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Historical landscape matters for threatened species in French mountain forests

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Abstract

Ancient forests are known to host a biodiversity of high ecological distinctiveness and are likely to provide habitat for red-listed species. Yet, few studies have investigated the role of forest continuity for the conservation of threatened species. We used species-presence data on red-listed species from 12 taxonomic groups (*Spermatophyta*, *Pteridophyta*, *Bryophyta*, *Lichens*, *Chiroptera*, *Aves*, *Squamata*, *Amphibia*, *Coleoptera*, *Lepidoptera*, *Odonata* and *Orthoptera*) to ascertain if ancient forests are an important habitat for threatened species in five mountain and subalpine protected areas in France. We compared the effect of the amount of historical forest (1853-1860) with the effect of the amount of current forest on the distribution of red-listed species in six circular buffers landscape ranging in radius from 100 to 1500m. We showed that the amount of historical forest in the landscape had a positive effect on forest *Spermatophyta*, *Bryophyta*, *Coleoptera* and edge forest *Pteridophyta* with a better predictive power than current forest area, highlighting a colonization credit in recent forests. Conversely, edge-forest lepidopterans were more negatively affected by historical than by current forest area, highlighting an extinction debt in recent forests. Our findings underline that implementing protective measures of ancient forests could be a better strategy than afforestation to preserve threatened forest species in mountain and subalpine forest landscapes.

1. Introduction

Forests with a long temporal continuity, i.e. forests with no change in land use for at least 150 years, also known as ancient forests (AF) as opposed to recent forests (RF), have particular conservation value because they host species guilds with low dispersal and competitive abilities that have trouble persisting after forest/habitat destruction (Bergès & Dupouey 2021; Hermy & Verheyen 2007). Even though the total surface area of temperate forests is currently expanding (Keenan *et al.* 2015; Mather 1992), AF area is still eroding. Indeed, it is estimated that 10 to 40% of the forests present in the 19th century have disappeared in European countries today (Bergès & Dupouey 2021). Despite this insidious erosion and behind the recommendations of the IUCN (IUCN 2016), only two European countries (Great Britain and Belgium) have adopted measures to protect AFs (Goldberg *et al.* 2007; Kervyn *et al.* 2017).

Species extinction probability is strongly related to population size, disturbances and the species' functional traits (Fischer & Lindenmayer 2007; Davies 2019). Therefore, extinction risk is likely to increase for species with low mobility, low dispersal and competition abilities and high habitat specialisation (Kotiaho *et al.* 2005; Cooke *et al.* 2020). In addition, rare species are particularly sensitive to past human activities (Lavergne *et al.* 2005) and the proportion of extinct or threatened species is better explained by 1900's indicators of human activities than by current one, showing a time lag effect (Gosselin & Callois 2021). Threatened species may therefore share many traits with ancient forest species. However, whereas many studies have highlighted the high ecological distinctiveness of AF biodiversity, only a few focused on the importance of these forests for threatened species (Bergès & Dupouey 2021). Two studies found a positive correlation between ancient forest species richness and threatened species richness for bryophytes, lichens, macro fungi, beetles, butterflies and spiders, one in Czech Republic (Hofmeister *et al.* 2019) and the other in Sweden (Fritz *et al.* 2008). However, these studies did not directly characterise forest continuity and only studied correlations between biodiversity indices. Only Flensted *et al.* (2016) actually evaluated the effect of past landscape context on the distribution of threatened forest species. The authors showed that threatened forest species

richness in Danish forests was better correlated with historical forest area (mapped between 1760 and 1820) than with current forest area for mammals, saproxylic beetles, butterflies, vascular plants and four groups of fungi. However, this study was carried out in a highly fragmented landscape (14% of Denmark is currently forested) and did not explore the response of non-forest species, although they might react differently to the temporal continuity of the forest and be relevant for the implementation of conservation measures. Indeed, open-habitat dependent species can persist in recent forests for several reasons: (1) the canopy cover may remain rather low, (2) they are close to the forest edge (Harper *et al.* 2005), and (3) their occurrence may be related to an extinction debt (Jackson & Sax 2010; Milberg *et al.* 2019).

To date, the role of past land use on forest biodiversity has rarely been studied in mountain forests (Janssen 2016; Bergès & Dupouey 2021). These forests have globally been less affected by deforestation and have undergone less intense silvicultural management than their lowland counterparts, which might lead to weaker impacts on threatened species than those observed by Flensted *et al.* (2016).

Our aim was to analyse the response of threatened species from multiple taxonomic groups to historical and current landscape contexts, using species observations in forest only. We used a large dataset of threatened forest and non-forest species presence from 12 taxonomic groups (*Spermatophyta*, *Pteridophyta*, *Bryophyta*, lichens, *Chiroptera*, *Aves*, *Squamata*, *Amphibia*, *Coleoptera*, *Lepidoptera*, *Odonata* and *Orthoptera*) in five protected areas in the French mountains. We assessed the probability of observing a threatened species within each taxonomic group as a function of the amount of historical or current forest in concentric circular buffers of different radii. More specifically, we tested the following hypothesis: 1- Due to habitat limitation, the occurrence of threatened forest species should increase with the increasing amount of current forest in the landscape, while the occurrence of non-forest species should decrease. 2- A delayed response to land-use change would occur in recent forests (former open lands) due to dispersal and recruitment limitations of threatened forest species (colonisation credit) and persistence of threatened non-forest species (extinction debt). Thus, the occurrence of threatened forest species should increase with the amount of historical forest in the landscape, and should be better predicted by the amount of historical forest than by the amount of current forest. Conversely, the occurrence of non-forest species should increase with the amount of historical open land in the landscape (and thus should decrease with the amount of historical forest in the landscape), and should be better predicted by the amount of historical open land than by the amount of current open land.

II. Materials and methods

II.1. Study area

The study area encompassed five National Parks (NP) in the southern half of France. The Vanoise, the Ecrins and the Mercantour NPs cover a large part of the French Alps and benefit from a mountain climate with a continental influence. The Cevennes and the Pyrenees NPs cover part of the Massif Central and the Pyrenean range and have a mountain climate with, respectively, a mediterranean and oceanic influence. The study covered all the elevation range where forest is naturally present. Current forest cover in the five parks ranges from 19% to 68%, while historical forest cover ranges from 10 to 17% (**Table 1**). Deforestation represents 5.5% to 17% of the historical forested area but forest is currently in expansion and increased by +97% to +347% since 1853-1864. The Vanoise NP displayed the lowest forest cover with the largest share of AFs, while the Cevennes NP had the highest forest cover with the smallest share of AFs. Conifers dominated in the Vanoise, Ecrins and Mercantour NPs, while broadleaves dominated in the Cevennes and Pyrenees NPs.

Table 1 : Description of the forest context in the five National Parks of our study area. Surface areas are in km² and percentages in brackets for current and historical forest area are relative to the total surface area while the historical forest loss is relative to the historical forest area. Forest expansion is relative to the historical forest area, and the share of ancient, deciduous, coniferous and mixed forests are relative to the current forest area.

National parks	Vanoise	Ecrins	Mercantour	Cevennes	Pyrenees
Total surface area	1 577	1 702	2 134	3 731	2 523
Current forest area	298.1 (19%)	571.8 (34%)	1 122.1 (52%)	2 523.2 (68%)	740.6 (29%)
Historical forest area (1853-1864)	151.3 (10%)	179.8 (11%)	374.9 (18%)	564 (15%)	392.6 (16%)
Historical forest loss since mid-19 th century	23.7 (16%)	29 (16%)	27.4 (7%)	31.5 (5.6%)	52.8 (13%)
Forest expansion since mid-19 th century	+ 97%	+ 218%	+ 199%	+ 347%	+ 89%
Current forest					
Share of ancient forest	43%	26%	31%	21%	46%
Share of deciduous forest	16%	25%	16%	44%	59%
Share of coniferous forest	76%	54%	71%	35%	22%
Share of mixed forest	8%	21%	13%	21%	19%
Elevation range (m)	[636 ; 2 480]	[670 ; 2 443]	[153 ; 2 728]	[104 ; 1 698]	[293 ; 2 555]

II.2. Species presence data

We prepared our database by assembling existing databases from the National Park managers, the National Botanical Conservatories and the French Nature and Landscape Information System (<https://openobs.mnhn.fr/>). These data are based on opportunistic observations and do not contain information on species absence but they include a high number of observations of red-listed species, which are invaluable for describing the distribution of these species. Twelve taxonomic groups were considered: *Spermatophyta*, *Pteridophyta*, *Bryophyta*, lichens, *Chiroptera*, *Aves*, *Squamata*, *Amphibia*, *Coleoptera*, *Lepidoptera*, *Odonata* and *Orthoptera*. We selected observations made from January 2000 to July 2018 and retained only those made in closed forest (i.e. tree cover $\geq 40\%$ according to the French National Forest map BD FORET[®] V2) at least 10 m from the forest edge and more than 1 500 m from the boundaries of the study area. Data were thinned using `spThin` R package (Aiello-Lammens *et al.* 2015) by setting the minimum distance between observations of each species to 200m for birds and chiropterans and 100m for other taxonomic groups. Species classified as "Vulnerable", "Endangered" and "Critically Endangered" in the IUCN regional red lists were considered threatened. If the species status was not available at the regional level (no regional list, species classified "Data Deficient" or omitted from the regional list), we used the national or European red list status instead (IUCN 2012). This information was derived from Gargominy and Régnier (2021) and synonyms were solved according to the official French taxonomic nomenclature (Gargominy *et al.* 2020). As there is no official national or regional IUCN red list for lichens in France, we used the information provided by Roux (2020). Based on the references listed in **Appendix S1**, the species were classified into three categories (Schneider *et al.* 2021): forest-dependent species (forest species: "FS"), open habitat-dependent species (non-forest species: "NFS") and forest-edge or generalist species (edge species: "ES").

As the dataset contained only presence data, we generated a set of pseudo-absences at the nodes of a 200 x 200 m grid. Then, we applied a list of filters to only keep: (1) pseudo-absences located in sectors (on a 2x2 km grid) with at least one observation of a threatened or non-threatened species from the corresponding taxonomic group, (2) pseudo-absences located in closed forests, and (3) pseudo-absences located more than 10 m from the forest edge and more than 1500 m from the boundaries of the study area.

II.3. Environmental factors

Large-scale context may determine local responses but the landscape scale of effect is difficult to determine a priori (Avon *et al.* 2015). One common method is to measure landscape characteristics at different nested spatial scales and then determine which scale best explains the ecological response to the landscape context (Jackson and Fahrig 2015). We therefore calculated the percentage of historical or current forest area in six circular buffers with radii of 100, 250, 500, 750, 1 000 and 1 500 m (noted B_{100} to B_{1500}) for each threatened species observation point and each pseudo-absence point. We calculated the forested area in the current landscape using the BD FORET[®] V2 map (consistent with the FAO's definition of "forest", FAO 2012), drawn in our study area between 2014 and 2018 by the French National Geographical Institute. We identified historical forests using the Ordnance survey maps drawn between 1853 and 1864, which are the reference in France for identifying long-continuity forests (Bergès & Dupouey 2021). All the maps had previously been vectorised and georeferenced according to Favre *et al.* (2013) by the National Research Institute for Agriculture, food and the Environment (INRAE) and the National Parks (Thomas *et al.* 2017). We also included elevation (from the French DEM BD ALTI[®] 25 m) and stand tree species composition (coniferous/deciduous/mixed, from the BD FORET[®] V2 forest map) to control for local biotic and abiotic conditions. To control for potential sampling bias, we also included slope and distance to the closest path in the analyses.

The data were processed with the `sf` (Pebesma 2018) and `raster` (Hijmans 2020) packages from the R 4.1.1 application (R Core Team 2021).

II.4. Statistical analyses

We used logistic regressions to analyse the effect of the selected environmental variables on the probability (p) of observing a threatened species. We analysed forest, edge and non-forest species separately for each taxonomic group. In each case, the parks where the number of observations of threatened species was below five for a taxonomic group were excluded from the analyses of the taxonomic group concerned.

