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Alpine mires support distinct and vulnerable plant–pollinator networks compared to grasslands

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Alpine mires support distinct and vulnerable plant–pollinator networks compared to grasslands

Abstract

Alpine mires are highly threatened habitats that support specialized biodiversity, yet their pollinator communities and plant–pollinator interactions remain poorly known. We compared plant and pollinator communities and their interaction networks in five alpine mires and five adjacent grasslands across the Western Italian Alps to assess differences in composition, network structure and robustness to species loss. Vegetation and pollinators, including hoverflies, bees, beetles and butterflies, were surveyed using standardized protocols. Mires supported lower plant and pollinator richness than grasslands, although 57.3% of mire plants and 47.2% of mire pollinators were recorded exclusively in this habitat. Plant and pollinator communities differed significantly between habitats, and macroplots with more similar plant communities also tended to support more similar pollinator communities. Both habitats hosted species of conservation concern, but mires were notable for several threatened hoverflies, including three Endangered *Cheilosia* species recorded exclusively there, whereas grasslands hosted two butterfly species listed in Annex IV of the Habitats Directive. Hoverflies showed similar richness and abundance in both habitats and dominated mire communities, whereas bees, beetles and butterflies were richer and more abundant in grasslands. Mire networks were smaller, contained fewer interactions and showed lower network-level specialization. Mire pollinator communities were less robust to the preferential loss of habitat-exclusive plants, while no habitat differences emerged under random plant-loss scenarios. These findings show that alpine mires and grasslands make complementary contributions to pollinator conservation, while small and fragmented mires support distinctive communities and interaction networks particularly vulnerable to vegetation change.

Keywords: ecological networks · peatlands · alpine grassland · flower visitors · network robustness · hoverflies

1. INTRODUCTION

Although peatlands cover only 3-4% of the Earth's land surface (United Nations Environment Programme 2022), they store large amounts of carbon, regulate freshwater, and support numerous highly specialized plant and animal species (Rydin and Jeglum 2013; Lehmitz et al. 2020). They also sustain rare and threatened taxa and may act as climate-change refugia (Słowińska et al. 2022; Słowińska et al. 2026). At the same time, peatlands are among the most threatened ecosystems worldwide. In Europe, mires have the highest proportion of threatened habitat types, with 85% classified as threatened in the European Red List of Habitats (Janssen et al. 2016). Their major threats include direct human activities (e.g., peat extraction, pollution, grazing) and indirect effects caused by climate change (Dieleman et al. 2015; Janssen et al. 2016; Spitale 2021; Pollo et al. 2022). In the Alps, mires occur near the southern margin of their European distribution, mainly as small, fragmented, and isolated patches (Li et al. 2025; Pérez-Haase and Ninot 2025). This marginal position is associated with low and declining climatic suitability (Tahitu et al. 2025), while limited extent and poor connectivity may further constrain ecological resilience (Słowińska et al. 2026). Local pressures, particularly cattle grazing and drainage, further increase their vulnerability (Spitale 2021). Recent vegetation resurveys have already revealed declining habitat integrity, with losses of mire-specialist plants and increases in generalist and woody species (Pollo et al. 2026).

Grasslands are among the most species-rich ecosystems worldwide (Wilson et al. 2012) and provide multiple ecosystem services, including forage production, soil-erosion control, water regulation, carbon storage, pollinator support and cultural values (Bengtsson et al. 2019). Since below the forest limit, grasslands are semi-natural systems whose long-term persistence depends on agro-pastoral practices (Targetti et al. 2010; Assandri et al. 2019), while agricultural intensification and the abandonment of traditional management practices are their major pressures in Europe (Janssen et al. 2016). In addition to

widespread land abandonment in the Alps, grasslands are increasingly affected by climate change (Dibari et al. 2021). Vegetation resurveys across the Alps have documented substantial temporal turnover, including the loss of characteristic grassland species and increasing contributions of generalist, nutrient-demanding and woody plants (Kindermann et al. 2024; Bonari et al. 2025).

