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Stronger legacy effects of cropland than of meadows or pastures on soil conditions and plant communities in French mountain forests

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Highlights

- We compared current soil conditions and understory plant communities in forests with different past land uses.
- The legacy effects of past agricultural activities on current soil conditions and plant communities are stronger in former cropland than in former pastures or meadows.
- It is necessary to consider the nature of the former agricultural activities in recent forests when studying the effect of forest continuity.

Abstract

Question

Differences in understory vegetation between ancient and recent forests have been thoroughly explored; however, few studies have investigated the legacies of different former land uses in recent forests. Indeed, due to more intense agricultural practices (tillage and fertilisation), legacy effects are expected to be stronger in former cropland or meadows than in former pastures. Our objectives were to compare soil conditions, taxonomic composition and functional composition of understory plant communities in recent forests located on former pastures, meadows or cropland, with ancient forests as a reference.

Location

Tarentaise Valley, Savoy, France

Methods

Based on land-use maps surveyed between 1862 and 1864, we selected 82 forest sites with different former land uses in mountain forests in the French Alps and carried out soil

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sampling and botanical surveys. To account for potential confounding factors (altitude, canopy cover, tree species composition), we applied multiple linear regressions to analyse soil properties, canonical correspondence analysis to analyse plant taxonomic composition and multi-species generalized linear mixed-effects models to analyse relationships between plant functional composition and former land uses.

Results

The soils of former cropland were richer in nutrients and more alkaline compared to other past land uses, while soils on former pastures and meadows differed only slightly from ancient forests. Ancient forests were characterised by acidophilic, shade-tolerant, low-stature, forest-dependent species, whereas former cropland was characterised by calcicolous non-forest species. Former pasture and meadow communities displayed a distinct taxonomic composition compared to other past land uses, but a functional composition closer to ancient forest than to former cropland.

Conclusion

Former cropland has a stronger legacy effect than former pastures or meadows. This could explain small differences between ancient and recent forests observed in previous studies conducted in mountain landscapes where former cropland was rare.

Keywords

Past land use, Functional composition, Understory vegetation, Ancient forest, Former cropland, Former pasture, Former meadow, Soil chemistry

Nomenclature

French national taxonomic reference TAXREF v15.0 (<https://inpn.mnhn.fr>)

1. Introduction

Ancient forests (AF), i.e. forests in which land use has not changed for a long period of time, are known to harbour a specialised species composition (Bergès & Dupouey, 2021) because of dispersal and recruitment limitations which constrain the colonisation, establishment and persistence of some species in recent forests (Flinn & Vellend, 2005). Recruitment is in part limited by persistent soil modifications caused by past agricultural activities; however, these modifications may vary depending on soil type, the nature of the agricultural activities and time since land abandonment (Flinn & Vellend, 2005).

The nature of the agricultural activities preceding afforestation is likely to be an important source of variability in the soil properties of recent forests. Indeed, during the 19th century, cropland was located on the most suitable sites for agricultural activities (Flinn et al., 2005) and subjected to modifications such as removal of stones, fertilisation (e.g. manuring and/or liming amendments) and homogenisation of soils by harrowing and ploughing. Meadows, intended to produce hay to feed livestock during winter, were more frequently located on fertile, wetter areas in valley bottoms or mid-slope, and were regularly fertilised, harrowed and irrigated. In contrast, pastures were more frequently located on soils unsuitable for cultivation and often had communal landownerships. Pasture soils were not ploughed but fertilisation by animal faeces could be locally important (Mouthon, 2019). Repeated fertilisation and ploughing in cropland enriched the soil and modified the original forest soil structure, contributing to soil homogenisation. Conversely, the lack of these types of disturbances under grazing better preserved the characteristics of the original forest soils (Holmes & Matlack, 2017; Burst et al., 2020). Forest soils on former cropland are thus generally richer, more alkaline and have lower carbon content than soils on former pastures (Koerner et al., 1997; von Oheimb et al., 2008). These differences in soil conditions are likely to result in differences in understory vegetation between cropland and pastures. Several

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studies have reported that former cropland support higher plant specific richness, with more nitrogen-demanding species and shrubs, while former pastures host plant communities more similar to those of ancient forest communities (Koerner et al., 1997; Dyer, 2010; Wulf, 2004; Abadie et al., 2021).

To date, no study seems to have explored how legacy effects in forested mountain landscapes differ between lands subjected to different agricultural activities in the past, even though such landscapes provide a favourable context for investigating such effects. Indeed, mountain areas of central Europe followed broadly the same temporal pattern of forest cover as described by Mather (1992): a decrease of forest area until mid-19th century followed by continuous increase. However, the deforestation rate before the industrial revolution was lower in mountain areas than in lowlands areas (Thomas et al., 2017). The current forest cover in mountain areas is thus less fragmented than in lowland areas and species may therefore be less limited by dispersal than by recruitment capacity (Jamoneau et al., 2012). The legacy effects of past land use (PLU) may be more pronounced in mountains because the limited availability of flat surfaces motivated for terrace cultivation to gain arable land on slopes, leading to considerable change in soil properties (Abadie et al., 2018a). Moreover, since the beginning of the Middle Ages, an agro-pastoral system has existed in French mountains, with large areas of pasture on steep slopes and in low fertility zones (Mouthon, 2019). In addition, mountain forests may currently be subject to less timber harvesting pressure than their lowland counterparts, thus leaving clearer signs of past land use effects that could otherwise be obscured by more intensive forest management (Depauw et al., 2019). Finally, mountain soils, which are generally not very productive, may be more sensitive to fertilisation. In case, this may accentuate the soil legacies of former agricultural activities and the recruitment limitation for forest species after afforestation.

The aim of this study is to assess whether different PLUs (pastures, meadows, cropland and forests), identified from historical Ordnance survey maps, have different legacy effects on soil properties and on the taxonomic and functional composition of the understory flora in mountain forests. We base our comparisons on soil and floristic surveys carried out in the French Alps, controlling for potential confounding environmental factors. We focus on soil properties that are likely to have determined the location of the different former land uses, or to have been affected by former agricultural activities; these two factors being hard to separate (Bergès & Dupouey, 2021). We then analysed the taxonomic and functional composition of the plant communities by selecting traits related to dispersal capacity, stress tolerance and species ecological preference (Weiher et al., 1999).

