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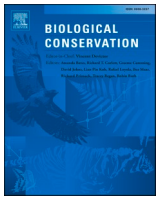

Landscape-scale diversity of plants, bumblebees and butterflies in mixed farm-forest landscapes of Northern Europe: Clear-cuts do not compensate for the negative effects of plantation forest cover

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ABSTRACT

To assess the biodiversity consequences of contemporary land-use trends in Northern Europe, where agriculture is being replaced by forestry, we need a better knowledge of the contributions of constituting habitats to biodiversity. Here, we use purposefully collected data from 87 sites to model how agricultural habitats, including semi-natural pastures, sown temporary grassland (leys), cereal crops, and forest habitats comprising both mature production forests and clear-cuts, contribute to landscape-scale diversity of plants, bumblebees and butterflies in boreonemoral Sweden. At the local scale, species richness was highest in semi-natural pastures, intermediate in cereal crops and leys and lowest in forest. In clear-cuts, species richness was similarly high to that in semi-natural pastures. Countryside species-area models show that at a landscape scale, the high local richness in clear-cuts was more than offset by the low species richness encountered in forest. At landscape scale, semi-natural pastures, and in the case of plants also cereal crops, were major contributors of unique species. Leys and semi-natural pastures were both important contributors to bumblebee diversity. The effect of the surrounding landscape composition on local diversity was weak, suggesting that area-based approximations of landscape-scale species richness were reasonable. We conclude that clear-cuts constitute habitats for open-land species but cannot maintain landscape-scale diversity in the face of agricultural abandonment when open land is replaced by even-aged production forests. Maintaining farmland, in particular semi-natural pastures but also cereals and leys, is therefore critical to maintaining the landscape-scale species richness of plants and insects in forestry-dominated areas.

1. Introduction

Biodiversity loss from farmland is largely driven by changes in land use, where both agricultural intensification and abandonment of farming, including afforestation, are threats to species that thrive in open landscapes, in particular species-rich semi-natural grasslands but also other farmland habitats (Beilin et al., 2014; Queiroz et al., 2014). Forests are expanding across Europe through both afforestation and regeneration (Palmero-Iniesta et al., 2021). Landscapes dominated by production forests are prevalent in Northern Europe where farmland abandonment and afforestation in an area previously dominated by large expanses of semi-natural grasslands threatens the remnants of open-land species communities (Auffret et al., 2018). In agriculture-dominated landscapes, farm management, cover of semi-natural habitats, crop diversity and field size are major landscape-scale drivers of species diversity (Sirami et al., 2019), and have been used to model consequences of different landscape-scale land-management scenarios on biodiversity (Hodgson et al., 2010; Kirchweger et al., 2020). However, such models cannot be straightforwardly applied to forestry-dominated landscapes where agricultural land may make up only a

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small proportion of the landscape, because the contribution of forest and agricultural habitats to landscape-scale diversity is unclear.

The even-aged monoculture forests that make up the bulk of forests in Northern Europe (95 % of Swedish forests, Axelsson and Angelstam, 2011) constitute a mosaic of clear-cuts, regrowing stands and closed forests (Fig. 1). When such habitats expand onto farmland following afforestation, many farmland species (including species of conservation concern) may be replaced by (initially mainly ubiquitous) forest species. However, the situation is more complex, because forest cannot be considered an inert matrix even for open-land species. Forests can offer resources such as nesting sites for bumblebees, or food resources for open-land insects in e.g. forest edges and clear-cuts. Clearings and open areas in forests have disproportionately diverse assemblages of a range of species of different functional groups, including both open land and forest species (Hilmers et al., 2018; Milberg et al., 2021). Species occurrence and richness within open habitats, such as semi-natural grasslands, can be higher when these are surrounded by forests rather than by cropland (e.g. Bergman et al., 2018), which has been hypothesized to be partly due to early-successional stages such as clear-cuts and power-lines within the forested area. The importance of clear-cuts for species tied to open habitats has been highlighted (Ram et al., 2020; Viljur and Teder, 2016). However, the relative value of clear-cuts when compared to other habitats has rarely been investigated even at local scales, and their contribution to biodiversity at larger scales (sensu Gabriel et al., 2010) is unexplored.

Open landscapes and biodiversity are largely public goods, which is an important part of the rationale for support to farming through subsidies. In the EU, area-based payments under the Common Agricultural Policy (CAP) that incentivize farmers to keep the landscape open by continuing farming, have slowed down but not halted the loss of farmland (Brady et al., 2017; Trubins, 2013). Land-use is changing also within agriculturally used land, with unexplored consequences for biodiversity. For instance, in southern Sweden, the last 10 years have seen an increase in cereals and a decrease in leys, which are sown temporary grasslands, usually based on grass and clover mixtures, as well as a substitution away from milk production towards suckler beef (a more extensive form of production) (Statistics Sweden 2010–2021, Jönköping county). In addition, increased demand for forest products and changes in diets with decreased demand for meat (Gong et al., 2022; Kok et al., 2018; Röös et al., 2016) can act as drivers of further land-use change in these regions.

The potential consequences of present and future dynamics of landscape-scale land use for biodiversity are poorly assessed because parametrized models that can predict the biodiversity based on the relative contribution of different agricultural and forest habitats are lacking. This is an obstacle for informing policy on how to halt and reverse biodiversity declines at the regional and national level, as well as improving global assessments whose ability to model biodiversity changes within human-dominated landscapes is still limited (Leclère et al., 2020).

