

Article

Forest Disturbances Threatening *Cypripedium calceolus* Populations Can Improve Its Habitat Conditions

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Abstract: Inappropriate forest management activities, above all clear-cutting, are recognized as the major threats to an iconic orchid species—the lady’s slipper orchid (*Cypripedium calceolus*), the flagship species of nature protection in Europe. Although clear-cutting in protected species’ localities is strongly regulated in many European countries, salvage logging is allowed in some circumstances (e.g., following windstorms, and insect outbreaks) and can threaten *C. calceolus* populations. In this paper, we review a database of recently registered populations of this species in the Czech Republic and study historical maps, to better understand the history of local habitat conditions and assess threats to *C. calceolus* populations by bark beetle outbreaks. We found that about one-third of the *C. calceolus* populations have suffered in coniferous or mixed tree plantations with a high proportion of spruce trees, which are forests with a high risk of bark beetle infestation. We review bark beetle management measures and distinguish management efforts in areas with known *C. calceolus* populations that result in no damage to the population and, at times, improve habitat conditions for the species. Thus, the bark beetle—usually understood as the enemy—can be transformed into a savior if smart management measures will replace the panic salvage logging.

Keywords: *Cypripedium calceolus*; orchids; conservation biology; threatening processes; bark beetle outbreak; appropriate management



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1. Introduction

According to the IUCN, habitat destruction, agriculture intensification, collecting from the wild, and inappropriate forest management are recognized as the major threats to an iconic orchid species—the lady’s slipper orchid (*Cypripedium calceolus*) [1]. Large-scale deforestation and converting natural or semi-natural forests to plantations are controversial practices of commercial forestry that are still widely applied in many European countries, and it is well-known that these practices can severely threaten *C. calceolus* [2]. Clear-cutting of the woods has been recognized as one of the three most important threats to this species around Europe. Specifically, 19 European countries reported that clear-cutting of habitats, where *C. calceolus* populations occur, threatened their populations [3]. For example, one of the largest *C. calceolus* populations growing in a state forest in SW Poland was destroyed as a result of clear-cutting in 2017 [3]. However, clear-cutting in the protected species’ localities is prohibited or strongly regulated in some European countries, including the Czech Republic. Nature protection authorities can successfully eliminate this threat when approving forest management plans. However, clear-cutting is a serious danger in the case of unplanned forest management measures applied after some extraordinary events (e.g., windstorms, snow-breaks, insect outbreaks), when the forest managers hectically apply salvage logging and cleaning the woods to avoid additional damages; protection of rare species is a minor issue compared to the economic benefits of commercial forestry in forests where this species grows.

Both frequency and intensity of extraordinary events affecting the European forests have increased during the last few decades [4]. Large windstorms and insect outbreaks have caused changes in many European forests; spruce forests belong to the most strongly affected habitats. We know that some populations of *C. calceolus* are growing in spruce monocultures and mixed tree plantations with a high proportion of spruce trees, which have replaced native habitats. To avoid the destruction of these *C. calceolus* populations, we decided: (i) to review a database of recently registered populations of this species in the Czech Republic, (ii) to study historical maps to better understand the historical evolution of local habitat conditions, (iii) to assess threats to *C. calceolus* populations by bark beetle outbreaks and inappropriate forest management measures. Our goal was to improve the preparation of post-disturbance management plans for sites at risk. Preliminary agreements on appropriate forest management measures in sites where *C. calceolus* populations occur are essential because salvage logging and post-disturbance forest management measures are usually applied very fast to prevent bark beetle outbreaks. We conclude with an account of which appropriate bark beetle measures could be applied in forests, where the *C. calceolus* populations occur. At the end of this paper, we discuss that, paradoxically, although bark beetle infestation is threatening the *C. calceolus* populations, nevertheless it can improve habitat conditions of these species populations, which are suffering in spruce plantations.

2. Materials and Methods

2.1. Study Species

The genus *Cypripedium* includes about 45 species [5], from which the lady's slipper orchid (*Cypripedium calceolus* L.) is the most widely distributed species. It ranges from Great Britain and Scandinavia across northern and central Europe to north-east Spain and northern Italy, and from western Europe through southern Siberia to Rebnun Island [6,7]. In Europe, this orchid with large ornamental flowers is exceedingly rare [8]. It is a long-lived, rhizomatous, terrestrial, cross-fertilized species [7,8], usually growing in slightly shaded deciduous and mixed woodlands (rarely in full sunlight, often in coppiced forests) and in meadows, predominantly on calcareous soils [7,8], as well as in deciduous and coniferous forests with an understory of grasses and other herbs, in forest clearings and lean pastures, often near stream banks, and in bushy hillsides.

Being rhizomatous, *C. calceolus* grows in smaller or larger patches or clusters that may belong to one or several clones. Clones identified by isozyme analysis are seldom larger than 70 cm in diameter [8]. *C. calceolus* is a geophyte. The rhizome with buds perennates through the winter. Vegetative reproduction which occurs by rhizome ramification is supposed to be the main reproduction strategy in many locations. However, in populations with vigorous sexual reproduction, where juveniles make up nearly half of the total ramet numbers, vegetative reproduction is less important [9]. The vegetative period before flowering lasts at least 6–10 years [8,10]. Flowering ramets may have one or two flowers, very seldom three, which are pollinated by medium-sized female solitary bees [11]. It is a long-lived species: many plants are more than 30 years old, and some live for more than 100 years [12].

C. calceolus belongs to the flagship species of nature protection and is legally protected in all European countries. It is also protected at the supranational level by the Convention on the Conservation of European Wildlife and Natural Habitats (Bern Convention), European Union Directive CE/92/43 on the Conservation of Natural Habitats and of Wild Fauna and Flora (Habitats Directive), and the Convention on International Trade in Endangered Species (Washington Convention) [13]. Besides cutting flowers and digging rhizomes (more common before the 1970s), habitat destruction with logging and habitat alteration with overgrowing grassland habitats by dense brush or closing up of the tree canopy are mentioned as the main threats to *C. calceolus* in Europe [3,8,13].

2.2. Study Sites

In the Czech Republic, *C. calceolus* occurs mainly in mesophytic and thermophytic regions [14]. Most sites are located in central and eastern Bohemia, central and southern Moravia, and in the White Carpathians. The species is absent in many regions of the Czech Republic.

The sites are believed to be long-lived [15]. The current occurrence is a remnant of the historical occurrence, only in rare cases new locations were created by planting or by conservation transfer. In this study, we used data on the occurrence of *C. calceolus* from the Natura 2000 species monitoring [16]. The basic monitoring unit is the bunch (i.e., a closely growing group of stems with a common root system) or individual plants with one stem. For this monitoring project, bunches more than 8–10 cm apart are considered to be different individuals. A location is defined as the occurrence of one or more individuals at least 500 m apart from the nearest other occurrences. Data about population sizes were used from the Species Occurrence Database [17] and Gola's thesis [18]. The population sizes of each population were calculated as the average of all records from the past 10 years.

2.3. Natura 2000 Habitats

The Czech Republic, like all other EU member states, had to implement the Natura 2000 Directives (i.e., Habitats Directive 92/43/EEC and Bird Directive 2009/147/EC) and Natura 2000 habitats mapping [19] was conducted as a part of the EU-integration process. To determine a list of suitable SCIs (Sites of Community Importance), which is required by the Habitats Directive, the habitats and species across the whole country were mapped by experts. More detailed vegetation units called biotopes [20] were mapped and later aggregated for habitats. Usually, 1–3 biotopes formed one habitat *sensu* Annex I of Habitats Directive 92/43/EEC. The mapping consisted in dividing the country into segments (polygons on the map), each of which contained only one forest/grassland/marshland biotope. Data from this complex and unique biotope mapping are publicly available from the Agency for Nature Conservation and Landscape Protection of the Czech Republic and are often used in many conservation projects. The Habitat Occurrence Database [21] contains data on habitats from the projects Habitat and Landscape Mapping of the Czech Republic (2000–2004) and Habitat Mapping Update (2006—present). In this paper, we used data about the habitats mapped in the sites where the *C. calceolus* populations occur. Some of the populations occur in the sites where the Natura 2000 grassland or forest habitats were mapped, other populations occur outside the Natura 2000 habitats, where we distinguished grassland, scrubland, and grassland as land cover categories, using current aerial photos.

We distinguished two types of forest habitats: (1) Natura 2000 forest habitats listed in Annex I of the Habitats Directive and (2) plantations, i.e., forests with artificial species composition and structure, often spruce monocultures, which replaced the natural habitats. We also distinguished two types of grassland habitats: (3) Natura 2000 grassland habitats listed in Annex I of the Habitats Directive and (4) no Natura 2000 grasslands, i.e., semi-natural grasslands without Natura 2000 habitat classification. The last defined habitat included (5) shrubs, i.e., scrublands or bushes without Natura 2000 habitat classification.