We hypothesise that former cropland was located in the most suitable areas for cultivation and have undergone tillage and fertilisation at higher rates than the other PLUs. Accordingly, we predict higher pH, higher cation exchange capacity, higher phosphorus content and lower C/N ratio in former cropland than in land with other PLUs. Conversely, we assume that former pastures and ancient forests were relegated to areas less favourable for cultivation, not intensively ploughed or fertilized. We therefore predict more acidic and less fertile soils on those sites compared to former cropland. Finally, we assume that former meadows were located on more fertile soils and subjected to fertilisation but not ploughed. Accordingly, they are expected to be intermediate between former cropland and ancient forests in most soil characteristics.

We expect plant species composition to vary with PLU. We expect more shade-tolerant, less dispersive and less competitive species in AF. Conversely, in former cropland, due to fertilisation and tillage, we expect more nitrogen-demanding, calcicolous and competitive species. We hypothesise that in former meadows, which are usually located in wetter areas and more often subjected to fertilisation than AFs and former pastures, hygrophilous and nitrogen-demanding non-forest species are more frequent. Finally, we expect communities on

former pastures to be more similar to those on AF sites than to those on former cropland because of less modified soils, spatial proximity to AFs and the likely persistence of scattered trees, making forest plant recruitment easier (Holmes, 2020). We also expect higher species richness on former pastures than on former cropland, due to higher environmental heterogeneity (Holmes & Matlack, 2017) and the persistence of grassland species (Milberg et al., 2019).

2. Material and methods

2.1. Study area

The study area was located in the forests on the north-facing slopes of the Tarentaise Valley in the French Alps in Savoy (45.4°N to 45.6°N and 6.5°E to 6.8°E). South-facing slopes, characterised mainly by open land still used today as pasture and by limited ancient forest cover, were discarded. The study area has a mountain climate with a continental influence (Köppen climate class Dfb/Dfc according to Beck et al. (2018)), with cold winters and summers (average temperature in January -1.8°C and in July 16.6°C). The average annual precipitation and temperature are 984 mm and 8.2 °C for the period of 1981-2000, respectively. The geology is characterised by eroded sediments of the Hercynian orogenic belt (black shales and micaceous sandstones), partly covered by glacial deposits. Current forests are predominantly coniferous, dominated by *Picea abies* and *Abies alba*. In the mid-19th century, forests covered 10% of the landscape but agriculture abandonment and reforestation policies have led to widespread forest recovery. At present, forest covers 19% of the study area (Thomas et al., 2017).

2.2. Forest continuity and past land use

We extracted current forest cover (according to the FAO definition of “forest” (FAO, 2012)) from the BD FORET® V2 map (scale=1:25 000) drawn for our study area using 2014 airborne images by the French National Geographic Institute. We identified past land use by use of Ordnance Survey maps (scale=1:40 000), used in France as a reference for identification of forests with a long temporal continuity (Bergès & Dupouey, 2021). The Ordnance surveyed our study area between 1862 and 1864. These maps were vectorised and georeferenced by the Vanoise National Park in 2017 (Thomas et al., 2017). This allowed us to identify: (i) current forests that were present as forests also in 1864 (ancient forests, AF); and current forests emerging (ii) on former pastures (RF_Pastu); (iii) on former meadows (RF_Mead); and (iv) on former cropland (RF_Crop).

2.3. Vegetation sampling

We used QGIS 3.16 to identify potential sampling areas. We first selected stands with closed canopy from aerial photographs taken in 1958 to exclude very recent forests and ancient forests that may have undergone a land-use change between 1850 and present. Then, we discarded slopes with inclination greater than 60% and south-facing sides. To eliminate areas with uncertain land use (errors during historical map production or the vectorisation process), a buffer of 20 m at the edge of each polygon was removed before placement of sampling sites. Within the selected polygons, 140 points were randomly placed (35 in each PLU) with a minimum distance of 250m between points sharing the same polygon. These sites were then prospected between June and September 2020 to carry out vegetation survey where: (1) *in situ* land-use remnants (terraces, stacks of stones, stone walls marking property boundaries) matched historical map information (Abadie et al., 2018a); (2) undergrowth vegetation cover was above 5%; (3) canopy cover was above 40% ; and (4) the surface was homogeneous. Coppice stands and sites with signs of recent soil or vegetation disturbances were avoided. Finally, 82 plots were retained for botanical surveys.

In the selected plots, we delineated rectangles of 20 x 12 m (240 m²) and recorded species occurrence. Shrubs and trees were excluded from our study because their trait values are difficult to compare with those of herbaceous species and they are considered to be more dependent on stand composition and successional stage than herbaceous species. A total of 243 herbaceous species were observed in the plots, of which 167 were present in more than two plots. The species list is given in Appendix S1.

2.4. Soil sampling

Samples of the upper soil layer were collected with a metal cylinder, 5 cm high and with radius 8 cm, after removal of the humus layer. Samples collected from the four corners of each plot were mixed before chemical analyses carried out by the INRAE soil analysis laboratory (Arras, France). Analyses included granulometry, total lime content (CaCO₃), total phosphorus content (Total P), organic carbon content (Organic C), total nitrogen content (Total N), C/N ratio, pH, available phosphorus extracted with the Duchaufour method (a method recommended for forest soils; Duchaufour & Bonneau 1959), effective cation exchange capacity (CEC), and exchangeable cation concentrations (Al, Ca, Fe, Mg, Mn, K and Na).

2.5. Plant traits and ecological preferences

Plant functional traits were extracted from the TRY database (Kattge et al., 2020) by selecting the datasets that were geographically most relevant for our study area (see the list of datasets used in Appendix S2). We included traits related to dispersal ability and stress tolerance, as recommended by Weiher et al. (1999). We also included species' ecological preferences using ecological indicator values (EIV) for light (L), temperature (T), soil moisture (F), soil reaction (R) and nitrogen (N), according to the Baseflor database (Julve, 1998) and forest habitat preferences according to Heinken et al. (2019) (Table 1).

The databases lacked trait values for 18 species out of 167 for SLA, 15/167 for LDMC and 24/167 for seed mass. These missing values were filled in by use of the `MissForest` R package (Stekhoven & Bühlmann, 2012), a non-parametric missing-value imputation method based on a random-forest model which assigns missing values using other traits as predictors (Penone et al., 2014).