From the 69 126 potential pseudo-absences generated, 10 000 were drawn at random and weighted so that the total weight of pseudo-absences equalled the total weight of presences in each model, as recommended by Barbet-Massin *et al.* (2012). We then fitted and compared three logistic regression models. First, we started with a full model (M_{full}) with the following environmental variables as predictors: national park identity, elevation, stand tree species composition, distance to the closest path and slope (see equation 1).

$$\text{Eq. 1} \quad M_{full} \quad \text{logit}(p) = \alpha + \beta_1.Park + \beta_2.Elevation + \beta_3.Stand_composition + \beta_4.Distance_to_path + \beta_5.Slope$$

Second, using `dredge` function of package `MuMIn` (Kamil 2020), we selected the best set of environmental variables as the environmental model (M_{Env}) by choosing the model with the lowest Akaike information criterion (AIC) and the fewest predictors.

Third, two models based on M_{Env} were compared: $M_{Act[i]}$, which included the effect of the current forest area in the buffer i , and $M_{Hist[i]}$, which included the effect of the historical forest area in 1853-1864 in the same buffer i (equation 2).

$$\begin{aligned} \text{Eq. 2} \quad M_{Act[i]} \quad \text{logit}(p) &= M_{Env} + \beta_i.Surf_{Act[i]} \\ M_{Hist[i]} \quad \text{logit}(p) &= M_{Env} + \beta'_i.Surf_{Hist[i]} \quad \text{with } i \in [B_{100} : B_{1500}] \end{aligned}$$

We calculated the difference in AIC (Δ_{AIC}) between each model and the model M_{Env} and estimated the values of the coefficients (β_i and β'_i) associated with historical and current forest area in each model. We used the coefficient of the model with the lowest AIC for interpretation.

To ensure that pseudo-absence random-draws had no effect, we repeated this procedure 20 times using 20 random draws of 10 000 pseudo-absences and results were summarised by their mean \pm standard deviation. The coefficients for each buffer size are provided in **Appendix S2**.

III. Results

III.1. Data summary

Of the 8 061 species recorded, 696 were identified as threatened. *Spermatophyta*, *Coleoptera* and *Lepidoptera* were the most diverse groups while *Spermatophyta* and *Aves* had the largest number of observations. All three habitat preferences (forest species: FS, edge species: ES and non-forest species: NFS) were present in the different taxonomic groups, except for *Squamata*, *Amphibia*, *Odonata* and *Orthoptera*, which contained only non-forest species (see the list of threatened species in **Appendix S3**).

III.2. Response of threatened species to current or historical forest area in the landscape

In accordance with our first hypothesis, the probability of observing a threatened forest species rose with increasing current forested area in the landscape while non-forest species were negatively

affected (**Figure 16** and **Appendix S2**). Current forested area had a significant positive effect on threatened FS spermatophytes ($\beta_{750} = 2.6 \pm 0.1$), birds ($\beta_{1000} = 1.2 \pm 0.08$) and beetles ($\beta_{250} = 5.4 \pm 0.06$). Conversely, NFS spermatophytes ($\beta_{100} = -2.8 \pm 0.1$) and birds ($\beta_{250} = -2.7 \pm 0.1$) as well as ES lepidopterans ($\beta_{1500} = -3.5 \pm 0.07$) were negatively affected by the current forested area in the landscape.

Our second hypothesis was also verified for several taxonomic groups. Some groups of threatened forest species responded to landscape changes with delay and their presence was better explained by the historical landscape than by the current one (Figure 1). FS Spermatophytes ($\beta_{1500} = 1.5 \pm 0.08$), bryophytes ($\beta_{500} = 0.8 \pm 0.04$) and beetles ($\beta_{250} = 2.0 \pm 0.02$), as well as ES pteridophytes ($\beta_{250} = 1.4 \pm 0.03$) were positively affected by the amount of historical forest in the landscape, M_{hist} being a better model than M_{Act} . In addition, historical forested area negatively affected ES lepidopterans ($\beta_{100} = -1.7 \pm 0.03$).

Neither historical nor current forested area in the landscape affected odonatan, Orthopterans, chiropterans, reptiles, amphibians, lichens, NFS pteridophytes, NFS and ES bryophytes (Figure 1).

Results were robust to pseudo-absence random-draws, Δ_{AIC} varied very little and all the β coefficients were included into the $\text{IC}_{95\%}$ calculated by the first model of the 20 iterations of pseudo-absence random-draws (**Appendix S2**).

The optimal landscape scale of effect varied among taxonomic groups and the effect tested (current or historical forested area). Historical forest affected bryophytes, beetles and lepidopterans at a rather small landscape scale, whereas spermatophytes were influenced at a large landscape scale. On the other hand, current forest area affected spermatophytes and coleopterans at a small landscape scale while birds and lepidopterans were influenced at a large landscape scale (Figure 1).



Figure 1: Differences in AIC between models M_{Act} or M_{Hist} and M_{Env} for each taxonomic group and type of threatened species (forest, edge or non-forest). Δ_{AIC} between -2 and +2 (shaded area) means there is no statistical difference between models M_{Act} or M_{Hist} and M_{Env} . Error bars represent standard deviation between the 20 iterations. The higher the Δ_{AIC} , the more explanatory the model. Empty boxes = non-applicable model.

IV. Discussion

IV.1. Effect of historical and current landscape context on the probability of observing a threatened species

Several forest taxonomic groups responded positively to the amount of current forest in the landscape. These results confirm our first hypothesis and show the importance of preserving habitats for the maintenance of threatened species (Pykälä 2019). However, FS chiropterans did not respond to current forest cover but this lack of effects for chiropterans may be due to the small number of observations that may have led to a limited statistical power of the models (N=24). FS bryophytes did not respond to current forest cover but this group include both epiphytic and non-epiphytic species that may be poorly affected by the amount of forest in the landscapes (McCune *et al.* 2021; Nordén *et al.* 2014). Conversely, current forested area negatively affected NFS spermatophytes and birds with a small landscape scale of effect, suggesting these species can be found in forests, but they might not tolerate dense forest cover. More investigation is needed, mixing observations inside and outside forest habitats, to properly analyse the effect of land abandonment and afforestation on threatened non-forest species.

Historical forested area better explained the presence of threatened forest spermatophytes than did current forested area at the largest landscapes scale, indicating that these species can be better maintained in large historically wooded areas, i.e. probably the areas least influenced by human activities. Indeed, forest cores may have been less affected by wood and litter extraction or by grazing, which led to the degradation of the forest cover during the 20th century (Jalut *et al.* 1998; Leroy 1957; Tochon 1872). Our results agree with Lavergne *et al.* (2005), who showed that rare species are maintained in the least anthropogenised ecosystems, and with Kimberley *et al.* (2014), who showed that AFs support more rare species than RFs when AF patches are large. Flensted *et al.* (2016) showed that the richness of red-listed spermatophytes was better correlated to former forested area than to the current one on 10x10km grids, as did Paltto *et al.* (2006) in Sweden with 5-km-radius circles. These studies, as well as our own results, suggest that i) the optimal landscape scale of effect is certainly greater than the 1.5-km radius covered by our largest buffer and ii) that the effect occurs in forest landscapes with various degrees of forest fragmentation.

ES pteridophytes were also positively affected by historical forest area while current forest had no effect. However, this taxonomic group was dominated by *Dryopteris oreades* and *Dryopteris ardechensis* which are mostly found in screes, an unfavourable habitat for cultivation that is usually found in ancient forests, which may indirectly explain our result.

Current forest area had a greater impact on FS and NFS birds than historical forest area. These species are highly mobile and are probably not limited by their dispersion ability, which explains the large landscape scale effect for current forest area. High forest cover is beneficial for FS birds but has a significant negative effect on NFS birds and management should be adapted according to conservation objectives (Ram *et al.* 2020).

The stronger effect of historical than current landscape on threatened forest beetles is in agreement with Flensted *et al.*'s (2016) results. Most of the threatened forest beetles we analysed were actually saproxylic beetles. These species are highly dependent on the forest context and may have a limited dispersal ability (Irmeler *et al.* 2010), which could induce a colonization credit in RFs (Brin *et al.* 2016). However, when the landscape is slightly fragmented, the distribution of saproxylic beetles seems to be more affected by the habitat quality (the abundance and diversity of dead wood, in particular) than by dispersal limitation (Janssen *et al.* 2016). Furthermore, forest continuity and stand maturity may have additive effects on the species richness and functional composition of saproxylic

beetle communities (Janssen *et al.* 2017). If forest continuity is a necessary (but insufficient) condition to obtain very mature stands (Nordén *et al.* 2014), it is also true that past human societies cleared forests for agriculture and pasture in the most favourable and accessible areas. AFs are thus more frequently found in the least accessible or steepest areas (Abadie *et al.* 2018; Flinn *et al.* 2005; Thomas *et al.* 2017). Therefore, AFs may be subject to less logging pressure and thus become more mature than RFs, which could result in an indirect effect of historical forest cover. Our study did not distinguish between these two effects. Further investigation is required to properly disentangle the forest continuity and maturity effects on the response of species, especially in mountain forests (Janssen *et al.* 2019).

Forest bryophytes were also positively affected by the amount of historical forest in the landscape. Because of their low dispersion capacities and their sensitivity to habitat change, bryophytes appear to be good indicator species for forest continuity (Mölder *et al.* 2015) and our results show the importance of ancient forests for the conservation of threatened species. However, the model M_{Hist} is only slightly better than M_{Env} . This weak difference is probably due to the heterogeneity of the FS group that includes both epiphytic and non-epiphytic species able to persist in residual canopy areas in cultural landscapes, which may mitigate our results (Fenton & Frego 2005).

Historical forested area negatively affected ES lepidopterans at the smallest landscape scale, whereas current forested area had no effect at this landscape scale. This suggests that these species occur in forest but only in recent forest due to an extinction debt. Indeed, past land use can indirectly affect butterfly communities because some grassland species may persist in forests for more than 100 years after canopy closure (Burst *et al.* 2017). Thus, clearcuts in post-agricultural forests have been shown to contain 35% more grassland species than clearcuts in AFs (Milberg *et al.* 2019). Therefore, vegetation that develops in forest clearcuts on former grasslands favours typical grassland-dependant lepidopterans (Ibbe *et al.* 2011), even in clearcuts more than 10 years old (Ram *et al.* 2020). Our study did not take forest management into account; some lepidopteran observations could have been located in former clearcuts even though the forest was considered closed on the BD FORET® V2 map (the canopy cover threshold of 40% can be reached in less than 10 years in mountain areas; Fuhr *et al.* 2015). Agricultural land abandonment and tree canopy closure are the two main threats for *Lepidoptera* (Erhardt 1995; Öckinger *et al.* 2006) and our results show that forest-edge *Lepidoptera* species were negatively affected by the amount of current forest in the landscape at the largest landscape scale. Targeted management in recent forests, for example, maintaining a network of clearings, could be an efficient tool for the conservation of lepidopterans threatened by intensive agricultural practices (Ram *et al.* 2020).

The amount of current forest or the amount of historical forest in the landscape did not affect the other taxonomic groups included in our study. Orthopterans are ectothermic organisms that depend mainly on the amount of heat reaching the ground and are generally negatively affected by forest cover. Thus, the abundance of threatened orthopterans is negatively affected by tree cover and advanced successional stages (Helbing *et al.* 2014) and the presence of forest near dry grasslands has a negative effect on their species richness (Bieringer & Zulka 2003). Our models probably did not detect any effect due to the low number of observations ($n=18$) in our dataset. While reptiles are also ectotherms, our results do not show any effect of forested area in the landscape. However, the link between reptile species richness and forested area is unclear in the literature. Indeed, the meta-analysis carried by Thompson & Donnelly (2018) does not conclude on differences in species richness or abundance between secondary forests and open areas or between old-growth and secondary forests. In addition, threatened lichens did not respond to either historical or current landscape in our study contrary to Fritz *et al.*'s (2008) results. However, these authors used a larger continuity gradient

(more than 350 years) and used correlation between ancient-forests species richness and threatened species richness. Moreover, lichens are particularly sensitive to the quality of their habitat (substrate, shade, humidity, air pollution, etc.) and maybe not strongly limited by their dispersal ability in slightly fragmented ecosystems (Nordén *et al.* 2014; Janssen *et al.* 2019). Finally, odonates may not respond to forest area in our study because they spend most of their life cycle in the larval stage and depend almost exclusively on the quality of the aquatic environment in which they develop. In addition, their high dispersal capacity at the adult stage probably make them rather independent of the landscape context (McPeck 2008).