2.4. Historical Land Cover

We used imprints of historical maps of the Stable Cadastre for half of the 19th century [22] provided by the Czech Office for Surveying, Mapping, and Cadastre (<https://www.cuzk.cz> (accessed on 15 February 2021)) to learn about the historical land cover of the sites where the *C. calceolus* populations were recently recorded. We defined ten categories of historical land cover (Table 1).

Table 1. Historical land cover categories.

Code	Land Cover Category	Historical Land Cover of the Site Where the <i>C. calceolus</i> Population Recently Occurs
ConFragm	Coniferous forest – fragmented	The site was historically located in a coniferous forest of size < 1 km ² OR in a mosaic of coniferous forests and grasslands.
ConLarge	Coniferous forest – large	The site was historically located in a coniferous forest of size > 1 km ² .
MixFragm	Mixed forest – fragmented	The site was historically located in a mixed forest of size < 1 km ² OR in a mosaic of mixed forests and grasslands.
MixLarge	Mixed forest – large	The site was historically located in a mixed forest of size > 1 km ² .
DecFragm	Deciduous forest – fragmented	The site was historically located in a deciduous forest of size < 1 km ² OR in a mosaic of deciduous forests and grasslands.
DecLarge	Deciduous forest – large	The site was historically located in a deciduous forest of size > 1 km ² .
Field	Fields – arable land	The site was historically located in properties mapped as a field or arable land. The intensity and types of applied management measures could have changed over time.
Garden	Garden	The site was historically mapped as a garden. The intensity and types of applied management measures could have changed over time.
Meadow	Meadow	The site was historically mapped as a meadow. It was probably a permanent (semi-natural) grassland habitat.
Pasture	Pasture	The site was historically mapped as a pasture. It was probably a permanent (semi-natural) grassland habitat.

2.5. Bark Beetle Infestation Risk

To assess the risk of bark beetle infestation in forests where the *C. calceolus* populations occur, we distinguished three categories of forests growing in a 3 km buffer zone around each *C. calceolus* population (Table 2).

Table 2. Risk categories of bark beetle infestation in forests where the *C. calceolus* populations occur.

Code	Risk Category	Description of Forest in the Vicinity of <i>C. calceolus</i> Population
Risk 0	a zero-risk forest	without spruce trees OR spruce trees cover <10% of the buffer zone and no occurrence of bark beetle trees was recorded during the last five years
Risk 1	a low-risk forest	mixed forests with less than 50% of spruce trees
Risk 2	a high-risk forest	spruce monoculture OR mixed forests with less than 50% of spruce trees and occurrence of bark beetle trees during the last five years OR mixed forests with more than 50% of spruce trees and no occurrence of bark beetle trees recorded during the last five years

2.6. Statistical Analyses

Using data on *C. calceolus* populations, current habitat conditions, historical land cover, and bark beetle infestation risk, we performed factorial ANOVA with factors “BB risk” and “habitat type” to test for differences in sensitivity to bark beetle infestation between sites located in different habitats. We also performed factorial ANOVA with factors “BB risk” and “stable cadaster category” to test for differences in sensitivity to bark beetle infestation between sites with different land cover. Because tested groups differed in the number of populations per group, we performed factorial ANOVAs in General linear models. Duncan’s tests were applied for post hoc comparisons where appropriate. Statistical analyses were performed in STATISTICA 12 [23].

3. Results

3.1. Current Occurrence

Population sizes of the studied populations varied from one bunch (i.e., an individual) to 462 bunches. However, most of the populations were small with only one or a few individuals (Figure 1). We have no data about population sizes from six of 136 populations; however, 30 populations had only one bunch of *C. calceolus*. More than 20 bunches were recorded in 30% of the populations and more than 100 individuals of *C. calceolus* were found only in seven populations.

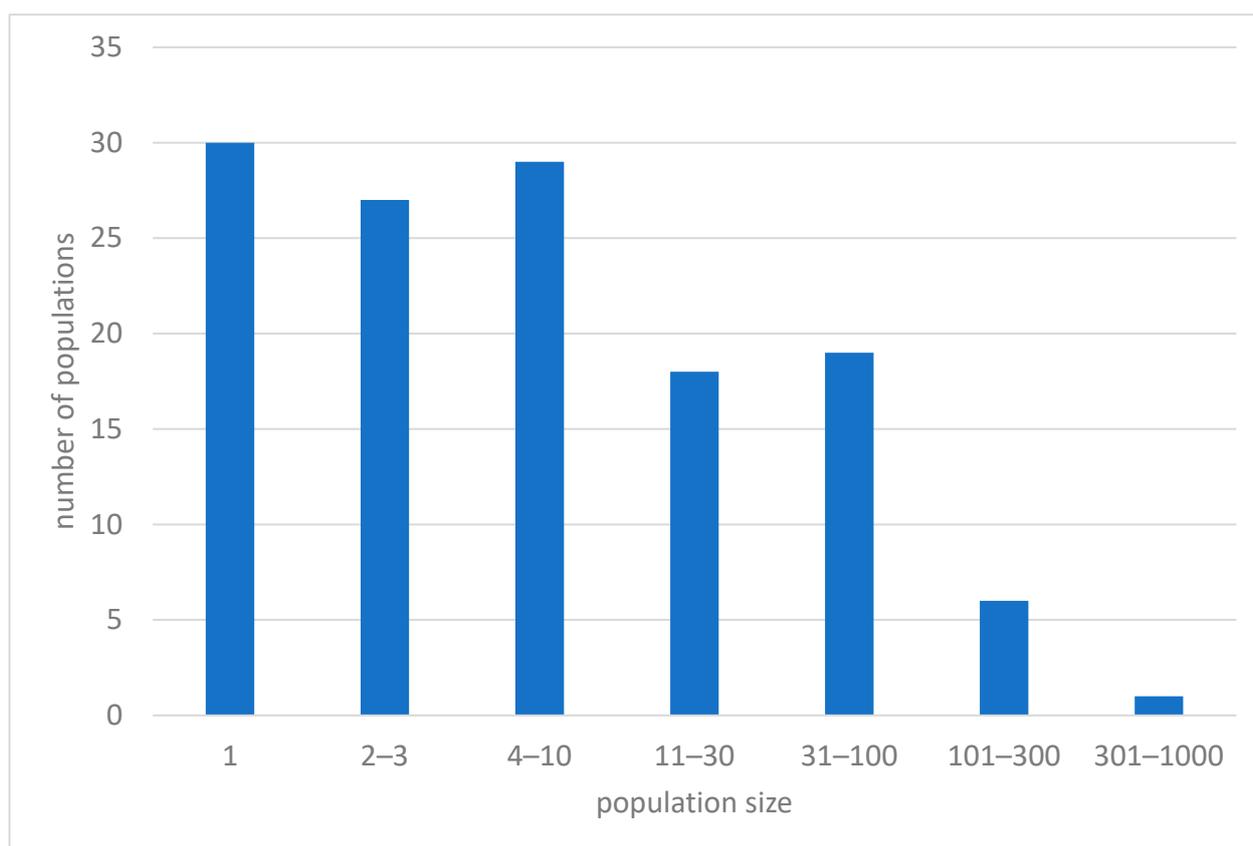


Figure 1. Population sizes of *Cypripedium calceolus* populations in the Czech Republic. Numbers of populations of different population sizes are shown.

Forests are the main habitat of the *C. calceolus* populations in the Czech Republic: 88% of the studied populations are growing in forest habitats, 8% in grassland habitats, and 4% in scrublands (Figure 2). Seventy of the forest populations occur in Natura 2000 habitats, mostly in habitats 9170—Galio-Carpinetum oak-hornbeam forests, 9130—Asperulo-Fagetum beech forests, and 9150—Medio-European limestone beech forests

(Table 3). Forty-eight of the forest populations occur in plantations, from which two-thirds are coniferous plantations, often spruce monocultures.