The ecological consequences of these compositional changes may extend beyond vegetation. Because flower-visiting insects depend on floral resources and many plants rely on animal-mediated pollination, shifts in plant composition may alter pollinator communities and plant–pollinator interaction networks (Trunschke et al. 2024). Research on alpine pollinators has concentrated primarily on grasslands (Lefebvre et al. 2018; Sommaggio et al. 2022; Hederström et al. 2024), which typically support high plant diversity and abundant floral resources (Fontana et al. 2020; Probo et al. 2025). Research on European mires, in turn, has largely focused on vegetation, hydrology, carbon dynamics and restoration, while species-level knowledge remains limited for nearly all non-plant taxonomic groups, particularly invertebrates (United Nations Environment Programme 2022). Existing research on mire fauna has mainly consisted of taxon-specific surveys and faunal inventories (Desrochers and van Duinen 2006; Batzer and Boix 2016). In the Alps, some studies have focused primarily on Odonata and Heteroptera, confirming that mires support specialized communities including boreo-alpine and often rare species at the southern margin of their range (Sindaco et al. 2007; Montagna et al. 2008; Bionda et al. 2013). Koch et al. (2021) showed that wetland environments support several rare hoverfly species, highlighting their conservation relevance. To our knowledge, descriptions of pollinator communities in mire habitats remain rare and geographically scattered, limited largely to a handful of temperate (Small 1976) and tropical (Beyer et al. 2023) case studies. Plant–pollinator network descriptions and analyses of alpine or temperate mires remain virtually absent. Ecological networks quantify the identity and frequency of interactions between plants and pollinators, allowing emergent properties such as interaction distribution, specialization and robustness to species loss to be assessed (Memmott et al. 2004; Blüthgen et al. 2006; Bascompte and Jordano 2007; Bascompte and Scheffer 2023). This framework is particularly relevant where pollinators depend on a

74 restricted set of floral resources, because losses of interacting plant species may propagate through
75 pollinator communities and increase the risk of secondary declines (Weiner et al. 2014).

76 Here, we investigated plant and pollinator communities and their interaction networks in mires in the
77 Western Italian Alps by comparing them with adjacent grasslands, which served as a well-studied reference
78 habitat for alpine pollinator communities. Specifically, we investigated whether (1) plant and pollinator
79 communities differ in composition between alpine mires and adjacent grasslands; (2) plant–pollinator
80 networks differ between the two habitats in size, interaction distribution and specialization; and (3) network
81 robustness to species loss differs between mires and grasslands. Overall, we aimed to assess whether plant–
82 pollinator interactions buffer or further amplify the vulnerability of these already threatened habitats.
83 Addressing these questions is particularly important at the southern margin of mire distribution, where
84 climatic constraints, habitat fragmentation, and ongoing vegetation change may increase the vulnerability
85 of both species and their interactions.

86 ## 2. MATERIALS AND METHODS

87 ### 2.1 Study area and sampling design

88 The study was conducted in 10 macroplots in the Western Italian Alps (45.14° N, 7.12° E), comprising five
89 alpine mires and five nearby grasslands distributed along an elevational gradient from 1,700 to 2,400 m
90 a.s.l. The macroplots were distributed across five study sites and covered 400 m² each. They were selected
91 to be representative of the respective habitat, marked with stakes and georeferenced (Fig. 1, Table S1).

92 **Fig. 1**

93 ### 2.2 Sampling and identification

94 Both vegetation and pollinators were sampled using a standardized protocol to ensure comparability across
95 habitats and reduce sampling bias.