Here, we empirically assess the contributions of five different habitat types (cereals, leys, semi-natural pastures, mature coniferous forest and clear-cuts) to the diversity of plants, bumblebees and butterflies at local scale, as well as to the landscape-scale species richness predicted by countryside-species area relationship models (cSAR; Pereira and Daily, 2006). These three species groups are known to be diverse in open habitats, including natural or anthropogenic early-successional forest stages (Lehnert et al., 2013; Viljur and Teder, 2016). We purposefully collected data in the highlands of Jönköpings län, Småland, Sweden, from 87 sites selected across independent gradients of landscape-scale cover of forest, cereal crops, leys and semi-natural pastures, allowing us to assess the effect of the surrounding landscape on local diversity and

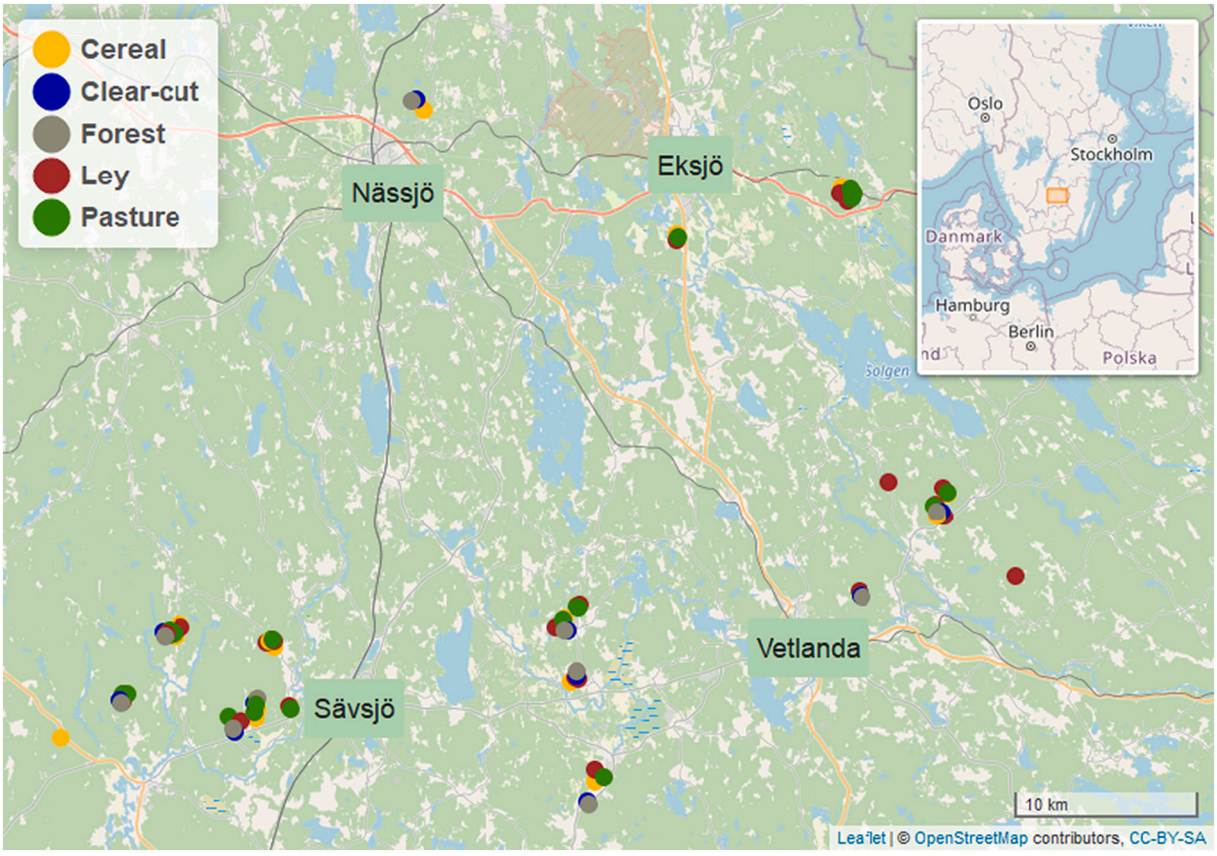

Fig. 1. Map of the study area, with an inset placing the study area, outlined with a red rectangle, within the region. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the validity of the area-based approaches. We use the cSARs to simulate landscape-scale species richness outcomes for different agricultural and forest habitat mixtures. In particular, we assess whether the relative contribution of clear-cuts to biodiversity in forest-farmland mosaics is sufficient to compensate for the expected negative effects of losing marginal farmland to forest habitats. We also assess how important the contribution of leys and/or cereal crops is to landscape-scale richness, as these habitats are have received much less attention than semi-natural grasslands.

2. Material and methods

2.1. Study sites

In the study region (Jönköping county, Småland, Sweden), even-aged coniferous forests (mainly spruce, but also pine; Nilsson et al., 2021), interspersed with clear-cuts, are the dominant land use types. Embedded within the forests are open areas cultivated by small farms, with cereal crops and leys (grasslands, often in rotation, established on arable land, mostly by sowing grass and clover mixtures), as well as semi-natural (non-improved) pastures mainly grazed by cattle. Broad-leaved tree cover is low and often restricted to forest edges, and non-improved hay meadows are very rare; these habitats were therefore not considered here (see Nilsson et al. (2013) for detailed descriptions of the region and habitats). Using a procedure explained in detail in the Supplementary Information (SI Text and Fig. S1) we selected 19 cereal, 24 ley, 24 semi-natural pasture, 10 clear-cut and 10 mature forest sites, based on GIS data and field visits. The selected clear-cuts were 2 to 7 years in age. The selection was done such that landscape surrounding the sites within a 1 km-radius would cover gradients in composition of forest, cereal, ley, and semi-natural pasture, thereby allowing the assessment of both local and landscape-scale effects of habitats on local communities. We chose clusters of sites containing one of each (or as many as possible) of the land-use types, both to optimize travel times and to create a natural clustering of sites to fit cSAR models for upscaling species richness from local to landscape-scale.

2.2. Surveys

2.2.1. Plants

We surveyed plants in all sites in one to two visits per site between June 10th and August 13th, 2019, using 1 × 1 m sample quadrats in which we recorded the presence of all vascular plant species, including trees and grasses. The number of quadrats was adapted to the accumulation of species as the surveys progressed, as we aimed for a similar sample completeness (Chao and Jost, 2012) across habitats and landscapes (see Fig. S2). Therefore, for leys and cereals that had been cut, harvested and/or ploughed, as well as in most forests, we only surveyed 10–15 squares per site, while in most semi-natural pastures and clear-cuts, as well as some leys, we surveyed 60 quadrats. For the agricultural sites and the clear-cuts, which have a higher edge density than mature forest patches, we placed five squares at the edge (inside the field or clear-cut). The other squares we placed haphazardly by throwing the squares out in the site turning at different directions each time. A deviation from this method was applied in the cereal crops, where distance between quadrats were based on estimated throwing distance in other habitats.