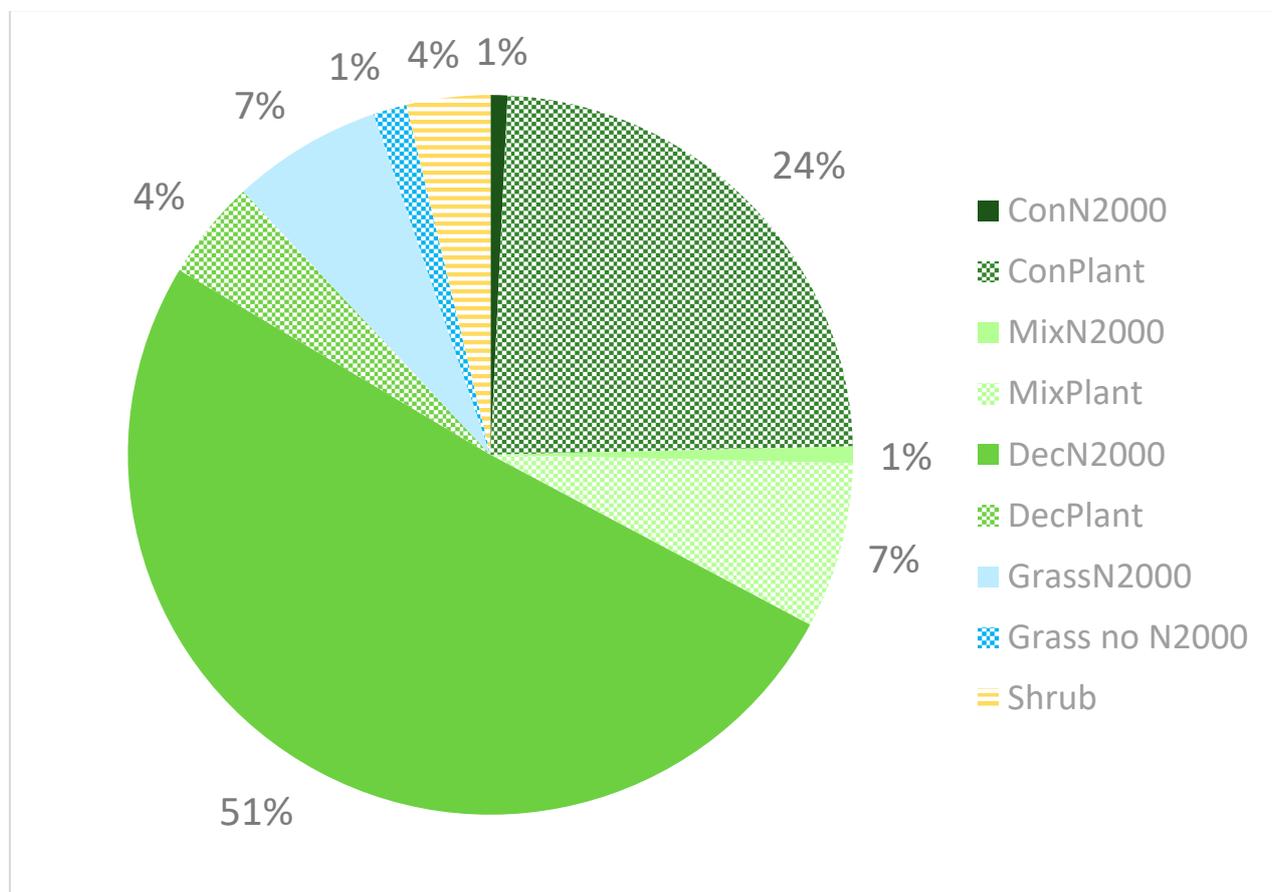


Figure 2. Habitats in which the present *Cypripedium calceolus* populations occur. ConN2000—coniferous forests, Natura 2000 habitats, ConPlant—coniferous plantations, MixN2000—mixed forests, Natura 2000 habitats, MixPlant—mixed tree plantations, DecN2000—deciduous forests, Natura 2000 habitats, DecPlant—deciduous plantations, GrassN2000—grasslands, Natura 2000 habitats, Grass no N2000—grasslands, no Natura 2000 habitats, Shrub—scrublands, no Natura 2000 habitats.

We found no significant differences between the sizes of the *C. calceolus* populations growing in different habitat types (Table 3). Many of the large populations occur in plantations that replaced the natural habitats. The largest population with 462 bunches occurs in the mixed tree plantations where spruce and beech trees dominate. In deciduous plantations, most *C. calceolus* populations have 20 or more individuals. On the contrary, only three of the populations growing in the coniferous plantations have more than 20 individuals; most of these populations are very small with one or only a few *C. calceolus* individuals.

Most of the grassland habitats where *C. calceolus* populations occur were mapped as the Natura 2000 grassland habitats and only two populations are growing in grasslands without the Natura 2000 classification. The habitat 6210-Semi-natural dry grasslands and scrubland facies on calcareous substrates (*Festuco-Brometalia*), a priority habitat *sensu* the Habitats Directive 92/43/EEC, is the most common grassland habitat, where the Czech *Cypripedium* populations occur. From the forest Natura 2000 habitats, five priority habitats were recognized as habitats where the *Cypripedium* populations occur (Table 3).

Table 3. Habitats of *Cypripedium calceolus*. Numbers of populations recorded in each habitat together with population sizes (mean, minimum, and maximum) are presented. Priority habitats according to Annex I of the Habitats Directive 92/43/EEC are marked with *.

Natura 2000	Habitat Code	Habitat Name	Number of Populations	Population Size		
				Mean	Min	Max
yes	9110	Luzulo-Fagetum beech forests	1	1.00	1	1
yes	9130	Asperulo-Fagetum beech forests	12	35.09	1	169
yes	9150	Medio-European limestone beech forests of the Cephalanthero-Fagion	11	11.40	2	64
yes	9170	Galio-Carpinetum oak-hornbeam forests	31	21.48	1	120
yes	9190	Old acidophilous oak woods with <i>Quercus robur</i> on sandy plains	1	1.00	1	1
yes	9180 *	Tilio-Acerion forests of slopes, screes, and ravines.	4	28.00	1	95
yes	91E0 *	Alluvial forests of <i>Alnus glutinosa</i> and <i>Fraxinus excelsior</i> (Alno-Padion, Alnion incanae, Salicion albae)	3	3.67	3	4
yes	91G0 *	Pannonic woods with <i>Quercus petraea</i> and <i>Carpinus betulus</i>	1	4.00	4	4
yes	91G0 *, 91I0 *	mosaic of 91G0 * & 91I0 *	1	8.00	8	8
yes	91H0 *	Pannonian woods with <i>Quercus pubescens</i> .	1	32.00	32	32
yes	91H0 *, 91I0 *	mosaic of 91H0 * & 91I0 *	1	62.00	62	62
yes	91I0 *	Euro-Siberian steppe oak woods	2	3.50	2	5
yes	91U0	Sarmatic steppe pine forests	1	25.00	25	25
no	ConPlant	Coniferous plantations, often spruce monocultures	33	8.41	1	76
no	DecPlant	Deciduous plantations	6	44.33	1	135
no	MixPlant	Mixed tree plantations or mixture of succession and planted trees	11	61.64	1	462
yes	6210 *	Semi-natural dry grasslands and scrubland facies on calcareous substrates (Festuco-Brometalia)	8	6.63	1	25
yes	6510	Lowland hay meadows (<i>Alopecurus pratensis</i> , <i>Sanguisorba officinalis</i>)	1	46.00	46	46
no	Grass no N2000	Grasslands, no Natura 2000 habitats	2	18.50	4	33
no	Shrubs	Scrublands, no Natura 2000 habitats—usual succession of abandoned meadows or edges of forests	5	12.60	1	47

3.2. Historical Occurrence

Three-quarters of the sites, where *C. calceolus* populations occur, were historically mapped as forests, 15% were pastures, and only 1% of the sites were historically mapped as meadows and gardens. The rest, i.e., 9% of the sites, were mapped as fields or arable land (Figure 3). Of the sites historically mapped as forests, more than half (specifically, 53 sites where *C. calceolus* populations occur at present) were located in coniferous forests. Thirty-five sites were mapped inside large coniferous forest segments and eighteen sites were in fragmented or small coniferous forests. Nineteen percent of the present *C. calceolus* sites occur in sites historically mapped as mixed forests, mostly in large segments of mixed forests. Only two sites are located in historically mapped small or fragmented segments of mixed forest. The rest of the sites are historically located in the forests, i.e., 15% of all current *C. calceolus* sites, were mapped as deciduous forests. Fourteen sites were mapped as large complexes of deciduous forest and seven as small or fragmented segments of this forest type.

We found significant differences between the *C. calceolus* population sizes among sites, which were historically mapped as forests, grasslands, and fields (ANOVA; $F = 4.132$, $p = 0.018$). The two largest recent populations of *C. calceolus* (462 and 169 individuals) occur in the sites historically mapped as field or arable land. There were no significant

differences in the population sizes of the *Cypripedium* populations occurring in forested sites that had different histories (Table 4). Except for the two largest populations occurring in sites mapped as a field and one population occurring in a site historically mapped as a pasture, all other populations of this species with more than 50 individuals occur in sites historically mapped as different types of forest.