IV.2. Use of biodiversity data: limits and perspectives

Like any natural history collection dataset (Newbold 2010), our dataset has several limitations. The first concerns the over-sampling of some taxonomic groups, and even of some species due to societal preferences (Troudet *et al.* 2017). In our dataset, birds and spermatophytes were better represented than other taxonomic groups, and some charismatic species were more sampled than other species in the same taxonomic group. These species therefore weighted more in our models. The second limitation concerns the spatial distribution of the recorded observations. In the absence of a pre-planned sampling design, observers may have selected sites based on previous observations, restricting themselves to easily accessible areas and resampling the same sector over time. Finally, since the sampling protocols, if any, are unknown, the dataset contains no information on species absence. However, despite these weaknesses, these types of databases also has several advantages: they cover large areas and provide information on rare species; they allow a multi-taxonomic approach, which should provide more general results (Westgate *et al.* 2014) and finally, they can help refine niche models when they are combined with standardised presence/absence data (Coron *et al.* 2018) or processed with deep learning techniques (Botella *et al.* 2018). These types of databases are therefore particularly important tools for ecological research and will become increasingly important with the development of participative science and the era of big data in biodiversity research (Hampton *et al.* 2013). We strongly encourage managers to complement biodiversity inventory efforts on taxonomic groups that have been under-sampled because of their low societal interest or due to lack of observers with the necessary scientific skills for species determination.

IV.3. Implications for conservation

In accordance with previous works (Flensted *et al.* 2016), our results show that forest continuity matters for red-listed species in landscapes with limited forest fragmentation. They confirm the importance of ancient forests for red-listed species and we therefore encourage policy makers to follow the IUCN recommendations (IUCN 2016) by adopting protective measures for AFs in order to preserve biodiversity.

The current forest area had less effect than the historical forest area (or had no effect) on threatened forest species for some taxonomic groups. On the other hand, high current forest area had a negative effect on some threatened non-forest species. This result questions the effectiveness of afforestation measures to preserve both forest and non-forest red-listed species. Indeed, while afforestation appears to be an effective measure for preserving forest species (Newmark *et al.* 2017), the objective could be missed due to the colonisation credit of threatened forest species in recent forests while being detrimental to non-forest threatened species. Landscape planning should be adapted to the conservation objectives but protecting ancient forests is a good compromise to preserve both forest and non-forest threatened species and can be more effective and less expensive than untargeted reforestations.

In addition, plantations and intensive management may also induce loss of forest biodiversity (Bremer & Farley 2010; Paillet *et al.* 2010), which could mitigate differences between recent and

ancient forests. Indeed, plantation may cause a recruitment limitation of threatened species in recent forests while intensive management of ancient forest can lead to the loss of their conservation value attributes (Bergès *et al.* 2017; Depauw *et al.* 2019). The protection of ancient forests is thus not only about fighting deforestation, but also about sustainable forest management and further research is needed in this way (Bergès & Dupouey 2021).

Some authors argue that forest continuity matters more than tree age for conservation of biodiversity (McMullin & Wiersma 2019), however, we agree with Janssen *et al.* 2019 that forest continuity and stand maturity are complementary components because they affect biodiversity by different ways: ancientness is related to species dispersal limitations while stand maturity is related to habitat requirements (Janssen *et al.* 2017). Nevertheless, ancient forests are easier to map than mature forests and managers should use historical maps to identify new high-priority conservation areas.

V. Conclusion

Our results confirm the role of temporal forest continuity in maintaining threatened forest species for multiple taxonomic groups in mountain ecosystems and highlight that the landscape scale of effect differ dramatically among taxonomic groups. Our results also show that for some group current forest cover rate is detrimental to non-forest threatened species. Thus, conservation measures will need to strike a balance between the conservation of both groups of species. We encourage stakeholders to prioritise ancient forest conservation measures over afforestation measures to preserve threatened forest species with the least impact on non-forest species.

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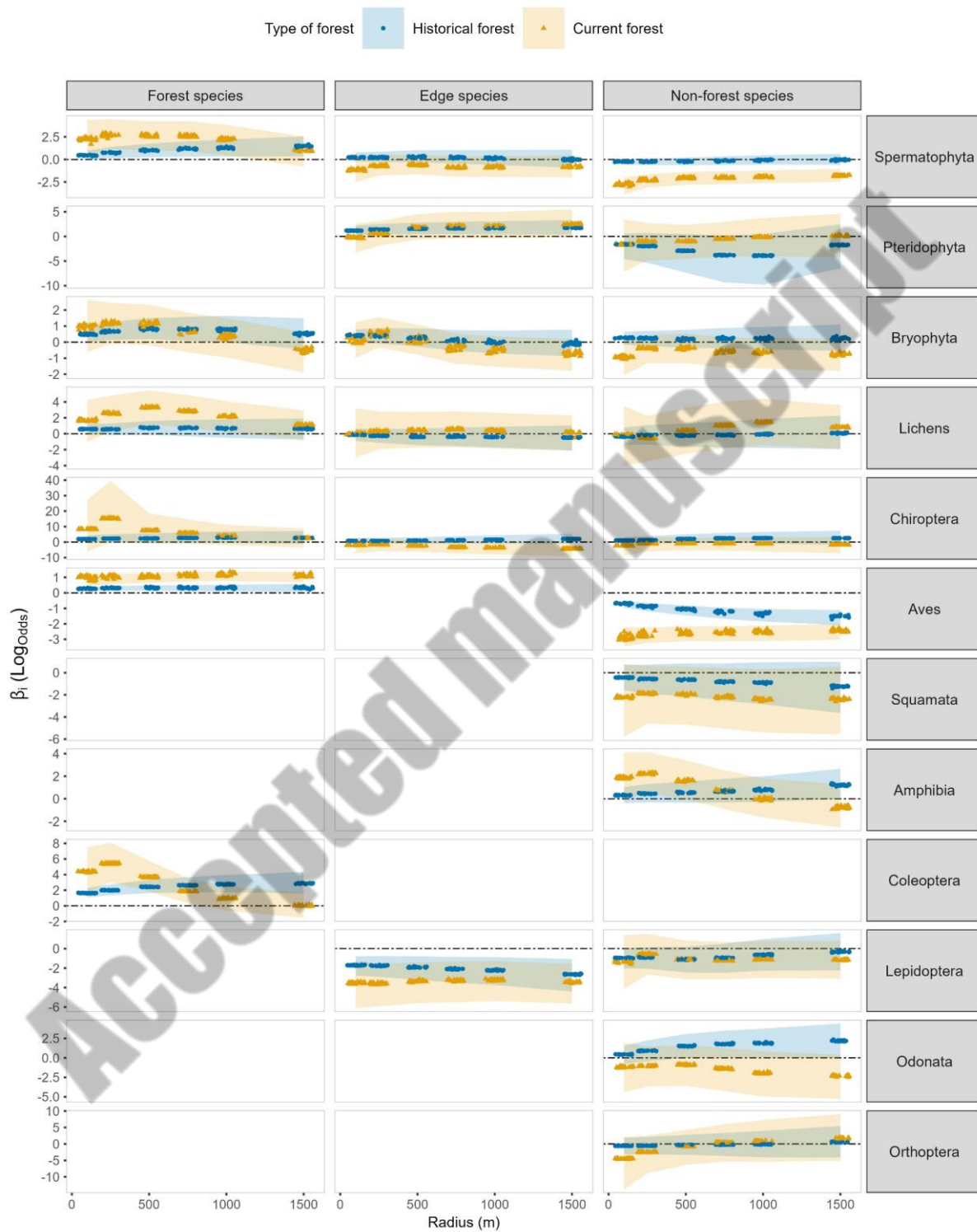
Appendices

Appendix S1: List of references used to classify species according to their preferred habitat.

Taxonomic groups	References
Spermatophyta/ Pteridophyta	Julve, P., 2002. Baseflor. Index botanique, écologique et chorologique de la Flore de France. Version 2019. Programme Catminat. URL http://perso.wanadoo.fr/philippe.julve/catminat.htm
Bryophyta	<p>Atherton, I., Bosanquet, S.D.S., Lawley, M., British Bryological Society (Eds.), 2010. Mosses and liverworts of Britain and Ireland: a field guide, 1st ed. ed. British Bryological Society, Middlewich ;</p> <p>Bernhardt-Römermann, M., Poschlod, P., Hentschel, J., 2018. BryForTrait – A life-history trait database of forest bryophytes. <i>Journal of Vegetation Science</i> 29, 798–800. https://doi.org/10.1111/jvs.12646;</p> <p>Hill, M.O., 2007. BRYOATT: attributes of British and Irish mosses, liverworts and hornworts. Centre for Ecology and Hydrology, Huntingdon, Cambridgeshire ;</p> <p>Julve, P., 2021. Basebryo. Base de données des végétations bryophytiques de France, Version 2021. Programme Catminat. [WWW Document]. URL http://perso.wanadoo.fr/philippe.julve/catminat.htm</p>
Lichens	Roux, C., 2020. Catalogue des lichens et champignons lichénicoles de France métropolitaine, 3rd ed. Association française de lichénologie (AFL), Fontainebleau
Chiroptera	Arthur, L., Lemaire, M., 2010. Les chauves-souris de France, Belgique, Luxembourg et Suisse. Biotope ; Muséum national d'histoire naturelle, Mèze (Hérault); Paris
Aves	<p>Oiseaux.net, 2021. oiseaux.net. oiseaux.net. URL https://www.oiseaux.net/ (accessed 4.12.21) ;</p> <p>Roché, J.E., Witté, I., Comolet-Tirman, J., Siblet, J.-P., Cochet, G., DECEUNINCK, Be., FROCHOT, B., GUILLOT, G., MULLET, Y., NICOLAU-GUILLAUMET, P., Olioso, G., 2016. Proposition de classification par l'habitat des oiseaux nicheurs de France. Test de l'influence du niveau typologique sur des diagnostics de tendances. <i>Alauda</i> 84, 111–144</p>
Squamata	Vacher, J.-P., Geniez, M., 2010. Les reptiles de France, Belgique, Luxembourg et Suisse, Collection Parthénope. Biotope Éditions, Mèze.
Amphibia	Duguet, R. (Ed.), 2003. Les Amphibiens de France, Belgique, et Luxembourg, Collection Parthénope. Biotope Éditions, Mèze.
Coleoptera	<p>Bouget, C., Brustel, H., Noblecourt, T., Zagatti, P., 2019. Les coléoptères saproxyliques de France: catalogue écologique illustré. Publications scientifiques du MNHN, Paris ;</p> <p>Schneider, A., Blick, T., Pauls, S.U., Dorow, W.H.O., 2021. The list of forest affinities for animals in Central Europe – A valuable resource for ecological analysis and monitoring in forest animal communities? <i>Forest Ecology and Management</i> 479, 118542. https://doi.org/10.1016/j.foreco.2020.118542</p>
Lepidoptera	<p>Lafranchis, T., Sauter, P., 2015. La vie des papillons: écologie, biologie et comportement des Rhopalocères de France. Diatheo, Paris</p> <p>Schneider, A., Blick, T., Pauls, S.U., Dorow, W.H.O., 2021. The list of forest affinities for animals in Central Europe – A valuable resource for ecological analysis and monitoring in forest animal communities? <i>Forest Ecology and Management</i> 479, 118542. https://doi.org/10.1016/j.foreco.2020.118542;</p> <p>Wolfgang, W., 2021. European Lepidoptera and their ecology [WWW Document]. European Lepidoptera and their ecology. URL http://www.pyrgus.de (accessed 4.13.21) ;</p>
Odonata	Dijkstra, K.-D., Lewington, R., 2007. Guide des libellules: de France et d'Europe. Delachaux et Niestlé, Paris.

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Appendix S2: Values of the 20 β_i coefficients estimated with different pseudo-absence random draws for the effect of the historical or current forested area according to different buffer sizes. The shaded area correspond to the 95% confidence interval of the coefficient estimates in the first iteration of pseudo-absence random draws. Empty boxes = non-applicable models. Points for the 20 pseudo-absence random-draws are jittered on the x axis for a better visualisation.



