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Can *Larix* sp. Mill. Provide Suitable Habitats for Insects and Lichens Associated with Stems of *Picea abies* (L.) H. Karst. in Northern Europe?

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Abstract: Recent observations suggest that climate change affects the growth conditions and range of tree species distribution in Europe. This may also have a major effect on communities of different organisms associated with these tree species. We aimed to determine whether *Larix* sp. could provide suitable habitats to insects and lichens associated with *P. abies* to conserve their biodiversity under climate change. The study sites were 10 *Larix* sp. and 10 *P. abies* forest stands in Lithuania. Both living and dead trees were included. Sticky traps, bark sheets, and exit hole methods were used for the assessment of insects. Independent plots on tree stems were established for the assessment of lichens. There were 76 and 67 different insect species on dead and living *P. abies*, respectively, using sticky traps. Similarly, there were 64 and 68 on dead and living *Larix* sp., respectively. The overall community of xylophagous insects consisted of nine and eight species, which were detected using the bark sheet and exit hole methods, respectively. The bark area colonized by lichens was 34.3% on dead *P. abies* and 63.2% on dead *Larix* sp., and 40.4% on living *P. abies* and 78.0% on living *Larix* sp. Taken together, the results demonstrate that native *P. abies* and introduced *Larix* sp. support similar diversity of stem-associated insect and lichen species.

Keywords: biodiversity; climate change; Norway spruce; larch; insects; lichens; forest management

1. Introduction

The ongoing process of climate change can be expected to have profound consequences for European forests, especially if species-specific climatic thresholds are surpassed. Prominent climatic changes, which are primarily affecting tree productivity, are mainly associated with increased droughts [1]. Droughts, especially in combination with different biotic factors, such as attacks by pests and pathogens, are known to make trees weaker or even cause mortality [1]. Consequently, the distributional range of different tree species and the composition of European forests can be expected to change in the future [2–4]. In north temperate and boreal European forests, the most economically, ecologically, and spatially important and abundant tree species are Scots pine (*Pinus sylvestris*, L.) and Norway spruce (*Picea abies*, (L.) H. Karst.), which are regionally experiencing increased mortality rates [2,5–12].

Picea abies is one of the most canonical tree species in the forest ecosystems of Eurasia. The area of its natural distribution is vast and ranges from western Siberia to Fennoscandia and the mountain ranges of central Europe [13]. It grows under a wide range of climatic conditions and tolerates a cool and wet climate. It predominantly grows on fertile soils and is a relatively shade-tolerant tree species, forming pure or mixed forest stands with different tree species [14,15]. As it produces valuable timber and its stands are relatively easy to manage, *P. abies* has been extensively planted both within and outside the natural range of

distribution, resulting in a considerable increase in its stands during the last century [14]. However, observations suggest that climate change is one of the most important factors leading to growth disturbances of *P. abies* throughout its distribution range [15–17]. A relatively shallow root system makes the tree species prone to both drought stress [8,18] and wind damage [19–21]. In addition, in the past decades, *P. abies* has been increasingly damaged over vast areas by the European spruce bark beetle (*Ips typographus* L., Coleoptera: Curculionidae). Outbreaks of *I. typographus* are frequently triggered by major storms and/or severe droughts [13,22–24]. Such disturbances can be expected to increase in the future, particularly at the edge of the current distribution range of *P. abies*, as the effects of climate change are likely to be most pronounced in these areas [25]. Consequently, the observed and predicted vulnerability of *P. abies* to abiotic and biotic damage requires special attention [13,26,27]. Indeed, different alternatives and solutions on how to mitigate the negative effects of climate change should be carefully considered [28].

Several studies provide valuable insights into the cultivation of some introduced coniferous tree species as an alternative to *P. abies*. In Western and Northern Europe, several exotic tree species within Pinaceae, namely, Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco), Lodgepole pine (*Pinus contorta* Doug. ex. Loud. var. latifolia Engelm.), Monterey pine (*Pinus radiata* D. Don.), and Sitka spruce (*Picea sitchensis* (Bong.) Carrière), presently constitute important portions of forested ecosystems [29,30]. Larch (*Larix* sp.) trees have also been considered as an alternative to *P. abies*, as it grows successfully in similar habitats to *P. abies* [31]. In addition, *Larix* sp. grows naturally in many areas of the northern hemisphere, being one of the components in boreal and mountain subalpine forests.

In Lithuania, *P. abies* constitutes ca. 21% of the forest area and is of great economic and ecological importance. However, as this area is close to the south-eastern edge of the natural distribution of *P. abies* in Europe, it is increasingly subjected to abiotic and biotic damage. In Lithuania, *Larix* sp. was introduced early in the 19th century as an exotic tree species. Nowadays, it is planted in monocultures or in mixed forest stands [32] but occupies only ca. 900 ha of forest area [33]. In comparison to *P. abies*, *Larix* generally possesses faster growth, more durable wood, and higher adaptability to different environmental conditions, which is partly due to the deep root system, making trees more resistant to windthrows and droughts [34]. *Larix* is an early successional tree species, and after disturbances such as large-scale windfall, it is able to establish on *Picea* sites [35]. *Larix* is a much more light-demanding tree species as compared to *P. abies*. Additionally, it requires large openings for regeneration and juvenile growth, while *P. abies* can regenerate in much smaller gaps or under the canopy [36]. Forest managers have attempted to cultivate several different *Larix* species in forest stands (*L. leptolepis*, *L. decidua*, and *L. polonica*), but *L. decidua* ssp. Polonica Ostenf et. Syrach shows the best growth rate (apart from its hybrids). Moreover, its productivity is significantly higher as compared to other coniferous tree species [37]. However, the productivity of *Larix* sp. can be reduced by insect pests, some of which are also able to damage *P. abies* or *P. sylvestris* [38].

The large-scale planting of introduced tree species instead of native species requires an evidence-based evaluation [30]. In addition to the productivity and adaptability or resilience to climate change, other factors, such as impacts on native flora and fauna communities, should be considered. Indigenous tree species are commonly associated with and/or provide habitats for a variety of different organisms, such as fungi, lichens, or insects. These organisms can be associated with their hosts [39]. Changes in the native forest structure and composition could lead to disturbances in the diversity and composition of these organisms and thus may affect the functioning of forest ecosystems.

Insects represent a key component in forest ecosystems [39], as they are involved in food web interactions (as herbivores, saprophages, predators, and parasites), ecosystem processes (such as pollination, energy flow, biogeochemical cycling, or ecological succession), and eco-evolutionary processes [40,41]. Epiphytic lichens are also an important component of forest biodiversity associated with coniferous forests in Europe [42]. Several studies have highlighted the importance of lichen diversity as an indicator of environmental change,

which is based on their response to air pollution [43,44], climatic conditions [45–47], and forest structure and dynamics [48–50]. The specific association between certain epiphytic lichens and host trees was demonstrated by Roper [51], and this is probably due to differences in the structure and acidity of the bark, thereby leading to sharp differences in lichen cover and diversity between different tree species. Although *Larix* sp. is often considered as an alternative tree species to *P. abies* for the future, the comparative analysis of insect and epiphytic lichen diversity on the stems of these tree species is generally lacking.

The aim of the present study was to determine whether *Larix* sp. could provide suitable habitats to insects and lichens associated with *P. abies* to conserve their biodiversity under climate change.