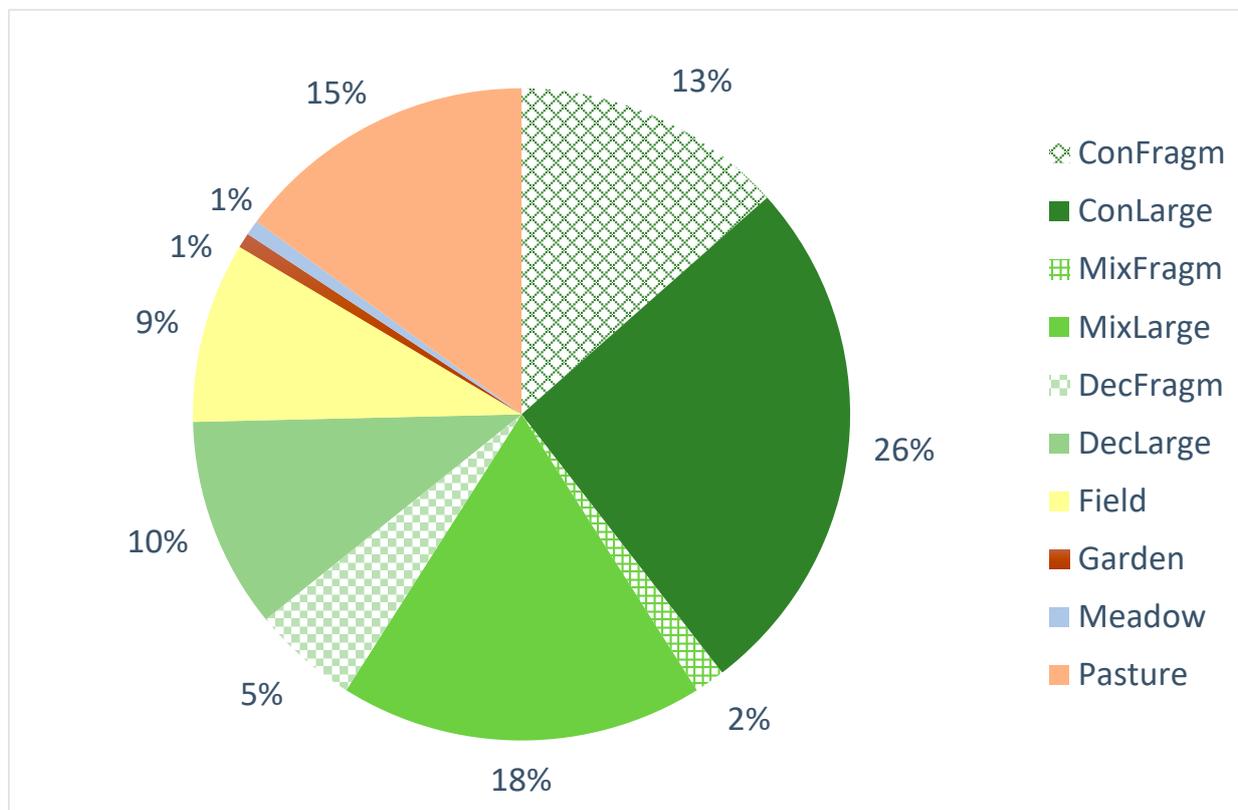


Figure 3. Categories of landscape cover historically mapped in the sites, where the recent populations of *Cypripedium calceolus* occur. ConFragm—fragmented coniferous forest, ConLarge—large segment of coniferous forest, MixFragm—fragmented mixed forest, MixLarge—large segment of mixed forest, DecFragm—fragmented deciduous forest, DecLarge—large segment of deciduous forest.

Comparing data from historical maps and Natura 2000 mapping, we found that habitat types have caused changes in the number of sites where the *C. calceolus* populations occur at present (Figure 4) and there are differences between habitats in patterns of changes (Figure 4). The number of sites located in grasslands increased over time. At least half of originally opened habitats (historical pastures, meadows, fields, or gardens) are currently mapped as forests: Natura 2000 forest habitats or plantations (Figure 4). On the other hand, there are some sites historically mapped as deciduous forests and recorded as no-Natura 2000 meadows now. We found that most of the *C. calceolus* populations currently occurring in Natura 2000 forest habitats are located in sites that were historically mapped as forest habitats (Figure 5). Nevertheless, about 25% of the sites currently occurring in habitats 9130 and 9170 were historically mapped as pastures, meadows, or fields.

Partly different patterns of changes have appeared in the numbers of sites currently occurring in plantations—out of them: 33% were historically mapped as fields or gardens; more than 55% were historically mapped as coniferous forests, and many were located in large segments of a coniferous forest. Two-thirds of sites currently recorded in deciduous plantations were historically mapped as coniferous forests (Figure 5). On the contrary, coniferous forests were historically mapped in less than 50% of sites, which are currently described as coniferous plantations (Figure 5). Historically, more than half of these sites were mapped as mixed forests, fields, or pastures.

Table 4. Categories of land cover historically mapped in the sites, where the present populations of *Cypripedium calceolus* occur. The numbers of populations recorded in each category of the land cover together with population sizes (mean, minimum and maximum) are presented.

Code of Historical Land Cover Category	Number of Populations	Population Size		
		Mean	Min	Max
ConFragm	18	17.60	1	124
ConLarge	35	21.51	1	120
MixFragm	2	25.50	4	47
MixLarge	24	12.46	1	102
DecFragm	7	15.29	2	33
DecLarge	15	17.50	1	160
Field	12	58.83	1	462
Garden	1	46.00	46	46
Meadow	2	1.50	1	2
Pasture	20	18.67	1	75

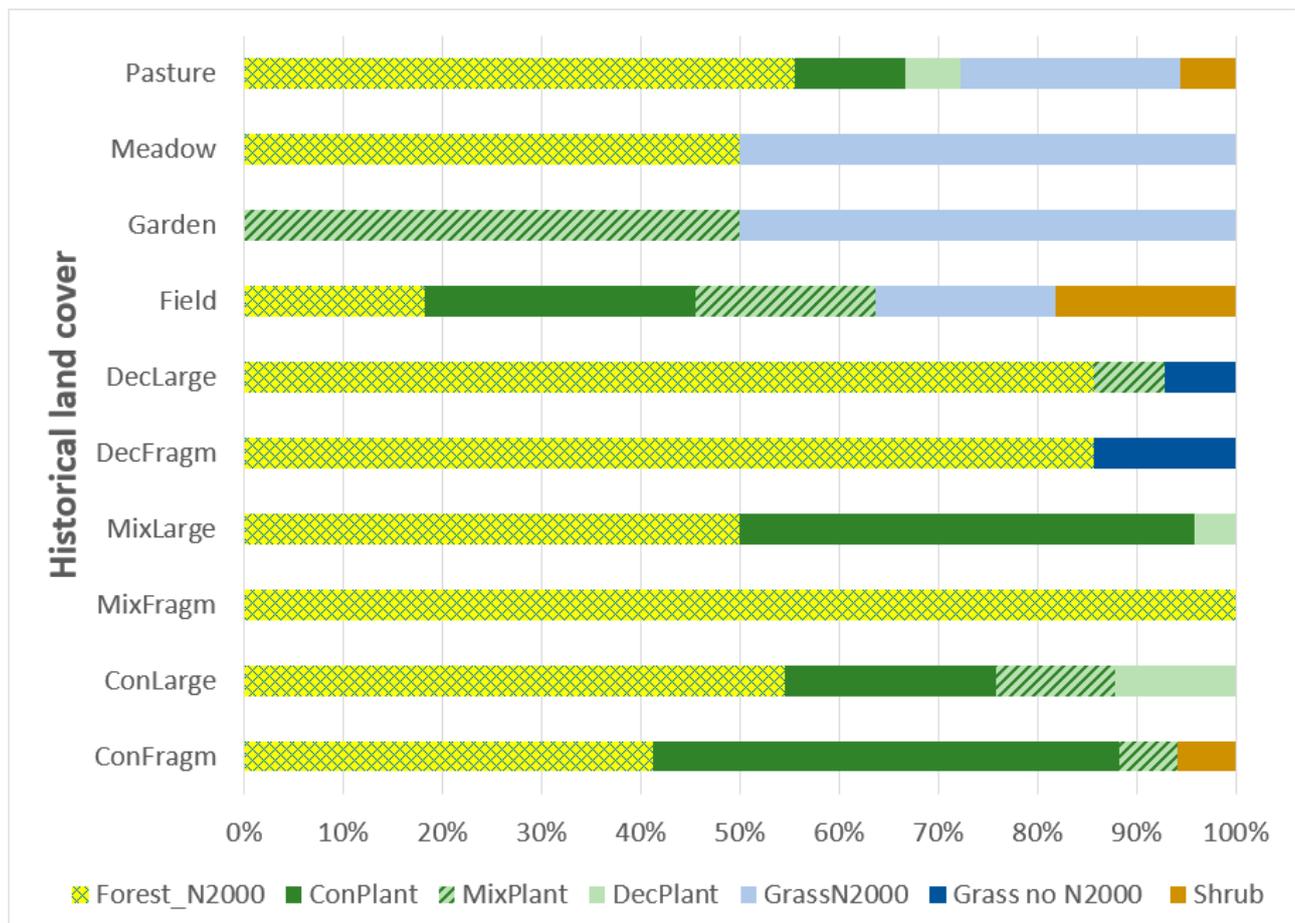


Figure 4. Changes in land cover types historically mapped in the sites, where the present populations of *Cypripedium calceolus* occur. Habitats: Forest_N2000—all Natura 2000 habitats, ConPlant—coniferous plantations, MixPlant—mixed tree plantations, DecPlant—deciduous plantations, GrassN2000—grasslands, Natura 2000 habitats, Grass no N2000—grasslands, no Natura 2000 habitats, Shrub—scrublands, no Natura 2000. Historical land cover categories: ConFragm—fragmented coniferous forest, ConLarge—large segment of coniferous forest, MixFragm—fragmented mixed forest, MixLarge—large segment of mixed forest, DecFragm—fragmented deciduous forest, DecLarge—large segment of deciduous forest.