2.6. Statistical analyses

To account for potential confounding factors when testing the effect of past land use (PLU), we included elevation, distance to the nearest forest edge, canopy cover and stand composition (2 levels: coniferous or deciduous) as predictors in our models and applied a model preselection procedure. We used the variance inflation factor (VIF) to detect collinearities among all these variables; none of the VIF values was greater than 1.6 (Appendix S3). We used R v 4.1.1 (R Core Team, 2021) to perform all analyses.

Soil properties

First, soil chemical properties were regressed against the potential confounding factors (elevation, distance to the forest edge, canopy cover, stand composition) by use of a linear model. To select the best subset of variables, we used the `dredge` function of package `MuMIn` (Kamil, 2020) to obtain all possible models. Thereafter we chose the model with the fewest predictors among the set of models with a delta Akaike information criterion (AIC) of less than two. Second, a PLU effect was added and its significance tested by a type III ANOVA test. When the PLU effect was significant, post-hoc pairwise tests were carried out to compare the different past land uses with the `emmeans` function (Lenth, 2021).

Species richness and taxonomic composition

Species richness (SR) was analysed by use of a linear model, following the procedure described above. To assess the taxonomic composition, we applied a canonical correspondence analysis (CCA, `cca` function, Legendre et al., 2012) on the presence/absence matrix of species using the same potential confounding factors as before. A backward stepwise model selection was carried out to select the best subset of variables (`ordistep` function, Blanchet et al., 2008). Then, a PLU effect was added. The significance of the effect of each variable was assessed with a type III ANOVA-like permutation test (`anova.cca` function, Legendre et al., 2011). Variance partitioning was then carried out to identify the unique and shared variance components explained by PLU and the other potential confounding factors (`varpart` function). To visualize the PLU effect, a partial canonical correspondence analysis (pCCA) was applied with PLU as a constraint and the other confounding factors as conditions. Unconditional CCA is shown in Appendix S4. These analyses were performed using the `vegan` R package (Oksanen et al., 2020). Species with only one or two occurrences were discarded from the analyses (n=167). We also conducted a complementary analysis to test the fidelity of species for each PLU with Pearson's phi coefficient of association (Chytrý et al., 2002) calculated with `multipatt` function of the `Indicspecies` R package (De Cáceres & Legendre, 2009; De Cáceres et al., 2010). These results are provided in Appendix S1.

Functional composition

To link plant functional traits to PLU and potential confounding factors, we adapted the generalized linear mixed-effects model (GLMM) framework proposed by Jamil et al. (2013) to presence/absence data with one trait and several environmental variables as predictors (Eq. 1).

$$\begin{aligned} \text{(Eq. 1)} \quad Y &= \text{Bernoulli}(p) \\ \text{logit}(p) &= \alpha + a + b + \beta_1 \text{trait} + \sum_{k=2}^{k=N_{+1}} ((\beta_k + c_k) \text{Envir}_k + \beta_{1k} \text{Envir}_k \times \text{trait}) \\ [a, b, c_k] &\sim \text{MVN}(0, \Sigma) \end{aligned}$$

This logit GLMM assesses the probability (p) of occurrence (Y) of each species in each site. The model includes an intercept (α), the main effect of the trait of the species (β_1), the main effects of the environmental variables (β_k with k varying from 2 to N_{+1} variables) and the interaction among them (β_{1k}) as fixed terms. The model also contains a random term for species (a), which allows different species to have different overall presence probabilities; a random term for sites (b), which allows sites to differ in mean species presence probability independently of the environmental variables; and a random term for each species-by-environment interaction (c_k), which allows different species to have different responses to the environmental variables. The three random effects follow a multivariate normal distribution (MVN) of mean zero and unstructured variance-covariance matrix Σ .

Using `glmer` in the R package `lme4` (Bates et al., 2015), we first computed a model including the random effects for sites and species (a and b) and all the potential confounding factors (elevation, stand comp, canopy cover and distance to the forest edge) as fixed and species-by-environment random interaction terms. A type-II ANOVA test was carried out to remove non-significant terms and obtain a parsimonious model, which will be referred to as M_0 .

In a second step, we computed a model (M_{trait}) for each trait by adding the main effect of trait (β_1) to M_0 ; then we selected the trait-environment interactions to add through tiered forward model selection. We used M_{trait} to test each trait-environment interaction separately, then added the interaction term that brought the strongest decrease in AIC (compared to M_{trait})

among all the tested models. This procedure was iteratively repeated with the other interaction terms until no further AIC decrease was obtained. Then, a type-II ANOVA test was carried out to remove non-significant interaction terms.

Finally, we added the main effect of PLU, the species-by-environment random interaction term for PLU, and the interaction term between trait and PLU to M_{trait} . We tested the significance of the interaction term with a type-II ANOVA test and carried out post-hoc pairwise comparison tests with the `emmeans` function for numerical traits and `emmeans` for categorical traits to assess differences between PLUs (Lenth, 2021). The p values of all the selected interaction terms are given in Appendix S5.

3. Results

3.1. Data summary and environmental differences among PLUs

The 82 sampled plots were equally distributed among PLUs (Table 2). The elevation ranged from 780 to 1900 m. Despite careful site selection, RF_Pastu and AF were situated 317 and 212 m higher than RF_Crop ($F=6.65$; $p<0.001$), respectively. Canopy cover was also larger in RF_Crop and RF_Mead than in AF and RF_Pastu ($F=4.66$; $p<0.01$). The AF and RF_Pastu plots mainly had a coniferous tree cover, while deciduous trees dominated RF_Crop plots ($\chi^2=12.8$; $p<0.01$). The AF plots tended to be located further from the forest edge than the other types of plots but the differences among PLUs were not significant ($F=1.8$; $p=0.15$).

3.2. Soil properties

Soils on former cropland differed significantly from soils with other PLUs by exhibiting the highest values for nitrogen, phosphorous, CEC, Ca^{2+} , Mg^{2+} and pH and the lowest values for Mn^{2+} , Al^{3+} and C/N. RF_Pastu and RF_Mead did not differ significantly from AF (Figure 1). The other soil properties investigated by us did not differ among PLUs.

