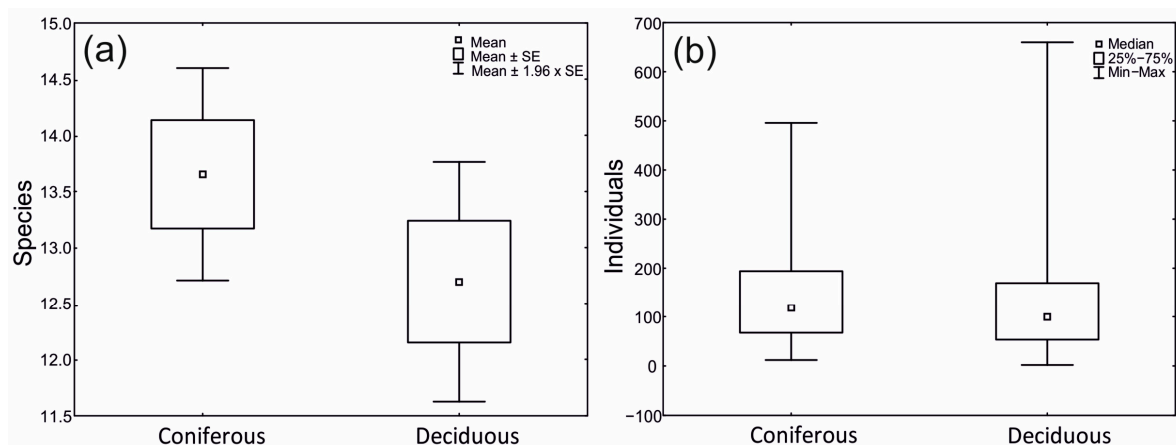


Figure 2. Mean number of carabid beetle species (a) and individuals (b) in coniferous and deciduous forest stands.

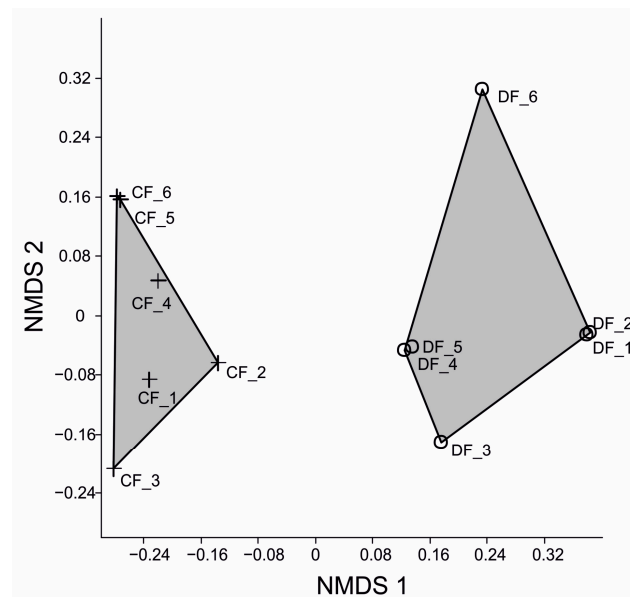


Figure 3. Non-metric multidimensional scaling analysis (NMDS) ordination of carabid beetle assemblages inhabiting coniferous (+ CF) and deciduous (O DF) forests (NMDS stress = 0.087; ANOSIM: $R = 0.981$, $p = 0.0024$). Numbers 1–6 indicate the transect number.

Carabid beetles with different life traits occupied deciduous and coniferous forest stands unevenly (Figure 4). However, we found a few exceptions. According to the Mann–Whitney U test, carnivorous species, for example, used both forest habitats similarly ($Z = 1.14$; $p = 0.254$), whereas omnivorous species were primarily found in coniferous forests ($Z = 4.24$; $p < 0.001$) (Figure 5a,b). Herbivorous species were not analyzed due to the low number of species captured. Macropterous carabids were equally distributed in deciduous and coniferous forests ($Z = 0.47$; $p = 0.64$), whereas dimorphic and brachypterous species occurred mostly in deciduous and coniferous forest stands, respectively ($Z = -5.84$; $p < 0.001$ and $Z = 3.21$; $p = 0.001$, respectively) (Figure 6a–c). Autumn breeders were caught mainly in deciduous forests ($Z = -2.91$; $p = 0.004$), while spring breeders were caught in coniferous ones ($Z = 6.66$; $p < 0.001$) (Figure 7a,b). Since only results related to the occurrence of omnivorous and autumn breeding carabids in both forest types supported our expectations, P2.1 was accepted only partially.

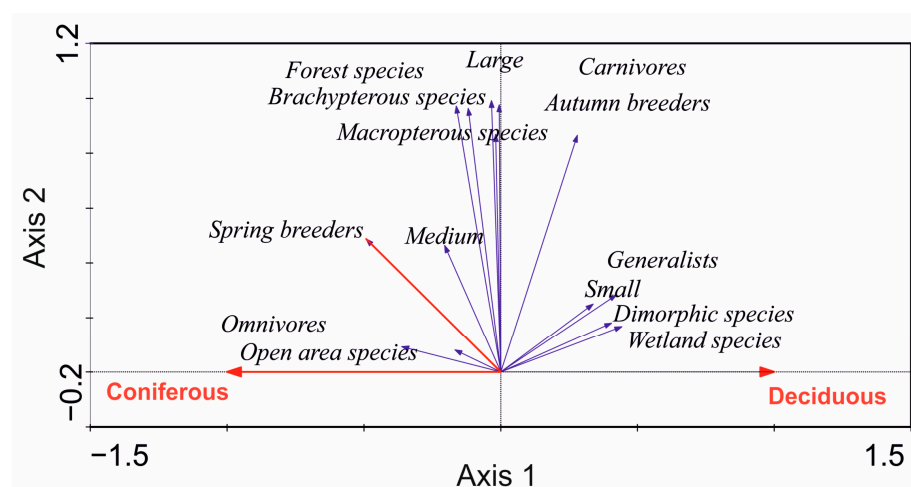


Figure 4. Redundancy analysis (RDA) for the ecological groups of carabid beetles caught in coniferous and deciduous forest stands.