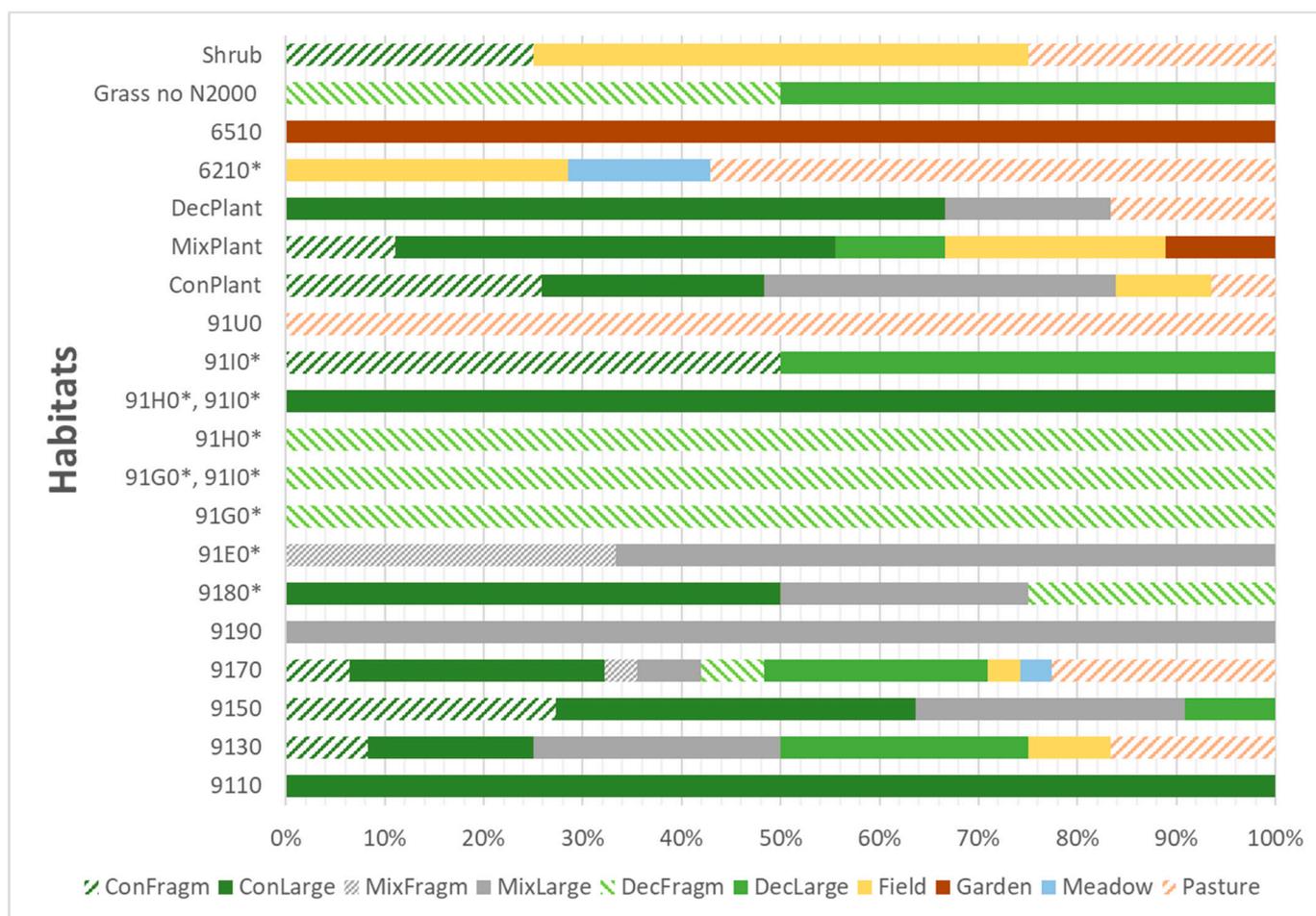


Figure 5. Proportions of land cover types historically mapped in the sites, where the present populations of *Cypripedium calceolus* occur. Changes in the habitats of the current occurrence of *C. calceolus* populations are shown separately. Habitats: Natura 2000 habitats are in codes (see Table 1), priority habitats according to Annex I of the Habitats Directive 92/43/EEC are marked with *; ConPlant—coniferous plantations, MixPlant—mixed tree plantations, DecPlant—deciduous plantations, GrassN2000—grasslands, Natura 2000 habitats, Grass no N2000—grasslands, no Natura 2000 habitats, Shrub—scrublands, no Natura 2000. Historical land cover categories: ConFragm—fragmented coniferous forest, ConLarge—large segment of coniferous forest, MixFragm—fragmented mixed forest, MixLarge—large segment of mixed forest, DecFragm—fragmented deciduous forest, DecLarge—large segment of deciduous forest.

3.3. Risks

Forest habitat types, where the *C. calceolus* populations occur, significantly differ in their sensitivity to bark beetle infestations (ANOVA, $p < 0.01$). We found no bark beetle risk in most of Natura 2000 habitats, in which the *C. calceolus* populations occur (Figure 6). Almost all the Natura 2000 habitats are broadleaf or mixed forests without spruce trees. Also, deciduous plantations showed a very low risk, because spruce trees are very rare in these forest types. On the contrary, a high risk was recognized in coniferous and mixed tree plantations. They are much more threatened by bark beetle outbreaks and following salvage logging than other forest habitats. Over the last five years, salvage logging of bark beetle-infected trees was recorded in close vicinity of five *C. calceolus* populations, and five others were recognized as sites with a very high risk of bark beetle outbreak. All these sites occur in spruce monocultures or mixed forests with a high proportion of spruce trees.

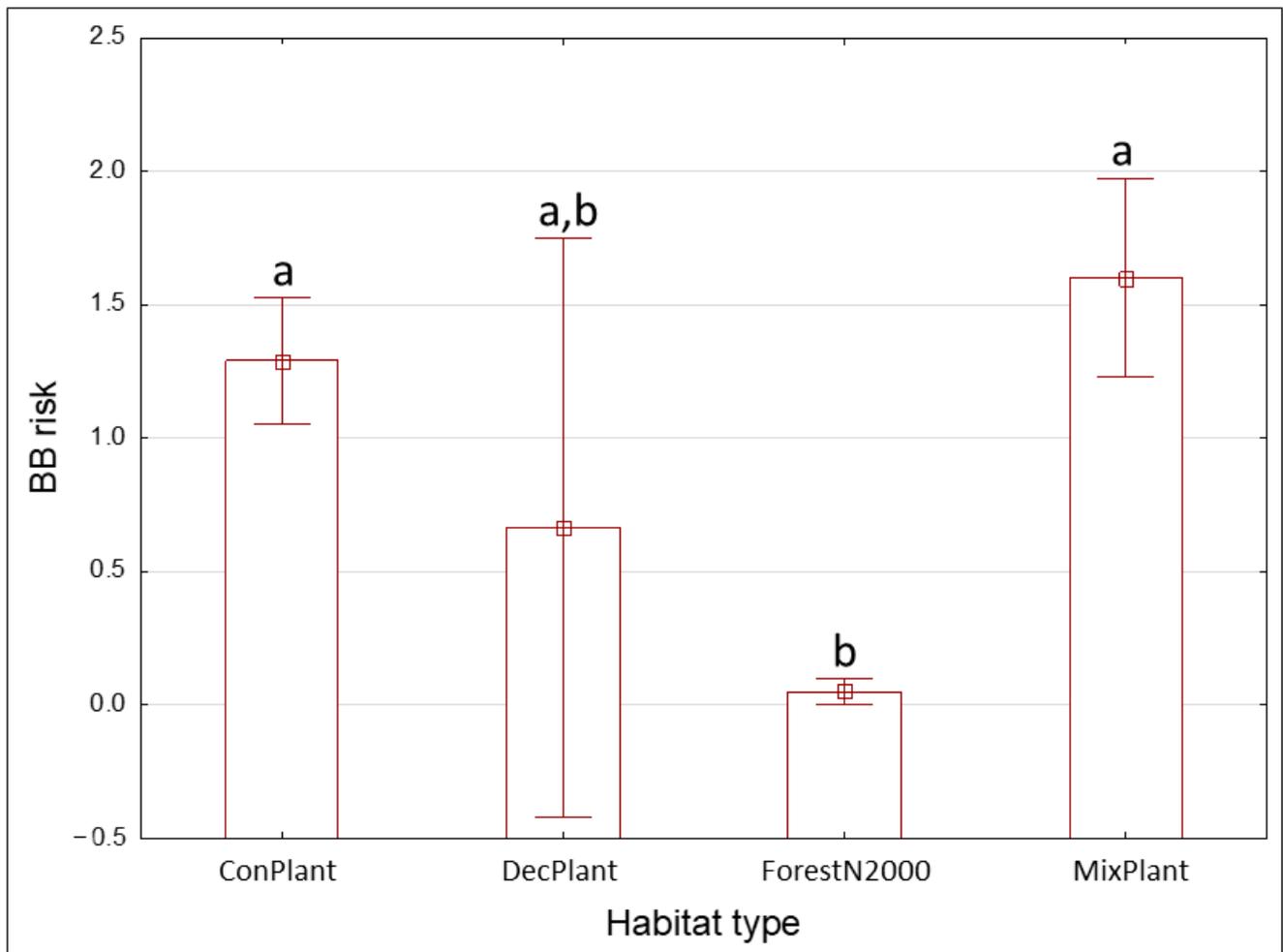


Figure 6. Risks of bark beetle infestation (BB risk) of different forest habitat types: Forest N2000—Natura 2000 forest habitats, ConPlant—coniferous plantations, DecPlant—deciduous plantations, ForestN2000—Natura 2000 forest habitats, MixPlant—mixed tree plantations. Means and 95% confidential intervals are shown. Letters above the bars indicate the results of post-hoc comparisons, i.e., different letters mark statistically different values.