2. Materials and Methods

2.1. Study Site and Observation

The study sites were in *P. abies* and *Larix* sp. forest stands at 10 different locations in Lithuania (Figure 1 and Table 1).
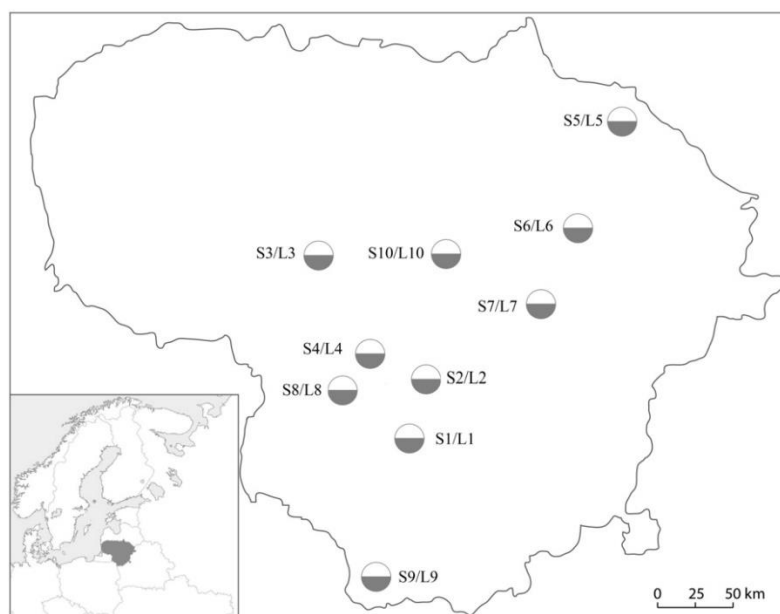

Figure 1. Map of Lithuania showing the distribution of study sites. Gray color in the circle indicates *Larix* sp. stands (L1–L10), and white color represents *P. abies* stands (S1–S10).

The identification of larch species is problematic due to their frequent hybridization [52,53], so in this study, they are referred to as *Larix* sp. At each site, there was one *P. abies* and one *Larix* sp. stand, which were within a radius of 200 m, so they were within the same geographical area and exposed to similar climatic conditions. The topography was similar in these areas. Information on the stand and site characteristics is in Table 1.

Study sites were selected based on forest inventory data from the State Forest Cadastre database. The criteria used for the selection of each study site were: (i) *P. abies* or *Larix* sp. trees were the prevailing species at the site; (ii) similar soil type [54]; and (iii) similar vegetation type [55]. Most of the study sites were characterized by soils of moderate fertility and normal humidity and by an *oxalidosa* vegetation type (Table 1).

At each *P. abies* or *Larix* sp. study site, up to five healthy-looking and up to five dead trees (dead trees were not always available) were randomly selected and used for the assessment of insects and lichens, which was carried out in 2018 and 2019.

Table 1. Characteristics of investigated *Picea abies* and *Larix* sp. stands. Information is based on forest inventory data obtained from the State Forest Cadastre as of 1 December 2020.

Site *	Geographical Position	Age (y)	Mean Height (m)	Mean Diameter (cm)	Stocking Level	Forest Site Type **	Forest Vegetation Type ***	Tree Species Composition (%) ****
S1	54°33′18.88″ N, 23°53′14.53″ E	47	21.7	23.5	1.3	Ncs	ox	100S
L1	54°33′19.82″ N, 23°53′17.18″ E	47	28.1	34.3	0.9	Ncs	ox	100L
S2	54°51′36.84″ N, 24°4′25.17″ E	57	25.2	29.0	0.9	Ncp	ox	40S 20L 20Q 10T 10B
L2	54°51′37.18″ N, 24°4′29.02″ E	37	28.5	33.7	0.8	Ncp	ox	90L10T
S3	55°17′10.6″ N, 23°26′11.7″ E	55	23.6	26.0	0.9	Lds	hox	100S
L3	55°17′10.56″ N, 23°26′23.63″ E	50	29.1	43.5	0.7	Ldp	aeg	100L
S4	55°3′19.44″ N, 23°31′8.07″ E	67	24.6	26.2	0.8	Ncp	ox	80S 10P 10S
L4	55°3′18.74″ N, 23°31′4.2″ E	72	35.9	42.8	0.8	Ncl	ox	90L 10P
S5	55°55′53.91″ N, 25°36′33.16″ E	35	19.0	24.0	0.6	Ldp	oxn	80S 20Q
L5	55°57′51.93″ N, 25°37′7.89″ E	80	28.0	34.0	0.6	Ldp	aeg	70L 20Pt 10B
S6	55°30′46.23″ N, 25°5′33.21″ E	50	19.0	18.0	0.9	Ncl	ox	50S 30P 20T
L6	55°30′46.9″ N, 25°5′35.92″ E	55	25.0	24.0	0.9	Lcl	ox	50P 30L 20S
S7	55°15′4.99″N, 24°48′58.27″ E	38	17.5	19.4	0.6	Ncl	ox	90S 10P
L7	55°15′53.53″ N, 24°48′50.76″ E	38	24.7	29.4	0.9	Ncl	ox	100 L
S8	54°48′57.86″ N, 23°25′24.43″ E	66	25.5	27.9	1.0	Nbl	m	80S 20P
L8	54°49′24.5″ N, 23°25′29.83″ E	66	32.7	32.2	0.8	Ncl	ox	80L 20P
S9	54°0′24.82″ N, 23°44′31.7″ E	84	25.4	28.0	0.7	Nbl	v	60S 10P 10S 20S
L9	54°0′20.68″ N, 23°38′7.07″ E	59	32.2	38.6	0.6	Ncl	ox	100L
S10	55°23′12.67″ N, 24°7′10.42″ E	58	24.4	20.5	1.2	Nds	hox	90S 10B
L10	55°23′14.38″ N, 24°7′13.74″ E	58	26.4	29.2	0.7	Nds	hox	90L 10B

* S1–S10: *Picea abies* stands; L1–L10: *Larix* sp. stands as in Figure 1. ** N: Normal humidity; L: temporarily waterlogged mineral soils; b: low fertility; c: moderate fertility; d: high fertility; l: light soil texture; p: two-layered soil structure with a light fraction on a heavy fraction or vice versa; s: heavy soil texture [54]. *** v: *vacciniosa*; m: *myrtilliosa*; ox: *oxalidosa*; hox: *hepatico-oxalidosa*; oxn: *oxalido-nemorosa*; aeg: *aegopodiosa* [55]. **** S: *Picea abies*; L: *Larix* sp.; P: *Pinus sylvestris*; Q: *Quercus robur*; B: *Betula pendula*; T: *Tilia cordata*; Pt: *Populus tremula*. In each stand, tree species composition is based on the volume.

2.2. Assessment of Insects Associated with Tree Stems

Three different methods were used for the assessment of insects: (i) using sticky traps, which were used to capture insects occurring on the surfaces of living and dead *P. abies* and *Larix* sp. trees, (ii) recording signs of xylophagous insects under the bark of dead trees, and (iii) recording exit holes of xylophagous insects on the bark of dead trees. For the capture of insects on the surface of tree stems [56], two sticky traps, which were made of 20 × 20 cm polyethylene sheets treated with non-drying glue (Pestifix, "Flora", Talinn, Estonia), were attached to each of the five living and five dead *P. abies* standing tree stems. Both traps were placed at the same height of ca. 1.5 m above the ground to prevent interference from grasses and shrubs. Sticky traps on living and dead *Larix* sp. tree stems were established in the same way. The assessment of insects using sticky traps was carried out between May and August 2019. During this period, sticky traps with trapped insects were collected once a month and replaced with new ones, which resulted

in three time points (June, July, and August). Collected sticky traps were transported to the laboratory the same day and stored at 5 °C until the identification of insect species using a binocular Zeiss Stemi 2000-C microscope (Oberkochen, Germany) and morphological insect identification keys [57–62]. Many insects were identified to the species level, while others were identified to the order, family, or genus level. Several insects remained unidentified, which was largely because they were missing body parts or were heavily covered by glue from sticky traps, thereby making reliable identification impossible. After the identification of insect species, accidentally trapped insects, i.e., species specifically associated with the tree crowns or non-target species, the development and feeding of which are not dependent on tree stems, were excluded from further analyses. However, predators and parasites of insects associated with tree stems were included in analyses.

Xylophagous insects, which are wood- and bark-boring insects, were assessed on dead *P. abies* and *Larix* sp. trees, and the signs and areas of their activity under the bark, i.e., larval tunnels, pupal chambers, and adult holes in the wood, were recorded. This was carried out once in August 2019 by removing a 20 × 20 cm bark sheet at a height of ca. 1.5 m above the ground [56]. In each study site, one bark sheet was removed from each of the five dead trees of each tree species, resulting in a total of 0.4 m² bark area in each site. The area of removed bark was photographed, signs of insect activity were analyzed in the laboratory, and insect species were identified.