2.2.2. Insects

We surveyed bumblebees and butterflies (including burnet moths) three times in 2019, between June 10th and August 13th, in each of 78 sites (a subset of the total 87 sites, as some could not be accessed during cattle grazing or for other reasons, see SI Text). These included 17 cereal, 10 clear-cut, 10 forest, 23 ley and 18 pasture sites. The surveys took place between 9:00 in the morning and 18:00 in the evening with temperatures above 16 degrees Celsius and winds 4 or less on the Beaufort scale. The insect surveys were conducted along five transects within each site. Each transect originated from the field border and reached 50 m out into the site. We walked along each transect for 10 min, not including time spent catching, handling and identifying, noting all species of butterflies and bumblebees within 2.5 m on each side of the transect, five meters ahead and five meters up. In addition to the transects, we surveyed flower-rich areas for bumblebees and butterflies at each of the sites for a further 10 min. We caught the insects in the field when necessary, and identified them to species (or species complexes).

2.3. Statistical analysis

We calculated the total species richness (observed number of species) per site for plants, bumblebees and butterflies (in the latter two cases, by aggregating species by site data across the three survey rounds), including only individuals identified to species (or species complex/section).

We modelled the effect of local habitat on local species richness separately for plants, bumblebees and butterflies, using linear mixed models fitted in R v4.0.2 (R Core Team, 2020) using the package lme4 v1.1.23 (Bates et al., 2015). The raw observed species richness was used as a response for plants, while observed species richness for the two insect groups were square-root transformed, resulting in Gaussian distribution and variance homogeneity among model residuals. To account for the spatial pattern obtained through the site selection procedure as well as potential regional effects, we fit random intercepts per spatial cluster of sites, defined as a group of sites being within a distance of 500 m, 1000 m or a higher value (up to 20 km, in 1000 m steps), chosen based on AICc values. We verified normality and homoscedasticity of residuals using the package DHARMa v0.3.2.0. (Hartig, 2020). For plants, we repeated the analysis for an equal-sampling-effort sample of 15 quadrats.

For each species group, we also assessed for the open habitats (cereal, ley, pasture, and clear-cut) the importance of the landscape-scale land-use in the surrounding 1000 m radius for the site-scale species richness, using a multi-model approach. Given the inherent multicollinearity in compositional data, we defined rules for suitable candidate models. All subset models contained the categorical factor "habitat type" and could contain up to three additional landscape-scale variables out of the following four: proportion forest cover (here including clear-cut), proportion cereal crops, leys or pasture. All 20 candidate models were fitted and the best model subset was obtained (threshold: $\Delta AIC < 4$), this was done using helper functions in MuMin v1.43.17 (Barton, 2020). We verified that there were no significant departures from the model assumptions, as described above, for all candidate models. The analysis was repeated separating forest into clear-cuts (2 to 7 years in age) and mature forest.

To generate predictions for species richness at larger scales, we applied the countryside-species area relationship (cSAR) approach (Martins and Pereira, 2017; Pereira and Daily, 2006) to each of the three taxonomic groups separately. This approach has been used in biodiversity upscaling from local-to-landscape scales (e.g. Merckx et al., 2019) and up to large regional scales (among others as part of global analyses such as Leclère et al., 2020) for linking landscape-scale land-use to biodiversity. The cSARs are built by splitting the species community into habitat affinity groups (e.g. "specialist habitat A", "specialist habitat B", "generalist"; based on the data or on prior knowledge) and fitting non-linear models linking the area of the different habitats to the species richness for each habitat affinity group. In local-to-landscape applications, the curves are built on presence-absence data that stem from non-adjacent sites and that are successively aggregated between neighboring sites in an approach akin to the construction of type IIIA species area curves (Scheiner, 2003). We build such an incremental aggregation, starting from considering all sites individually, then constructing intermediate-size pseudo-landscapes using complete-linkage hierarchical clustering of the matrix of distances between sites, resulting in site

aggregations ranging from two to 54 individual sites (only 49 for insects). Finally, we added a single large pseudo-landscape consisting of all 87 sites (only 78 for insects). Here, unlike previous applications, we more conservatively consider that the species richness estimates refer to the sum of the aggregated sampled area, rather than the sum of the area covered by the non-continuous grid. We consider that each sampled site corresponded to 1 ha, with the resulting pseudo-landscapes covering between two to 87 ha (78 ha for insects).

To group the species into habitat affinity groups, given the level of detail for the habitats, we could not rely on readily available information from the literature or trait databases, and chose a data-driven approach. Instead of defining habitat specialist groups based on the relative abundance as in Merckx et al. (2019), we allowed for groups with more complex patterns of habitat preference using a clustering approach to define these groups from the data. We computed the species-level frequency of occurrence in the different habitats, which we used to compute a Euclidean distance matrix. We applied Ward's method for hierarchical clustering on the distance matrix, after assessing whether the data was clusterable using the Hopkins statistic for cluster tendency. We determined the optimal number of clusters by applying the majority rule to the outcome of three approaches (silhouette, gap and elbow; Kassambara and Mundt, 2020), with the constraint that smallest cluster should hold more than two species. For each i-th habitat affinity group, we fitted $S_i = c_i \times \left(\sum_j h_{ij} A_j\right)^{z_i}$. This was done using the *nls* function. The starting values for c_i and z_i were the exponential of the intercept and slope, respectively, of a log-log linear model between S_i and the sum of the areas of habitat for which the group was expected to have high habitat affinity values. The parameters h_{ij} were set equal to one for the habitat j for which the highest frequency was observed. Starting values for all other h_{ij} values were based on the mean frequencies of occurrence for the species affinity group in habitat j. The $h_{ij} \cdot A_j$ terms were omitted where a habitat affinity group i did not at all occur in a particular habitat j. Estimates of total species richness were obtained by summing the S_i values across habitat affinity groups, where more than a single group had been identified.