When testing whether the history of land cover can explain the sensitivity of forest stands to bark beetle infestation, we found significant differences between the categories of historical land cover (ANOVA, $p < 0.05$; Figure 7). Zero-risk forests occur in the sites, which were historically mapped as fragmented deciduous and mixed forests. Forests with the highest risk of bark beetle infestation are growing in the sites historically mapped as fragmented coniferous forests, large mixed forests, and fields or gardens. Mainly spruce monocultures or mixed tree plantations with a high proportion of spruce trees were planted in these sites.

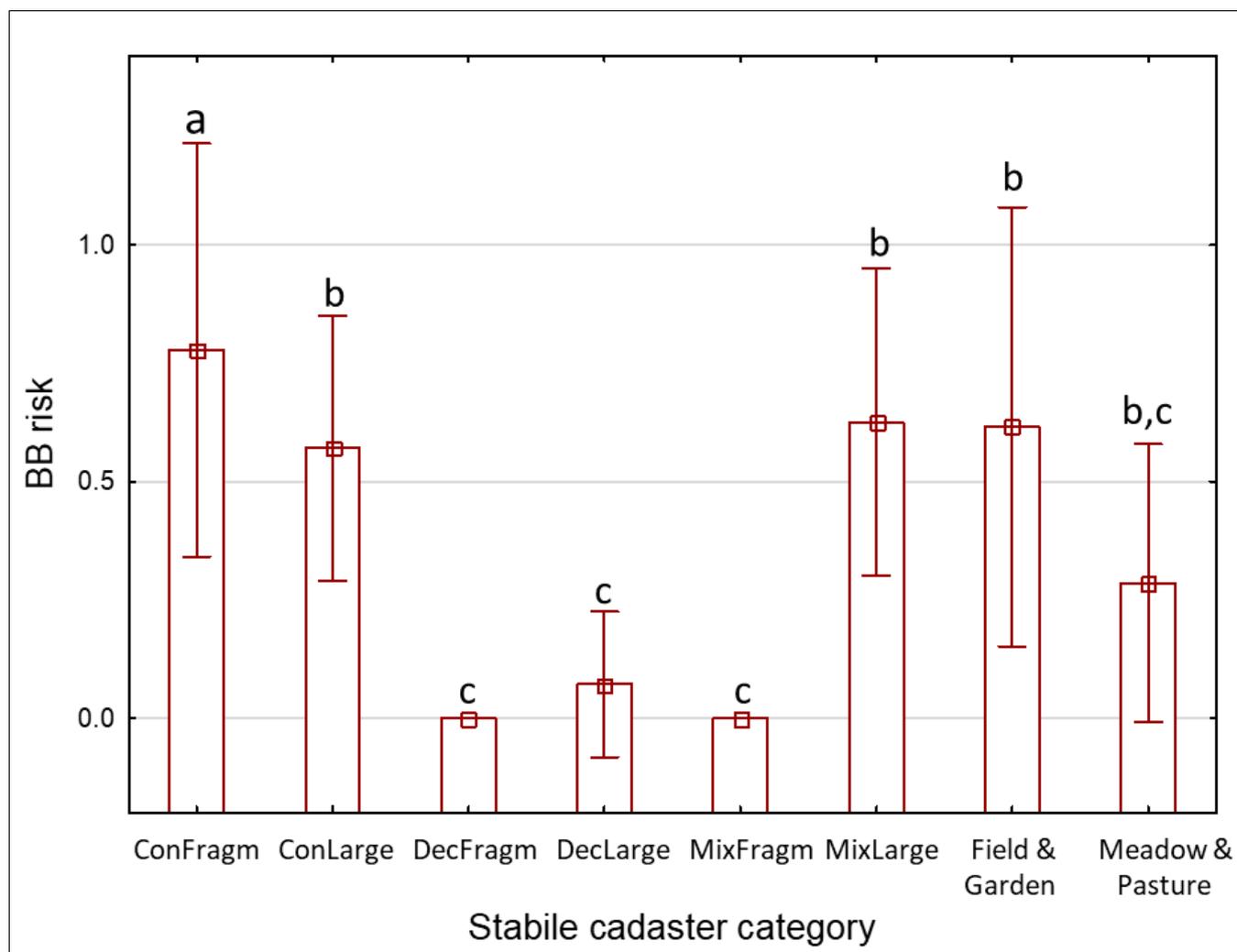


Figure 7. Risks of bark beetle infestation (BB risk) in sites with different historical land covers: ConFragm—fragmented coniferous forests, ConLarge—large segments of coniferous forest, DecFragm—fragmented deciduous forests, DecLarge—large segments of deciduous forest, MixFragm—fragmented mixed forests, MixLarge—large segments of mixed forest, Field&Garden—arable land or gardens, Meadow&Pasture—permanent grasslands (meadows or pastures). Means and 95% confidence intervals are shown. Letters above the bars indicate the results of post-hoc comparisons, i.e., different letters mark statistically different values.

4. Discussion

Similarly, to other European countries [3], the Czech populations of *C. calceolus* differ in population sizes and many populations are extremely threatened with extinction. From more than 25% of the Czech studied sites, only one bunch (i.e., one individual) of *C. calceolus* was reported. Similar declines in population sizes were reported for example from Poland [24], or Romania, where many still-existing populations are getting smaller and smaller by each year with only a few flowering specimens [25–27]. Also in Central Germany, where Kretzschmar [28] calculated an absolute decrease of 57% of the occurrence, many occurrences only consist of small populations or individual plants.

Grasslands represent only a small, but very important minority among the current sites of *C. calceolus* occurrence. The habitat 6210, i.e., calcareous Festuco-Brometalia grasslands, was recognized as the most common grassland habitat in which *C. calceolus* populations occur in the Czech Republic and many other Central European countries [3]. Calcareous grasslands belong to the most species-rich plant communities in Europe and contain a

large number of rare and endangered species [29,30]. Habitat 6210 is considered a priority habitat *sensu* the Habitats Directive 92/43/EEC if it is an important orchid site [31]. Most calcareous grasslands are of secondary origin, replacing former thermophilous forests, and are products of former extensive grazing. In Central Europe, some of them are remnants of early Holocene steppes [32] and can be recognized as prehistoric sites of *C. calceolus*. The Czech *C. calceolus* populations, currently occurring in habitat 6210, were historically mapped as pastures (both private and common pastures), meadows, or fields. We can only speculate about the details of the traditional management of these sites. However, we can expect a long-term continuum of sparse calcareous grasslands suitable for *C. calceolus*. At present, successional changes negatively affect most of these locations in the Czech Republic and only small *C. calceolus* populations (1–25 individuals) are reported from these sites.

Forests are the main habitat of the *C. calceolus* populations in Central Europe [8], as well as in Czechia. The 9170, 9130, and 9150 are the most common Natura 2000 habitats which contain *C. calceolus* sites also in Germany, Poland, Romania, Croatia, and Slovenia [3]. Nevertheless, many forests where the Czech populations of the lady's slipper orchids occur are not natural habitats for the species. During the last century, spruce monocultures have been planted in the originally natural habitats and the *C. calceolus* populations suffer there. In many current sites, the *C. calceolus* populations persist in some gaps in the spruce canopy, edges of forest roads, or edges of old clearings. We found that more than half of the Czech forest populations of this species grow in plantations, from which two-thirds are coniferous plantations, often spruce monocultures. Occurrences of *C. calceolus* populations in coniferous or mixed tree plantations with a high proportion of spruce trees are reported also from other European countries (e.g., Poland, Germany, Latvia, or Austria) [33–38]. However, the numbers of these cases are unknown. Habitat conditions in such locations are not the best for the lady's slipper orchids: plants suffer from shading, pollinators are missing and acidic litter from needles adversely affects soil conditions [3,18].