Appendix S3: List of threatened species classified by taxonomic group with species' forest affinity (FS: forest species; ES: edge species; NFS: non-forest species) and number of occurrences.

Species	Forest affinity	Number of occurrences
Spermatophyta		
<i>Achillea erba-rotta</i> subsp. <i>erba-rotta</i> All., 1773	ES	1
<i>Achillea nobilis</i> L., 1753	NFS	1
<i>Aconitum napellus</i> subsp. <i>burnatii</i> (Gáyer) J.-M.Tison, 2010	NFS	13
<i>Adonis aestivalis</i> L., 1762	NFS	1
<i>Adonis flammea</i> Jacq., 1776	NFS	1
<i>Adonis vernalis</i> L., 1753	NFS	18
<i>Aethionema saxatile</i> (L.) W.T.Aiton, 1812	ES	1
<i>Alchemilla plicata</i> Buser, 1893	NFS	1
<i>Anacamptis coriophora</i> (L.) R.M.Bateman, Pridgeon & M.W.Chase, 1997	NFS	5
<i>Anacamptis laxiflora</i> (Lam.) R.M.Bateman, Pridgeon & M.W.Chase, 1997	NFS	1
<i>Androsace septentrionalis</i> L., 1753	NFS	3
<i>Apera interrupta</i> (L.) P.Beauv., 1812	NFS	1
<i>Aphyllanthes monspeliensis</i> L., 1753	NFS	2
<i>Arabis auriculata</i> Lam., 1783	NFS	2
<i>Arenaria ligericina</i> Lecoq & Lamotte, 1847	NFS	3
<i>Arenaria montana</i> L., 1755	ES	54
<i>Artemisia chamaemelifolia</i> Vill., 1779	NFS	1
<i>Asperula tinctoria</i> L., 1753	ES	1
<i>Aster amellus</i> L., 1753	ES	2
<i>Aster pyrenaicus</i> Desf. ex DC., 1805	NFS	3
<i>Astragalus alopecuroides</i> L., 1753	NFS	1
<i>Astragalus penduliflorus</i> Lam., 1779	NFS	1
<i>Astragalus vesicarius</i> subsp. <i>pastellianus</i> (Pollini) Arcang., 1882	NFS	8
<i>Astragalus vesicarius</i> subsp. <i>vesicarius</i> L., 1753	NFS	2
<i>Blitum virgatum</i> L., 1753	ES	3
<i>Brachypodium retusum</i> (Pers.) P.Beauv., 1812	NFS	2
<i>Briza minor</i> L., 1753	NFS	3
<i>Buglossoides incrassata</i> subsp. <i>permixta</i> (Jord.) L.Cecchi & Selvi, 2014	ES	1

Species	Forest affinity	Number of occurrences
<i>Bupleurum longifolium</i> L., 1753	ES	2
<i>Bupleurum rotundifolium</i> L., 1753	NFS	1
<i>Calamagrostis pseudophragmites</i> (Haller f.) Koeler, 1802	ES	5
<i>Carduus personata</i> (L.) Jacq., 1776	NFS	6
<i>Carex depauperata</i> Curtis ex With., 1787	FS	5
<i>Carex depressa</i> Link, 1800	FS	9
<i>Carex flava</i> L., 1753	NFS	8
<i>Carex hordeistichos</i> Vill., 1779	NFS	2
<i>Carex limosa</i> L., 1753	NFS	1
<i>Carex mairei</i> Coss. & Germ., 1840	NFS	1
<i>Carex maritima</i> Gunnerus, 1772	NFS	1
<i>Carex oedipostyla</i> Duval-Jouve, 1870	NFS	19
<i>Carex olbiensis</i> Jord., 1846	NFS	1
<i>Carex pauciflora</i> Lightf., 1777	NFS	2
<i>Carlina biebersteinii</i> Bernh. ex Hornem., 1819	NFS	1
<i>Circaea alpina</i> L., 1753	FS	9
<i>Cirsium carniolicum</i> subsp. <i>rufescens</i> (Ramond ex DC.) P.Fourn., 1940	NFS	17
<i>Cirsium glabrum</i> DC., 1815	NFS	2
<i>Cirsium heterophyllum</i> (L.) Hill, 1768	NFS	25
<i>Cistus laurifolius</i> L., 1753	ES	5
<i>Cistus umbellatus</i> L., 1753	ES	21
<i>Cochlearia pyrenaica</i> DC., 1821	NFS	6
<i>Coeloglossum viride</i> (L.) Hartm., 1820	NFS	2
<i>Colchicum alpinum</i> DC., 1805	NFS	5
<i>Corallorhiza trifida</i> Châtel., 1760	FS	2
<i>Cotoneaster nebrodensis</i> (Guss.) K.Koch, 1853	ES	1
<i>Crocus vernus</i> (L.) Hill, 1765	NFS	1
<i>Cruciata glabra</i> (L.) Ehrend., 1958	ES	3
<i>Cynoglossum germanicum</i> Jacq., 1767	ES	2
<i>Cytinus hypocistis</i> (L.) L., 1767	ES	2
<i>Daboecia cantabrica</i> (Huds.) K.Koch, 1872	ES	19

Species	Forest affinity	Number of occurrences
<i>Daphne cneorum</i> L., 1753	ES	6
<i>Daphne striata</i> Tratt., 1814	NFS	1
<i>Dasiphora fruticosa</i> (L.) Rydb., 1898	NFS	1
<i>Delphinium consolida</i> L., 1753	NFS	1
<i>Dichoropetalum carvifolia</i> (Vill.) Pimenov & Kljuykov, 2007	NFS	1
<i>Draba incana</i> L., 1753	NFS	2
<i>Draba nemorosa</i> L., 1753	NFS	7
<i>Dracocephalum austriacum</i> L., 1753	NFS	1
<i>Drosera rotundifolia</i> L., 1753	NFS	1
<i>Epipogium aphyllum</i> Sw., 1814	FS	26
<i>Eriophorum gracile</i> Koch ex Roth, 1806	NFS	1
<i>Eryngium alpinum</i> L., 1753	NFS	23
<i>Euphorbia illirica</i> Lam., 1788	NFS	8
<i>Euphorbia seguieriana</i> subsp. <i>loiseleurii</i> (Rouy) P.Fourn., 1936	ES	3
<i>Festuca airoides</i> Lam., 1788	NFS	3
<i>Festuca amethystina</i> L., 1753	NFS	1
<i>Festuca longifolia</i> Thuill., 1799	NFS	1
<i>Fritillaria moggridgei</i> Baker, 1879	NFS	16
<i>Gagea bohemica</i> (Zauschn.) Schult. & Schult.f., 1829	NFS	1
<i>Galium pusillum</i> L., 1753	NFS	11
<i>Galium tricornutum</i> Dandy, 1957	NFS	1
<i>Gentiana utriculosa</i> L., 1753	NFS	7
<i>Gratiola officinalis</i> L., 1753	NFS	1
<i>Gymnadenia odoratissima</i> (L.) Rich., 1817	NFS	7
<i>Hackelia deflexa</i> (Wahlenb.) Opiz, 1838	ES	43
<i>Hedysarum boutignyanum</i> (A.Camus) Alleiz., 1928	NFS	11
<i>Hedysarum brigantiacum</i> Bourn., Chas & Kerguélen, 1992	NFS	1
<i>Herminium monorchis</i> (L.) R.Br., 1813	NFS	7
<i>Hieracium isolanum</i> (Besse & Zahn) Zahn, 1916	NFS	1
<i>Horminum pyrenaicum</i> L., 1753	NFS	33
<i>Hypochaeris uniflora</i> Vill., 1779	NFS	3

Species	Forest affinity	Number of occurrences
<i>Hyssopus officinalis</i> L., 1753	NFS	17
<i>Iberis carnosus</i> Willd., 1800	ES	1
<i>Illecebrum verticillatum</i> L., 1753	NFS	1
<i>Impatiens noli-tangere</i> L., 1753	ES	13
<i>Inula bifrons</i> (L.) L., 1763	ES	1
<i>Iris graminea</i> L., 1753	ES	1
<i>Juncus capitatus</i> Weigel, 1772	NFS	15
<i>Juniperus phoenicea</i> L., 1753	ES	1
<i>Kalmia procumbens</i> (L.) Gift, Kron & P.F.Stevens ex Galasso, Banfi & F.Conti, 2005	NFS	2
<i>Lamium galeobdolon</i> subsp. <i>montanum</i> (Pers.) Hayek, 1929	FS	16
<i>Lappula squarrosa</i> (Retz.) Dumort., 1827	ES	2
<i>Laserpitium gallicum</i> L., 1753	ES	1
<i>Lathraea squamaria</i> L., 1753	FS	21
<i>Lathyrus cirrhosus</i> Ser., 1825	ES	1
<i>Lepidium villarsii</i> Gren. & Godr., 1847	NFS	6
<i>Linaria angustissima</i> (Loisel.) Borbás, 1900	NFS	1
<i>Linaria pelisseriana</i> (L.) Mill., 1768	NFS	3
<i>Linaria supina</i> (L.) Chaz., 1790	NFS	3
<i>Linnaea borealis</i> L., 1753	FS	31
<i>Linum austriacum</i> L., 1753	NFS	1
<i>Lunaria rediviva</i> L., 1753	FS	42
<i>Luzula desvauxii</i> Kunth, 1841	NFS	4
<i>Lysimachia minima</i> (L.) U.Manns & Anderb., 2009	NFS	4
<i>Lysimachia tenella</i> L., 1753	NFS	2
<i>Lythrum hyssopifolia</i> L., 1753	NFS	1
<i>Matthiola valesiaca</i> J.Gay ex Boiss., 1867	NFS	16
<i>Mentha arvensis</i> L., 1753	NFS	1
<i>Micranthes clusii</i> (Gouan) B.Bock, 2012	NFS	21
<i>Moehringia lebrunii</i> Merxm., 1965	NFS	6
<i>Molopospermum peloponnesiacum</i> (L.) W.D.J.Koch, 1824	NFS	36
<i>Muscari botryoides</i> (L.) Mill., 1768	NFS	16

Species	Forest affinity	Number of occurrences
<i>Myricaria germanica</i> (L.) Desv., 1824	ES	10
<i>Neotinea maculata</i> (Desf.) Stearn, 1974	NFS	1
<i>Neottia cordata</i> (L.) Rich., 1817	FS	8
<i>Nepeta nuda</i> L., 1753	ES	1
<i>Nothobartsia spicata</i> (Ramond) Bolliger & Molau, 1992	NFS	6
<i>Odontites luteus</i> subsp. <i>lanceolatus</i> (Gaudin) P.Fourn., 1937	NFS	1
<i>Omalotheca norvegica</i> (Gunnerus) Sch.Bip. & F.W.Schultz, 1861	ES	2
<i>Ophrys speculum</i> Link, 1799	NFS	1
<i>Orobanche rapum-genistae</i> Thuill., 1799	ES	10
<i>Orobanche salviae</i> F.W.Schultz ex W.D.J.Koch, 1833	FS	1
<i>Oxytropis fetida</i> (Vill.) DC., 1802	NFS	9
<i>Oxytropis pilosa</i> (L.) DC., 1802	NFS	3
<i>Phelipanche arenaria</i> (Borkh.) Pomel, 1874	NFS	1
<i>Phelipanche lavandulacea</i> (F.W.Schultz) Pomel, 1874	NFS	1
<i>Phyteuma cordatum</i> Balb., 1809	NFS	4
<i>Pinguicula alpina</i> L., 1753	NFS	1
<i>Pinguicula grandiflora</i> subsp. <i>rosea</i> (Mutel) Casper, 1962	NFS	1
<i>Pinguicula longifolia</i> subsp. <i>longifolia</i> Ramond ex DC., 1805	NFS	2
<i>Pinguicula reichenbachiana</i> Schindl., 1908	NFS	2
<i>Pinus nigra</i> subsp. <i>salzmannii</i> (Dunal) Franco, 1943	FS	41
<i>Poa hybrida</i> Gaudin, 1808	NFS	2
<i>Polemonium caeruleum</i> L., 1753	NFS	1
<i>Polygala alpina</i> (DC.) Steud., 1821	NFS	1
<i>Potamogeton natans</i> L., 1753	ES	2
<i>Potentilla alba</i> L., 1753	ES	11
<i>Potentilla cinerea</i> Chaix ex Vill., 1779	NFS	1
<i>Potentilla delphinensis</i> Gren. & Godr., 1848	NFS	12
<i>Potentilla fagineicola</i> Lamotte, 1877	NFS	1
<i>Psilurus incurvus</i> (Gouan) Schinz & Thell., 1913	NFS	3
<i>Quercus cerris</i> L., 1753	FS	8
<i>Radiola linoides</i> Roth, 1788	NFS	6