2.4. Simulating biodiversity levels from cSAR models

In a first step, we used the cSAR models to compute the species area curves separately for the different habitats, to assess how differences in species richness between habitats change with the area of habitat considered. Bootstraps were generated by sampling (N = 1000) with replacement from the original pool of sites and pseudo-landscapes, keeping the original habitat affinity groups. For values between one to 40 ha, we calculated model predictions as well as bootstrap-based bias-corrected and accelerated confidence intervals (Kropko and Harden, 2020). We compared the results with resampling-based estimates of beta-diversity partitions (species turnover and nestedness) on presence-absence data, using the package betapart (Baselga et al., 2021).

In a second step, we predicted and plotted the effects of different agricultural land-use mixes for three levels of forest cover, assuming clear-cuts constitute 10 % of the forest area, an assumption verified using the public clear-cut data from the Swedish Forest Agency (Skogsstyrelsen) (see SI for details). Ternary plots for model predictions were made using ggtern v3.3.0 (Hamilton and Ferry, 2018).

In a third step, to assess the effect of forest and clear-cut cover on landscape-scale species richness, we simulated the species richness outcomes in response to afforestation for a 40 ha landscape consisting at the outset 45 % of forest and 55 % of agriculture, with equal shares of cereal crops, leys and pastures. In the simulation, the forest cover increases from 45 to 95 %, assuming that the forest has 0, 10 or 20 % of its area that is clear-cut. The afforestation was simulated without discrimination between agricultural habitats during the simulated afforestation. Additionally, we repeated this by starting to afforest on pastures, and only when that is used up switch to land used for cereal crops and ley, as well as the reverse, that is start afforesting on land used for cereal crops and ley. The simulations did not include temporal aspects such as forest growth dynamics, but only considered end-points, technically meaning that afforestation leads immediately to both mature forests and clear-cuts. To assess the uncertainty in the cSAR simulations, we computed bootstrapped confidence intervals for total species richness, using the procedure described previously.

3. Results

3.1. Observed communities and sampling completeness

We observed 362 plant, 48 butterfly (and burnet moth) and 17 bumblebee species. Mean site-level sample completeness relative to the Chao estimators (computed using *specpool* function in the package vegan; Oksanen et al., 2019) was between 70 and 78 % for plants, 57 to 70 % for butterflies and 75 and 82 % for bumblebees. Completeness, assessed for all sites for which at least one species was detected (all 87 sites for plants, 71 for butterflies and 75 for bumblebees) did not differ between habitats for any of the three groups (Fig. S2; plants: $F_{4,82} = 0.853$, $P = 0.496$; butterflies: $F_{4,66} = 1.352$, $P = 0.260$; bumblebees: $F_{4,70} = 0.359$, $P = 0.837$). For the assessment of butterfly and bumblebee completeness, we treated the surveys of flower-rich areas as an additional transect, since they had the same time duration. The surveys of flower-rich areas added 27 % of butterfly species, with significantly higher values observed in cereals (36 %) than in clear-cuts and pastures (23 and 13 % respectively) (binomial GLM, Likelihood-ratio tests for overall habitat effect: $\chi^2_{df=4} = 12.29$, $P = 0.015$, followed by Tukey posthoc test). They contributed 17 % of bumblebee species, with no significant differences between habitats ($\chi^2_{df=4} = 7.15$, $P = 0.128$).

3.2. Local species richness

At the scale of the individual site, all open habitats, including clear-cuts, had significantly higher species richness of plants, butterflies and bumblebees than forests (Fig. 2, Table S1; Likelihood-ratio tests for overall habitat effect for plants: $\chi^2_{df=4} = 93.26$, $P < 0.001$; butterflies: $\chi^2_{df=4} = 105.94$, $P < 0.001$; bumblebees: $\chi^2_{df=4} = 39.76$, $P < 0.001$). There were higher number of plant species in both pastures and clear-cuts compared to cereal and leys (Fig. 2). Pastures also harbored higher numbers of butterfly species compared to cereals and leys, while the species richness in clear-cuts was intermediate and not significantly different to that in the other three open habitats. Bumblebee species numbers were only higher in pastures compared to cereals, while in both leys and clear-cuts species numbers were intermediate and not significantly different to those in pastures or cereals. The spatial clusters minimizing AICc were determined to be at a distance of 1000 m for plants, 4000 m for butterflies and 500 m for bumblebees, accounting for 7 %, 25 % and 11 % of the variation in the random effect components, respectively. When analyzing equal-sampling-effort plant species richness values, results were similar, but clear-cuts were under-sampled with values being closer to those in leys and cereal crops rather than those in pastures (Fig. S3).

3.3. Landscape-scale species richness

To upscale species richness, we clustered species into habitat affinity groups resulting in four groups for plants, three for butterflies, and one for bumblebees. We fitted cSAR models for each of these habitat affinity groups (Table 1; Table S2 for habitat affinity group membership of individual species). Plant groups included pasture, cereal and clear-cut specialists, and a more generalized group. The butterfly groups included pasture and clear-cut specialists and a more generalized group (Table 1). The cSAR single-habitat predictions for areas between 1 and 40 ha showed that plant species in leys fell behind that of cereal crops at