3.3. Plant species richness and taxonomic composition of plant communities

On average (\pm SD), 30 (\pm 10) species were found in AF plots, 35 (\pm 10) in plots on former pastures, 29 (\pm 6) in plots on former meadows and 29 (\pm 11) in former cropland plots. These differences were not significant ($F=0.39$, $p=0.76$). Also, at the gamma diversity level (total number of species recorded for each PLU), we recorded little variation: 164 species in AF, 161 species in RF_Pastu, 150 species in RF_Mead and 164 species in RF_Crop.

The stepwise model preselection by CCA failed to select the distance to the forest edge effect. The marginal effect of PLU was significant ($\chi^2=0.18$, $p=0.02$) according to the ANOVA-like permutation test. The CCA explained 6.9% of the total variation in the species dataset.

Variance partitioning indicated that the pure effect of elevation was high (42.2%), while the pure effect of PLU accounted for only 10.7% of the total explained variation. The joint effect of the three components, PLU, elevation, and stand composition and canopy cover, amounted to 24.5% of the total explained variation (Figure 2).

The first pCCA axis (Figure 3) contrasted RF_Crop with the three other land uses, the second axis placed AF and RF_Pastu at opposite ends and the third axis isolated the remaining PLU, RF_Mead. According to their positions on pCCA diagrams, we identified groups of species closely linked to each PLU. *Anthoxanthum odoratum*, *Festuca heterophylla*, *Hepatica nobilis*, *Luzula pilosa*, *Milium effusum*, *Orthilia secunda*, *Saxifraga cuneata* and *Scrophularia nodosa* were associated with AF. *Agrostis stolonifera*, *Campanula barbata*, *Circaea lutetiana*, *Deschampsia caespitosa*, *Dryopteris dilatata*, *Imperatoria ostruthium*, *Lactuca alpina*, *Luzula luzulina* and *Saxifraga rotundifolia* were associated with RF_Pastu; *Galium aparine*, *Equisetum arvensis*, *Rubus fruticosus* and *Veratrum album* were associated with RF_Mead; and *Ervillia sylvatica*, *Galium mollugo*, *Knautia arvensis* and *Laserpitium latifolium* were associated with RF_Crop. Indicator species analysis (Appendix S1) provided essentially the same results without considering confounding factors.

3.4. Functional composition

Distance to nearest forest edge was not selected in the first model selection step. Among the functional traits included in our analyses, the interactions between PLU and seed mass, plant height, specific leaf area (SLA), ecological indicator value for light (L), soil reaction (R) and forest affinity were significant. Significant interaction terms were also found between several traits and elevation [longevity, SLA, forest affinity, L, soil moisture (F), temperature (T) and Raunkiær life form], stand composition (longevity, seed mass, F, R and Raunkiær life form) and canopy cover [SLA, L, F and nitrogen (N)]. For dispersal mode, leaf dry matter content (LDMC) and phenology, no significant interaction term with any environmental variable was found (Appendix S5).

The probability of species' occurrence decreased with increasing plant height and light requirements in AF and RF_Mead plots whereas no relationship to these traits was found for the other PLUs (Figure 4A). Species' presence probability rose with seed mass, but only for RF_Crop and RF_Mead. Species' presence probability increased with SLA for all PLUs but rose more slowly for RF_Crop than for the other PLUs, indicating a higher proportion of species with small SLA in RF_Crop plots. The probability of species' occurrence decreased with ecological indicator value for soil reaction for AF, RF_Pastu and RF_Mead while no relationship was found for RF_Crop. Nitrogen-demanding species tended to be favoured by all RF types while hygrophilous and anemochorous species tended to be favoured by RF_Pastu; however, these effects were not significant (Figure 4A–B).

Forest species were more frequent in AF than in RF_Crop plots while non-forest species showed the opposite pattern (Figure 4B). Forest-edge species were more frequent in RF_Pastu than in AF and RF_Mead plots.

4. Discussion

4.1. Legacy effects on soil properties

Our results show a nutrient gradient related to past land use, with RF_Crop showing the highest levels of nitrogen, phosphorus and magnesium and the lowest C/N ratio compared to other PLUs, indicating soils richer in nutrients. Furthermore, results for pH, Ca^{2+} , CEC, Al^{3+} and Mn^{2+} indicate that RF_crop has the most alkaline and RF_Pastu the most acidic soils. These differences in soil condition among PLUs may be due to two factors that are inseparable by the available information (Bergès & Dupouey, 2021): the differences may have existed before deforestation because the areas selected for cultivation were more favourable with respect to topography (flats, sites close to a watercourse, low-altitude sites), soil type (stoniness, texture, colour) and/or vegetation (biomass, indicator species); but they may also be legacies of past agricultural activities (fertilisation, liming, ploughing). However, historically, meadows played a central role in mountain agricultural systems as they provided the hay necessary for the wintering livestock. Hay meadows were therefore usually located on fertile soils and subjected to regular manuring and irrigation (Mouthon, 2019). Therefore, plots on former meadows are expected to display soil conditions similar to those of former cultivated areas. Surprisingly, our results contrast this expectation, as the soil conditions of former meadows were more similar to those of former pastures and ancient forests than to former cropland, from which they differ significantly. In addition, phosphorus levels are higher in RF_Crop than in the other PLUs, which is an indication of higher fertilisation levels (Dupouey et al., 2002). These results suggest that the soil enrichment observed in RF_Crop is due to a legacy effect of tillage that may have strengthened the effect of fertilisation by burying manure, rather existing before deforestation. Our results are consistent with previous findings (Koerner et al., 1997; von Oheimb et al., 2008; Burst et al., 2020) and suggest that the recovery of forest soil properties may be slower and land-use legacies stronger in formerly tilled soils than in former grassland soils.

4.2. Legacy effects on taxonomic and functional composition

Our second hypothesis is partly confirmed, as the four types of PLUs show distinct understory plant communities. Common forest-core species are typically associated with AFs while those associated with RF_Pastu are mostly hygrophilous species typical of tall-forb communities. Species associated with RF_Crop and RF_Mead are typically non-forest, nitrogen-demanding species.