Species	Forest affinity	Number of occurrences
<i>Ranunculus trichophyllus</i> subsp. <i>eradicatus</i> (Laest.) C.D.K.Cook, 1967	ES	2
<i>Rhaponticum centauroides</i> (L.) O.Bolòs, 1970	NFS	7
<i>Rhynchospora alba</i> (L.) Vahl, 1805	NFS	4
<i>Ruscus hypoglossum</i> L., 1753	FS	12
<i>Salix daphnoides</i> Vill., 1779	ES	1
<i>Salvia aethiopsis</i> L., 1753	ES	5
<i>Saussurea alpina</i> (L.) DC., 1810	NFS	1
<i>Saxifraga cuneifolia</i> subsp. <i>cuneifolia</i> L., 1759	FS	1
<i>Saxifraga hirculus</i> L., 1753	NFS	1
<i>Saxifraga iratiana</i> F.W.Schultz, 1851	NFS	1
<i>Schoenus ferrugineus</i> L., 1753	NFS	5
<i>Scrophularia pyrenaica</i> Benth., 1846	NFS	1
<i>Silene inaperta</i> L., 1753	NFS	1
<i>Silene noctiflora</i> L., 1753	NFS	2
<i>Silene viridiflora</i> L., 1762	ES	9
<i>Spergula segetalis</i> (L.) Vill., 1789	NFS	1
<i>Spiranthes aestivalis</i> (Poir.) Rich., 1817	NFS	7
<i>Stipa pennata</i> L., 1753	NFS	2
<i>Streptopus amplexifolius</i> (L.) DC., 1805	NFS	5
<i>Swertia perennis</i> L., 1753	NFS	13
<i>Symphytum bulbosum</i> K.F.Schimp., 1825	ES	3
<i>Tephrosia helenitis</i> (L.) B.Nord., 1978	NFS	27
<i>Thalictrum lucidum</i> L., 1753	ES	1
<i>Trichophorum alpinum</i> (L.) Pers., 1805	NFS	1
<i>Trifolium saxatile</i> All., 1773	NFS	3
<i>Trinia glauca</i> (L.) Dumort., 1827	NFS	1
<i>Trochiscanthes nodiflora</i> (All.) W.D.J.Koch, 1824	ES	35
<i>Turgenia latifolia</i> (L.) Hoffm., 1814	NFS	1
<i>Utricularia minor</i> L., 1753	ES	2
<i>Vaccinium microcarpum</i> (Turcz. ex Rupr.) Schmalh., 1871	ES	1
<i>Veronica montana</i> L., 1755	NFS	1

Species	Forest affinity	Number of occurrences
<i>Veronica spicata</i> L., 1753	NFS	2
<i>Vicia cassubica</i> L., 1753	ES	5
<i>Vicia disperma</i> DC., 1813	NFS	1
<i>Viola pinnata</i> L., 1753	ES	2
<i>Viscaria vulgaris</i> Bernh., 1800	NFS	1
Pteridophyta		
<i>Allosorus hispanicus</i> (Mett.) Christenh., 2012	NFS	1
<i>Allosorus tinaei</i> (Tod.) Christenh., 2012	NFS	2
<i>Botrychium matricariifolium</i> (Retz.) W.D.J.Koch, 1845	NFS	11
<i>Cystopteris dickieana</i> R. Sim, 1848	NFS	3
<i>Diphasiastrum alpinum</i> (L.) Holub, 1975	ES	2
<i>Dryopteris ardechensis</i> Fraser-Jenk., 1981	ES	59
<i>Dryopteris oreades</i> Fomin, 1911	ES	22
<i>Lycopodiella inundata</i> (L.) Holub, 1964	NFS	4
<i>Spinulum annotinum</i> (L.) A.Haines, 2003	ES	7
Bryophyta		
<i>Amblyodon dealbatus</i> (Hedw.) P.Beauv., 1804	NFS	1
<i>Andreaea rothii</i> subsp. <i>falcata</i> (Schimp.) Lindb., 1879	NFS	1
<i>Andreaea rothii</i> subsp. <i>rothii</i> F. Weber & D. Mohr, 1807	NFS	2
<i>Anthoceros agrestis</i> Paton, 1979	ES	2
<i>Atrichum angustatum</i> (Brid.) Bruch & Schimp., 1844	ES	15
<i>Barbilophozia lycopodioides</i> (Wallr.) Loeske, 1907	FS	13
<i>Bartramia stricta</i> Brid., 1803	NFS	2
<i>Bazzania flaccida</i> (Dumort.) Grolle, 1972	FS	2
<i>Biantheridion undulifolium</i> (Nees) Konstant. & Vilnet, 2010	NFS	1
<i>Blasia pusilla</i> L., 1753	NFS	1
<i>Brachydontium trichodes</i> (F. Weber) Milde, 1869	FS	2
<i>Brachytheciastrum velutinum</i> (Hedw.) Ignatov & Huttunen, 2002	FS	10
<i>Brachythecium glareosum</i> (Bruch ex Spruce) Schimp., 1853	ES	4
<i>Brachythecium mildeanum</i> (Schimp.) Schimp., 1862	ES	1

Species	Forest affinity	Number of occurrences
<i>Brachythecium tenuicaule</i> (Spruce) Kindb., 1900	FS	3
<i>Brachythecium tommasinii</i> (Sendtn. ex Boulay) Ignatov & Huttunen, 2002	NFS	1
<i>Bryum gemmiparum</i> De Not., 1865	NFS	4
<i>Bryum ruderale</i> Crundw. & Nyholm, 1963	NFS	1
<i>Buckia vaucheri</i> (Lesq.) D.Ríos, M.T.Gallego & J.Guerra, 2018	NFS	1
<i>Calypogeia arguta</i> Nees & Mont., 1838	ES	15
<i>Calypogeia suecica</i> (Arnell & J.Perss.) Müll.Frib., 1904	FS	1
<i>Campyliadelphus chrysophyllus</i> (Brid.) R.S.Chopra	ES	6
<i>Campylium protensum</i> (Brid.) Kindb., 1894	ES	4
<i>Campylophyllopsis calcarea</i> (Crundw. & Nyholm) Ochyra, 2010	FS	10
<i>Campylopus pilifer</i> Brid., 1819	NFS	15
<i>Cephaloziella baumgartneri</i> Schiffn., 1905	NFS	2
<i>Cephaloziella dentata</i> (Raddi) Steph., 1897	NFS	2
<i>Cephaloziella hampeana</i> (Nees) Schiffn.ex Loeske, 1903	ES	9
<i>Cephaloziella integerrima</i> (Lindb.) Warnst., 1902	FS	1
<i>Cephaloziella phyllacantha</i> (C.Massal. & Carestia) Müll.Frib., 1913	FS	1
<i>Cephaloziella rubella</i> (Nees) Warnst., 1902	FS	1
<i>Cephaloziella stellulifera</i> (Taylor ex Carrington & Pearson) Croz., 1903	NFS	2
<i>Cephaloziella turneri</i> (Hook.) Müll.Frib., 1913	NFS	6
<i>Cinclidotus danubicus</i> Schiffn. & Baumgartner, 1906	NFS	1
<i>Codonoblepharon forsteri</i> (Dicks.) Goffinet, 2004	FS	18
<i>Conardia compacta</i> (Drumm. ex Müll.Hal.) H.Rob.	FS	1
<i>Coscinodon cribrus</i> (Hedw.) Spruce, 1849	NFS	20
<i>Crossocalyx hellerianus</i> (Nees ex Lindenb.) Meyl., 1939	FS	1
<i>Cynodontium strumiferum</i> (Hedw.) Lindb., 1864	ES	2
<i>Dicranum fuscescens</i> Sm.	FS	1
<i>Dicranum muehlenbeckii</i> Bruch & Schimp., 1847	FS	1
<i>Dicranum spadiceum</i> J.E.Zetterst., 1865	ES	3
<i>Didymodon acutus</i> (Brid.) K.Saito, 1975	NFS	5
<i>Didymodon ferrugineus</i> (Schimp. ex Besch.) M.O.Hill, 1981	NFS	3
<i>Didymodon glaucus</i> Ryan, 1901	NFS	1

Species	Forest affinity	Number of occurrences
<i>Didymodon spadiceus</i> (Mitt.) Limpr., 1888	ES	1
<i>Didymodon tophaceus</i> (Brid.) Lisa, 1837	NFS	5
<i>Douinia ovata</i> (Dicks.) H.Buch, 1928	FS	9
<i>Encalypta vulgaris</i> Hedw., 1801	ES	7
<i>Entosthodon attenuatus</i> (Dicks.) Bryhn, 1908	ES	2
<i>Entosthodon fascicularis</i> (Hedw.) Müll.Hal., 1848	NFS	1
<i>Entosthodon muhlenbergii</i> (Turner) Fife, 1985	NFS	2
<i>Entosthodon obtusus</i> (Hedw.) Lindb., 1865	NFS	4
<i>Entosthodon pulchellus</i> (H.Philib.) Brugués	NFS	1
<i>Eucladium verticillatum</i> (With.) Bruch & Schimp., 1846	ES	48
<i>Eurhynchium angustirete</i> (Broth.) T.J.Kop., 1967	FS	3
<i>Fissidens exilis</i> Hedw., 1801	ES	1
<i>Fissidens gracilifolius</i> Brugg.-Nann. & Nyholm, 1986	FS	1
<i>Fissidens osmundoides</i> Hedw., 1801	NFS	1
<i>Fissidens rivularis</i> (Spruce) Schimp., 1851	NFS	2
<i>Fossombronia angulosa</i> (Dicks.) Raddi, 1818	NFS	20
<i>Fossombronia caespitiformis</i> (Raddi) De Not. ex Rabenh., 1860	ES	1
<i>Fossombronia pusilla</i> (L.) Nees, 1838	NFS	3
<i>Fossombronia wondraczekii</i> (Corda) Dumort. ex Lindb., 1873	ES	1
<i>Fuscocephaloziopsis lunulifolia</i> (Dumort.) Vána & L.Söderstr., 2013	FS	1
<i>Gongylanthus ericetorum</i> (Raddi) Nees, 1836	NFS	12
<i>Grimmia elatior</i> Bruch ex Bals.-Criv. & De Not., 1838	NFS	6
<i>Grimmia funalis</i> (Schwägr.) Bruch & Schimp., 1845	NFS	6
<i>Grimmia incurva</i> Schwägr., 1811	NFS	2
<i>Grimmia longirostris</i> Hook., 1818	NFS	4
<i>Grimmia muehlenbeckii</i> Schimp., 1860	ES	2
<i>Grimmia orbicularis</i> Bruch ex Wilson, 1844	NFS	7
<i>Grimmia tergestina</i> Tomm. ex Bruch & Schimp., 1845	NFS	2
<i>Gymnostomum viridulum</i> Brid., 1826	NFS	1
<i>Gyroweisia tenuis</i> (Hedw.) Schimp., 1876	ES	1
<i>Habrodon perpusillus</i> (De Not.) Lindb., 1863	FS	38