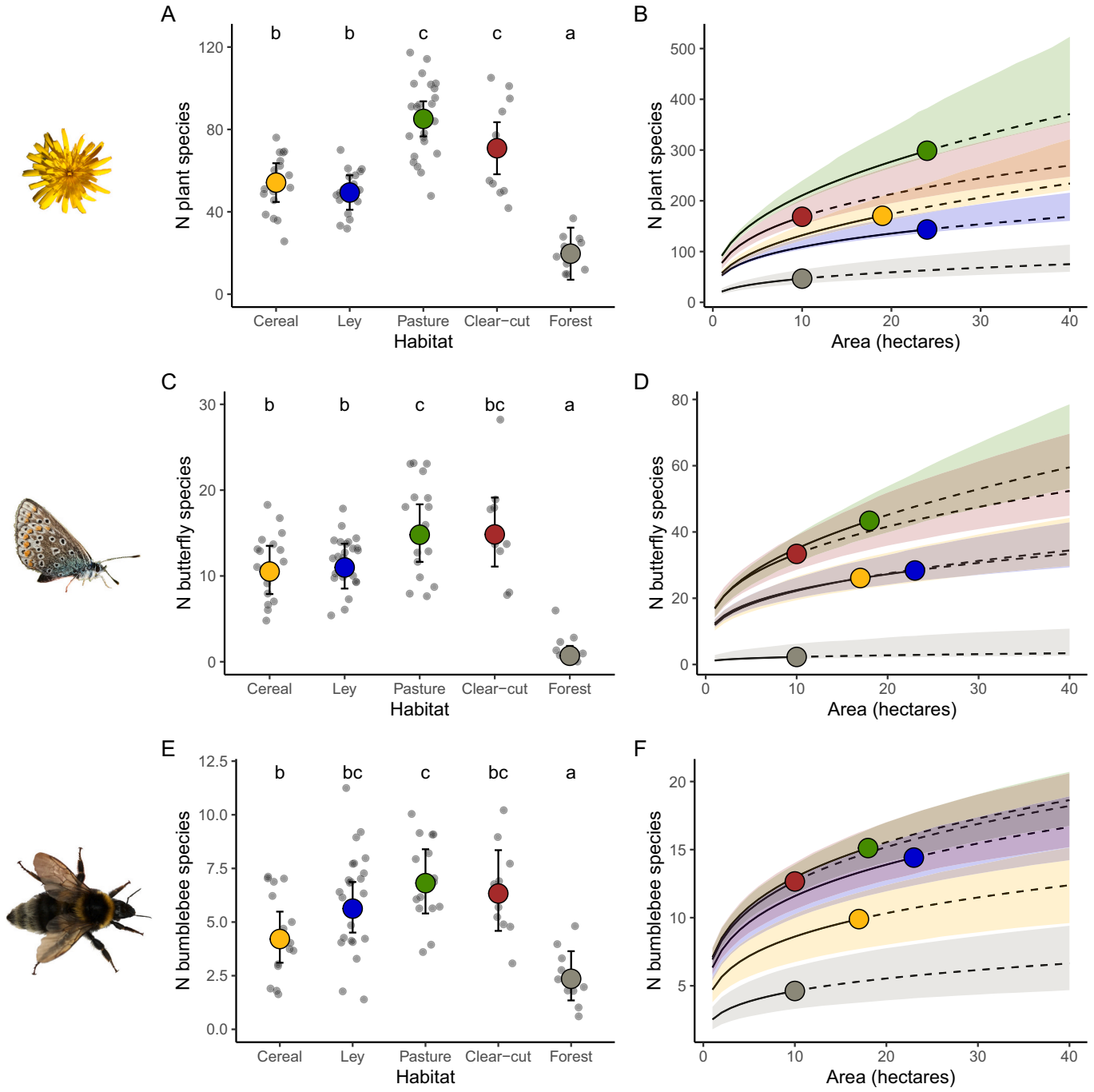

Fig. 2. Observed and predicted species richness for plants (A, B), butterflies (C, D) and bumblebees (E, F). The site-level predictions (A, C, E) are extracted from the best models (back-transformed from square-root in the case of the two insect groups). Coloured points are model estimates, grey points are observations, and error bars are 95 % confidence intervals for the model estimates. Letters indicate habitats not significantly different from each other based on post-hoc tests. The area-based predictions (B, D, F, black lines) are based on species from countryside species-area models. Points indicate the number of sampled sites (we assume a site corresponds to a hectare). Ribbons in B, D, and F are 95 % bootstrap intervals.

larger spatial scales (Fig. 2B), which contrasted with the pattern in butterflies where the similarly low values in cereals and leys persisted even at larger scales (Fig. 2D). Species richness of plants in clear-cuts fell back behind that of pastures as scales increased. For butterflies and bumblebees the patterns at larger scales were similar to those observed at site level (Fig. 2D, F), but with bumblebee species numbers in leys becoming more similar to those in pastures and clear-cuts than those in cereals. Species turnover accounted for the largest component of total beta-diversity, and differences in species turnover between habitats reflected cSAR trends (Table S3).

Comparison of the cSAR-based, simulated effects of the mixture of agricultural habitats at the landscape scale (again 40 ha; Fig. 3) showed that landscapes with a high share of pasture had the highest species richness values for all three groups. Fig. 3 illustrates which habitats were most important when the share of pasture was lower. Approximately 95 % of the maximal plant species richness could be obtained with 60 % pasture and 40 % cereal or 75 % pasture and 25 % ley. The reverse pattern was observed in bumblebees, where approximately 95 % of the maximal species richness values were observed at 70 % pasture and 30 % ley or 40 % pasture and 60 % ley. The patterns did not qualitatively

Table 1

Parameter estimates for the nine cSAR models $S_i = c_i \times \left(\sum_j h_{ij} A_j\right)^{z_i}$. Habitat affinity values h_{ij} are given for cereal crops (h_a), clear-cut (h_c), ley (h_l), forest (h_f) and pasture (h_p), for each group (j). Estimated values in bold are significant (t-test, $P < 0.05$).

Taxon	group	c	z	Cereal h_a	Clear-cut h_c	Ley h_l	Forest h_f	Pasture h_p	N species
Plants	S_1	**55.00**	**0.30**	**0.49**	**0.04**	**0.47**	0.00	1.00[a]	148
	S_2	**56.48**	**0.35**	0.01	1.00[a]	0.01	**0.04**	**0.21**	129
	S_3	**4.02**	**0.82**					1.00[a]	53
	S_4	**2.90**	**0.82**	1.00[a]					32
Butterflies	S_1	**1.54**	**0.70**	**0.23**	0.12	0.10		1.00[a]	14
	S_2	**14.03**	**0.23**	**0.35**	**0.77**	**0.43**	0.00	1.00[a]	25
	S_3	**3.37**	**0.44**	0.00	1.00[a]	0.01	0.00	**0.11**	9
Bumblebees	S	**6.92**	**0.26**	**0.23**	1.00[a]	**0.71**	0.02	**1.09**	17

[a] These values were set to one, not estimated.