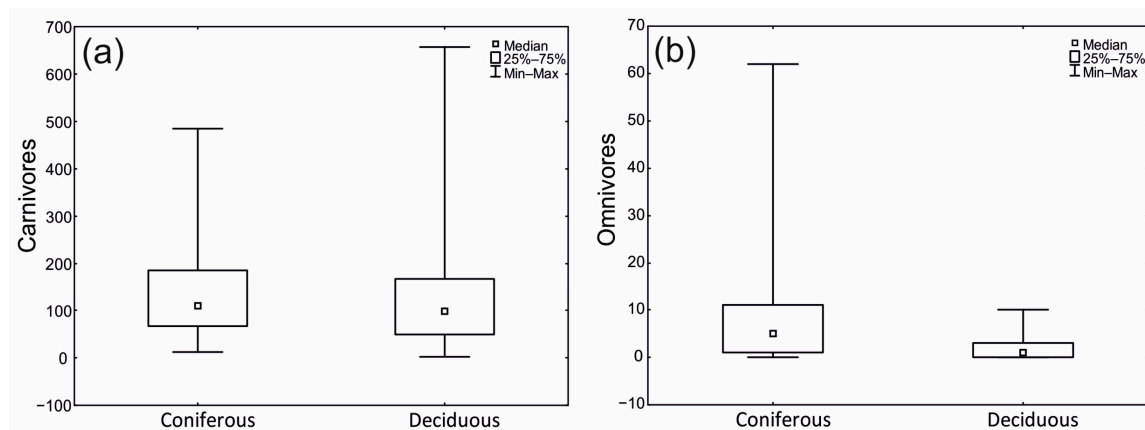


Figure 5. Mean number of carnivorous (a) and omnivorous (b) carabid beetles in coniferous and deciduous forest stands.

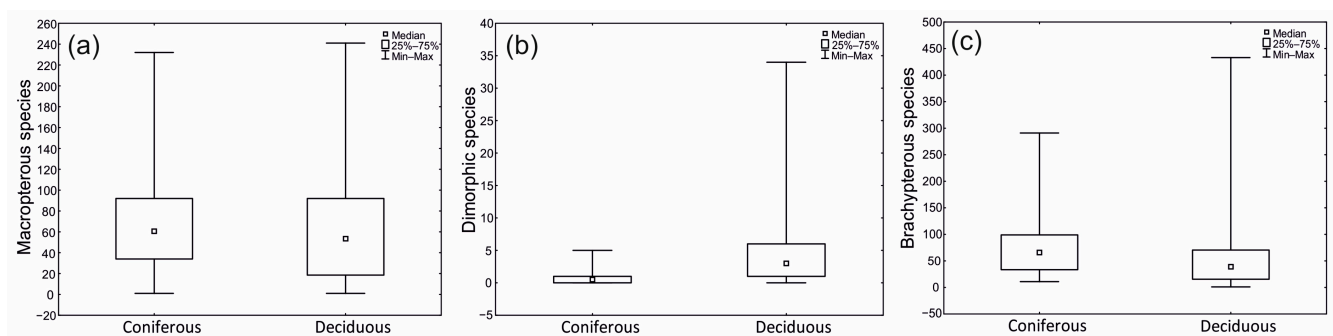


Figure 6. Mean number of macropterous (a), dimorphic (b) and brachypterous (c) carabid beetles in coniferous and deciduous forest stands.

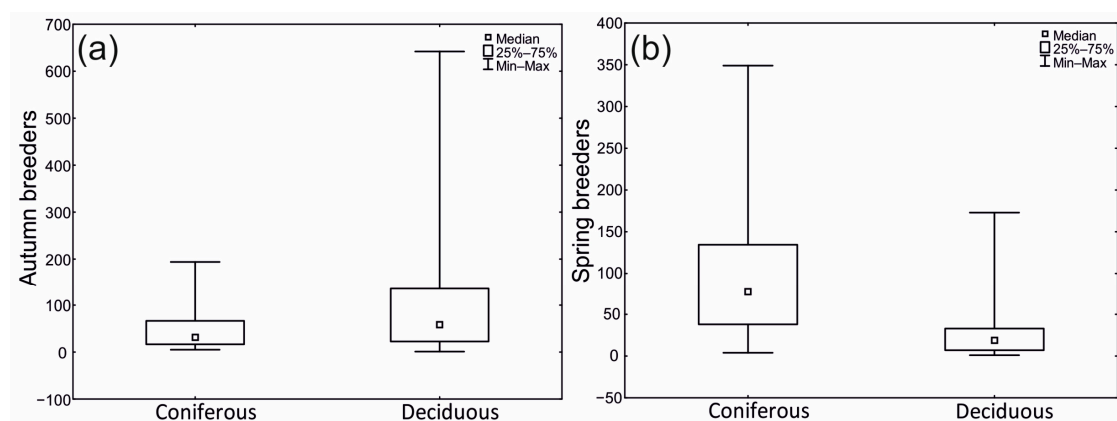


Figure 7. Mean number of carabid beetles with autumn (a) and spring (b) breeding life cycle caught in coniferous and deciduous forest stands.

Habitat preferences and body size were important descriptors of forest use by carabid beetles. The Mann–Whitney U test revealed that forest specialists were mainly recorded in coniferous forests ($Z = 2.97$; $p = 0.003$), while generalists and wetland-preferring species were more prevalent in deciduous forests ($Z = -5.38$; $p < 0.001$ and $Z = -7.13$; $p < 0.001$, respectively) (Figure 8a–c). Open-area carabid beetles utilized both forest types similarly ($Z = 1.19$; $p = 0.231$), although we trapped almost twice as many individuals in coniferous forests as in deciduous forests (460 vs. 252, respectively) (Figure 8d; Figure 4).