Species	Forest affinity	Number of occurrences
<i>Heterocradiella dimorpha</i> (Brid.) Ignatov & Fedosov, 2019	NFS	4
<i>Heterocladium wulfsbergii</i> I.Hagen, 1909	FS	3
<i>Homalothecium philippeanum</i> (Spruce) Schimp., 1851	ES	3
<i>Hydrogonium croceum</i> (Brid.) Jan Kucera, 2013	NFS	3
<i>Hygrohypnum luridum</i> (Hedw.) Jenn., 1913	ES	12
<i>Hylocomiastrum umbratum</i> (Hedw.) M.Fleisch. ex Broth., 1925	FS	1
<i>Hyocomium armoricum</i> (Brid.) Wijk & Margad., 1961	ES	29
<i>Isopterygiella pulchella</i> (Hedw.) Ignatov & Ignatova, 2020	NFS	2
<i>Kiaeria starkei</i> (F.Weber & D.Mohr) I.Hagen, 1915	NFS	1
<i>Leptodon smithii</i> (Hedw.) F.Weber & D.Mohr, 1803	FS	23
<i>Lescurea plicata</i> (Schleich. ex F.Weber & D.Mohr) Broth.	NFS	7
<i>Lescurea radicata</i> (Mitt.) Mönk., 1927	NFS	1
<i>Lescurea saxicola</i> (Schimp.) Molendo, 1864	NFS	1
<i>Lewinskya acuminata</i> (H.Philib.) F.Lara, Garilleti & Goffinet, 2016	ES	28
<i>Lewinskya shawii</i> (Wilson) F.Lara, Garilleti & Goffinet, 2016	NFS	1
<i>Lophocolea fragrans</i> (Moris & De Not.) Gottsche, Lindenb. & Nees, 1845	FS	2
<i>Lophozia ascendens</i> (Warnst.) R.M.Schust., 1952	FS	3
<i>Mannia androgyna</i> (L.) A.Evans, 1938	NFS	9
<i>Mannia fragrans</i> (Balb.) Frye & L.Clark, 1937	NFS	1
<i>Mannia triandra</i> (Scop.) Grolle, 1975	NFS	4
<i>Marchantia quadrata</i> Scop., 1772	NFS	31
<i>Meesia uliginosa</i> Hedw., 1801	NFS	3
<i>Mesoptychia bantriensis</i> (Hook.) L.Söderstr. & Vána, 2012	NFS	13
<i>Mesoptychia heterocolpos</i> (Thed. ex Hartm.) L.Söderstr. & Vána, 2012	NFS	5
<i>Mesoptychia turbinata</i> (Raddi) L.Söderstr. & Vána, 2012	NFS	8
<i>Mnium marginatum</i> (Dicks.) P.Beauv.	FS	4
<i>Mnium spinosum</i> (Voit) Schwägr., 1816	FS	8
<i>Mnium thomsonii</i> Schimp., 1876	ES	8
<i>Mylia anomala</i> (Hook.) Gray, 1821	NFS	1
<i>Myurella julacea</i> (Schwägr.) Schimp., 1853	NFS	7
<i>Neoorthocaulis attenuatus</i> (Mart.) L.Söderstr., De Roo & Hedd., 2010	ES	3

Species	Forest affinity	Number of occurrences
<i>Neorthocaulis floerkei</i> (F. Weber & D. Mohr) L. Söderstr., De Roo & Hedd., 2010	NFS	2
<i>Obtusifolium obtusum</i> (Lindb.) S. W. Arnell, 1956	FS	4
<i>Odontoschisma fluitans</i> (Nees) L. Söderstr. & Vána, 2013	NFS	1
<i>Orthothecium intricatum</i> (Hartm.) Schimp., 1851	FS	15
<i>Orthotrichum pumilum</i> Sw. ex anon.	NFS	7
<i>Orthotrichum rogeri</i> Brid., 1812	ES	11
<i>Orthotrichum scanicum</i> Grönvall, 1885	ES	2
<i>Orthotrichum stellatum</i> Brid., 1826	ES	1
<i>Orthotrichum tenellum</i> Bruch ex Brid., 1827	NFS	18
<i>Oxyrrhynchium schleicheri</i> (R. Hedw.) Röll	FS	4
<i>Palustriella commutata</i> (Hedw.) Ochyra, 1989	ES	26
<i>Palustriella decipiens</i> (De Not.) Ochyra, 1989	NFS	2
<i>Pedinophyllum interruptum</i> (Nees) Kaal., 1893	FS	7
<i>Phaeoceros carolinianus</i> (Michx.) Prosk., 1951	NFS	2
<i>Phaeoceros laevis</i> (L.) Prosk., 1951	NFS	7
<i>Philonotis calcarea</i> (Bruch & Schimp.) Schimp., 1856	NFS	2
<i>Philonotis capillaris</i> Lindb., 1867	NFS	14
<i>Philonotis rigida</i> Brid., 1827	NFS	3
<i>Philonotis tomentella</i> Molendo, 1864	NFS	5
<i>Plagiomnium elatum</i> (Bruch & Schimp.) T. J. Kop., 1968	NFS	3
<i>Plagiomnium medium</i> (Bruch & Schimp.) T. J. Kop., 1968	FS	4
<i>Plagiomnium rostratum</i> (Schröd.) T. J. Kop., 1968	ES	5
<i>Plagiothecium laetum</i> Schimp., 1851	FS	9
<i>Plagiothecium piliferum</i> (Sw.) Schimp., 1851	NFS	5
<i>Plagiothecium platyphyllum</i> Mönk., 1927	FS	4
<i>Plasteurhynchium striatulum</i> (Spruce) M. Fleisch., 1925	FS	9
<i>Platydictya jungermannioides</i> (Brid.) H. A. Crum, 1964	FS	10
<i>Platyhypnum duriusculum</i> (De Not.) Ochyra, 2013	NFS	2
<i>Pogonatum nanum</i> (Schreb. ex Hedw.) P. Beauv., 1805	ES	2
<i>Pohlia bulbifera</i> (Warnst.) Warnst., 1904	NFS	1
<i>Pohlia prolifera</i> (Kindb.) Lindb. ex Broth.	ES	2

Species	Forest affinity	Number of occurrences
<i>Pohlia sphagnicola</i> (Bruch & Schimp.) Broth., 1903	NFS	1
<i>Polytrichastrum alpinum</i> (Hedw.) G.L.Sm., 1971	ES	16
<i>Porella obtusata</i> (Taylor) Trevis., 1877	NFS	7
<i>Pottiopsis caespitosa</i> (Brid.) Blockeel & A.J.E.Sm.	NFS	1
<i>Pterygoneurum ovatum</i> (Hedw.) Dixon, 1934	NFS	1
<i>Ptilidium pulcherrimum</i> (Weber) Vain.	FS	4
<i>Ptilium crista-castrensis</i> (Hedw.) De Not., 1867	FS	27
<i>Ptychostomum creberrimum</i> (Taylor) J.R.Spence & H.P.Ramsay, 2005	NFS	1
<i>Ptychostomum elegans</i> (Nees) D.Bell & Holyoak, 2020	ES	5
<i>Ptychostomum imbricatum</i> (Müll.Hal.) Holyoak & N.Pedersen, 2007	NFS	5
<i>Ptychostomum torquescens</i> (Bruch & Schimp.) Ros & Mazimpaka, 2013	ES	5
<i>Ptychostomum zieri</i> (Hedw.) Holyoak & N.Pedersen, 2007	NFS	7
<i>Racomitrium ericoides</i> (Brid.) Brid., 1819	ES	2
<i>Racomitrium sudeticum</i> (Funck) Bruch & Schimp., 1845	NFS	4
<i>Rhizomnium pseudopunctatum</i> (Bruch & Schimp.) T.J.Kop., 1968	ES	1
<i>Rhynchostegiella curviseta</i> (Brid.) Limpr., 1896	ES	8
<i>Rhynchostegium murale</i> (Hedw.) Schimp., 1852	ES	5
<i>Rhytidiadelphus subpinnatus</i> (Lindb.) T.J.Kop., 1971	FS	1
<i>Riccardia chamedryfolia</i> (With.) Grolle, 1969	ES	8
<i>Riccia beyrichiana</i> Hampe, 1838	NFS	18
<i>Riccia ciliata</i> Hoffm., 1795	NFS	1
<i>Riccia ciliifera</i> Link ex Lindenb.	NFS	2
<i>Riccia crozalsii</i> Levier, 1902	NFS	5
<i>Riccia gougetiana</i> Durieu & Mont., 1849	NFS	3
<i>Riccia nigrella</i> DC., 1815	NFS	7
<i>Riccia subbifurca</i> Warnst. ex Croz., 1903	FS	2
<i>Riccia warnstorffii</i> Limpr. ex Warnst., 1899	NFS	11
<i>Saccogyna viticulosa</i> (L.) Dumort., 1831	FS	10
<i>Saelania glaucescens</i> (Hedw.) Broth., 1894	NFS	16
<i>Scapania aequiloba</i> (Schwägr.) Dumort., 1835	ES	10
<i>Scapania aspera</i> M.Bernet & Bernet, 1888	ES	14

Species	Forest affinity	Number of occurrences
<i>Scapania compacta</i> (Roth) Dumort., 1835	ES	26
<i>Scapania cuspiduligera</i> (Nees) Müll.Frib., 1915	NFS	3
<i>Scapania paludicola</i> Loeske & Müll.Frib., 1915	NFS	1
<i>Scapania scandica</i> (Arnell & H.Buch) Macvicar, 1926	NFS	17
<i>Scapania umbrosa</i> (Schrad.) Dumort., 1835	FS	8
<i>Schistochilopsis opacifolia</i> (Culm. ex Meyl.) Konstant., 1994	NFS	1
<i>Schistostega pennata</i> (Hedw.) F. Weber & D. Mohr, 1803	FS	9
<i>Sciuro-hypnum curtum</i> (Lindb.) Ignatov, 2008	FS	1
<i>Scleropodium touretii</i> (Brid.) L.F.Koch, 1949	ES	11
<i>Scorpidium cossonii</i> (Schimp.) Hedenäs, 1989	NFS	1
<i>Scorpiurium circinatum</i> (Brid.) M.Fleisch. & Loeske, 1907	ES	16
<i>Seligeria donniana</i> (Sm.) Müll.Hal., 1848	FS	2
<i>Seligeria pusilla</i> (Hedw.) Bruch & Schimp., 1846	FS	2
<i>Serpoleskea confervoides</i> (Brid.) Loeske, 1904	NFS	1
<i>Solenostoma confertissimum</i> (Nees) Schljakov, 1981	NFS	1
<i>Solenostoma hyalinum</i> (Lyell) Mitt., 1870	ES	3
<i>Solenostoma sphaerocarpum</i> (Hook.) Steph., 1901	NFS	1
<i>Southbya tophacea</i> (Spruce) Spruce, 1850	NFS	4
<i>Syntrichia montana</i> var. <i>montana</i> Nees, 1819	NFS	4
<i>Syntrichia virescens</i> (De Not.) Ochyra, 1992	NFS	1
<i>Targionia hypophylla</i> L., 1753	NFS	15
<i>Thuidium recognitum</i> (Hedw.) Lindb., 1874	FS	6
<i>Timmia austriaca</i> Hedw., 1801	ES	1
<i>Tortella inclinata</i> (R.Hedw.) Limpr., 1888	NFS	3
<i>Tortula atrovirens</i> (Sm.) Lindb., 1864	NFS	1
<i>Tortula inermis</i> (Brid.) Mont., 1832	NFS	1
<i>Tortula marginata</i> (Bruch & Schimp.) Spruce, 1845	ES	2
<i>Trichostomum brachydontium</i> Bruch, 1829	ES	49
<i>Trichostomum crispulum</i> Bruch, 1829	ES	17
<i>Ulota hutchinsiae</i> (Sm.) Hammar, 1852	ES	4