In addition, five species associated with AFs on the pCCA diagrams (*Festuca heterophylla*, *Hepatica nobilis*, *Luzula pilosa*, *Millium effusum*, *Scrophularia nodosa*) have been reported as ancient woodland indicator species (AWIs) in the previous literature, being found more frequently in ancient than in recent forests (Hermy et al., 1999; Sciana et al., 2009; Jabs-Sobocińska et al., 2022). Some of known AWIs (*Circea lutetiana*, *Deschampsia caespitose*, *Driopteris dilatata*) are associated with former pastures in our study while none are associated with RF_crop or RF_Mead. These results suggest that some AWIs are more able to colonise or have persisted in recent forests located on former pastures than in recent forests located on former cropland or meadows. Type of former land use can therefore partly explain the regional variability in the lists of AWIs established so far (Jabs-Sobocińska et al., 2022). A large fraction of the total explained variation in plant communities (24.5%) is shared between PLU, elevation, stand composition and canopy cover. This reflects that, despite careful site selection, we did not manage to design a data set that is fully balanced, with similar range of environmental conditions for all PLUs. A substantial part of the past land-use effect is therefore confounded with effects of other factors in our study, precluding full disentanglement. The use of databases covering large territories, with a large number of occurrences in which the type of former land use and potential confounding factors are taken into account, would open for establishment of more robust species lists (Schmidt et al., 2014; Bergès et al., 2016).

Among the 15 traits included in our study, seed mass, plant height, SLA, light preference, soil reaction preference and forest affinity vary among types of former land use, while the other traits are mostly affected by elevation, stand composition or canopy cover (Appendix S5). Plant height is positively correlated with a species' ability to compete and disperse (Weiher et al., 1999; Thomson et al., 2011). The higher proportion of small species found in AFs thus confirms the preference of low-competition and low-dispersal species for ancient forests (Flinn & Vellend, 2005). Forest-dependent and shade-tolerant species are also more frequent in ancient forests compared to recent forests, as expected from reports in previous studies, as ancient forests are known to host more core forest species whereas recent forests host more forest-edge species (Bergès et al., 2016, 2017; Abadie et al., 2021). However, former pastures and meadows have values intermediate between AFs and RF_Crop in terms of heliophilia, SLA and forest affinity. This result suggests that repeated tillage in former cropland restricted the recruitment and colonisation of forest species (Baeten et al., 2009) more than did practices in former pastures and meadows where tillage was absent or rare. Finally, acidophilic species are more frequent in ancient forests, former pastures and meadows, whereas calcicolous species tend to be more frequent in former cropland. This result can be related to differences in soil properties among PLUs, suggesting a recruitment limitation in former cropland, as the more alkaline soils of RF_Crop may facilitate development of calcicolous plants and be detrimental to acidophilic plants. Our results are consistent with those of Koerner et al. (1997), Dyer (2010) and Abadie et al. (2021), who also observed that the understory plant communities of former pastures are more similar to those of ancient forests than to those of former cropland. However, these studies also indicate that ploughing in former cropland is detrimental to rhizomatous plants and species with non-assisted dispersal, whereas we do not find any interaction between PLU and these two traits.

Regarding seed mass, Sciama et al., (2009) show that species associated with recent forests have larger seeds than species associated with ancient forests while Kimberley et al., (2013) show the opposite; larger seeds of AWIs than of other forest species. Our results are in line with the results of Sciama et al., (2009): species with large seeds are more frequent than species with small seed mass on former cropland and meadows, but not on former pastures or AF. However, we did not focus on traits specific for ancient forest or recent forest specialist species but rather analysed the distribution of trait values across the whole plant community in each PLU. One possible explanation for our results is that species with large seed mass survive better under a variety of different seedling hazards, such as competition from established vegetation, defoliation, or drought (Westoby, 1998). Large seed mass may thus indicate higher recruitment capacity which may be advantageous for species that have colonized fertile soils such as cropland or disturbed sites such as regularly mown meadows and have persisted beyond canopy closure.

4.3. Applying a functional approach to the study of past land uses: interest and perspectives

The multi-species model applied in this study for analysis of trait-environment relationships respects the structure of the sample design by incorporating random effects for sites, species and species-by-environment interactions (Jamil et al., 2013). Furthermore, it allowed us to estimate the conditional effects of each term, whereas classical approaches like RLQ and fourth-corner analysis only detect simple correlations (Dray et al., 2014). Moreover, multi-species models have lower type-I error rates compared to other approaches and are recommended for complex analyses (Miller et al., 2019). We therefore argue that the multi-species model approach is suitable for investigating relationships between species' traits and ecological variables of interest, such as past land use legacies on current biodiversity, since the model allows isolation of the unique contribution of the focal variable from potential confounding effects.

Suggestions for future research include model refinement by use of abundance data instead of simple presence/absence data. Furthermore, intra-specific variability of functional traits could be included to prevent blurring of the trait responses (Funk et al., 2017). For example, Baeten et al. (2011) showed that the tissues of individual plants located in recent forests had lower phosphorous content and N/P ratio than individuals of the same species located in ancient forests.

5. Conclusion

The nature of former agricultural use, as recorded in 1862–1864, is an important explanatory factor of variability in current forest soil conditions, forest plant taxonomic and functional composition. Cultivation affects soil chemical properties for centuries while grazing and mowing have shorter-lasting effects. Dispersal limitation may partly explain the differences in understory species composition between ancient and recent forests but recruitment limitations may also explain differences among past land uses in recent forests, due to differences in soil properties. Most of the studies published in forest historical ecology concern lowland areas, where recent forests have developed mainly on former cropland. In contrast, as in Mediterranean forest landscapes (Abadie et al., 2018b), mountain areas were characterised by a traditional agro-pastoral system where pastures were more extensive than cropland. This may explain the smaller differences between ancient and recent forests observed in some mountain areas (Janssen et al., 2018). This shows that a raw comparison between ancient and recent forest is not sufficient and that different types of former land use within recent forests need to be taken into account.

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Data availability statement

Plant community surveys (L), site descriptions (R), trait data (Q, available upon request) and the R script used for our analyses are available on the INRAE data portal at <https://doi.org/10.15454/BGMNQY>.

Author contributions

S.M., L.B., G.K. and J-L.D. designed the research questions; S.M. collected data with contributions from J-L.D. and P.M.; S.M. performed the statistical analyses and wrote the paper with contributions from G.K., J-L.D., P.M. and L.B.; all authors discussed the results and commented on the manuscript.

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Figure legends list

Figure 1. Estimated means (\pm CI95%) of the physical and chemical soil properties according to past land use at the average value of the other predictors. AF: ancient forest, RF_Pastu: recent forest on former pasture, RF_Mead: recent forest on former meadow, RF_Crop: recent forest on former cropland. The groups with the same letters were not significantly different.