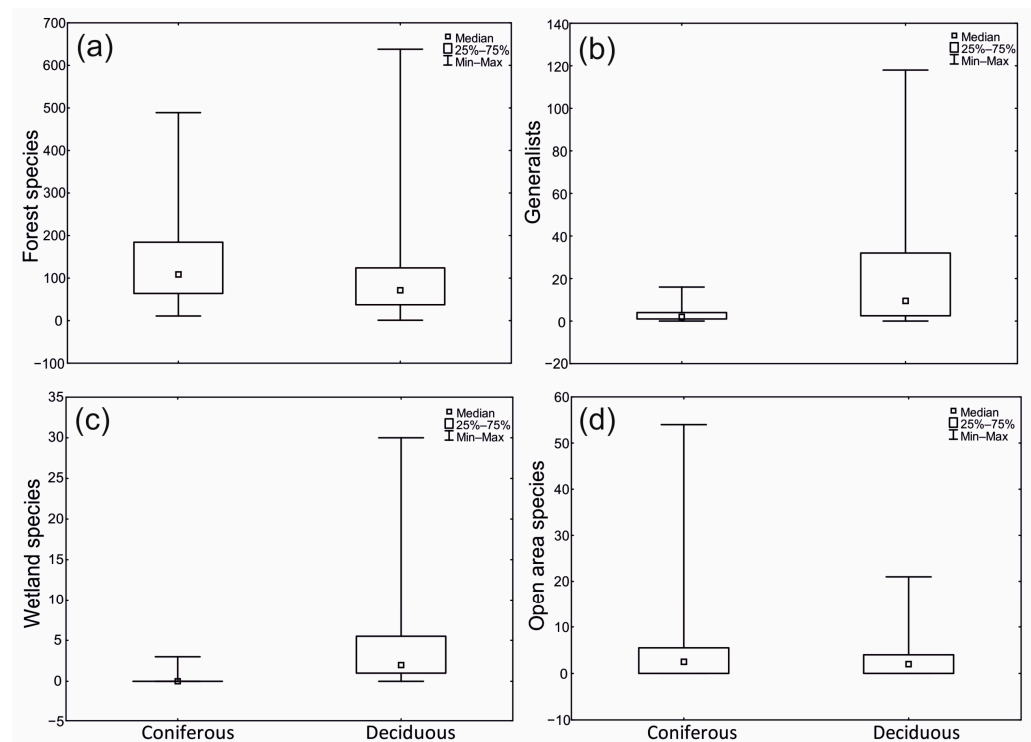


Figure 8. Mean number of forest (a), generalist (b), wetland (c) and open-area (d) species of carabid beetles caught in coniferous and deciduous forest stands.

Considering carabid beetle body size, our results showed that large-bodied species occurred similarly in both forest stands ($Z = 1.75$; $p = 0.079$), whereas medium-sized species and small-bodied species were more frequently captured in coniferous and deciduous forests, respectively ($Z = 2.73$; $p = 0.006$ and $Z = 3.12$; $p = 0.002$) (Figure 9a–c). Therefore, with the exception of large carabids, likely, only medium- and small-bodied species had a significant impact on MIB levels in deciduous and coniferous forests: 272 vs. 302 mg, respectively ($Z = 3.41$; $p < 0.001$) (Figure 10). Consequently, as only trends in the occurrence of open area and wetland carabids in both forests types were in line with our prediction, we accepted P2.2 partially. Although our results did not fully support P2.1 and P2.2, a large number of carabid beetle life traits (e.g., omnivorous, dimorphic, brachypterous, autumn breeding, spring breeding, forest specialists, generalists, wetland-preferring, medium-sized and small-bodied species) were distributed unevenly over deciduous and coniferous forests. Hence, H2 was partially accepted.

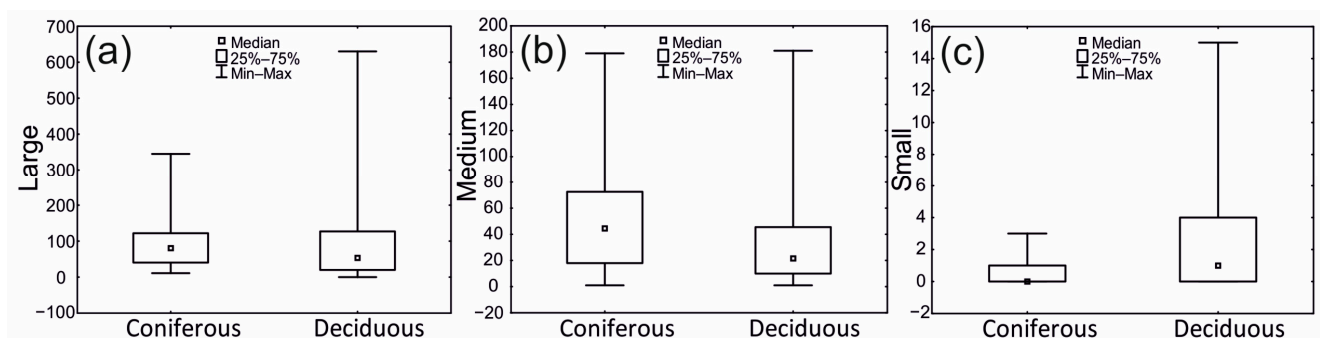


Figure 9. Mean number of large (a), medium (b) and small-bodied (c) carabid beetles caught in coniferous and deciduous forest stands.

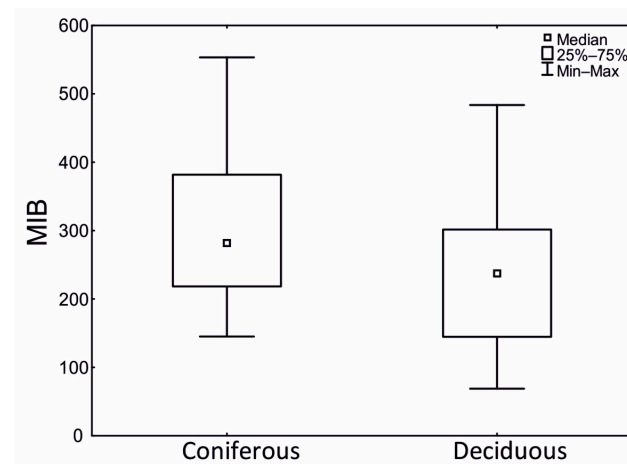


Figure 10. Mean individual biomass (MIB) values for carabid beetle assemblages from coniferous and deciduous forest stands.