Species	Forest affinity	Number of occurrences
Lichens		
<i>Acarospora admissa</i> (Nyl.) Kullh., 1871	NFS	1
<i>Acrocordia salweyi</i> (Leight. ex Nyl.) A. L. Sm., 1911	FS	2
<i>Ainoa mooreana</i> (Carroll) Lumbsch & I. Schmitt, 2001	NFS	1
<i>Alyxoria ochrocheila</i> (Nyl.) Ertz & Tehler, 2011	FS	1
<i>Anaptychia crinalis</i> (Schleich.) Vezda	FS	3
<i>Anema moedlingense</i> Zahlbr., 1908	NFS	1
<i>Arthonia leucopellaea</i> (Ach.) Almq., 1880	FS	3
<i>Aspicilia laevata</i> (Ach.) Arnold, 1887	ES	3
<i>Bacidina caligans</i> (Nyl.) P. Clerc	ES	1
<i>Baeomyces placophyllus</i> Ach., 1803	NFS	4
<i>Bellemerea diamarta</i> (Ach.) Hafellner & Cl.Roux	NFS	1
<i>Bellemerea sanguinea</i> (Kremp.) Hafellner & Cl.Roux	ES	2
<i>Biatora chrysantha</i> (Zahlbr.) Printzen, 1994	FS	2
<i>Biatora nylanderi</i> Anzi, 1860	FS	1
<i>Biatora ocelliformis</i> (Nyl.) Arnold, 1870	FS	1
<i>Biatoridium monasteriense</i> J. Lahm ex Körb., 1860	FS	1
<i>Bryonora rhypariza</i> (Nyl.) Poelt, 1983	ES	2
<i>Bryoria bicolor</i> (Ehrh.) Brodo & D.Hawksw., 1977	ES	13
<i>Bryoria implexa</i> (Hoffm.) Brodo & D.Hawksw., 1977	FS	1
<i>Bryoria subcana</i> (Nyl. ex Stizenb.) Brodo & D.Hawksw., 1977	ES	3
<i>Buellia epigaea</i> (Pers.) Tuck.	NFS	1
<i>Calicium trabinellum</i> (Ach.) Ach., 1810	FS	2
<i>Caloplaca conversa</i> (Kremp.) Jatta, 1900	NFS	1
<i>Caloplaca exsecuta</i> (Nyl.) Dalla Torre & Sarnth., 1902	NFS	1
<i>Catolechia wahlenbergii</i> (Ach.) Körb., 1855	ES	13
<i>Chaenotheca brunneola</i> (Ach.) Müll.Arg., 1862	FS	3
<i>Chaenotheca phaeocephala</i> (Turner) Th.Fr., 1861	ES	2
<i>Chaenothecopsis epithallina</i> Tibell, 1975	FS	1
<i>Chaenothecopsis pusiola</i> (Ach.) Vain., 1927	FS	1

Species	Forest affinity	Number of occurrences
<i>Chaenothecopsis savonica</i> (Räsänen) Tibell, 1984	FS	1
<i>Chaenothecopsis subparoica</i> (Nyl.) Tibell, 1995	ES	1
<i>Cladonia sulphurina</i> (Michx.) Fr., 1831	FS	1
<i>Cliostomum corrugatum</i> (Ach.) Fr., 1845	ES	2
<i>Collema glebulentum</i> (Nyl. ex Cromb.) Degel., 1952	NFS	1
<i>Cyphelium inquinans</i> (Sm.) Trevis., 1862	FS	1
<i>Cyphelium karelicum</i> (Vain.) Räsänen, 1939	FS	1
<i>Cyphelium notarisii</i> (Tul.) Blomb. & Forssell, 1880	ES	2
<i>Cyphelium pinicola</i> Tibell, 1969	ES	1
<i>Degelia atlantica</i> (Degel.) P. M. Jørg. & P. James	FS	6
<i>Fuscidea austera</i> (Nyl.) P. James, 1980	NFS	1
<i>Fuscidea gothoburgensis</i> (H. Magn.) V. Wirth & Vezda	ES	1
<i>Fuscopannaria sampaiana</i> Tav.	FS	1
<i>Graphis betulina</i> (Pers.) Ach.	ES	1
<i>Gyalecta derivata</i> (Nyl.) H. Olivier, 1911	FS	3
<i>Hypocenomyce anthracophila</i> (Nyl.) P. James & Gotth. Schneid.	ES	1
<i>Hypogymnia austerodes</i> (Nyl.) Räsänen, 1943	ES	2
<i>Ionaspis obtecta</i> (Vain.) R. Sant., 2004	NFS	1
<i>Ionaspis suaveolens</i> (Fr.) Th.Fr. ex Stein	NFS	1
<i>Lecanora caesiosora</i> Poelt, 1966	ES	1
<i>Lecanora eurycarpa</i> Poelt, Leuckert & Cl. Roux non Nyl.	NFS	1
<i>Lecanora orbicularis</i> (Schaer.) Vain., 1899	NFS	1
<i>Lecidea albohyalina</i> (Nyl.) Th.Fr., 1874	FS	1
<i>Lecidea paupercula</i> Th.Fr., 1874	NFS	1
<i>Lepraria lobificans</i> Nyl., 1873	NFS	8
<i>Leptogium corticola</i> (Taylor) Tuck., 1849	FS	1
<i>Leptogium furfuraceum</i> (Harm.) Sierk, 1964	ES	1
<i>Llimoniella phaeophysciae</i> Diederich, Ertz & Etayo, 2010	FS	1
<i>Lobaria linita</i> (Ach.) Rabenh., 1845	ES	1
<i>Lobaria virens</i> (With.) J. R. Laundon	FS	9
<i>Lobothallia parasitica</i> (B. de Lesd.)	NFS	1

Species	Forest affinity	Number of occurrences
<i>Massalongia carnos</i> (Dicks.) Körb., 1855	ES	5
<i>Megalospora tuberculosa</i> (Fée) Sipman, 1983	FS	1
<i>Melanelia panniformis</i> (Nyl.) Essl., 1978	ES	1
<i>Melanelia tominii</i> (Oksner) Essl.	NFS	1
<i>Menegazzia terebrata</i> (Hoffm.) A.Massal., 1854	ES	14
<i>Micarea adnata</i> Coppins, 1983	FS	1
<i>Micarea lutulata</i> (Nyl.) Coppins, 1980	NFS	1
<i>Microcalicium disseminatum</i> (Ach.) Vain., 1927	FS	3
<i>Neocatapyrenium radicescens</i> (Nyl.) Breuss, 1996	NFS	1
<i>Ochrolechia szatalaensis</i> Vers.	FS	1
<i>Opegrapha vulpina</i> Vondrák, Kocourk. & Tretiach, 2008	NFS	1
<i>Parmeliella testacea</i> P. M. Jørg.	FS	2
<i>Peltigera neopolydactyla</i> (Gyeln.) Gyeln., 1932	ES	1
<i>Peltigera scabrosa</i> Th.Fr., 1861	NFS	1
<i>Pertusaria glomerata</i> (Ach.) Schaer., 1826	ES	1
<i>Physcia phaea</i> (Tuck.) Thoms.	NFS	2
<i>Placopsis gelida</i> (L.) Linds., 1866	NFS	1
<i>Placynthium lismorense</i> (Cromb.) Vain., 1909	NFS	1
<i>Porina hoehneliana</i> (Jaap) R. Sant., 1952	FS	2
<i>Porina leptosperma</i> Müll.Arg., 1883	FS	1
<i>Porpidia platycarpoides</i> (Bagl.) Hertel, 1987	NFS	1
<i>Pycnora sorophora</i> (Vain.) Hafellner, 2001	ES	2
<i>Ramboldia elabens</i> (Fr.) Kantvilas & Elix, 2007	ES	2
<i>Ramonia subsphaeroides</i> (Tav.) Vezda	FS	3
<i>Rhizocarpon postumum</i> (Nyl.) Arnold, 1870	ES	1
<i>Rhizocarpon subgeminatum</i> Eitn.	NFS	1
<i>Rosellinula haplospora</i> (Th.Fr. & Almq.) R. Sant., 1986	NFS	1
<i>Sarcogyne fallax</i> H. Magn., 1935	NFS	2
<i>Schaereria cinereorufa</i> (Schaer.) Th.Fr., 1861	ES	1
<i>Solenopsora liparina</i> (Nyl.) Zahlbr., 1919	NFS	1
<i>Sticta fuliginosa</i> (Dicks.) Ach., 1803	FS	26

Species	Forest affinity	Number of occurrences
<i>Sticta limbata</i> (Sm.) Ach., 1803	FS	23
<i>Sticta sylvatica</i> (Huds.) Ach., 1803	FS	19
<i>Strigula angustata</i> Cl.Roux & Sérus.	FS	3
<i>Strigula buxi</i> Chodat, 1912	FS	4
<i>Strigula endolithe</i> a Cl.Roux & Bricaud	ES	1
<i>Strigula minor</i> (Vezda) Cl.Roux & Sérus.	FS	3
<i>Thelidium dionantense</i> (Hue) Zschacke	NFS	1
<i>Thelotrema lepadinum</i> (Ach.) Ach., 1803	FS	5
<i>Trapelia placodioides</i> Coppins & P. James, 1984	ES	2
<i>Usnea longissima</i> Ach., 1810	FS	3
<i>Usnea schadenbergiana</i> Göp. & Stein	ES	1
<i>Verrucaria constricta</i> Zschacke, 1933	NFS	1
<i>Verrucaria geophila</i> Zahlbr.	ES	1
<i>Verrucula polycarparia</i> Nav.-Ros. & Cl.Roux	ES	1
<i>Xylographa trunciseda</i> (Th.Fr.) Minks. ex Redinger	FS	2
Chiroptera		
<i>Miniopterus schreibersii</i> (Natterer in Kuhl, 1817)	NFS	2
<i>Myotis bechsteinii</i> (Kuhl, 1817)	FS	11
<i>Myotis blythii</i> (Tomes, 1857)	NFS	11
<i>Myotis capaccinii</i> (Bonaparte, 1837)	NFS	1
<i>Nyctalus lasiopterus</i> (Schreber, 1780)	FS	10
<i>Nyctalus noctula</i> (Schreber, 1774)	FS	3
<i>Rhinolophus euryale</i> Blasius, 1853	ES	2
<i>Rhinolophus ferrumequinum</i> (Schreber, 1774)	ES	31
Aves		
<i>Acrocephalus scirpaceus</i> (Hermann, 1804)	NFS	1
<i>Actitis hypoleucos</i> (Linnaeus, 1758)	NFS	5
<i>Aegolius funereus</i> (Linnaeus, 1758)	FS	562
<i>Alcedo atthis</i> (Linnaeus, 1758)	NFS	4
<i>Alectoris graeca</i> (Meisner, 1804)	NFS	110

Species	Forest affinity	Number of occurrences
<i>Alectoris rufa</i> (Linnaeus, 1758)	NFS	10
<i>Anser anser</i> (Linnaeus, 1758)	NFS	1
<i>Anthus campestris</i> (Linnaeus, 1758)	NFS	2
<i>Anthus pratensis</i> (Linnaeus, 1758)	NFS	3
<i>Ardea alba</i> Linnaeus, 1758	NFS	2
<i>Ardea purpurea</i> Linnaeus, 1766	NFS	10
<i>Ardeola ralloides</i> (Scopoli, 1769)	NFS	1
<i>Bonasa bonasia</i> (Linnaeus, 1758)	FS	97
<i>Bubo bubo</i> (Linnaeus, 1758)	NFS	30
<i>Bubulcus ibis</i> (Linnaeus, 1758)	NFS	1
<i>Carduelis carduelis</i> (Linnaeus, 1758)	NFS	27
<i>Carduelis citrinella</i> (Pallas, 1764)	FS	54
<i>Ciconia ciconia</i> (Linnaeus, 1758)	NFS	1
<i>Ciconia nigra</i> (Linnaeus, 1758)	FS	7
<i>Columba livia</i> Gmelin, 1789	NFS	1
<i>Columba oenas</i> Linnaeus, 1758	FS	60
<i>Corvus corax</i> Linnaeus, 1758	NFS	222
<i>Coturnix coturnix</i> (Linnaeus, 1758)	NFS	4
<i>Delichon urbicum</i> (Linnaeus, 1758)	NFS	2
<i>Dendrocopos leucotos</i> (Bechstein, 1803)	FS	277
<i>Dendrocopos medius</i> (Linnaeus, 1758)	FS	1
<i>Dendrocopos minor</i> (Linnaeus, 1758)	FS	6
<i>Egretta garzetta</i> (Linnaeus, 1766)	NFS	6
<i>Emberiza cia</i> Linnaeus, 1766	NFS	86
<i>Emberiza citrinella</i> Linnaeus, 1758	NFS	40
<i>Emberiza hortulana</i> Linnaeus, 1758	NFS	17
<i>Emberiza schoeniclus</i> (Linnaeus, 1758)	NFS	1
<i>Falco naumanni</i> Fleischer, 1818	NFS	3
<i>Falco peregrinus</i> Tunstall, 1771	NFS	157
<i>Ficedula hypoleuca</i> (Pallas, 1764)	FS	72
<i>Gallinago gallinago</i> (Linnaeus, 1758)	NFS	1