For the assessment of exit holes of adult insects and the identification of their species, five dead trees of *P. abies* and *Larix* sp. per study site were visually inspected in August 2018. On each tree stem (1–1.5 m above the ground), insect exit holes were recorded on five plots, each 0.01 m² in size, and were situated along the stem and from four different geographical directions (N, S, E, and W), resulting in a 0.2 m² area per tree in total. This method was adopted from Asta et al. [63]. The number of exit holes was recorded for each insect species separately. Insect species for which exit holes were clearly species-specific, e.g., *Ips typograhus* and *Pityogenes chalcographus*, were identified to the species level, while others were identified to the family or genus level.

2.3. Assessment of Epiphytic Lichens

Epiphytic lichens were assessed at the same study sites in August 2018 (Figure 1 and Table 1). In each *P. abies* or *Larix* sp. study site, five healthy and five dead trees were selected. The selected trees were ca. 18–20 cm in diameter at a height of 1.3 m above the ground, stem inclination was not more than 20°, trees were without wounds on the stem, and bark structure and bark thickness were similar for all trees of each tree species. For the assessment of lichens, on each tree, four independent plots, each 10 × 10 cm in size and each facing a different geographical direction (N, S, E, or W), were established at ca. 1.5 m above the ground [63]. All lichen species present within each plot and the area covered by each of them were recorded. Most of the lichen specimens were identified to the species, genus, or family level, but several species remained unidentified.

2.4. Statistical Analysis

Differences in the richness of insect or lichen taxa between dead or living trees of *P. abies* and *Larix* sp. were compared by nonparametric chi-square test [64], taking into account the Bonferroni correction. The Shannon diversity index, qualitative Sorensen similarity index, and nonmetric multidimensional scaling (NMDS) in Canoco 5 [65–67] were used to characterize the diversity and composition of insect and lichen communities. The nonparametric Mann–Whitney test in Minitab v.19.2 (Minitab® Inc., Pennsylvania State University, State College, PA, USA) was used to test if the Shannon diversity index among different samples differed significantly or not. ANOVA in Minitab was used to evaluate whether the bark area colonized by lichens differed among different tree species.

3. Results

3.1. Insects

In total, there were 20,226 insects trapped using sticky traps (Table 2). When all sites were taken together, on dead *P. abies*, there were 76 different insect species identified among 10,858 (53.3%) insects trapped, while on dead *Larix* sp., there were 64 different species identified among 1017 (5%) insects trapped.

Table 2. Diversity of insects detected in sticky traps at different *Picea abies* and *Larix* sp. study sites.

Site	Tree State	Tree Species	Relative Abundance, % (No. of Insects)	Richness, % (No. of Insect Species)	Shannon H	Sørensen Cs *
S1/L1	Live	*Picea*	0.4 (74)	22.1 (21)	2.34	0.44
		Larix	0.3 (69)	15.8 (15)	2.16	
	Dead	*Picea*	0.3 (63)	24.2 (23)	2.53	-
		Larix	-	-	-	
	Total		**1.0 (206)**	**40.0 (38)**	**2.35**	**0.48**
S2/L2	Live	*Picea*	0.5 (109)	25.3 (24)	2.46	0.36
		Larix	0.2 (32)	15.8 (15)	2.33	
	Dead	*Picea*	29.1 (5885)	25.3 (24)	0.07	0.42
		Larix	0.1 (16)	9.5 (9)	1.85	
	Total		**29.9 (6042)**	**43.2 (41)**	**0.22**	**0.50**
S3/L3	Live	*Picea*	0.4 (82)	18.9 (18)	2.14	0.39
		Larix	1.1 (221)	18.9 (18)	1.86	
	Dead	*Picea*	0.71 (144)	27.4 (26)	2.32	0.40
		Larix	1.6 (325)	25.3 (24)	1.63	
	Total		**3.8 (772)**	**48.4 (46)**	**2.24**	**0.54**
S4/L4	Live	*Picea*	0.5 (102)	29.5 (28)	2.81	0.46
		Larix	0.4 (91)	21.1 (20)	2.16	
	Dead	*Picea*	4.5 (918)	34.7 (33)	0.86	0.57
		Larix	0.3 (64)	24.2 (23)	2.52	
	Total		**5.8 (1175)**	**56.8 (54)**	**1.68**	**0.60**
S5/L5	Live	*Picea*	0.6 (127)	18.9 (18)	2.06	0.46
		Larix	0.5 (99)	22.1 (21)	2.58	
	Dead	*Picea*	1.4 (286)	28.4 (27)	2.21	-
		Larix	-	-	-	
	Total		**2.5 (512)**	**44.2 (42)**	**2.66**	**0.41**
S6/L6	Live	*Picea*	0.6 (120)	23.2 (22)	1.76	0.41
		Larix	0.4 (78)	17.9 (17)	1.94	
	Dead	*Picea*	0.9 (194)	29.5 (28)	2.48	0.46
		Larix	0.7 (146)	25.3 (24)	2.01	
	Total		**2.7 (538)**	**53.7 (51)**	**2.49**	**0.56**
S7/L7	Live	*Picea*	31.5 (6369)	30.5 (29)	0.25	0.49
		Larix	0.6 (122)	25.3 (24)	2.22	
	Dead	*Picea*	1.2 (241)	30.5 (29)	2.32	0.46
		Larix	0.8 (165)	29.5 (28)	2.24	
	Total		**34.1 (6897)**	**62.1 (59)**	**0.64**	**0.54**

Table 2. *Cont.*

Site	Tree State	Tree Species	Relative Abundance, % (No. of Insects)	Richness, % (No. of Insect Species)	Shannon H	Sørensen Cs *
S8/L8	Live	*Picea*	0.5 (110)	28.4 (27)	2.57	0.59
		Larix	0.3 (54)	17.9 (17)	2.25	
	Dead	*Picea*	8.4 (1705)	36.8 (35)	1.05	0.56
		Larix	0.4 (82)	20.0 (19)	2.49	
	Total		**9.6 (1951)**	**51.6 (49)**	**1.53**	**0.60**
S9/L9	Live	*Picea*	1.0 (207)	25.3 (24)	2.10	0.58
		Larix	0.5 (95)	25.3 (24)	2.38	
	Dead	*Picea*	6.0 (1222)	35.8 (34)	0.99	0.39
		Larix	0.6 (117)	23.2 (22)	2.39	
	Total		**8.1 (1641)**	**55.8 (53)**	**1.74**	**0.52**
S10/L10	Live	*Picea*	0.6 (120)	28.4 (27)	2.71	0.55
		Larix	0.3 (70)	17.9 (17)	2.00	
	Dead	*Picea*	1.0 (200)	33.7 (32)	2.68	0.57
		Larix	0.5 (102)	25.3 (24)	2.68	
	Total		**2.4 (492)**	**53.7 (51)**	**2.84**	**0.57**
All sites	**Live *Picea***		**36.7 (7420)**	**70.5 (67)**		
	Live *Larix*		**4.6 (931)**	**71.6 (68)**		
	Dead *Picea*		**53.7 (10,858)**	**80 (76)**		
	Dead *Larix*		**5.0 (1017)**	**67.4 (64)**		
	All total		**100 (20,226)**	**100 (95)**		

* Sørensen similarity index in rows Total shows the comparison between all *Picea abies* and all *Larix* sp. trees within adjacent study sites, e.g., S2 and L2.

Consequently, the chi-square test showed that the richness of insect species was significantly higher on dead *Larix* sp. than on dead *P. abies* ($p < 0.0001$). Similarly, on living *P. abies*, there were 67 different insect species among 7420 (36.7%) insects trapped, while on living *Larix* sp., there were 68 different species among 931 (4.6%) insects trapped. The richness of insect species was significantly higher on living *Larix* sp. than on living *P. abies* ($p < 0.0001$).