4. Discussion

Although our data collection was carried out in 2013 and 2014, the goal of this study seems to be still important. We believe that such a comparison of carabid beetle assemblages in forests with different stand compositions, although it does not provide temporal trends, still present relevant mechanisms underlying species responses to habitat conditions. Our results provide some initial state we can use in future studies examining effects of ongoing changes in forest ecosystems.

The number of carabid beetles captured (approx. 20,000) in the studied forests represented 79 species. This accounted for 16% of the total number of species in the family Carabidae in Poland (approx. 500) and 9% in Central Europe (approx. 900) [52,60,61]. In studies by other authors (e.g., refs. [22,24,62]), the recorded carabid richness in assemblages was lower, with fewer species and individuals. The high species richness recorded in the coniferous forest area studied (62 species) may also reflect the fertility of the habitats on which the pine stands were growing. Pine forests growing on fertile sites are a consequence of post-war Polish forest management, which responded to the enormous demand for timber. This resulted in the establishment of monoculture plantations of Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) [63]. Pine forests growing on fertile sites create microhabitats that provide living conditions for a relatively large number of Carabidae species. Therefore, given the assumption that sample size determines the representativeness of results, we believe that our study accurately reflects the state of carabid beetle assemblages in the forests studied.

Our results did not confirm the trend that deciduous forests, compared with coniferous forests, are characterized by higher richness and diversity of carabid beetle assemblages; the values observed in both forest stands were similar. This could be related to species affinity to the habitat or environment variables they live in. In this context, the carabid beetles of the studied forests exhibited high ecological plasticity: most species showed neither a strict association with, nor an affinity for, forest habitats in either coniferous or deciduous stands. These carabids were ubiquitous across both forest stand types studied, and their influence on differences in carabid assemblage richness and diversity was negligible. Nor did the presence of highly specialized carabid species play a significant role in this respect. However, such species are usually regarded as the elements that determine the richness and diversity of the entire carabid beetle assemblages. This is because even within forest habitats with similar stand characteristics, such as tree species composition and spatial structure, these conditions may differ for these ecologically specialized carabids [64]. Therefore, the number of species with a high ecological specialization tends to increase with the

extent to which their habitat conditions in a given forest environment correspond to their requirements. In this context, deciduous forests are indicated as habitats with richer and more diverse carabid beetle communities [14,65]. In the forests we studied, however, we recorded only a few ecologically specialized carabid species in each forest type. As a result, so far, we have observed only differences in species composition between the assemblages studied.

The carabid beetle assemblages in the studied forests showed distinct differences in the proportions of ecological groups. Carabid beetles with an autumn breeding cycle and those inhabiting moist habitats were more numerous in deciduous forests. This could suggest that deciduous forests provide favorable habitat conditions for more specialized species. However, the distribution of other ecological groups seems to contradict this interpretation. Forest-associated and wingless carabids were more common in coniferous forests. Furthermore, although some authors consider large-bodied and carnivorous species to be highly specialized due to their requirements for suitable sites for shelter, feeding, and oviposition [35], these species were distributed relatively evenly across our study area. This, in turn, may reflect that both forest types ensure similarly favorable habitat conditions for carabid beetles sharing these traits. However, winged species, small- to medium-bodied species, eurytopic species, species adapted to open habitats, and species with a predominantly spring breeding cycle were also well represented in the forests studied. This finding is somewhat surprising, as these groups are frequently reported to be associated with disturbed, unsuitable or unstable habitats [22,36,37]. Consequently, our results largely deviated from the initial pattern expected at the outset of the study. This template suggests that carabid beetle assemblages in forests, especially deciduous ones, are primarily composed of large, brachypterous forest predators that exhibit an autumn breeding strategy. Therefore, as a result, the partial explanation may be that neither forest type we studied provided the favorable habitat conditions that carabids usually find in such environments [66,67].

There may be several reasons for such results. According to Skłodowski [21,68] and Stanek et al. [69], similar patterns in the ecological structure and diversity of carabid beetle assemblages have often been associated with the managed character of forests. For example, in studies comparing carabid assemblages similar to ours, but conducted in protected areas without anthropogenic pressure, such as nature reserves, forests with deciduous stands were characterized by a higher richness and diversity of carabid beetle assemblages. Moreover, it has been previously shown that the species composition and ecological structure were typical of forest assemblages, with a predominance of large, forest, predatory and wingless carabids with an autumn breeding type [21,62,68]. By contrast, in forests with managed stands, many carabids representing these ecological groups may not occur in the unfavorable habitat conditions. Many authors have suggested that a side effect of silvicultural treatments in forest stands may be the impoverishment and homogenization of the range of ecological niches available to carabids. Stanek et al. [69], for example, indicate clear-fell milling as an unsuitable forestry activity for carabid beetles. Canopy opening, soil desiccation, and a reduction in dead wood are also mentioned in this context [14,65,68].

As some authors indicate, the severity of these changes in stand structure for carabid beetles may be further intensified by the extensive spatial and temporal scale of the consequences of silvicultural treatments and climate change [65,70,71]. It should be noted here that similar disturbances in forest environmental conditions, such as gaps or openings in the tree canopy, also occur in forests unaffected by human activity, including the death of individual trees. Nevertheless, as some articles have shown, they are usually neither as numerous nor as strongly influential on the forest environment as in managed forests, where

one-time, large-scale felling of numerous trees leads to a substantial reduction in canopy closure [72]. Both forest habitats where we collected carabids had moderate canopy closure. Although microclimatic variables and soil properties were not measured during our study, we believe they could provide important background for the patterns observed here.