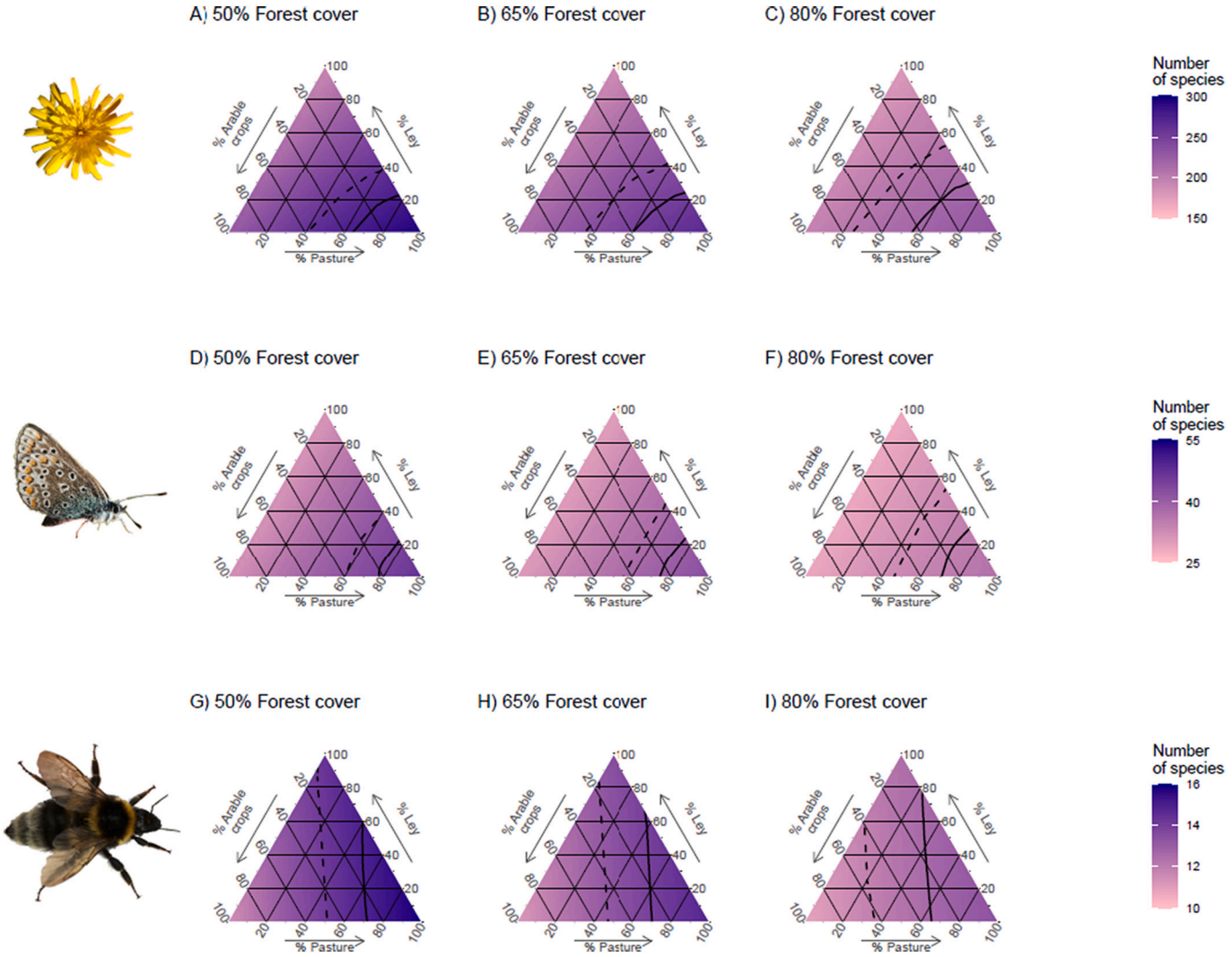

Fig. 3. Landscape-scale species richness predicted from countryside species-area relationships (cSAR) models given land-use composition (%A: arable crops, %L: leys, %P: semi-natural pastures). Predictions were made assuming the forest consists of 90 % mature coniferous forest and 10 % clear-cuts (see Fig. 4 for effects of alternative clear-cut proportions), and that arable crops are cereals (see methods). The two lines (stippled and solid) in each panel indicate the zone where species richness is within 90 % (stippled) and 95 % (solid) of the maximum value in that panel.

change with the share of forest in the landscape (comparing across columns in Fig. 3). Here we considered forests to have 10 % clear-cut between zero and 10 years of age, based on analyses of the clear-cut data showing that in the study region the share of clear-cuts was approximately 10 % considering forest ages 0–10 years (see Fig. S4).

3.4. Effects of simulating increasing forest cover

Further simulations using the fitted cSAR models varying the cover of forest and share of clear-cut showed that predicted landscape-scale species richness decreased with increasing forest cover across all three taxonomic groups in nearly all cases (Fig. 4; Figs. S5, S6). The decrease

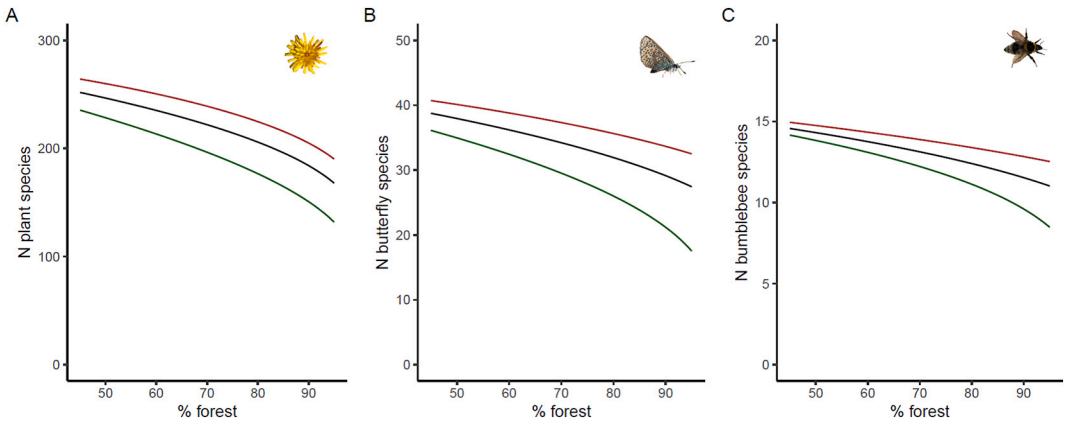

Fig. 4. Effects of increasing forest cover with different proportions of clear-cuts on landscape-scale species richness of plants (A), butterflies (B) and bumblebees (C) predicted from countryside species-area relationships (cSAR) models for an area of 40 ha. Share of clear-cut (relative to forest area) is 0 % (green lines), 10 % (black lines) or 20 % (brown lines). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