Figure 2. Variance partitioning of the CCA showing the unique and shared variance components for past land use (PLU), elevation, stand composition and canopy cover.

Figure 3. Partial canonical correspondence analysis (pCCA) diagrams for axes 1 and 2 (A and B) and 1 and 3 (C and D) for species (A and C) and sites (B and D). The pCCA included PLU as constraining and the other environmental variables as conditional variables. Species names are given in Appendix S4. The tips of the star branches on figures B and D indicate site positions and the centres of the stars with PLU labels are placed at the centroid of the sites for each PLU. AF: ancient forest; RF_Pastu: recent forest on former pasture; RF_Mead: recent forest on former meadow; RF_Crop: recent forest on former cropland.

Figure 4. (A) Estimated slopes of the trait effect for each PLU (\pm CI95%) at the average value of the other predictors. (B) Estimated species presence probability according to ecological preference and PLU (\pm CI95%) at the average value of the other predictors. AF: ancient forest; RF_Pastu: recent forest on former pasture; RF_Mead: recent forest on former meadow; RF_Crop: recent forest on former cropland. PLUs with the same letters were not significantly different.

Supplementary materials

Appendix S1. List of species recorded.

Appendix S2. Datasets used in the TRY database for each trait

Appendix S3. Variance-inflation factors for each variable included in the linear models.

Appendix S4. Unconditional CCA.

Appendix S5. Significance of the interaction terms between traits and environmental variables.

Tables and figures

Table 1. Functional traits and ecological preferences retrieved from databases. N= Numerical, I=Integer, C=Categorical.

Trait	Function	Type	Unit	Range of values
Seed mass	Dispersal distance, longevity in seed bank, establishment success, fecundity	N	mg	From 0.005 to 203.5
Plant height	Competitive ability, dispersal distance	N	m	From 0.07 to 1.7
Dispersal mode	Dispersal distance, longevity in seed bank	C	.	Myrmecochorous Barochorous Anemochorous Zoochorous
Leaf dry matter content (LDMC)		N	g/g	From 0.08 to 0.54
Specific leaf area (SLA)	Relative growth rate, plasticity, stress tolerance, evergreenness, leaf longevity	N	mm ² /mg	From 12.8 to 77.1
Raunkiaer life form		C	.	Hemicryptophyte Therophyte Geophyte Chamaephyte
Onset of flowering	Stress and disturbance avoidance	I	Month	From 1 (January) to 9 (September)
Duration of flowering		I	Month	From 0 (less than 1 month) to 7 months
Longevity		C	.	Annual, Perennial
Light EIV (L)		I	.	From 2 (persciaphilic = 50 lux) to 9 (hyperheliophilic = 100 000 lux)
Soil moisture EIV (F)		I	.	From 4 (mesoxerophilic) to 8 (hydrophilic)
Soil reaction EIV (R)	Ecological preferences	I	.	From 1 (hyperacidophilic = 3 < pH < 4) to 9 (hypercalcolous = 8 < pH < 9)
Nitrogen EIV (N)		I	.	From 2 (peroligotrophilic = 200 µg N/l) to 9 (hypereutrophilic = 1500 µg N/l)
Temperature EIV (T)		I	.	From 1 (alpine) to 9 (thermo-Mediterranean)
Forest affinity	Habitat preference	C	.	1.1 = Forest species. Taxa which are found mainly in closed forest; 1.2 = Edge species. Taxa which are mainly typical of forest edges and forest openings. This includes species of forest edges, species which mainly occur in windthrows, burned or clear-cut areas, or during the regeneration phase after such events, species which mainly occur on exploitation roads and unpaved forest paths, species which are restricted to open forests due to extreme site conditions; 2.1 = Indifferent species. Taxa which can be found in forests as well as open areas; 2.2 = Non-forest species. Taxa which can be found occasionally in forests, but mainly in open areas.

Table 2. Summary of past land use attributes. For elevation, canopy cover and distance to edge, values indicate means \pm SD. Groups sharing the same letters were not significantly different according to a post-hoc pairwise comparison test.

PLU	Total number of plots	Number of plots in coniferous forest	Number of plots in deciduous forest	Elevation (m)	Canopy cover (%)	Distance to edge (m)
AF	22	18	4	1348 \pm 317(ac)	60 \pm 16 (a)	138 \pm 109 (a)
RF_Pastu	18	13	5	1453 \pm 293 (a)	61 \pm 14 (ab)	97 \pm 95 (a)
RF_Mead	21	10	11	1162 \pm 218 (bc)	74 \pm 14 (c)	89 \pm 44 (a)
RF_Crop	21	7	14	1136 \pm 196 (b)	72 \pm 16 (bc)	109 \pm 67 (a)