Many insect species were shared between dead trees and between living trees of both tree species. Among the 95 insect species identified, 5 were unique to living *P. abies*, and 4 were unique to living *Larix* sp. trees. Similarly, two insect species were unique to dead *P. abies*, and five were unique to dead *Larix* sp. (Figure 2).

Consequently, the Sørensen similarity index of insect communities was moderate when compared between dead trees of both tree species and living trees of both tree species (Table 2). The Mann–Whitney test showed that the Shannon diversity index of insect communities was similar between dead trees ($p > 0.05$) and between living trees ($p > 0.05$) when compared between *P. abies* and *Larix* sp., respectively. NMDS showed that insect communities on living *P. abies* and living *Larix* sp. were partially overlapping (Figure 3a). By contrast, insect communities on dead *P. abies* and dead *Larix* sp. were separated along the diagonal (Figure 3a). However, NMDS showed that there was a partial overlap between insect communities on living *P. abies* and dead *Larix* sp. (Figure 3a). Assessments that were conducted in June, July, and August showed that there were only minor variations in the abundance of dominant insect species on both living and dead *P. abies* and *Larix* sp. (Table 3). The most common insect species on *P. abies* were *Crypturgus pusillus*, *Ichneomonidae* sp., and *Eucnemidae* sp. 1, while on *Larix* sp., they were *Ichneomonidae* sp., *Eucnemidae* sp. 1, and *Eucnemidae* sp. 2 (Table 3). All insect species detected using sticky traps are in Table S1.
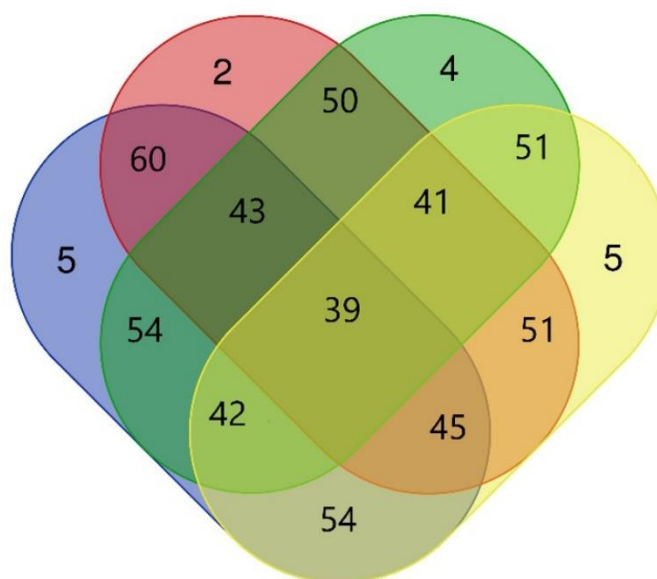
Figure 2. Venn diagram showing the species richness and overlap of insect species collected using sticky traps. The data from different study sites are combined. Different colors show: blue—living *Picea abies*; pink—dead *P. abies*; green—living *Larix* sp.; and yellow—dead *Larix* sp.

The overall community of xylophagous insects consisted of nine species detected using bark sheets and eight species detected using the exit hole method (Table 4). When all sites were taken together, the colonized bark area was 39.0% on dead *P. abies* and 47.3% on *Larix* sp. trees. Consequently, the chi-square test showed that the bark area colonized was significantly higher on dead *Larix* sp. trees than on *P. abies* ($p < 0.0001$). The number of exit holes of xylophagous insects was 2509 (75.4%) on dead *P. abies* and 819 (24.6%) on *Larix* sp. The number of exit holes was significantly higher on *P. abies* than on *Larix* sp. trees ($p < 0.0001$) (Table 4). More importantly, communities of xylophagous insects detected using bark sheet and exit hole methods were similar when compared between *P. abies* and *Larix* sp. (Figure 3b,c). In support, the Sørensen similarity index was 0.80, showing high species similarity between all dead *P. abies* and *Larix* sp. trees using both methods (Table 4). The Mann–Whitney test showed that the Shannon diversity index of xylophagous insect communities was similar using bark sheet ($p > 0.05$) and exit hole methods ($p > 0.05$) when a comparison was made between dead *P. abies* and *Larix* sp., respectively.

However, the species composition of xylophagous insects was quite different when compared between bark sheet and exit hole methods (Table 5). The most common xylophagous insects detected using bark sheets on *P. abies* were *Polygraphus poligraphus* (31.0%), *Molorchus* sp. (27.7%), and *Callidium* sp. (18.0%), while those on *Larix* sp. were *Callidium* sp. (35.7%), *Cerambycidae* sp. (27.2%), and *Rhagium* sp. (17.5%) (Table 5). The most common xylophagous insects detected using the exit hole method on *P. abies* were *Pityogenes chalcographus* (44.2%), *Hylurgops palliatus* (25.5%), and *Trypodendron lineatum* (16.6%), while on *Larix* sp., they were *Buprestidae* sp. (28.6%), *Scolytinae* sp. (22.6%), and *Cerambycidae* sp. (22.0%) (Table 5).
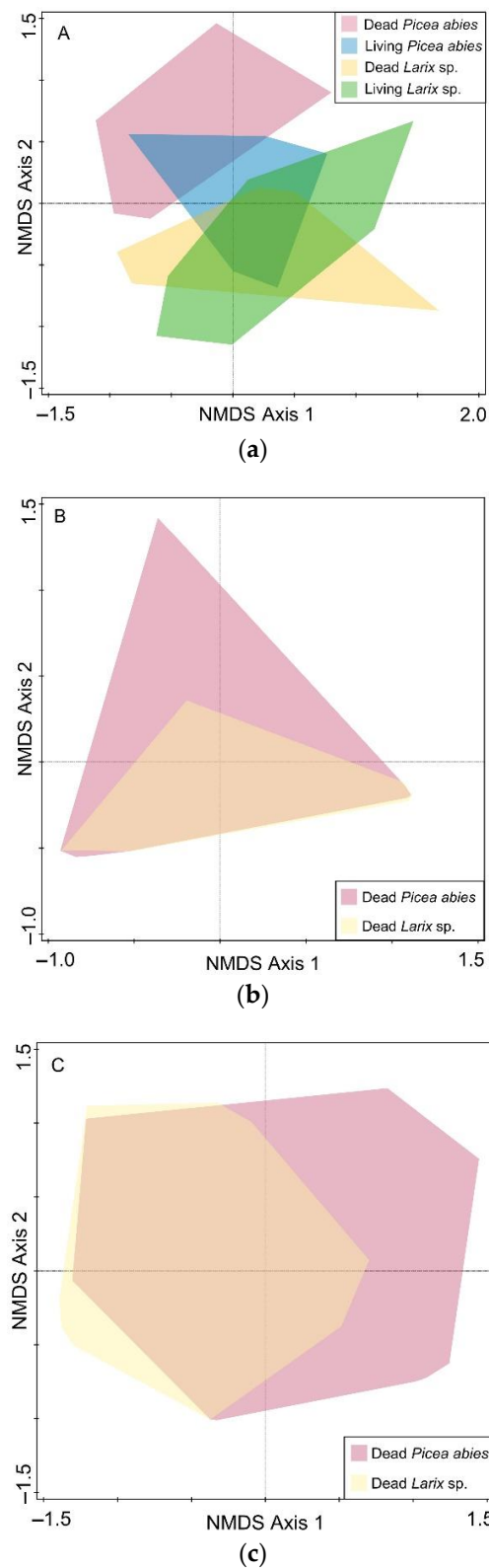
Figure 3. Ordination diagram based on nonmetric multidimensional scaling of insect communities detected in association with *Picea abies* and *Larix* sp. trees. Insects were assessed using: (**a**) sticky traps attached to the surface of dead and living trees (47.1% variation explained on axis 1 and 31.9% explained on axis2, (**b**) bark sheets removed from dead trees (52.7% on axis 1 and 31.8% on axis 2), and (**c**) insect exit holes recorded on dead trees (47.2% on axis 1 and 28.5% on axis 2).