Accordingly, vegetation was surveyed in four 16-m² subplots within each macroplot, following Chytrý and Otýpková (2003). Within each subplot, all vascular plant species were recorded, and their percentage cover was estimated. Flowering plants visited by each sampled flower-visiting insect were also identified and recorded, allowing quantitative plant–pollinator interactions to be reconstructed. Plant species were identified in the field whenever possible, whereas uncertain specimens were subsequently determined with the support of expert botanists. All specimens were identified to species level, except for the taxonomically critical taxa, which were retained as aggregates (i.e., *Alchemilla alpina* aggr., *Festuca ovina* aggr., *Festuca violacea* aggr., *Hieracium prenanthoides* aggr., and *Thymus serpyllum* aggr.). Vegetation was surveyed during the optimal phenological phase for grassland and mire plant communities in June-August 2024 (Jenačković et al. 2019). We standardized the taxonomic nomenclature following the Euro+Med PlantBase (Euro+Med 2025).

Flower-visiting insects (hereafter, 'pollinators') were sampled within macroplots, and each macroplot was visited six times between June and August 2024, at approximately 15-day intervals, to account for seasonal variation in pollinator activity and community composition (Schwarz et al. 2020). Mire and grassland macroplots belonging to the same site were surveyed on the same day. Pollinators were surveyed for 90 minutes during each visit, sampling only under suitable weather conditions for insect activity. Except for butterflies identified directly in the field, specimens were captured using an entomological net and preserved in tubes containing 70% ethanol for subsequent identification to species level (Table S2). Due to the taxonomic complexity of the collected material, species-level identification was not possible for all insect groups. We therefore focused on taxonomically well-resolved and ecologically well-studied taxa, in order to avoid taxonomic bias in the analysis (Blüthgen and Staab 2024). Hoverflies (Diptera: Syrphidae), wild bees (Hymenoptera: Anthophila; Andrenidae, Apidae, Colletidae, Halictidae and Megachilidae), beetles (Coleoptera: Buprestidae, Cantharidae, Cerambycidae, Coccinellidae, Curculionidae, Elateridae, Meloidae, Melyridae, Nitidulidae, Oedemeridae, Scarabaeidae, Scirtidae, and Tenebrionidae) and butterflies (Lepidoptera: Papilionidae, Pieridae, Lycaenidae, Nymphalidae, and Hesperiidae) were

identified. Nomenclature of hoverflies follows Speight (2026) with the exception of *Chrysotoxum fasciatum* here referred to as C. *arcuatum* following The International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature 1999). Nomenclature of wild bees follows Reverté et al. (2023). Nomenclature of beetles (Coleoptera) follows Löbl and Smetana (2007), Audisio et al. (2009, for Nitidulidae Meligethinae), Löbl and Löbl (2016), Danilevsky (2020), Iwan and Löbl (2020), and Alonso-Zarazaga et al. (2023). Nomenclature of butterflies follows Wiemers et al. (2018).

In addition, the following environmental variables were recorded for each macroplot at each sampling occasion: rock cover (%), bare soil cover (%), open water cover (%), flower cover (%), elevation (m a.s.l.), and mean herb-layer height (cm).

2.3 Data Analysis

We performed all statistical analyses with R Software version 4.6.0 (R Core Team 2026).

For analyses, vegetation cover values were averaged across the four subplots to obtain a single cover value for each plant species within each macroplot. Similarly, pollinator abundances were summed across the six sampling visits within each macroplot, yielding a macroplot × species abundance matrix.

Regional biodiversity patterns

Regional species richness was assessed for plants and pollinators as the total number of species recorded across the 10 macroplots, 5 within each habitat type. Regional plant cover was calculated as the mean of the macroplots and regional pollinator abundance was calculated as the sum of all specimens monitored across macroplots. Pooling the six temporal surveys provided a more comprehensive representation of the plant–pollinator interactions occurring within each macroplot over the flowering season, while retaining the macroplot as the independent unit of analysis and avoiding the pseudoreplication of repeated observations from the same location.

Plant and pollinator species were classified as "shared" when they occurred in both habitats and as "exclusive" when they were recorded only in mires or only in grasslands. Here, "exclusive" refers solely to species recorded visiting flowers in only one of the two habitat types during our surveys. It does not necessarily indicate ecological specialization or strict habitat dependence.