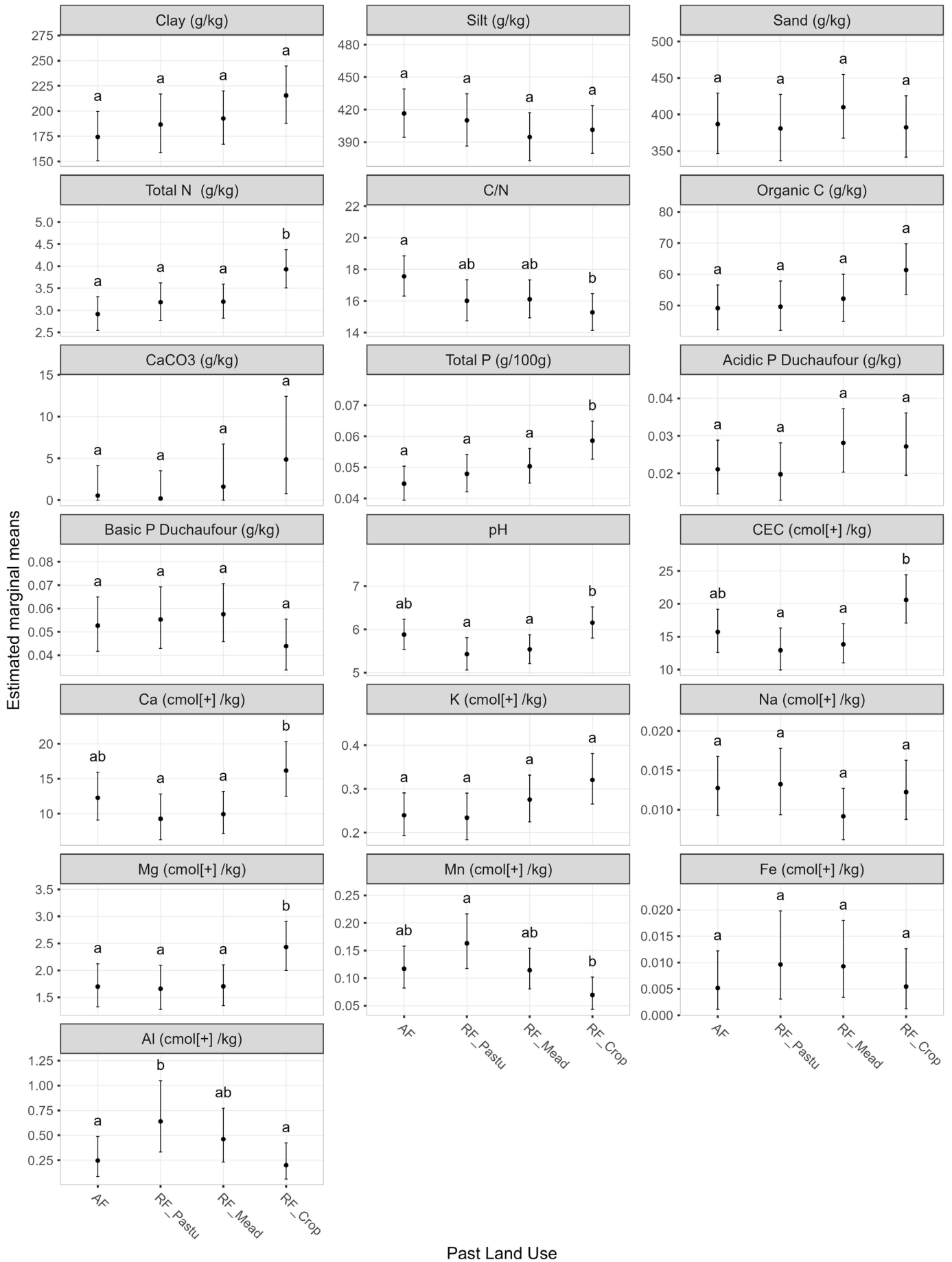


Figure 1. Estimated means (± CI_{95%}) of the physical and chemical soil properties according to past land use at the average value of the other predictors. AF: ancient forest, RF_Pastu: recent forest on former pasture, RF_Mead: recent forest on former meadow, RF_Crop: recent forest on former cropland. The groups with the same letters were not significantly different.

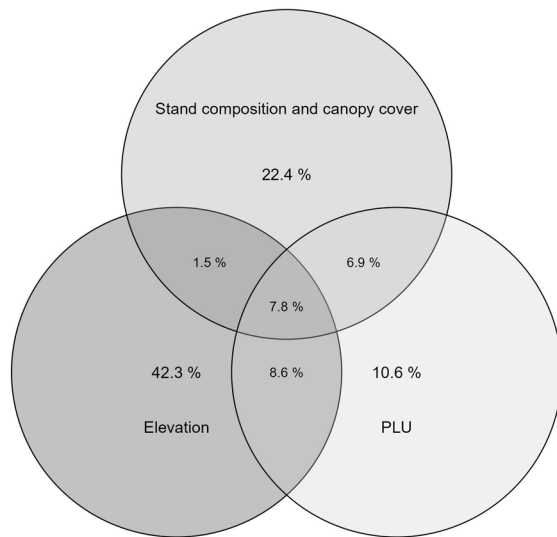


Figure 2. Variance partitioning of the CCA showing the unique and shared variance components for past land use (PLU), elevation, stand composition and canopy cover.