was strongest when assuming that the forest did not contain clear-cuts. When we assumed that, at the landscape-scale, a forest contained 10 % or 20 % clear-cuts, the negative effects of increasing forest cover were compensated to a higher degree – but never fully – in landscapes where the agricultural land-use had low proportions of high-quality habitat. For all groups, converting pastures to forest induced the steepest declines in species richness, with lower declines observed for the conversion of cereal crops and leys (Fig. S5). The differences between the three afforestation scenarios were greater for plants and butterflies than for bumblebees, which were also least affected overall by a higher share of forest. The only case where afforestation resulted in close to a null-sum for species richness was for butterflies, when afforestation was simulated on cereal crops or leys rather than semi-natural grasslands, and when we considered 10 % or 20 % clear-cuts (Fig. S5B).

3.5. Accounting for landscape context

Finally, to evaluate whether an area-based approach such as the cSAR model is appropriate, we assessed whether local species richness was affected by the surrounding landscape composition using a multi-model and model-averaging approach. Landscape effects were found not to be significant for plants or butterflies (Tables S4–S7). For bumblebees, however, the cover of leys within a 1000 m buffer of the site centroid was positively related to local species richness (Tables S4–S7). Fitting cSARs for bumblebees separately for the sites with low (<10 %) and high (10 % or more) cover of ley in the landscape suggested this did not have much effect on the cSAR model parameters, which did not differ significantly between the two models (Fig. S7).

4. Discussion

Quantitative knowledge on the contribution of different habitat types to biodiversity is essential for anticipating effects of future land-use and policy scenarios on biodiversity loss (Leclère et al., 2020). Here, we applied a countryside species-area approach across mosaic farmland-forest landscapes to assess the contribution of the main agricultural and forest habitats, including clear-cuts, to landscape-scale species richness of plants, butterflies and bumblebees in a region where active agriculture is vulnerable to policy changes (Brady et al., 2017; Renwick et al., 2013). We found that semi-natural pastures drove species richness patterns across scales and taxa. Cereal crops and leys made important contributions to landscape-scale species richness of plants and bumblebees, respectively. The results also show the negative impacts of even-aged coniferous forest cover on species richness of all three taxa. While clear-cuts are an important transient habitat for farmland species, their overall contribution at the landscape scale does not compensate for the negative effect that simulated shifts from farm to forested land have on species richness of the investigated taxa.

4.1. Semi-natural grasslands and other open habitats

Semi-natural grasslands with permanent extensive use for agriculture through mowing and grazing host the majority of the plant species of Central and Northern Europe (Pärtel et al., 2005). The area of these grasslands has decreased dramatically over the past couple of hundred years, accompanied by shifts in their management (Dengler et al., 2014; Nilsson et al., 2013). Their central role for biodiversity conservation is reflected in monitoring efforts and agri-environmental policy, where support to semi-natural pastures is an important component. Not surprisingly, the importance of semi-natural pastures is well supported by our data, where 15 % of plant species were restricted to that habitat. In addition, affinity for semi-natural pastures was also high for most habitat generalists across both plants and insects (Table 1). Semi-natural pastures were as a result associated with very high species richness values for all the taxonomic groups we studied, both at site and landscape levels. Conserving and even increasing the area and quality of these habitats, should thus continue to be a key priority.

The relative value for biodiversity of habitats other than semi-natural pastures in mixed agricultural and forest landscapes has been less well investigated. Leys were found to be almost as good habitats as semi-natural grasslands for bumblebees, likely due to the presence of white and red clover (*Trifolium repens*, *T. pratense*) which harbor important food resources for bumblebees (Goulson et al., 2008). Leys have also been reported to be likely suitable nesting habitats for bumblebees (Svensson et al., 2000). Cereal crops contributed little to the local diversity of the studied taxa (Fig. 1). However, they contributed plant species to the observed species pool that were not commonly found in any of the other surveyed habitats (Table 1). This set them apart from leys, which are also on arable land but hosted species common also elsewhere, for instance in pastures or cereals. Simulating species richness levels shows that while pasture-dominated agricultural landscapes were most species rich, landscapes with a mixture of pasture and cereal crops would host a larger number of plant species than landscapes with a mixture of pasture and leys (Fig. 2). This effect did not carry over to butterflies or bumblebees, however.

Cereal and ley field management may differ between farms and fields, which in turn could affect species richness of plants and insects (e.g. Tiainen et al., 2020). We expect our sites to represent a range in the variability of the current management, but systematic future changes in management (such as an intensification of leys, or a shift towards more protein crops, changes in the stocking rates of pastures) may reduce the representativeness of our data.

4.2. Clear-cuts and mature forest

Early successional stages of forest development (clear-cuts, clearings, etc.) often benefit light-demanding species, including tree associated species (saproxylic beetles, moths) (Hilmers et al., 2018). In Northern European countries that are dominated by dense commercial forest plantations, the area of clear-cuts is substantial. Past studies have already suggested that such transient open forest habitat can contribute to the local diversity of open farmland species (Ram et al., 2020; Viljur and Teder, 2016). Our models show that clear-cuts also contribute to landscape-wide species richness, in particular for bumblebees, but also for butterflies and plants, for which habitat affinity groups were identified that showed specialization towards clear-cuts (see habitat affinities in Table 1).

However, this is counterbalanced by the fact that under the current forestry practices the area of clear-cuts represents only about 10 % of the total forest area (Fig. 4). More mature commercial forests are often homogeneous with little light reaching the ground under the currently dominating forestry practices, which means that they harbor very low diversity of species. The species-area curve of bumblebees in forests is not quite as flat as that of plants and butterflies (Fig. 2), which can be explained by individual patches of flowers such as cow-wheat *Melampyrum* spp. being actively sought out within the forest by foraging bumblebees. Our simulations based on the field data showed that increasing forest area, in a region already dominated by forests, does not benefit any of the species groups considered, despite the beneficial effect of clear-cuts. This is also true if the extent of pastures is kept constant and the simulated afforestation is only conducted on arable land (cereal crops and ley).