In this context, the presence of specific carabid species may be helpful. It is possible that in coniferous forests, unfavorable habitat conditions for forest carabid beetles may have contributed to the abundant occurrence of, among others, *Amara communis* and *A. lunicollis*. According to Skłodowski and Szczeszek [35], both species are frequently found in single-layered, even-aged, sun-exposed, dry pine stands, where unstable microclimatic conditions seem to be common. In deciduous forests, ecological groups associated with open areas include *Bembidion lampros* and *Trechus quadristriatus*. Deciduous forests also hosted a significant number of wetland-associated carabids, such as *Carabus granulatus* and *Leistus terminatus*. The presence of these species may indicate a relatively moist habitat [73]. This, along with soil desiccation, may also impede larval development and decrease the availability of food resources, such as snails and earthworms, for many carabid species [14,74]. Thus, it can be suggested that the limited occurrence of forest carabid beetles could reflect the unfavorable microclimatic and soil conditions in the forests we studied.

Moreover, many previous studies have shown that overall landscape composition, including the frequency and spatial arrangement of specific habitats relative to one another, also appears to be of great importance for carabid beetles [65,75–77]. Currently, we can observe extensive patches of coniferous forests throughout entire forests. In our study area, the deciduous stands were meager—small and isolated patches. As a consequence, this probably provides a poor range of habitats. Meanwhile, as other authors also stated, the lack of sufficient deciduous habitat does not support the survival of carabid beetles that are strictly associated with this habitat type [40,78,79]. As a result, these species are particularly vulnerable to changes in abundance or to complete population disappearance due to rapid, widespread and long-lasting changes in forest habitat conditions [80–82].

This could ultimately support the possibility that only a limited number of large, forest-dwelling, predatory carabids of the autumn-breeding type occurred in our study area. This finding also seems to be supported by mean individual biomass index (MIB) values. However, the MIB value of 300 mg in coniferous forests, such as those in Jedwabno, is commonly observed in low-quality forest habitats and is considered the standard [53]. The coniferous stands in our study area ranged in age from 47 to 108 years, indicating that some sections have not yet matured. As these stands continue to age over the coming decades, the MIB value is expected to increase, particularly as populations of large, predatory carabid species that breed in the autumn begin to recover [83,84]. Nevertheless, we believe that many carabid species representing these ecological groups appear to have declined in the deciduous forests of Wipsowo. The MIB value in this case was only 272 mg, whereas in other deciduous stands it can reach 500–700 mg [54,85,86]. This increase is due to the abundance of species such as *C. coriaceus*, *C. violaceus*, and *C. convexus* [54,64,84,87]. The results of our research may therefore reflect the need to practice more sustainable forest management—e.g., leave some of the stands to age naturally and to increase the area of fertile deciduous forests. Stanek et al. [69] suggest that forestry planning, management diversification and the maintenance of continuity of commercial and non-interventional natural forests are of great importance for the large body of forest arthropod taxa.

Our study only compared carabid beetle assemblages in coniferous and deciduous forests. Therefore, we are aware of several limitations that occurred in our study. First, although forest composition is widely expected to change under climate change and forest management, our study did not directly assess the influence of climatic effects and forestry practices. Consequently, any implications regarding future biodiversity responses

to forestry- and climate-driven changes in vegetation should be treated as conjectural and considered within a broader ecological context rather than as a proven explanation of the observed patterns. Second, the Mean Individual Biomass (MIB) index may be influenced not only by habitat quality but also by local and regional species composition. Consequently, the differences in MIB values observed between coniferous and deciduous forests should not be interpreted as unequivocal evidence of differences in habitat conditions and should be evaluated together with other community characteristics. Furthermore, the observed patterns in carabid beetle assemblages may have been affected by the relatively high environmental similarity among study sites. All sampling locations were situated within the same geographical region of northeastern Poland and shared comparable climatic conditions and post-glacial landscape features. Although the studied forest types differed in tree species composition, the generally homogeneous environmental background may have reduced the magnitude of differences in species richness, life-history traits and community composition. Therefore, some of the relatively small differences detected among forest types likely reflect common regional environmental conditions rather than forest type alone. Future studies conducted across broader climatic, edaphic, and topographic gradients, combined with direct measurements of microclimatic conditions, soil properties and forest stand characteristics, would help disentangle the effects of forest type from those of regional environmental conditions and improve our understanding of future changes in forest fauna communities.

5. Conclusions

Our study may contribute to the understanding of the range of possible characteristics of carabid beetle assemblages in commercial forests and provide useful information for sustainable forest management. The results demonstrate a slight effect of forest habitat type on carabid beetle richness and diversity. Carabid beetle assemblages differ only in species composition and, to some extent, in ecological structure. However, these differences do not allow us to determine whether typical forest carabids prefer coniferous or deciduous forest habitats. This finding may partially reflect the influence of forestry practices, since even past forest use may still be of considerable importance today, highlighting the long-term impact on biota.

We believe that these changes may have had particularly negative consequences for deciduous forests. Such forests often resemble isolated islands and are surrounded by much younger stands, which, due to their very different structure and environmental conditions, do not favor carabid occurrence and hinder their dispersal. This may highlight the need for spatial planning in forest management to reduce habitat fragmentation, maintain ecological continuity and enhance the long-term sustainability and resilience of forest ecosystems.

Applying sustainable forest management in areas surrounding mature deciduous forests seems to be an effective strategy for improving the species composition and abundance of carabid beetle assemblages. Reducing management intensity in the younger and maturing stands that surround these older forests could help create protective buffer zones. Over time, increasing the area of older stands and incorporating them into ecological corridors may enhance the spatial coherence of valuable forest habitats. These measures align with the principles of sustainable development, balancing biodiversity conservation with the responsible use of forest ecosystems. Furthermore, incorporating biodiversity indicators such as carabid beetles into forest monitoring may support adaptive management and provide a valuable tool for assessing the ecological sustainability of managed forests. In this context, we believe that our results may serve as a baseline for a broader discussion of biodiversity conservation and future forest management.