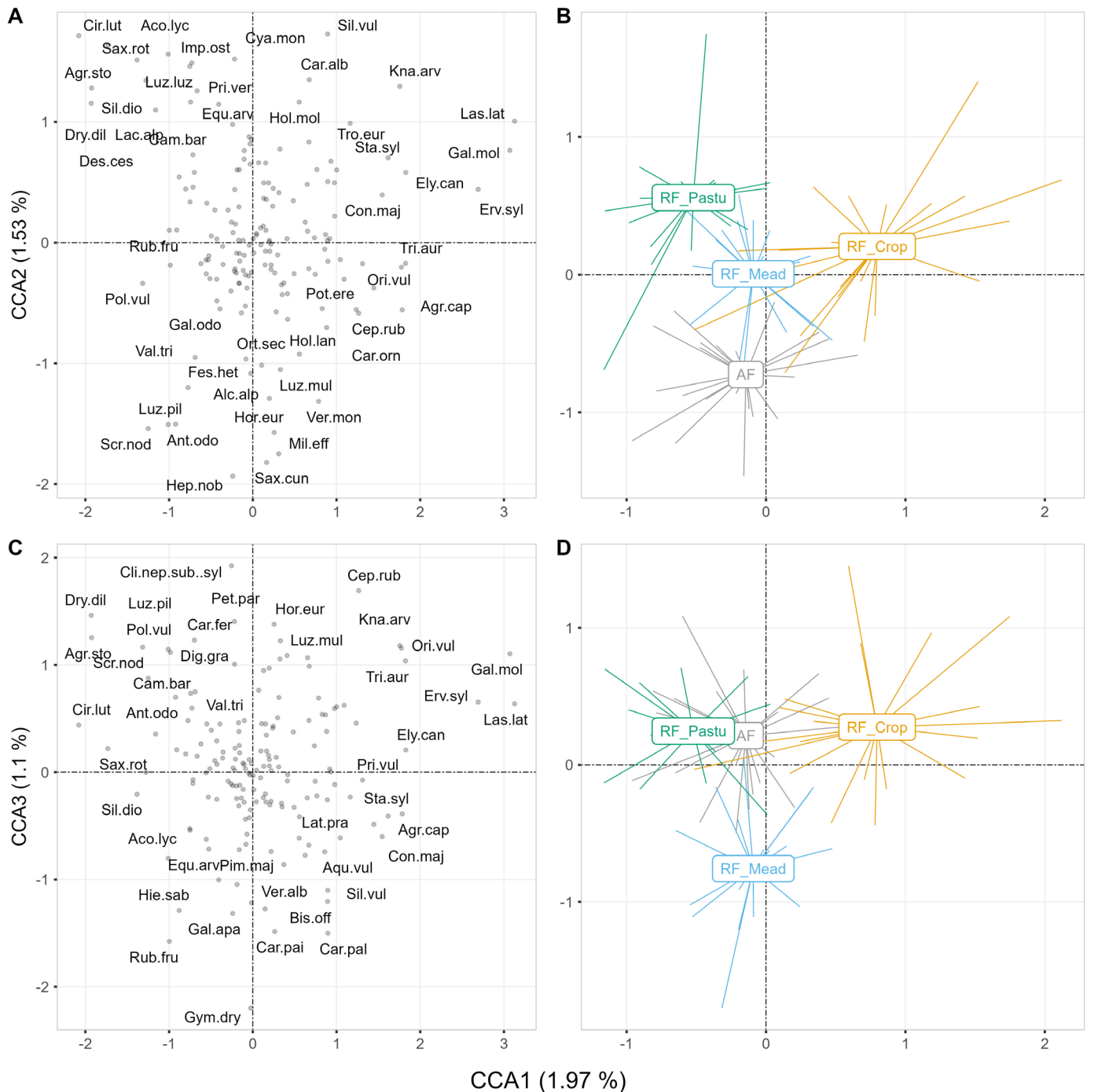


Figure 3. Partial canonical correspondence analysis (pCCA) diagrams for axes 1 and 2 (A and B) and 1 and 3 (C and D) for species (A and C) and sites (B and D). The pCCA included PLU as constraining and the other environmental variables as conditional variables. Species names are given in Appendix S4. The tips of the star branches on figures B and D indicate site positions and the centres of the stars with PLU labels are placed at the centroid of the sites for each PLU. AF: ancient forest; RF_Pastu: recent forest on former pasture; RF_Mead: recent forest on former meadow; RF_Crop: recent forest on former cropland.

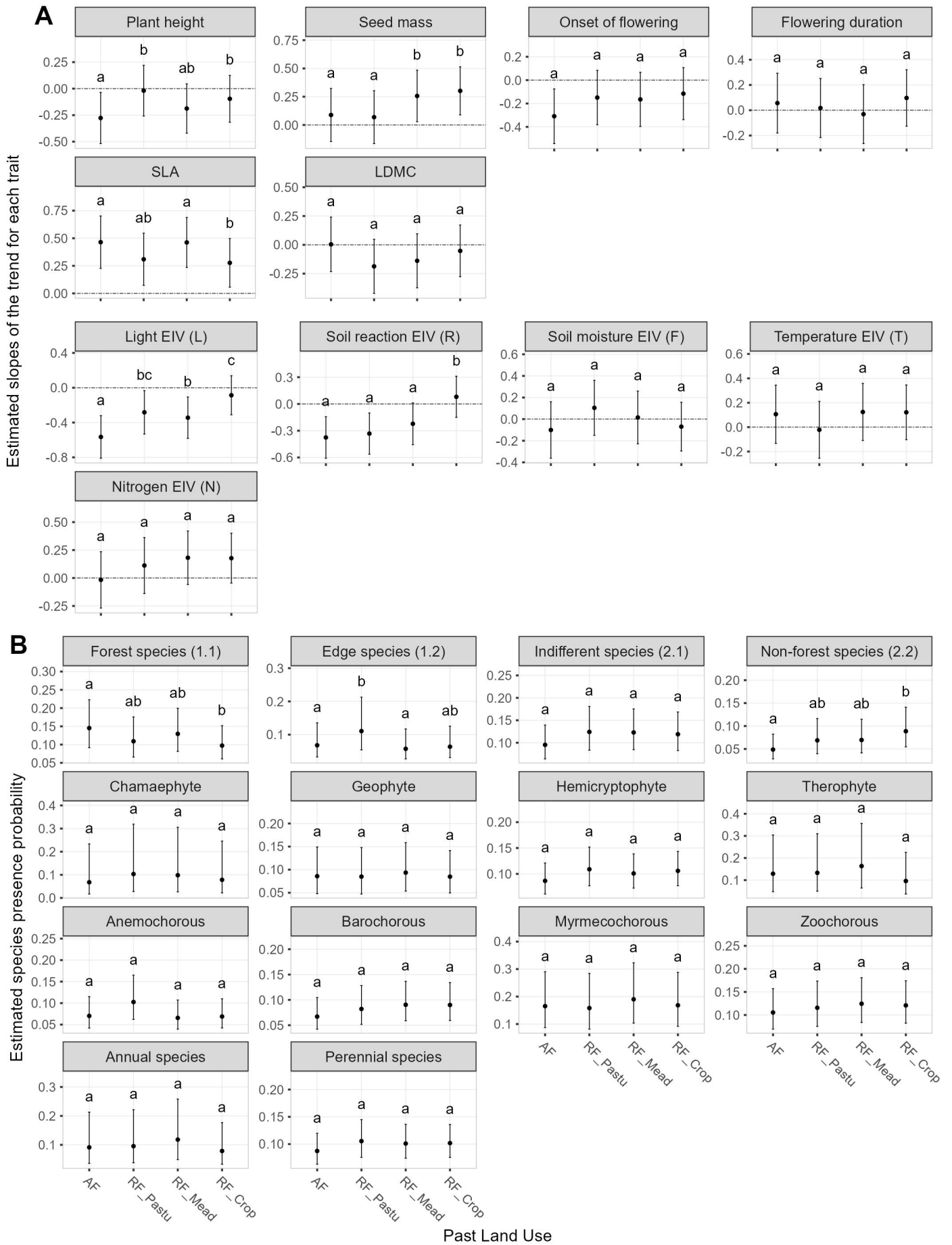


Figure 4. (A) Estimated slopes of the trait effect for each PLU (\pm CI_{95%}) at the average value of the other predictors. (B) Estimated species presence probability according to ecological preference and PLU (\pm CI_{95%}) at the average value of the other predictors. AF: ancient forest; RF_Pastu: recent forest on former pasture; RF_Mead: recent forest on former meadow; RF_Crop: recent forest on former cropland. PLUs with the same letters were not significantly different.