For each recorded species, the conservation status was identified by consulting the European Red Lists (Bilz et al. 2011; Cálix et al. 2018; Vujić et al. 2022; Van Swaay et al. 2025; Michez et al. 2026), while the protection was recorded using annexes of the Habitats Directive (Council of the European Union 1992). Floristic and faunistic records were compared with the available regional distribution information to detect possible new records for the administrative region (Piedmont) and/or for Italy.

Plant and pollinator community composition

Plant and pollinator community compositions were analyzed using non-metric multidimensional scaling (NMDS) based on Bray–Curtis dissimilarities. Ordinations were performed using the 'metaMDS' function in the 'vegan' package (Oksanen et al. 2025). Differences in community composition between mires and grasslands were tested separately for plants and pollinators using permutational multivariate analysis of variance (PERMANOVA), implemented with the 'adonis2' ('vegan' package) by setting 999 free-exchangeable permutations and with habitat type included as the explanatory variable. Homogeneity of multivariate dispersion was confirmed by 'betadisper' ('vegan' package). To identify environmental variables associated with plant and pollinator composition, we fitted all measured variables onto the respective NMDS ordinations ('envfit' function, 'vegan' package). Only variables showing significant associations were retained for interpretation and visualization.

Concordance between plant and pollinator community patterns was assessed by comparing their NMDS configurations using the Procrustes analysis ('procrustes' function, 'vegan' package), and the statistical significance of the resulting concordance was evaluated with the PROTEST randomization test ('protest' function, 'vegan' package).

Plant–pollinator network metrics

Quantitative plant–pollinator networks were constructed separately for each macroplot (10 networks in total). Interactions from the six temporal visits were pooled, producing five mire and five grassland networks, for a total of ten macroplot-level networks. These networks describe the observed floral visits and do not directly measure the actual pollination effectiveness, yet they can be regarded as an indicator of the structure of plant–pollinator interactions.

Network size, plant and pollinator richness, number of interactions and number of links were calculated for each network (metric details provided in Table S3). Interaction structure was further described by interaction evenness (E_2), network-level and species-level specialization (H_2' and d', respectively). The species-level specialization at the macroplot level was calculated as the mean of all species, separately for plants and pollinators. E_2 and H_2' were calculated using the 'networklevel' function, whereas d′ was calculated using the 'specieslevel' function ('bipartite' package; Dormann et al. 2008). Network size, plant and pollinator richness, and interaction number were evaluated as observed metrics. By contrast, because link number, interaction evenness, network-level specialization and species-level specialization may be influenced by variation in species richness, species-level interaction frequency and sampling effort, these metrics were standardized against null-model expectations (Blüthgen and Staab 2024). Null matrices were generated using the 'nullmodel' function in the 'bipartite' package with the Patefield algorithm (method = "r2dtable", Nnull = 999; Patefield 1981). The algorithm randomizes the distribution of network interactions while preserving all row and column marginal totals, and therefore the total interaction frequency and the interaction frequencies of individual plant and pollinator species. Each metric was calculated for the empirical matrix and for all corresponding null matrices. Z-scores were calculated as the deviation of observed values from null model means divided by the null model standard deviation. Positive z-scores indicate that a metric was higher than expected under the null model, whereas negative values indicate that it was lower than expected.

Finally, network robustness was assessed through extinction simulations following Memmott et al. (2004). Robustness was calculated as the area under the secondary-extinction curve, ranging from 0 to 1, with higher values indicating greater persistence of the non-removed guild (plants or pollinators). After each species removal, persistence was measured as the proportion of species in the other guild that retained at least one interaction relative to their initial richness; species with no remaining interaction partners were considered secondarily extinct. The curve included the intact network, with persistence equal to 1, and all subsequent removal steps, and its area was calculated by trapezoidal integration. Four scenarios were simulated for each network: 1) plant robustness following random pollinator removal, 2) plant robustness following preferential removal of habitat-exclusive pollinators, 3) pollinator robustness following random plant removal, and 4) pollinator robustness following preferential removal of habitat-exclusive plants. In random scenarios, all species in the removed guild were eliminated in random order. In preferential scenarios, habitat-exclusive species were removed first in random order, followed by the remaining species, also in random order. Species occurring in the grassland network but not in the mire network were classified as grassland-exclusive, whereas species occurring only in the mire network were classified as mire-exclusive. Each extinction scenario was repeated 100 times per network, and the mean area under the resulting secondary-extinction curves was retained as the robustness estimate. Robustness values were retained as observed metrics rather than expressed relative to null-model expectations, since the aim was to quantify the real robustness of the sampled network as such, including any effect of network size. Standardization against null expectations would have removed part of the size-related vulnerability that was itself ecologically relevant to the comparison.