The vegetation in clear-cuts has been shown to reflect past land-use history (Jonason et al., 2014). This suggests that clear-cuts may have potential for restoration of species-rich grasslands, but that their long-term contribution to plant diversity in a forest dominated landscape over multiple forest rotations may be limited. The exact land-use history of the clear-cuts used in the present study is not known, as distinguishing between different types of open habitat on historical maps is often not possible.

A caveat of the study is that our land-use categories are few and only representative of the current management. Forests were split into only two forest age classes (mature and clear-cut) and we limit ourselves to coniferous plantations that are harvested with clear-cutting, which is justified by their dominance in the study region. Habitats such as broadleaved forest, mixed forests, open (grazed) forests, naturally regenerating forest patches, with natural disturbances due to fire, windfall and/or bark beetle attack, may be more valuable habitat for the studied taxa (Hilmers et al., 2018; Lehnert et al., 2013), but these were much less common in our study area. The studied clear-cuts were 2 to 7 years in age and may not represent the full range of conditions resulting from the interaction of management (e.g. removal of stubs, degree of soil preparation, density of the planting) and clear-cut age. The clear-cut stages we studied may have been disproportionately good for the studied species groups (Milberg et al., 2021), meaning that our results at the landscape scale are over- rather than under estimating the contribution of clear-cuts. Our findings may have been different when considering taxonomic groups that have more forest-dependent species, such as fungi, wood-inhabiting insect taxa, or birds. This limitation is somewhat offset by the fact that forests are already the dominant land-use in these landscapes (which is also reflected in our simulations), and that the plantations that dominate the forests in the study region are considered species poor when compared to more diverse or older-growth forests (Larsson et al., 2011).

4.3. Accounting for landscape context

Simulating landscape-scale species richness using cSARs parametrized with replicated, multi-habitat field data provides a simple, data-driven solution to the challenge of assessing the impact of larger-scale land-use changes on mosaic landscapes. One limitation of the current approach is that it is correlational, but we avoided as far as possible correlations to unrelated background variables using a careful design. Another limitation of the cSAR approach is that it confines the assessment to the species richness metric of biodiversity, and makes it difficult to incorporate effects of landscape composition and configuration beyond area effects. The latter has to our knowledge not been previously done except for small, artificial landscapes (Loke et al., 2019) given the extensive data requirements. For our study, the landscape effects at the scale considered (1-km radius around the focal sites) were detected only for bumblebees. We did not find any beneficial effects of forests as reported elsewhere (Sõber et al., 2020), but species richness of bumblebees was higher when the landscape surrounding a local site had a high cover of ley, suggesting that the food resources and nesting habitat these offer also benefit bumblebees diversity in the surroundings (Persson and Smith, 2013). Refitting the cSAR model separately for sites from low and high ley landscapes separately showed that the bias caused by ignoring landscape effects in the main analysis are minor (Fig. S7), and that the upscaling of bumblebee species richness through cSARs, and the conclusions drawn from the simulations, are robust, at least at the landscape scales considered.

4.4. Conclusions and implications for management

Open habitats, including species-rich semi-natural grasslands, have decreased substantially during the last century, and land-use change has not been halted, especially in marginal farming areas (Dengler et al., 2014; Nilsson et al., 2013; Trubins, 2013). Even though the current agricultural subsidies are maintaining profitability of farming (Brady et al., 2017), abandonment and afforestation have led to detectable floristic changes in the past 15–30 years (Tyler et al., 2018). Current and future pressures, including changing diets (Röös et al., 2016) and increasing demands for wood products and afforestation for carbon storage (Gong et al., 2022; Kok et al., 2018), will continue to put pressure on agriculture in marginal farming areas, including the maintenance of semi-natural grasslands. Our study shows that shifts in land-use can have very large consequences for the species richness of plants, butterflies and bumblebees. In some cases, this can imply halving the number of species at the landscape-scale within the observed range of landscape composition. A shift towards a higher share of farmland dedicated to cereal crops would be deleterious for biodiversity, unless pastures are maintained. A continued increase in cover of production forests will decrease plant, butterfly and bumblebee diversity despite the high local species richness attained in clear-cuts. Changes to the Common Agricultural Policy (CAP) may also have significant impact in the near future. These could for example include a removal or a change in the formulation of coupled support to livestock, or changes in eco-schemes or agri-environmental schemes that affect the relative attractiveness of grazing animals on pastures or on leys. Sector-model simulations suggest we can expect moderate to high decreases in the cover of pastures in Sweden, depending on the size and distribution of funds to different agri-environmental mechanisms within the upcoming CAP (Söderberg and Hasund, 2021). Our parametrized models, including the bootstrapped versions for uncertainty quantification, can be integrated with e.g. economic agent-based or sectoral models (Brady et al., 2017; Hristov et al., 2020) predicting land-use changes, for further ex-ante assessment of specific alternative future policies or land-use targets. We show here that maintaining grazed semi-natural pastures in the landscape is the primary prerequisite for maintaining species richness across three taxa in mosaic forest-farmland landscapes, with cereal and ley production. Increasing the attractiveness of using semi-natural pastures for grazing, and ensuring that the number and distribution of farms with grazing animals is suitable for continued grazing should thus be of the highest priority for farmland biodiversity conservation. This should guide the formulation of the CAP Strategic plans of

countries with high shares of farmland in agriculturally marginal, forest-dominated regions.

CRediT authorship contribution statement

YC conceived the idea with support from HS and JE. YC, GKS, NBO and FR designed the study, GKS led the field work with support from YC. YC led the analysis with support from GKS and FR, YC led the writing of the initial version of the manuscript with support from GKS. All authors contributed with input to the final manuscript.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data and code necessary to reproduce the analyses, figures and tables are archived at Mendeley Data (DOI: https://doi.org/10.17632/xnh8zgvbtz.1)

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Appendix A. Supplementary information

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2022.109728.

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