Table 3. Relative abundance (%) of the 20 most common insect species trapped using sticky traps. All study sites are combined.

Order/Family	Species	*Picea abies* Trees								*Larix* sp. Trees							
		June		July		August		Total		June		July		August		Total	
		D *	L **	D	L	D	L	D	L	D	L	D	L	D	L	D	L
Coleoptera/Curculionidae	*Crypturgus pusillus* Erich.	91.6	80.0	69.8	87.0	59.2	-	83.8	82.7	-	-	0.3	-	-	-	0.2	-
Hymenoptera/Ichneomonidae	*Ichneomonidae* sp.	1.9	3.1	6.9	5.1	8.0	22.8	3.6	5.0	23.2	26.2	24.8	29.1	30.0	28.1	24.6	27.8
Coleoptera/Eucnemidae	*Eucnemidae* sp. 1	1.2	3.9	2.1	1.3	1.2	3.9	1.4	2.1	25.9	23.2	31.9	18.8	5.4	5.6	27.0	19.0
Coleoptera/Eucnemidae	*Eucnemidae* sp. 2	0.7	3.2	2.6	1.5	1.8	6.3	1.3	2.1	4.9	13.9	7.5	14.8	4.1	8.2	6.1	13.7
Coleoptera/Elateridae	*Dalopius marginatus* L.	0.7	2.9	-	-	-	-	0.4	0.8	19.0	11.5	-	-	-	-	7.8	4.5
Coleoptera/Anobiidae	*Hadrobregmus pertinax* L.	0.2	-	3.8	0.1	-	-	1.2	0.1	1.7	-	5.0	1.8	-	-	3.2	0.9
Coleoptera/Elateridae	*Conoderus* sp.	-	-	2.7	0.5	1.7	2.8	0.9	0.4	0.5	0.6	3.4	3.1	7.3	1.2	2.6	1.9
Coleoptera/Cleridae	*Tillus elongatus* L.	0.1	0.6	1.2	0.7	0.3	-	0.4	0.7	2.9	1.9	5.9	5.5	-	0.5	4.1	3.5
Coleoptera/Cleridae	*Thanasimus formicarius* L.	0.4	0.6	1.7	0.5	1.8	0.7	0.9	0.5	1.5	1.7	1.0	0.5	-	-	1.1	0.9
Coleoptera/Anthribidae	*Anthribus nebulosus* Forst.	0.1	0.6	0.5	0.6	2.0	15.3	0.3	1.0	1.1	0.3	0.6	1.8	7.4	10.3	1.4	2.2
Coleoptera/Ptinidae	*Anobium rufipes* Fabr.	0.1	0.3	1.5	0.3	0.3	2.5	0.5	0.4	-	2.3	3.3	-	-	-	1.6	0.9
Coleoptera/Scolytidae	*Polygraphus poligraphus* L.	0.2	-	0.0	0.1	12.1	1.0	0.7	0.1	0.8	-	0.2	-	0.6	1.1	0.5	0.1
Hymenoptera/Formicidae	*Formica rufa* L.	0.1	0.7	0.1	0.3	1.8	16.0	0.2	0.8	-	0.8	-	0.3	0.6	4.1	0.1	0.9
Coleoptera/Scolytidae	*Trypodendron lineatum* Ol.	0.8	0.4	0.2	-	0.3	0.7	0.6	0.1	1.6	0.3	-	0.2	3.2	4.5	1.0	0.7
Coleoptera/Cantharidae	*Malthodes* sp.	-	0.3	0.2	0.3	0.6	0.8	0.1	0.3	0.3	1.4	1.2	3.1	1.8	-	0.9	2.1
Coleoptera/Scolytidae	*Pityogenes chalcographus* L.	0.1	0.1	1.4	0.1	-	-	0.5	0.1	-	0.3	-	-	-	-	-	0.1
Coleoptera/Nitidulidae	*Glischrochilus hortensis* Geoffr.	0.2	0.2	0.3	-	-	0.3	0.2	0.1	1.3	0.9	0.8	0.3	-	-	0.9	0.5
Coleoptera/Trogossitidae	*Nemozoma elongatum* L.	2.2	0.1	0.6	-	0.3	-	0.3	0.1	-	-	-	-	-	-	-	-
Coleoptera/Dermestidae	*Megatoma undata* L.	0.1	0.1	0.5	0.1	-	-	0.2	0.1	0.5	1.2	0.2	-	-	-	0.3	0.5
Hymenoptera/Myrmicidae	*Myrmica* sp.	-	-	0.2	0.1	0.5	5.5	0.1	0.2	-	-	-	0.9	1.3	3.9	0.1	0.9
Total of 20 species		**98.7**	**97.2**	**96.4**	**98.9**	**91.9**	**78.6**	**97.7**	**97.9**	**85.1**	**86.5**	**86.3**	**80.0**	**61.8**	**67.5**	**83.5**	**81.1**

* D: dead trees; ** L: living trees.

Table 4. Diversity of xylophagous insects detected using bark sheet and exit hole methods on dead *Picea abies* and *Larix* sp.

Site	Tree Species	Bark Sheets				Exit Holes			
		Richness, % (No. of Insect Species)	Bark Area Colonized, %	Shannon H	Sørensen Cs	Richness, % (No. of Insect Species)	Amount, % (No. of Exit Holes)	Shannon H	Sørensen Cs
S1/L1	*Picea*	44.4 (4)	54.2	1.03	-	62.5 (5)	3.3 (109)	0.79	-
	Larix	-	-	-		-	-	-	
Total		**44.4 (4)**	**54.2**	**-**		**62.5 (5)**	**3.3 (109)**	**-**	
S2/L2	*Picea*	22.2 (2)	18.3	0.56	0.67	50.0 (4)	0.9 (3)1	0.84	1.00
	Larix	44.4 (4)	49.2	0.23		50.0 (4)	3.2 (108)	0.91	
Total		**44.4 (4)**	**40.0**	**0.58**		**50.0 (4)**	**4.2 (139)**	**1.08**	
S3/L3	*Picea*	22.2 (2)	35.7	0.69	0.67	50.0 (4)	2.9 (96)	0.95	0.33
	Larix	11.1 (1)	58.0	0.00		25.0 (2)	0.3 (10)	0.33	
Total		**22.2 (2)**	**45.0**	**0.57**		**62.5 (5)**	**3.2 (106)**	**1.18**	
S4/L4	*Picea*	44.4 (4)	42.5	0.97	0.00	75.0 (6)	8.2 (273)	1.46	0.44
	Larix	22.2 (2)	75.0	0.64		37.5 (3)	1.6 (53)	1.08	
Total		**66.7 (6)**	**49.0**	**1.48**		**87.5 (7)**	**9.8 (326)**	**1.64**	
S5/L5	*Picea*	44.4 (4)	55.0	1.27	-	50.0 (4)	3.0 (100)	0.60	-
	Larix	-	-	-		-	-	-	
Total		**44.4 (4)**	**55.0**	**-**		**50.0 (4)**	**3.0 (100)**	**-**	
S6/L6	*Picea*	55.6 (5)	13.8	1.10	0.57	62.5 (5)	9.0 (300)	1.13	0.50
	Larix	22.2 (2)	38.0	0.60		37.5 (3)	3.2 (108)	0.77	
Total		**55.6 (5)**	**23.1**	**1.01**		**75.0 (6)**	**12.3 (408)**	**1.34**	
S7/L7	*Picea*	22.2 (2)	71.0	0.59	0.40	62.5 (5)	18.3 (609)	0.83	0.60
	Larix	33.3 (3)	69.0	1.08		62.5 (5)	1.8 (60)	1.33	
Total		**44.4 (4)**	**70.0**	**1.24**		**87.5 (7)**	**20.1 (669)**	**1.09**	
S8/L8	*Picea*	22.2 (2)	23.5	0.52	0.00	87.5 (7)	10.0 (333)	0.81	0.73
	Larix	11.1 (1)	20.0	0.00		50.0 (4)	3.2 (106)	0.79	
Total		**33.3 (3)**	**22.0**	**0.98**		**87.5 (7)**	**13.2 (439)**	**0.93**	
S9/L9	*Picea*	44.4 (4)	53.3	1.00	0.33	87.5 (7)	16.7 (556)	1.35	0.55
	Larix	22.2 (2)	59.0	0.63		50.0 (4)	7.3 (242)	0.72	
Total		**55.6 (5)**	**55.9**	**1.43**		**100 (8)**	**24.0 (798)**	**1.72**	
S10/L10	*Picea*	22.2 (2)	31.4	0.66	0.80	37.5 (3)	3.1 (102)	0.85	0.40
	Larix	33.3 (3)	29.2	0.43		25.0 (2)	3.3 (111)	0.48	
Total		**33.3 (3)**	**30.4**	**1.07**		**50.0 (4)**	**3.4 (113)**	**1.21**	
All sites	*Picea*	88.9 (8)	39.0	1.65	0.80	100 (8)	75.4 (2509)	1.44	0.80
	Larix	77.8 (7)	47.3	1.55		87.5 (7)	24.6 (819)	1.61	
All total		**100 (9)**	**42.2**	**1.94**		**100 (8)**	**100 (3328)**	**1.77**	