Species	Forest affinity	Number of occurrences
<i>Glaucidium passerinum</i> (Linnaeus, 1758)	FS	408
<i>Grus grus</i> (Linnaeus, 1758)	NFS	7
<i>Hirundo rustica</i> Linnaeus, 1758	NFS	5
<i>Jynx torquilla</i> Linnaeus, 1758	NFS	10
<i>Lagopus muta</i> (Montin, 1776)	NFS	11
<i>Lanius senator</i> Linnaeus, 1758	NFS	1
<i>Linaria cannabina</i> (Linnaeus, 1758)	NFS	28
<i>Merops apiaster</i> Linnaeus, 1758	NFS	1
<i>Monticola saxatilis</i> (Linnaeus, 1766)	NFS	6
<i>Muscicapa striata</i> (Pallas, 1764)	NFS	9
<i>Nucifraga caryocatactes</i> (Linnaeus, 1758)	FS	432
<i>Nycticorax nycticorax</i> (Linnaeus, 1758)	NFS	1
<i>Otus scops</i> (Linnaeus, 1758)	NFS	10
<i>Pandion haliaetus</i> (Linnaeus, 1758)	NFS	17
<i>Petronia petronia</i> (Linnaeus, 1766)	NFS	2
<i>Phylloscopus sibilatrix</i> (Bechstein, 1793)	FS	16
<i>Poecile montanus</i> (Conrad von Baldenstein, 1827)	FS	421
<i>Prunella collaris</i> (Scopoli, 1769)	NFS	42
<i>Puffinus mauretanicus</i> P. R. Lowe, 1921	NFS	2
<i>Puffinus puffinus</i> (Brünnich, 1764)	NFS	1
<i>Pyrhacorax pyrrhacorax</i> (Linnaeus, 1758)	NFS	108
<i>Pyrrhula pyrrhula</i> (Linnaeus, 1758)	FS	727
<i>Rallus aquaticus</i> Linnaeus, 1758	NFS	1
<i>Saxicola rubetra</i> (Linnaeus, 1758)	NFS	18
<i>Saxicola rubicola</i> (Linnaeus, 1766)	NFS	11
<i>Scolopax rusticola</i> Linnaeus, 1758	FS	32
<i>Serinus serinus</i> (Linnaeus, 1766)	NFS	24
<i>Spatula clypeata</i> (Linnaeus, 1758)	NFS	1
<i>Spinus spinus</i> (Linnaeus, 1758)	FS	137
<i>Sternula albifrons</i> (Pallas, 1764)	NFS	1
<i>Streptopelia turtur</i> (Linnaeus, 1758)	NFS	9

Species	Forest affinity	Number of occurrences
<i>Sylvia borin</i> (Boddaert, 1783)	NFS	55
<i>Sylvia curruca</i> (Linnaeus, 1758)	NFS	72
<i>Sylvia undata</i> (Boddaert, 1783)	NFS	13
<i>Tachymarpis melba</i> (Linnaeus, 1758)	NFS	26
<i>Tetrao urogallus aquitanicus</i> Ingram, 1915	FS	433
<i>Tetrao urogallus</i> Linnaeus, 1758	FS	297
<i>Tichodroma muraria</i> (Linnaeus, 1766)	NFS	52
<i>Turdus pilaris</i> Linnaeus, 1758	NFS	113
<i>Turdus torquatus</i> Linnaeus, 1758	FS	158
<i>Tyto alba</i> (Scopoli, 1769)	NFS	2
<i>Upupa epops</i> Linnaeus, 1758	NFS	13
<i>Vanellus vanellus</i> (Linnaeus, 1758)	NFS	1
Squamata		
<i>Anguis fragilis</i> Linnaeus, 1758	NFS	14
<i>Coronella austriaca</i> Laurenti, 1768	NFS	5
<i>Emys orbicularis</i> (Linnaeus, 1758)	NFS	1
<i>Mauremys leprosa</i> (Schweigger, 1812)	NFS	1
<i>Natrix maura</i> (Linnaeus, 1758)	NFS	1
<i>Timon lepidus</i> (Daudin, 1802)	NFS	6
<i>Vipera aspis</i> (Linnaeus, 1758)	NFS	26
<i>Vipera aspis aspis</i> (Linnaeus, 1758)	NFS	1
<i>Vipera aspis zinnikeri</i> Kramer, 1958	NFS	4
<i>Vipera berus</i> (Linnaeus, 1758)	NFS	1
Amphibia		
<i>Alytes obstetricans</i> (Laurenti, 1768)	NFS	20
<i>Bombina variegata</i> (Linnaeus, 1758)	NFS	7
<i>Calotriton asper</i> (Al. Dugès, 1852)	NFS	92
<i>Pelophylax kl. esculentus</i> (Linnaeus, 1758)	NFS	1
<i>Rana pyrenaica</i> Serra-Cobo, 1993	NFS	35
<i>Triturus marmoratus</i> (Latreille, 1800)	NFS	1

Species	Forest affinity	Number of occurrences
Coleoptera		
<i>Aeletes atomarius</i> (Aubé, 1843)	FS	1
<i>Ampedus brunnicornis</i> Germar, 1844	FS	1
<i>Anthaxia istriana</i> Rosenhauer, 1847	FS	2
<i>Brachygonus ruficeps</i> (Mulsant & Guillebeau, 1855)	FS	4
<i>Buprestis haemorrhoidalis</i> Herbst, 1780	FS	1
<i>Calopus serraticornis</i> (Linnaeus, 1758)	FS	2
<i>Cardiophorus anticus</i> Erichson, 1840	FS	3
<i>Cerambyx cerdo</i> Linnaeus, 1758	FS	6
<i>Cerambyx welensii</i> (Küster, 1845)	FS	2
<i>Cetonischema speciosissima</i> (Scopoli, 1786)	FS	2
<i>Corticeus longulus</i> (Gyllenhal, 1827)	FS	1
<i>Dolotarsus lividus</i> (C.R. Sahlberg, 1833)	FS	5
<i>Elater ferrugineus</i> Linnaeus, 1758	FS	4
<i>Episernus striatellus</i> (Brisout de Barneville in Grénier, 1863)	FS	1
<i> Erotides cosnardi</i> (Chevrolat, 1831)	FS	2
<i>Eupotosia mirifica</i> (Mulsant, 1842)	FS	2
<i>Gnorimus variabilis</i> (Linnaeus, 1758)	FS	7
<i>Hyperisus declive</i> (Dufour, 1843)	FS	1
<i>Ischnomera cinerascens</i> (Pandellé in Grénier, 1867)	FS	1
<i>Judolia sexmaculata</i> (Linnaeus, 1758)	FS	2
<i>Kisanthobia ariasi</i> (Robert, 1858)	FS	1
<i>Lamia textor</i> (Linnaeus, 1758)	FS	1
<i>Melandrya dubia</i> (Schaller, 1783)	FS	1
<i>Merohister ariasi</i> (Marseul, 1864)	FS	1
<i>Morimus asper</i> (Sulzer, 1776)	FS	3
<i>Mycetochara quadrimaculata</i> (Latreille, 1804)	FS	1
<i>Necydalis ulmi</i> Chevrolat, 1838	FS	3
<i>Osmoderma eremita</i> (Scopoli, 1763)	FS	11
<i>Oxylaemus variolosus</i> (Dufour, 1843)	FS	1

Species	Forest affinity	Number of occurrences
<i>Philothermus evanescens</i> (Reitter, 1876)	FS	2
<i>Phloeostichus denticollis</i> W. Redtenbacher, 1842	FS	1
<i>Platysoma lineare</i> Erichson, 1834	FS	1
<i>Prostomis mandibularis</i> (Fabricius, 1801)	FS	9
<i>Pycnomerus terebrans</i> (Olivier, 1790)	FS	3
<i>Pytho depressus</i> Linnaeus, 1767	FS	2
<i>Rhizophagus brancsiki</i> Reitter, 1905	FS	4
<i>Rosalia alpina</i> (Linnaeus, 1758)	FS	37
<i>Sphaerites glabratus</i> (Fabricius, 1792)	FS	2
<i>Stephanopachys quadricollis</i> (Marseul, 1878)	FS	1
<i>Teredus cylindricus</i> (Olivier, 1790)	FS	1
<i>Triplax lacordairii</i> Crotch, 1870	FS	1
<i>Triplax melanocephala</i> (Latreille, 1804)	FS	1
<i>Wanachia triguttata</i> (Gyllenhal, 1810)	FS	1
<i>Xylita laevigata</i> (Hellenius, 1786)	FS	1
<i>Zilora obscura</i> (Fabricius, 1794)	FS	2
Lepidoptera		
<i>Aricia morronensis</i> (Ribbe, 1910)	NFS	1
<i>Boloria euphrosyne</i> (Linnaeus, 1758)	ES	2
<i>Brenthis ino</i> (Rottemburg, 1775)	ES	1
<i>Carterocephalus palaemon</i> (Pallas, 1771)	ES	2
<i>Chazara briseis</i> (Linnaeus, 1764)	NFS	9
<i>Coenonympha dorus</i> (Esper, 1782)	NFS	1
<i>Cupido minimus</i> (Fuessly, 1775)	NFS	2
<i>Erebia gorgone</i> Boisduval, 1833	NFS	1
<i>Erebia pronoe</i> (Esper, 1780)	NFS	2
<i>Eumedonia eumedon</i> (Esper, 1780)	ES	26
<i>Fabriciana niobe</i> (Linnaeus, 1758)	ES	1
<i>Hesperia comma</i> (Linnaeus, 1758)	NFS	1
<i>Hyponephele lycaon</i> (Rottemburg, 1775)	NFS	10

Species	Forest affinity	Number of occurrences
<i>Lysandra hispana</i> (Herrich-Schäffer, 1852)	NFS	2
<i>Melitaea diamina</i> (Lang, 1789)	ES	2
<i>Nymphalis antiopa</i> (Linnaeus, 1758)	ES	67
<i>Papilio alexanor</i> Esper, 1800	NFS	2
<i>Parnassius apollo</i> (Linnaeus, 1758)	NFS	9
<i>Parnassius mnemosyne</i> (Linnaeus, 1758)	ES	2
<i>Phengaris alcon</i> (Denis & Schiffermüller, 1775)	NFS	14
<i>Pieris ergane</i> (Geyer, 1828)	NFS	1
<i>Polygonia egea</i> (Cramer, 1775)	NFS	5
<i>Polyommatus amandus</i> (Schneider, 1792)	ES	1
<i>Polyommatus damon</i> (Denis & Schiffermüller, 1775)	NFS	6
<i>Polyommatus daphnis</i> (Denis & Schiffermüller, 1775)	ES	5
<i>Polyommatus dolus</i> (Hübner, 1823)	ES	2
<i>Polyommatus eros</i> (Ochsenheimer, 1808)	NFS	1
<i>Satyrus actaea</i> (Esper, 1781)	NFS	9
<i>Satyrus ferula</i> (Fabricius, 1793)	NFS	5
<i>Scolitantides orion</i> (Pallas, 1771)	NFS	1
<i>Zygaena hilaris</i> Ochsenheimer, 1808	ES	1
<i>Zygaena trifolii</i> (Esper, 1783)	ES	1
<i>Zygaena viciae</i> (Denis & Schiffermüller, 1775)	ES	1
Odonata		
<i>Aeshna juncea</i> (Linnaeus, 1758)	NFS	4
<i>Coenagrion hastulatum</i> (Charpentier, 1825)	NFS	1
<i>Cordulegaster bidentata</i> Selys, 1843	NFS	34
<i>Lestes dryas</i> Kirby, 1890	NFS	6
<i>Lestes sponsa</i> (Hansemann, 1823)	NFS	1
<i>Macromia splendens</i> (Pictet, 1843)	NFS	3
<i>Sympetrum danae</i> (Sulzer, 1776)	NFS	1
<i>Sympetrum flaveolum</i> (Linnaeus, 1758)	NFS	2
Orthoptera		

Species	Forest affinity	Number of occurrences
<i>Gampsocleis glabra</i> (Herbst, 1786)	NFS	14
<i>Polysarcus denticauda</i> (Charpentier, 1825)	NFS	1
<i>Polysarcus scutatus</i> (Brunner von Wattenwyl, 1882)	NFS	1
<i>Pseudochorthippus montanus</i> (Charpentier, 1825)	NFS	2

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