In the Czech Republic, most of the *C. calceolus* populations growing in the coniferous plantations are very small with one or only a few individuals. One could summarize that forests, specifically coniferous forests, are not a suitable habitat for this species. However, it is not that simple. Looking at the historical maps we can see that forests were the main habitat of the *C. calceolus* populations in the past. Specifically, 53 of the current locations of *C. calceolus* were located in sites mapped as coniferous forests, often in their large segments. Fourteen sites were historically mapped in large complexes of deciduous forest and several other sites were recorded as small, fragmented, or mixed forests. Obviously, deciduous and mixed forests, small segments (<1 km²) of all forest types, and mosaics of fragmented forest and grassland habitats have probably been long-term suitable habitats for *C. calceolus* populations [8]. However, even large-scale complexes of coniferous and mixed forests should not be considered unsuitable habitats for *C. calceolus* populations in the past. Until the beginning of the 20th century, the forests were much more open, lighter, and differently structured due to over-logging, coppicing, litter demand, and forest grazing [39]. Also, natural disturbances (fires, floods, windstorms, insect outbreaks, etc.) affected historical forests and created habitats suitable for the lady's slipper orchids. Historical forests considerably differed from current plantations, in which significant numbers of *C. calceolus* populations persist.

Currently, there are many spruce monocultures or mixed tree plantations with a high proportion of spruce trees where small populations of *C. calceolus* persist and these forests are highly sensitive to bark beetle infestation. This may cause the disappearance of a significant proportion of sites, as salvage logging or other quickly applied bark beetle measures (Table 5—management types A,B,C) can easily destroy the last *C. calceolus* individuals here and eliminate possible recovery of the *C. calceolus* in the affected locations. However, bark beetle may not only threaten *C. calceolus*—it can also help it, as we will now show.

Table 5. Types of bark beetle management and their effects on *C. calceolus* populations. Types of bark beetle measures were adapted from Jakuš and Blaženec [40].

Management Type	Bark Beetle Measures	Effect on <i>C. calceolus</i> Populations
Type A	Salvage logging: bark beetle-infected trees are logged, wood removed, litter burned, the site is cleaned, and new trees are planted.	Individual plants are destroyed, and the quality of the biotope fundamentally deteriorates. The movement of heavy forestry equipment, handling of the soil, and the modification of the site during the planting of new trees cause damage to the underground parts of orchids and seed banks. Natural recovery of the orchid population is not possible.
Type B	Salvage logging: bark beetle-infected trees are logged; debarked trunks are left on the ground to decompose, and new trees are planted.	
Type C	Salvage logging: bark beetle-infected trees are logged, debarked trunks are left on the ground to decompose, and natural regeneration is allowed.	Individual orchids are destroyed, and the quality of the biotope significantly deteriorates. Driving heavy forestry equipment and handling debarked trunks will significantly damage the underground parts of orchids and seed banks. Natural recovery of the orchid population is probably impossible.
Type D	Debarking of standing trees or bark-scratching of storm felled trees; bark beetle-infected trees are debarked or bark-scratched, the site is cleaned, and new trees are planted.	Some orchids are destroyed, and the quality of the biotope partially deteriorated. In the case of planting new trees, the underground parts of the orchids and the seed bank may be damaged. The natural recovery of the orchid population is significantly weakened.
Type E	Debarking of standing trees or bark-scratching of storm-felled trees; bark beetle-infected trees are debarked, or bark-scratched, and natural regeneration is allowed.	Some orchids are destroyed, and the quality of the biotope partially deteriorated. The natural recovery of the orchid population is limited.
Type F	Mixed management: salvage logging is applied only partly and at least 50% of standing trees must be left in a site (green, debarked, or bark-scratched) to maintain partial shade for <i>C. calceolus</i> . No planting of new trees or natural regeneration is allowed.	In zones where active bark beetle management is applied, damage to orchids, including their underground parts, may occur. However, the <i>C. calceolus</i> population at least partially benefits from the removal of bark trees or their killing by the bark beetle.
Type G	No intervention: bark beetle-infected trees are not managed, and natural regeneration is allowed. All management measures are located in a buffer zone located at a distance of at least 30 m from <i>C. calceolus</i> specimens.	Orchids are not destroyed, and the habitat of the condition is improved. The <i>C. calceolus</i> population benefits from the removal of bark trees in the buffer zone. Dry bark trees in the <i>C. calceolus</i> site can provide desirable partial shade.

There exist smart and *C. calceolus* occurrence-sensitive bark beetle management measures—management types F, G in Table 5, which do not damage the sites with residual populations of *C. calceolus* but are even able to improve habitat conditions for *C. calceolus* in these sites. Most of the *C. calceolus* populations persisting in spruce plantations are very small, with one or only a few specimens. In these cases, a delimitation of a non-intervention zone in a site where the lady’s slipper orchids occur and implementation of all management measures at a distance at least 30 m from *C. calceolus* individuals (management type G) is the best choice. This type of management can help to suppress bark beetle infestation because smart bark beetle measures can be prepared in advance in a zone without conservation regulation and only a few bark beetle-infected/sensitive trees are left in the non-intervention zone. Trees left inside of the non-intervention zone (green trees and trees naturally killed by bark beetle) provide natural shading for the lady’s slipper orchids. Salvage logging, which is applied at a distance of more than 30 m from *C. calceolus* specimens does not threaten *C. calceolus* specimens directly, but it removes or at least thins dense surrounding stands, which is very typical for plantations.

If a high bark beetle risk or lack of manager’s courage does not allow to accept non-intervention management, then at least a mixed management (Table 5—management type F) should be applied. Some bark beetle-infected trees can be logged and at least 50% of standing trees must be left (green or debarked) in the site to maintain partial shade for *C. calceolus*. Logging or debarking of standing trees must be done very carefully, fully

respecting *C. calceolus* specimens. Some artificial cages or other temporary protection for the lady's slipper orchids are welcome. Removing of wood, burning of litter, and preparation of the site for planting or planting of new trees are not planned in management type F.

Debarking of standing bark beetle-infested trees (Table 5—management types D, E) is occasionally applied in locations of high conservation values, to protect biodiversity and support the natural regeneration process of forest ecosystems. It is a very time-consuming and expensive bark beetle measure. However, this is not very suitable management for sites where populations of *C. calceolus* persist, because tree climbers or falling bark strips can damage the lady's slipper orchids. Of course, even this is much better than salvage logging and persisting *C. calceolus* specimens can benefit from a partial shade of standing debarked trees.

5. Conclusions

We conclude that the relationship between bark beetle and *C. calceolus* is somewhat ambivalent. A significant number of the lady's slipper orchids grow in forest sites sensitive to bark beetle infestation. Usually, the bark beetle is understood as the enemy of the forest, and salvage logging, the most common response of forest managers to this challenge, strongly threatens the *C. calceolus* populations. However, we believe that not only in the Czech Republic, but also in other countries where *C. calceolus* thrives in coniferous monocultures, an enemy can be transformed into a savior, if smart bark beetle measures will replace the panic, chaotic, or unprofessional salvage logging. Smart management measures prepared in advance can effectively reduce bark beetle outbreaks and simultaneously improve habitat conditions of the lady's slipper orchids, which are now suffering in plantations. Of course, close cooperation and mutual trust among forest managers, conservationists, and scientists are necessary for this transformation of the bark beetle from an enemy to a savior.

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References

1. Terschuren, J. *Action Plan for Cypripedium calceolus in Europe—Report to the Council of Europe*; Convention on the Conservation of European Wildlife and Natural Habitats; T-PVS(98)20; Council of Europe: Strasbourg, France, 1998.
2. Bilz, M. *Cypripedium calceolus*, the IUCN Red List of Threatened Species. 2011. Available online: <https://www.iucnredlist.org/species/162021/5532694> (accessed on 18 December 2022).
3. Jakubská-Busse, A.; Tsiftsis, S.; Śliwiński, M.; Křenová, Z.; Djordjević, V.; Steiu, C.; Kolanowska, M.; Efimov, P.; Hennigs, S.; Lustyk, P.; et al. How to protect natural habitats of rare terrestrial orchids effectively: A comparative case study of *Cypripedium calceolus* in different geographical regions of Europe. *Plants* **2021**, *10*, 404. [CrossRef]
4. Lindner, M.; Maroschek, M.; Netherer, S.; Kremer, A.; Barbati, A.; Garcia-Gonzalo, J.; Seidl, R.; Delzon, S.; Corona, P.; Kolström, M.; et al. Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. *For. Ecol. Manag.* **2010**, *259*, 698–709. [CrossRef]
5. Cribb, P.; Syrylak Sandison, M. A preliminary assessment of the conservation status of *Cypripedium* species in the wild. *Bot. J. Linn. Soc.* **1998**, *126*, 183–190. [CrossRef]