Table 5. Relative abundance (%) of xylophagous insects colonizing dead wood of *Picea abies* and/or *Larix* sp. detected using bark sheet and exit holes methods.

Order/Family	Insect Species	Bark Sheets		Exit Holes	
		Picea abies	*Larix* sp.	*Picea abies*	*Larix* sp.
Coleoptera/Cerambycidae	*Callidium* sp. Fabr.	18.0	35.7	-	-
Coleoptera/Cerambycidae	*Cerambycidae* sp. Latr	0.2	27.2	4.3	22.0
Coleoptera/Curculionidae	*Ips typographus* L.	11.0	-	7.1	-
Coleoptera/Cerambycidae	*Molorchus* sp. Fabr.	27.7	5.6	-	-
Coleoptera/Curculionidae	*Polygraphus poligraphus* L.	31.0	-	-	-
Coleoptera/Curculionidae	*Rhagium* sp. Fabr.	7.0	17.5	-	-

Table 5. *Cont.*

Order/Family	Insect Species	Bark Sheets		Exit Holes	
		Picea abies	*Larix* sp.	*Picea abies*	*Larix* sp.
Coleoptera/Curculionidae	*Scolytinae* sp. Latr.	3.8	2.9	1.2	22.6
Hymenoptera/Siricidae	*Siricidae* sp. Fabr.	1.2	0.3	-	-
Coleoptera/Cerambycidae	*Tetropium* sp. Kirby	-	10.8	-	-
Coleoptera/Curculionidae	*Pityogenes chalcographus* L.	-	-	44.2	6.3
Coleoptera/Curculionidae	*Trypodendron lineatum* Oliv.	-	-	16.6	17.8
Coleoptera/Buprestidae	*Buprestidae* sp. Leach	-	-	0.9	28.6
Coleoptera/Curculionidae	*Hylurgops palliatus* Gyll.	-	-	25.5	-
Hymenoptera/Siricidae	*Sirex juvencus* L.	-	-	0.2	2.7

3.2. Lichens

The overall lichen community detected in the present study consisted of twelve species, among which eight were on dead *P. abies*, ten were on dead *Larix* sp., ten were on living *P. abies*, and eleven were on living *Larix* sp. (Table 6). The bark area colonized by lichens was 34.3% on dead *P. abies* and 63.2% on dead *Larix* sp., and 40.4% on living *P. abies* and 78.0% on living *Larix* sp. (Table 6).

Table 6. Diversity and occurrence of epiphytic lichens on the bark of dead and living *Picea abies* and *Larix* sp. trees.

Site	Tree State	Tree Species	Richness, % (No. of Lichen Species)	Bark Area Colonized, %	Shannon H	Sørensen Cs *
S1/L1	Live	*Picea*	66.6 (8)	89.5	1.18	0.71
		Larix	50.0 (6)	71.2	1.25	
	Dead	*Picea*	66.6 (8)	95.5	1.06	-
		Larix	-	-	-	
	Total		**75.0 (9)**	**85.8**	**1.31**	**0.80**
S2/L2	Live	*Picea*	58.3 (7)	51.8	1.61	0.62
		Larix	50.0 (6)	28.5	1.35	
	Dead	*Picea*	58.3 (7)	40.4	1.44	0.73
		Larix	33.3 (4)	26.8	1.09	
	Total		**75.0 (9)**	**47.7**	**1.54**	**0.62**
S3/L3	Live	*Picea*	8.3 (1)	20.0	0.00	0.20
		Larix	75.0 (9)	77.2	1.52	
	Dead	*Picea*	-	-	-	-
		Larix	33.3 (4)	86.1	1.11	
	Total		**75.0 (9)**	**50.2**	**1.44**	**0.20**
S4/L4	Live	*Picea*	50.0 (6)	37.3	1.17	0.62
		Larix	58.3 (7)	81.1	1.13	
	Dead	*Picea*	16.7 (2)	17.8	0.53	0.29
		Larix	41.7 (5)	49.5	0.85	
	Total		**83.3 (10)**	**48.7**	**1.17**	**0.57**
S5/L5	Live	*Picea*	16.7 (2)	19.0	0.65	0.36
		Larix	75.0 (9)	83.2	1.13	
	Dead	*Picea*	41.7 (5)	40.2	1.00	-
		Larix	-	-	-	
	Total		**75.0 (9)**	**49.6**	**1.32**	**0.71**

Table 6. *Cont.*

Site	Tree State	Tree Species	Richness, % (No. of Lichen Species)	Bark Area Colonized, %	Shannon H	Sørensen Cs *
S6/L6	Live	*Picea*	25.0 (3)	26.0	1.03	0.75
		Larix	41.7 (5)	84.9	0.67	
	Dead	*Picea*	8.3 (1)	5.0	0.00	0.29
		Larix	50.0 (6)	89.2	0.82	
	Total		**50.0 (6)**	**54.2**	**0.96**	**0.80**
S7/L7	Live	*Picea*	66.7 (8)	58.3	1.13	0.80
		Larix	58.3 (7)	71.7	0.70	
	Dead	*Picea*	8.3 (1)	12.0	0.00	0.00
		Larix	16.7 (2)	31.0	0.14	
	Total		**75.0 (9)**	**44.4**	**1.11**	**0.80**
S8/L8	Live	*Picea*	58.3 (7)	46.8	0.96	0.71
		Larix	58.3 (7)	57.4	1.42	
	Dead	*Picea*	58.3 (7)	55.9	1.34	0.75
		Larix	75.0 (9)	49.2	1.36	
	Total		**83.3 (10)**	**52.5**	**1.42**	**0.75**
S9/L9	Live	*Picea*	8.3 (1)	17.0	0.00	0.40
		Larix	33.3 (4)	80.9	1.21	
	Dead	*Picea*	25.0 (3)	28.7	0.58	0.67
		Larix	25.0 (3)	90.1	0.86	
	Total		**50.0 (6)**	**59.9**	**1.10**	**0.25**
S10/L10	Live	*Picea*	66.7 (8)	24.8	1.39	0.80
		Larix	58.3 (7)	4.8	1.17	
	Dead	*Picea*	41.7 (5)	22.5	1.28	0.33
		Larix	8.3 (1)	68.0	0.00	
	Total		**75.0 (9)**	**56.3**	**1.16**	**0.80**
All sites	Live *Picea*		83.3 (10)	40.4	1.42	0.86
	Live *Larix*		91.7 (11)	78.0	1.48	
	Dead *Picea*		66.7 (8)	34.3	1.38	0.89
	Dead *Larix*		83.3 (10)	63.2	1.11	
	All Total		**100 (12)**	**54.8**	**1.45**	**0.86**

* Sørensen similarity index in rows "Total" shows the comparison between all *Picea abies* and all *Larix* sp. trees within adjacent study sites, e.g., S2 and L2.