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Institutional Review Board Statement: In the case of insect species that are important for ecosystem functioning or rare species protected under species conservation regulations in Poland, their use in research is governed by the Act of 16 April 2004 on Nature Conservation: Act of 16 April 2004 on Nature Conservation (in Polish), as well as the implementing regulation following this Act, namely the Regulation of the Minister of the Environment of 16 April 2016 on Species Protection of Animals: Regulation of 16 April 2016 (in Polish), and its earlier versions from 2014: Regulation of 2014 (in Polish), and 2011: Regulation of 2011 (in Polish), on the basis of which we conducted our research. The above-mentioned documents listed all insect species belonging to the genus *Carabus* as animals under strict species protection (Regulation of 2011), and subsequently under partial protection only (Regulation of 2014). The use of Carabidae in nature research obtained permits from the Regional Directorate for Environmental Protection and the General Directorate for Environmental Protection. The insects were handled according to accepted regulations.

Informed Consent Statement: Not applicable.

Data Availability Statement: Data relating to the species composition and abundance of carabid beetles presented in this study are available by request from the first and corresponding author.

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Abbreviations

The following abbreviations are used in this manuscript:

CON Coniferous
DEC Deciduous

Appendix A

Table A1. Numbers of carabids trapped in coniferous and deciduous forest stands with diversity indexes.

Species	Forest	
	CON	DEC
<i>Agonum emarginatum</i> (Gyllenhal, 1827)	1	3
<i>Agonum fuliginosum</i> (Panzer, 1809)	54	17
<i>Agonum sexpunctatum</i> (Linnaeus, 1758)	0	2
<i>Amara bifrons</i> (Gyllenhal, 1810)	1	0
<i>Amara brunnea</i> (Gyllenhal, 1810)	11	3

Table A1. Cont.

Species	Forest	
	CON	DEC
<i>Amara communis</i> (Panzer, 1797)	219	21
<i>Amara consularis</i> (Duftschmid, 1812)	2	0
<i>Amara convexior</i> (Stephens, 1828)	12	1
<i>Amara curta</i> (Dejean, 1828)	1	0
<i>Amara equestris</i> (Duftschmid, 1812)	1	0
<i>Amara familiaris</i> (Duftschmid, 1812)	0	1
<i>Amara lunicollis</i> (Schiodte, 1837)	41	0
<i>Amara similata</i> (Gyllenhal, 1810)	0	1
<i>Anchomenus dorsalis</i> (Pontoppidan, 1763)	0	2
<i>Badister bullatus</i> (Schränk, 1798)	3	0
<i>Badister lacertosus</i> (Sturm, 1815)	1	0
<i>Badister peltatus</i> (Panzer, 1797)	1	0
<i>Badister sodalis</i> (Duftschmid, 1812)	0	3
<i>Badister unipustulatus</i> (Bonelli, 1813)	1	0
<i>Bembidion biguttatum</i> (Fabricius, 1779)	0	6
<i>Bembidion bipunctatum</i> (Linnaeus, 1761)	0	1
<i>Bembidion lampros</i> (Herbst, 1784)	0	34
<i>Bembidion properans</i> (Stephens, 1828)	1	0
<i>Bradycellus harpalinus</i> (Audinet-Serville, 1821)	0	1
<i>Calathus erratus</i> (Sahlberg, 1827)	3	0
<i>Calathus fuscipes</i> (Goeze, 1777)	12	2
<i>Calathus micropterus</i> (Duftschmid, 1812)	75	85
<i>Carabus arvensis</i> (Herbst, 1784)	2087	0
<i>Carabus cancellatus</i> (Illiger, 1798)	38	25
<i>Carabus convexus</i> (Fabricius, 1775)	472	0
<i>Carabus coriaceus</i> (Linnaeus, 1758)	693	82
<i>Carabus glabratus</i> (Paykull, 1790)	207	172
<i>Carabus granulatus</i> (Linnaeus, 1758)	6	178
<i>Carabus hortensis</i> (Linnaeus, 1758)	1027	2505
<i>Carabus marginalis</i> (Fabricius, 1794)	107	0
<i>Carabus nemoralis</i> (O.F.Müller, 1764)	676	55
<i>Cicindela campestris</i> (Linnaeus, 1758)	0	1
<i>Clivina fossor</i> (Linnaeus, 1758)	0	1
<i>Cychrus caraboides</i> (Linnaeus, 1758)	67	33
<i>Dyschiriodes globosus</i> Herbst, 1784	0	7
<i>Elaphrus riparius</i> (Linnaeus, 1758)	2	0
<i>Epaphius secalis secalis</i> (Paykull, 1790)	4	32
<i>Harpalus calceatus</i> (Duftschmid, 1812)	1	0

Table A1. Cont.