6. Hultén, E.; Fries, M. *Atlas of North European Vascular Plants*; Koeltz ScientiÆc Books: Köningstein, Germany, 1986.
7. Delforge, P. *Orchids of Europe, North Africa and the Middle East*; Timber Press: Portland, OR, USA, 2006.
8. Kull, T. *Cypripedium calceolus* L. *J. Ecol.* **1999**, *87*, 913–924. [[CrossRef](#)]
9. Kull, T. Genet and ramet dynamics of *Cypripedium calceolus* in different habitats. *Abstr. Bot.* **1995**, *19*, 95–104.
10. Rasmussen, H.N. *Terrestrial Orchids: From Seed to Mycotrophic Plant*; Cambridge University Press: Cambridge, UK, 1995.
11. Nilsson, L.A. Anthecological studies on the Lady's Slipper, *Cypripedium calceolus* (Orchidaceae). *Bot. Not.* **1979**, *132*, 329–347.
12. Kull, T. Identification of clones in *Cypripedium calceolus* (Orchidaceae). *Proc. Est. Acad. Sci.* **1988**, *37*, 195–199. [[CrossRef](#)]
13. Fay, M.F.; Taylor, I. 801. *Cypripedium calceolus*: Orchidaceae. *Curtis's Bot. Mag.* **2015**, *32*, 24–32. [[CrossRef](#)]
14. Chytrý, M.; Danihelka, J.; Kaplan, Z.; Wild, J.; Holubová, D.; Novotný, P.; Řezníčková, M.; Rohn, M.; Dřevojan, P.; Grulich, V.; et al. Pladias Database of the Czech Flora and Vegetation. *Preslia* **2021**, *93*, 1–87. [[CrossRef](#)]
15. Procházka, F.; Velíšek, V. *Orchideje Naší Přírody [Orchids of our Nature]*; Academia: Praha, Czech Republic, 1983.
16. Turoňová, D.; Gillová, L. Střevičník pantoflíček (*Cypripedium calceolus*)—Metodika Monitoringu [Monitoring Methods]. Master's Thesis, Agentura ochrany přírody a krajiny ČR: Praha, Czech Republic, 2011.
17. AOPK ČR. *Nálezová Databáze Ochrany Přírody [Species Occurrence Database, On-Line Database]*; Agency of Nature Conservation and Landscape Protection of the Czech Republic: Prague, Czech Republic, 2022; Available online: <https://portal.nature.cz/nd/> (accessed on 21 December 2022).
18. Gola, P. Ecobiological Exigencies of Wood Populations *Cypripedium calceolus* L. Master's Thesis, Department of Ecology and Environmental Sciences, University Palacky Olomouc, Olomouc, Czech Republic, 2011.
19. Härtel, H.; Lončáková, J.; Hošek, M. (Eds.) *Mapování Biotopů v České Republice. Východiska, Výsledky, Perspektivy [Biotope Mapping in the Czech Republic. Background, Results, Perspectives]*; Agency for Nature Conservation and Landscape Protection of the Czech Republic: Prague, Czech Republic, 2009.
20. Chytrý, M.; Kučera, T.; Kočí, M.; Grulich, V.; Lustyk, P. (Eds.) *Katalog Biotopů České Republiky [Catalog of Biotopes of the Czech Republic]*, 2nd ed.; Agency for Nature Conservation and Landscape Protection of the Czech Republic: Prague, Czech Republic, 2010.
21. FiNDB. *Nálezová Databáze Biotopů [Habitat Occurrence Database, On-Line Database]*; Agency of Nature Conservation and Landscape Protection of the Czech Republic: Prague, Czech Republic, 2022; Available online: https://portal.nature.cz/mb/mb_nalez.php?X=X (accessed on 21 December 2022).
22. Semotánová, E. *Historická Geografie Českých Zemí [Historical Geography of the Czech Lands]*; Institute of History of the Czech Academy of Sciences: Prague, Czech Republic, 1998.
23. *STATISTICA v. 12*; StatSoft Inc.: Tulsa, OK, USA, 2012; Available online: <http://www.statsoft.com> (accessed on 1 October 2021).
24. Jakubská-Busse, A.; Szcześniak, E.; Śliwiński, M.; Narkiewicz, C. Zanikanie stanowisk obuwika pospolitego *Cypripedium calceolus* L., 1753 (Orchidaceae) w Sudetach. *Przyr. Sudet.* **2010**, *13*, 43–52.
25. Pop, A. *Studiul Populației de Cypripedium calceolus L. din Împrejurimile Orașului Sovata, Județ Mures, Lucrare de Licență [Population Study of Cypripedium calceolus L. from the Surroundings of Sovata City; Mures County]*; Universitatea "Babeș-Bolyai": Cluj-Napoca, Romania, 2006; p. 80.
26. Balázs, Z.R.; Roman, A.; Balazs, H.E.; Căpraș, D.; Podar, D. Rediscovery of *Cypripedium calceolus* L. in the vicinity of Cluj-Napoca (Romania) after 80 years. *Contrib. Bot.* **2016**, *51*, 43–53.
27. Tomescu, C.V. *Cypripedium calceolus* L. în pădurea Dragomirna-județul Suceava, in: Horticultură, Viticultură și vinificație, Silvicultură și grădini publice. *Protecția Plantelor* **2018**, *47*, 421–427.
28. Kretzschmar, H. Die statistische Gefährdung des Frauenschuhs im mittleren Deutschland. *Ber. Arbeitskrs. Heim. Orchid.* **1996**, *13*, 39–40.
29. Karlik, P.; Poschlod, P. History or abiotic filter: Which is more important in determining the species composition of calcareous grasslands? *Preslia* **2009**, *81*, 321–340.
30. Wilson, J.B.; Peet, R.K.; Dengler, J.; Partel, M. Plant species richness: The world records. *J. Veg. Sci.* **2009**, *23*, 796–802. [[CrossRef](#)]
31. Olmeda, C.; ŠeffEROVÁ, V.; Underwood, E.; Millan, L.; Gil, T.; Naumann, S. (Eds.) *EU Action Plan to Maintain and Restore to Favourable Conservation Status the Habitat Type 6210 Semi-Natural Dry Grasslands and Scrubland Facies on Calcareous Substrates (Festuco-Brometalia) (*Important Orchid Sites)*; European Commission Technical Report; European Commission: Brussels, Belgium, 2022; Available online: <https://ieep.eu/publications/eu-habitat-action-plans-targeting-restoration-of-key-habitats-and-species> (accessed on 29 December 2022).
32. Chytrý, M.; Hoffmann, A.; Novák, J. Suché trávníky [Dry grasslands]. In *Vegetace České Republiky 1. Travninná a keříčková vegetace [Vegetation of the Czech Republic 1. Grassland and Heathland Vegetation]*; Chytrý, M., Ed.; Academia: Prague, Czech Republic, 2007; pp. 371–470.
33. Kucharczyk, M. *Cypripedium calceolus* L., Obuwik pospolity. In *Gatunki roślin. Poradniki Ochrony Siedlisk i Gatunków Natura 2000—Podręcznik Metodyczny. Tom 9*; Sudnik-Wojciechowska, B., Werblan-Jakubiec, H., Eds.; Ministerstwo Środowiska: Warszawa, Poland, 2004; pp. 107–111.
34. Kaźmierczakowa, R. *Polish Red List of Pteridophytes and Flowering Plants*; Institute of Nature Conservation Polish Academy of Sciences: Krakow, Poland, 2016.
35. Niklfeld, H.; Schratt-Ehrendorfer, L. Rote Liste gefährdeter Farn- und Blütenpflanzen (Pteridophyta und Spermatophyta) Österreichs. 2. Fassung. In *Rote Listen Gefährdeter Pflanzen Österreichs*; 2. Auflage; Grüne Reihe des Bundesministeriums für Umwelt, Jugend und Familie, Band 10; Niklfeld, H., Ed.; Austria Medien Service: Graz, Austria, 1999; pp. 33–152.

36. Gudžinskas, Z.; Ryla, M. *Lietuvos Gegužraibiniai (Orchidaceae)*, Botanikos Instituto Leidykla; Spausdino UAB, Petro Ofsetas: Žalgirio, Lithuania, 2006; p. 104.
37. Ingelög, T.; Andersson, R.; Tjernberg, M. *Red Data Book of the Baltic Region. Part 1: Lists of Threatened Vascular Plants and Vertebrates*; Swedish Threatened Species Unit Uppsala: Riga, Latvia, 1993.
38. Klavina, D.; Grauda, D.; Priede, A.; Rashal, I. The habitat diversity and genetic variability of *Cypripedium calceolus* in Latvia. In *Actions for Wild Plants, Proceedings of the 6th Planta Europa Conference on the Conservation of Plants, Kraków, Poland, 23–27 May 2011*; Committee on Nature Conservation, Polish Academy of Sciences: Kraków, Poland, 2011; pp. 91–97.
39. McGrath, M.J.; Luyssaert, S.; Meyfroidt, P.; Kaplan, J.O.; Bürgi, M.; Chen, Y. Reconstructing European forest management from 1600 to 2010. *Biogeosci. Discuss.* **2015**, *12*, 5365–5433. [[CrossRef](#)]
40. Jakuš, R.; Blaženec, M. (Eds.) *Principy Ochrany Dospelých Smrekových Porastov pred Podkorným Hmyzom [Principles of Protection of Adult Spruce Stands against Bark Beetles]*; Institute of Forest Ecology, the Slovak Academy of Sciences: Zvolen, Slovensko, 2015.

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