ANOVA showed that the bark area colonized by lichens was significantly larger on dead and living *Larix* sp. trees than on corresponding *P. abies* trees ($p < 0.0001$). The Mann–Whitney test showed that the Shannon diversity index of lichen communities was similar between living *P. abies* and *Larix* sp. trees ($p > 0.05$) and between dead *P. abies* and *Larix* sp. trees ($p > 0.05$) (Table 6).

The most abundant lichen species was *Lepraria* sp., which composed 69.9% of the total bark area colonized by lichens. The relative abundance of this species was 60.4% and 59.9% on dead and living *P. abies*, respectively, and 76.4% and 71.4% on dead and living *Larix* sp., respectively (Table 7). The other most common lichen species detected on dead and living *P. abies* were *Phlyctis argena* (13.6% and 19.9%, respectively) and *Lecidea elaeochroma* (6.7% and 7.7%, respectively), while those on dead and living *Larix* sp. were *Hypogimnia physodes* (14.3% and 6.5%, respectively) and Unidentified sp. 1 (4.3% and 6.7%, respectively). Unidentified sp. 2, with a relative abundance of 7.0%, was detected only on living *Larix* sp. trees (Table 7).

Table 7. Relative abundance (%) of epiphytic lichen species on colonized dead and living *P. abies* and *Larix* sp. trees. Different sampling sites are combined.

Family	Lichen Species	*Picea abies*		*Larix* sp.		Total
		Dead	**Living**	**Dead**	**Living**	
Stereocaulaceae	*Lepraria sp.* Ach.	60.4	59.9	76.4	71.4	69.9
Parmeliaceae	*Hypogimnia physodes* (L.) Nyl.	3.3	4.8	14.3	6.5	8.1
Phlyctidaceae	*Phlyctis argena* Spreng.	13.6	19.9	1.9	1.9	5.8
Unknown	Unidentified sp. 1	4.1	5.1	4.3	6.5	5.4
Lecanoraceae	*Lecidea elaeochroma* Ach.	6.7	7.7	1.4	2.4	3.4
Unknown	Unidentified sp. 2	-	-	-	7.0	3.2
Parmeliaceae	*Parmelia sulcate* Taylor.	5.5	1.0	0.9	1.3	1.6
Unknown	Unidentified sp. 3	4.8	1.1	0.2	0.3	0.9
Physciaceae	*Physcia stellaris* (L.) Nyl.	1.6	0.2	0.3	1.0	0.8
Teloschistaceae	*Xanthoria parietina* (L.) Th.Fr.	-	0.3	0.1	1.2	0.6
Unknown	Unidentified sp. 4	-	-	0.1	0.6	0.3
Unknown	Unidentified sp. 5	-	0.1			0.0

NMDS showed that lichen communities associated with dead and living trees of *P. abies* and *Larix* sp. were largely the same and thus overlapping (Figure 4). In agreement, the Sørensen similarity index of lichen communities was 0.86 between *P. abies* and *Larix* sp. trees, showing a high species similarity (all study sites combined) (Table 6).
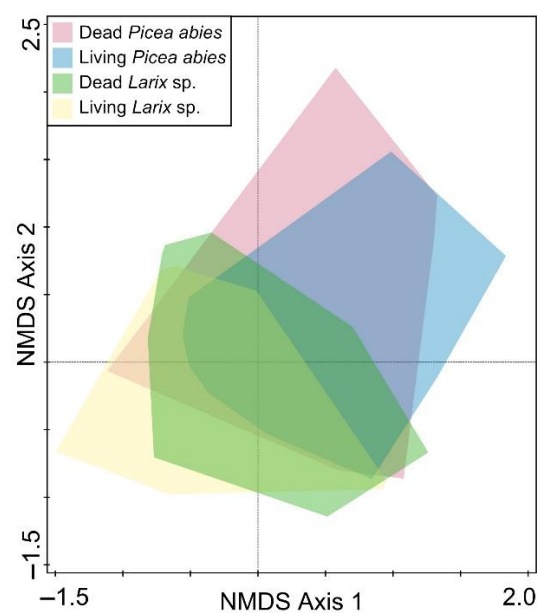
Figure 4. Ordination diagram based on nonmetric multidimensional scaling (NMDS) of lichen communities on dead and living trees of *Picea abies* and *Larix* sp. In NMDS, 44.2% variation was explained on axis 1, and 34.5% was explained on axis 2.

4. Discussion

The results demonstrate that the two coniferous tree species, namely, native *P. abies* and introduced *Larix* sp., support a similar diversity of stem-associated insect and lichen communities, but the species composition was only partially overlapping (Figures 2–4 and Tables 3–7). Consistently, for both insects and lichens, the Sørensen similarity index ranged from moderate to high, while the Shannon diversity index was similar between the two tree species. Therefore, *Larix* sp. has the potential to provide suitable habitats for some insect and lichen species associated with stems of *P. abies*. However, other organisms associated with these tree species should also be considered, as the replacement of native tree species

by introduced ones is a drastic event and may affect biodiversity at both local and regional scales [68]. In addition, different groups of organisms may respond to introduced tree species, i.e., to a new habitat, in different ways [69]. Several studies have evaluated the effect of introduced trees on a particular group of organisms, e.g., plants [70], insects [29,30,71,72], or birds [73,74]. Nevertheless, similar studies that simultaneously assessed different groups of organisms are scarce but can be particularly valuable [75], especially if a number of factors, such as the age of forest stands, microclimate conditions, the type of forest management, or the volume of deadwood, are taken into consideration [76–79], as these may also have a strong impact on associated biodiversity [80].

4.1. Insects

In the present study, the use of different assessment methods (sticky traps, bark sheets, and exit holes) provided a comprehensive comparison of the diversity and composition of stem-associated insects (Tables 3–5 and Figure 3), thereby allowing the overall insect diversity to be estimated [39,81,82]. Among these methods, sticky traps represent one of the most commonly used types of passive traps [83], but additional methods are often needed, as these may provide valuable complementary information [84,85]. However, to increase the accuracy of species identification, additional methods such as DNA sequencing may be needed, as for several insects trapped, the species identity could not be established using morphological methods (Table 3). Nevertheless, sticky traps allowed the collection of important and host-tree-specific insect species but, in some cases, also resulted in unspecific individuals, e.g., *Dalopius marginatus* L., *Conoderus* sp. (Coleoptera: Elateridae), *Formica rufa* L. (Hymenoptera: Formicidae), *Myrmica* sp. (Hymenoptera: Myrmicidae), or *Malthodes* sp. (Coleoptera: Cantharidae) (Table 3). Although the latter insects are abundant in the Palaearctic and Nearctic regions and play important roles in forest ecosystems [86], they are not specifically associated with *P. abies* or *Larix* sp. Beetles dominated insect communities in sticky traps, among which two species of aggressive bark beetles, i.e., *Polygraphus poligraphus* and *Pityogenes chalcographus*, which regularly attack and can kill living trees, were detected (Table 3). Interestingly, *P. poligraphus* and *P. chalcographus* are among the phloeophagous insect species, which are known to be specifically associated with the genus *Picea* [87], but in the present study, these were detected on both *P. abies* and *Larix* sp. (Table 3). Similarly, on both tree species, there were also several secondary bark beetle species, which are deadwood-dependent and colonize trees following attacks by aggressive bark beetles. These included *Crypturgus pusillus*, *Hadrobregmus pertinax*, *Anobium rufipes*, and *Trypodendron lineatum* (Table 3). Among these, *C. pusillus* is known to be a *P. abies*-dependent species that colonizes trees following attacks by *I. typographus* [87,88].