Species	Forest	
	CON	DEC
<i>Harpalus laevipes</i> (Zetterstedt, 1828)	167	26
<i>Harpalus latus</i> (Linnaeus, 1758)	35	13
<i>Harpalus luteicornis</i> (Duftschmid, 1812)	11	13
<i>Harpalus rufipalpis</i> (Sturm, 1818)	1	0
<i>Harpalus rufipes</i> (Degeer, 1774)	94	14
<i>Harpalus smaragdinus</i> (Duftschmid, 1812)	4	0
<i>Harpalus tardus</i> (Panzer, 1797)	10	1
<i>Harpalus xanthopus winkleri</i> (Schauberger, 1923)	10	0
<i>Leistus ferrugineus</i> (Linnaeus, 1758)	8	0
<i>Leistus rufomarginatus</i> (Duftschmid, 1812)	0	53
<i>Leistus terminatus</i> (Hellwig, 1793)	2	26
<i>Limodromus assimilis</i> (Paykull, 1790)	1	624
<i>Loricera pilicornis</i> (Fabricius, 1775)	0	22
<i>Microlestes minutulus</i> (Goeze, 1777)	1	0
<i>Nebria brevicollis</i> (Fabricius, 1792)	7	340
<i>Notiophilus biguttatus</i> (Fabricius, 1779)	22	2
<i>Notiophilus palustris</i> (Duftschmid, 1812)	13	22
<i>Oodes helopioides</i> (Fabricius, 1792)	0	2
<i>Oxypselaphus obscurus</i> (Herbst, 1784)	1	173
<i>Patrobus atrorufus</i> (Strom, 1768)	3	106
<i>Poecilus cupreus</i> (Linnaeus, 1758)	5	13
<i>Poecilus lepidus</i> (Leske, 1785)	2	0
<i>Poecilus versicolor</i> (Sturm, 1824)	19	8
<i>Pterostichus aethiops</i> (Panzer, 1797)	172	0
<i>Pterostichus anthracinus</i> (Illiger, 1798)	2	27
<i>Pterostichus diligens</i> (Sturm, 1824)	2	0
<i>Pterostichus melanarius</i> (Illiger, 1798)	67	1116
<i>Pterostichus niger</i> (Schaller, 1783)	1161	2605
<i>Pterostichus nigrita</i> (Paykull, 1790)	8	66
<i>Pterostichus oblongopunctatus</i> (Fabricius, 1787)	2931	756
<i>Pterostichus strenuus</i> (Panzer, 1797)	26	90
<i>Pterostichus vernalis</i> (Panzer, 1796)	5	5
<i>Stomis pumicatus</i> (Panzer, 1796)	1	4
<i>Syntomus foveatus</i> (Linnaeus, 1761)	1	0
<i>Synuchus vivalis</i> (Illiger, 1798)	0	15
<i>Trechus quadristriatus</i> (Schränk, 1781)	0	90
Total Individuals	10,619	9506
Total Species	62	54

Table A1. Cont.

Species	Forest	
	CON	DEC
MIB	302	272
Shannon H' Log Base 10,	1.021	0.983
Shannon J'	0.570	0.567

Table A2. Results of SIMPER analysis.

Species	Av. Dissim	Contrib. %	Cumulative %	Mean CON	Mean DEC
<i>Pterostichus oblongopunctatus</i>	10.9	16.53	16.53	489	126
<i>Carabus arvensis</i>	10.07	15.26	31.78	348	0
<i>Pterostichus niger</i>	7.294	11.05	42.84	194	434
<i>Carabus hortensis</i>	6.931	10.5	53.34	171	418
<i>Pterostichus melanarius</i>	5.112	7.748	61.09	11.2	186
<i>Carabus nemoralis</i>	3.337	5.058	66.15	113	9.17
<i>Carabus coriaceus</i>	3.08	4.669	70.82	116	13.7
<i>Limodromus assimilis</i>	2.974	4.507	75.32	0.167	104
<i>Carabus convexus</i>	2.489	3.772	79.1	78.7	0
<i>Nebria brevicollis</i>	1.507	2.284	81.38	1.17	56.7
<i>Amara communis</i>	1.363	2.066	83.45	36.5	3.5
<i>Carabus glabratus</i>	0.9599	1.455	84.9	34.5	28.7
<i>Harpalus latus</i>	0.8235	1.248	86.15	27.8	4.33
<i>Carabus granulatus</i>	0.8162	1.237	87.39	1	29.7
<i>Oxypselaphus obscurus</i>	0.8034	1.218	88.6	0.167	28.8
<i>Pterostichus aethiops</i>	0.7683	1.165	89.77	28.7	0
<i>Carabus marginalis</i>	0.6387	0.968	90.74	17.8	0
<i>Harpalus rufipes</i>	0.5612	0.8506	91.59	15.7	2.33
<i>Patrobus atrorufus</i>	0.4851	0.7352	92.32	0.5	17.7
<i>Trechus quadristriatus</i>	0.4835	0.7328	93.05	0	15
<i>Calathus micropterus</i>	0.4419	0.6698	93.72	12.5	14.2
<i>Pterostichus strenuus</i>	0.3461	0.5246	94.25	4.33	15
<i>Pterostichus nigrita</i>	0.3059	0.4636	94.71	1.33	11
<i>Cychrus caraboides</i>	0.3057	0.4634	95.18	11.2	5.5
<i>Leistus rufomarginatus</i>	0.2822	0.4277	95.6	0	8.83
<i>Agonum fuliginosum</i>	0.2639	0.3999	96	9	2.83
<i>Amara lunicollis</i>	0.2212	0.3352	96.34	6.83	0
<i>Bembidion lampros</i>	0.2146	0.3252	96.66	0	5.67
<i>Carabus cancellatus</i>	0.2118	0.321	96.99	6.33	4.17
<i>Epaphius secalis secalis</i>	0.1596	0.242	97.23	0.667	5.33
<i>Leistus terminatus</i>	0.1278	0.1937	97.42	0.333	4.33

Table A2. Cont.