Interactions between xylophagous insects and their predators are common in nature and may have a direct effect on the health and sustainability of forest stands [89]. Several predators were detected, among which probably the most interesting was *Nemozoma elongatum* (Coleoptera: Trogossitidae), as it is one of the most important predators of *P. chalcographus* [90]. However, *N. elongatum* was captured in low abundance and only on dead and living *P. abies* (Table 3), even though its trapping coincided with the flying period (June–July) of *P. chalcographus* [91]. Zahradník and Zahradníková [92], using pheromone baited traps, showed a strong positive correlation between the abundance of *P. chalcographus* (1–4%) and *N. elongatum* (up to 60%). Among other predatory insects captured on *P. abies* and *Larix sp.* tree stems were *Thanasimus formicarius*, *Tillus elongatus*, *Glischrochilus hortensis*, and *Anthribus nebulosus* (Table 3). *Thanasimus formicarius* and *Glischrochilus hortensis* are predators of many different bark beetle species from the subfamily Scolytinae, including *I. typographus* [89,93–96]. *Tillus elongatus* is also a predator of bark beetles, attacking them in larval tunnels [97]. *Anthribus nebulosus* is a predator of soft-scale insects from the family Coccidae [98]. Despite the detection, the relative abundance of predator insects was low, and in many cases, the host insects were absent, suggesting that their trapping could be accidental. The use of sticky traps also revealed the presence of *Tetropium gabrieli* on *Larix* sp. trees (Table S1), which is an important secondary pest of *Larix* sp. in Europe and was

detected for the first time in Lithuania [99]. Among the deadwood-dependent insects, there were two species from the family *Eucnemidae*, which were trapped on both *P. abies* and *Larix* sp. (Table 3). Larvae of these insects develop in the wood of dead or dying deciduous or coniferous trees [85,100]. *Eucnemidae* may play an important role in the interactions between trees, fungi, and forest regeneration and can be used as an indicator species of forest biodiversity [101].

Many previous studies have shown that deadwood is one of the most important substrates in forests and supports a high diversity of xylophagous insects [88,102–104]. Indeed, deadwood as a substrate is required for many species of beetles, bees, wasps, ants, flies, mosquitoes, and other invertebrates [100,105–110]. It may serve as a resource for feeding, breeding, overwintering, or refuge [39,88,111,112]. In the present study, xylophagous insects detected in dead trees of *P. abies* and *Larix sp.* using bark sheet and exit hole methods were rather different as compared to those detected using sticky traps (Tables 3–5), thereby repeatedly showing that all of these methods complemented each other. However, the diversity of xylophagous insects detected using bark sheet and exit hole methods was generally limited (Table 4). In comparison, other studies have shown a much higher diversity of xylophagous insect species associated with deadwood of *P. abies*. For example, there were 47 insect species reported by Jonsell and Weslien [113] and 66 species reported by Seedre [87]. The lower diversity of xylophagous insects could be due to specific stand characteristics, i.e., middle-aged monocultures with routine and intensive forest management and a relatively low occurrence of dead trees (Table 1). Intensive forest management was also shown to have a negative impact on the diversity of xylophagous insects [114]. In addition, the diversity and composition of xylophagous insects may also depend on other factors, such as tree species, degree of decay, and the cause of tree death [115].

Although on *P. abies* and *Larix* sp., the diversity and composition of xylophagous insects were similar (Figure 3b,c), the use of bark sheet and exit hole methods showed certain specificity, which can probably be attributed to the biology and ecology of specific insect species. For example, adults of *P. chalcographus* and *H. palliatus* make numerous exit holes on tree stems, but their larvae are relatively small and colonize a relatively small area as compared to large larvae of *Callidium* sp., which was detected using the bark sheet method (Table 5). Furthermore, *Trypodendron lineatum* was abundantly detected on both tree species, but only using the exit hole method (Table 5). Galleries of *T. lineatum* are found ca. 7 cm deep in the wood and are undetectable using the bark sheet method [116]. Similarly, *Sirex juvencus* was detected on both *P. abies* and *Larix sp.* using the exit hole method, as its larvae occur ca. 15–30 cm deep in the wood and leave no signs of activity under the bark [117]. *Siricidae* woodwasps make circular and smooth-edged exit holes of ca. 4–10 mm in diameter, making identification of the species relatively easy [118,119]. Despite the importance of the conservation of many xylophagous insect species and the promotion of deadwood habitats, the risk of bark beetle outbreaks should also be considered [120]. Bark beetle species such as *I. typographus*, *P. polygraphus*, or *P. chalcographus*, which usually colonize weakened and/or dying trees, can cause extensive damage [121]. In the present study, these were mainly associated with *P. abies*, suggesting that *Larix* sp. under the given conditions was less susceptible to their attack (Table 5). However, it was shown that *Larix* sp. can be vulnerable to attacks by bark beetles of the genus *Ips*, including *I. typographus* and *I. cembrae* [34,122]. Therefore, slight differences in the composition of xylophagous insects between *Larix sp.* and *P. abies* trees can probably be explained by certain host specificity. Xylophagous beetles colonizing fresh wood or dying trees need to overcome the tree resistance in the form of chemical barriers [123] and, therefore, are much more host-adapted than those of later decomposition stages [102]. Interestingly, Muller et al. [124] showed a low ranking of *Larix decidua* as the host, which was due to a generally lower number of herbivorous species, including saproxylic beetles, colonizing this tree species as compared to other coniferous tree species, e.g., *P. abies*.

4.2. Lichens

In the present study, the diversity of epiphytic lichens was generally low on both *P. abies* and *Larix* sp. trees (Tables 6 and 7). By contrast, Giordani et al. [50] reported a relatively high diversity of lichen species in mixed *P. abies* forests, but this diversity was similar between *P. abies* and *Larix decidua* trees. It is known that epiphytic lichens can be sensitive to several abiotic factors, such as light [125], temperature and annual precipitation [45–47,126], pH value and nutrient availability on the tree bark [42], and air pollution [43,44]. Forest structure and dynamics are among other determinants of the diversity of epiphytic lichens [48,49,127,128]. In addition, the diversity and biomass of epiphytic lichens appear to be higher in unmanaged old-growth forests than in managed ones [128]. Indeed, Marmor et al. [125] showed that on *P. abies*, the diversity of lichen species significantly increases with the age of trees. In the present study, similarly to insect species (see above), specific characteristics of *P. abies* and *Larix* sp. stands (Table 1) were likely among the main determinants of the low diversity of epiphytic lichens.

In agreement with results of the present study, Hauck [42] and Marmor et al. [125] showed that *Lepraria* sp. and *H. physodes* were among the most dominant lichen species on *P. abies* in boreal forests of Europe. Interestingly, both lichen species showed a higher preference for dead or living *Larix* sp. than for corresponding *P. abies* (Table 7). By contrast, *P. argena* showed a higher preference for dead or living *P. abies* than for corresponding *Larix* sp. (Table 7). Several studies have emphasized the effect of the tree species on the diversity and composition of lichen communities, e.g., [129,130]. This effect appears to be mainly due to species-specific differences in chemical and physical traits of the bark, e.g., [129,131]. Bark pH, which is usually between 3.0 and 4.0 for different conifer tree species [42], is among the principal factors that determine the occurrence and abundance of epiphytic lichens [132]. As the pH of the bark for both *P. abies* and *Larix sp.* was shown to be similar [133,134], this has likely led to the overlap of lichen communities associated with dead or living *P. abies* and *Larix* sp. (Figure 4). Consequently, the detected lichen species appear to be generalists, i.e., adapted to different tree species, as they only showed a preference for a particular tree species to a small extent. On the other hand, the larger bark area colonized by lichens on dead and living *Larix* sp. than on corresponding *P. abies* (Table 6) shows that the growth of lichens is faster on the former tree species.

In summary, the results revealed that *P. abies* and *Larix* sp. share a large number of stem-associated insect and lichen species. As climate change can be expected to have a strong negative effect on *P. abies* in the area, its gradual replacement by *Larix* sp. is likely to provide appropriate habitats for investigated insects and lichens, thereby supporting forest biodiversity. However, the possibility should not be excluded that some wood-boring insect species will not be able to jump between host tree species and may be lost if the mortality of *P. abies* drastically increases in the future.

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