Species	Av. Dissim	Contrib. %	Cumulative %	Mean CON	Mean DEC
<i>Harpalus luteicornis</i>	0.1265	0.1918	97.61	5.83	2.17
<i>Notiophilus biguttatus</i>	0.1239	0.1878	97.8	3.67	0.333
<i>Poecilus versicolor</i>	0.123	0.1864	97.99	3.17	1.33
<i>Pterostichus anthracinus</i>	0.1198	0.1815	98.17	0.333	4.5
<i>Poecilus cupreus</i>	0.1104	0.1674	98.34	0.833	2.17
<i>Loricera pilicornis</i>	0.09956	0.1509	98.49	0	3.67
<i>Synuchus vivalis</i>	0.0921	0.1396	98.63	0	2.5
<i>Notiophilus palustris</i>	0.07617	0.1155	98.74	2.17	3.67
<i>Amara brunnea</i>	0.07384	0.1119	98.85	1.83	0.5
<i>Calathus fuscipes</i>	0.07111	0.1078	98.96	2	0.333
<i>Amara convexior</i>	0.07086	0.1074	99.07	2	0.167
<i>Harpalus laevipes</i>	0.06225	0.09436	99.16	1.83	2.17
<i>Leistus ferrugineus</i>	0.05606	0.08497	99.25	1.33	0
<i>Harpalus tardus</i>	0.05213	0.07901	99.33	1.67	0.167
<i>Harpalus xanthopus winkleri</i>	0.05	0.07578	99.4	1.67	0
<i>Dyschiriodes globosus</i>	0.04941	0.07489	99.48	0	1.17
<i>Pterostichus vernalis</i>	0.04163	0.06309	99.54	0.833	0.833
<i>Bembidion biguttatum</i>	0.02786	0.04223	99.58	0	1
<i>Harpalus smaragdinus</i>	0.0235	0.03561	99.62	0.667	0
<i>Stomis pumicatus</i>	0.01988	0.03013	99.65	0.167	0.667
<i>Badister bullatus</i>	0.01761	0.0267	99.68	0.5	0
<i>Agonum emarginatum</i>	0.01575	0.02387	99.7	0.167	0.5
<i>Anchomenus dorsalis</i>	0.01412	0.0214	99.72	0	0.333
<i>Pterostichus diligens</i>	0.01301	0.01972	99.74	0.333	0
<i>Badister sodalis</i>	0.01286	0.01949	99.76	0	0.5
<i>Calathus erratus</i>	0.01205	0.01827	99.78	0.5	0
<i>Oodes helopioides</i>	0.01188	0.01801	99.8	0	0.333
<i>Amara consularis</i>	0.01059	0.01605	99.81	0.333	0
<i>Poecilus lepidus</i>	0.009791	0.01484	99.83	0.333	0
<i>Agonum sexpunctatum</i>	0.009109	0.01381	99.84	0	0.333
<i>Elaphrus riparius</i>	0.008333	0.01263	99.85	0.333	0
<i>Amara curta</i>	0.007234	0.01096	99.86	0.167	0
<i>Badister peltatus</i>	0.007234	0.01096	99.88	0.167	0
<i>Bradycellus harpalinus</i>	0.007059	0.0107	99.89	0	0.167
<i>Cicindela campestris</i>	0.007059	0.0107	99.9	0	0.167
<i>Amara similata</i>	0.006718	0.01018	99.91	0	0.167
<i>Bembidion properans</i>	0.00642	0.009731	99.92	0.167	0
<i>Harpalus calceatus</i>	0.00642	0.009731	99.93	0.167	0
<i>Badister unipustulatus</i>	0.00642	0.009731	99.94	0.167	0

Table A2. Cont.

Species	Av. Dissim	Contrib. %	Cumulative %	Mean CON	Mean DEC
<i>Badister lacertosus</i>	0.00642	0.009731	99.95	0.167	0
<i>Syntomus foveatus</i>	0.005774	0.008751	99.95	0.167	0
<i>Amara familiaris</i>	0.004822	0.007309	99.96	0	0.167
<i>Bembidion bipunctatum</i>	0.004287	0.006498	99.97	0	0.167
<i>Clivina fossor</i>	0.004287	0.006498	99.97	0	0.167
<i>Harpalus rufipalpis</i>	0.004167	0.006315	99.98	0.167	0
<i>Amara equestris</i>	0.004167	0.006315	99.99	0.167	0
<i>Amara bifrons</i>	0.004167	0.006315	99.99	0.167	0
<i>Microlestes minutulus</i>	0.004017	0.006089	100	0.167	0

Table A3. Results of IndVal analysis.

Species	Group	Indval	p Value	Freq
<i>Carabus nemoralis</i>	CON	0.90	0.001	106
<i>Carabus arvensis</i>	CON	0.88	0.001	63
<i>Pterostichus oblongopunctatus</i>	CON	0.80	0.001	136
<i>Carabus convexus</i>	CON	0.78	0.001	56
<i>Carabus coriaceus</i>	CON	0.55	0.001	72
<i>Pterostichus aethiops</i>	CON	0.54	0.001	39
<i>Carabus marginalis</i>	CON	0.5	0.001	36
<i>Harpalus laevipes</i>	CON	0.48	0.001	59
<i>Amara communis</i>	CON	0.41	0.001	41
<i>Amara lunicollis</i>	CON	0.29	0.001	21
<i>Agonum fuliginosum</i>	CON	0.29	0.003	42
<i>Harpalus rufipes</i>	CON	0.24	0.013	29
<i>Notiophilus biguttatus</i>	CON	0.20	0.001	18
<i>Harpalus tardus</i>	CON	0.10	0.028	9
<i>Harpalus xanthopus winkleri</i>	CON	0.10	0.02	7
<i>Pterostichus melanarius</i>	DEC	0.71	0.001	86
<i>Carabus hortensis</i>	DEC	0.66	0.004	131
<i>Carabus granulatus</i>	DEC	0.60	0.001	49
<i>Pterostichus niger</i>	DEC	0.60	0.005	126
<i>Oxypselaphus obscurus</i>	DEC	0.59	0.001	44
<i>Limodromus assimilis</i>	DEC	0.58	0.001	43
<i>Nebria brevicollis</i>	DEC	0.45	0.001	38
<i>Patrobus atrorufus</i>	DEC	0.42	0.001	34
<i>Pterostichus strenuus</i>	DEC	0.37	0.001	51
<i>Trechus quadristriatus</i>	DEC	0.28	0.001	20
<i>Pterostichus nigrita</i>	DEC	0.26	0.001	26

Table A3. Cont.

Species	Group	Indval	p Value	Freq
<i>Leistus rufomarginatus</i>	DEC	0.22	0.001	16
<i>Leistus terminatus</i>	DEC	0.22	0.001	19
<i>Pterostichus anthracinus</i>	DEC	0.17	0.002	15
<i>Bembidion lampros</i>	DEC	0.17	0.002	12
<i>Synuchus vivalis</i>	DEC	0.14	0.002	10
<i>Loricera pilicornis</i>	DEC	0.14	0.002	10
<i>Epaphius secalis secalis</i>	DEC	0.12	0.023	13

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