Differences between mire and grassland networks were tested separately for each metric using Wilcoxon tests (‘wilcox.test’ function, ‘stats’ package).

3. RESULTS

3.1 Regional biodiversity patterns

At the regional level, mires and grasslands showed marked differences in both gamma diversity and the cover or abundance of plant and pollinator communities (Fig. 2, Tables S4 and S5).

Mires supported lower overall richness than grasslands for both plants (82 and 152 species, respectively) and pollinators (106 and 156 species, respectively), with a larger difference in vegetation than in pollinators. This pattern was consistent for three of the four pollinator taxa considered, namely bees (23 and 45, respectively), butterflies (11 and 26, respectively) and beetles (18 and 30, respectively). Hoverflies represented an exception, showing almost identical richness in mires and grasslands (54 and 55 species, respectively). Although the proportion of exclusive species was generally higher in grasslands, mires still supported a substantial habitat-specific component: 57.3% of the plants and 47.2% of the pollinators in mires were habitat-exclusive species. This contribution was consistent across pollinator groups, with mire-exclusive species representing 55.6% of beetle richness, 48.1% of hoverfly richness, 45.5% of butterfly richness and 39.1% of bee richness.

As observed for species richness, the mean regional vegetation cover was lower in mires than in grasslands (77.0% and 95.0%, respectively). Total pollinator abundance showed the same pattern, with 349 individuals recorded in mires and 627 in grasslands. Hoverflies were the only group with identical abundance in the two habitat types, with 204 individuals recorded in each. All other pollinator groups were less abundant in mires than in grasslands: bees numbered 76 and 245 individuals, beetles 44 and 99, and butterflies 25 and 79, respectively. Cover- and abundance-based patterns revealed a clear difference between plants and pollinators in mires. Although plant species found exclusively in mires represented only slightly more than half of total plant richness, they accounted for 85.5% of total vegetation cover. Thus, mire vegetation was largely dominated by mire-exclusive plant species. In contrast, pollinator communities in mires were numerically dominated by species also occurring in grasslands, which accounted for 65.9% of total pollinator abundance and mire-exclusive pollinator species contributing only 34.1% of overall pollinator abundance. Their contribution differed among taxonomic groups, accounting for 42.2% of hoverfly abundance, 38.6% of beetle abundance, 28.0% of butterfly abundance, and only 11.8% of bee abundance.

Among pollinator groups, hoverflies were the richest and most abundant taxon in mires, showing values similar to those recorded in grasslands. Bees were also relatively species-rich and abundant in mires, although both richness and abundance were considerably higher in grasslands. Beetles showed lower richness and abundance than hoverflies and bees, with substantially higher values in grasslands than in mires. Butterflies were the least represented group overall, both in terms of species richness and abundance, and were consistently richer and more abundant in grasslands. Nevertheless, every pollinator group included species recorded exclusively in mires and absent from the surrounding grasslands.

Fig. 2

The two habitats also differed in terms of the conservation relevance of the recorded species. No plant species were listed under the Habitats Directive (Council of the European Union 1992), whereas two butterfly species, *Parnassius apollo* and *Phengaris arion*, are protected under Annex IV and were recorded exclusively in grasslands. Among plants, no species were classified as threatened according to the European Red List of Vascular Plants (Bilz et al. 2011). By contrast, eight pollinator species recorded in grasslands and/or mires were classified as threatened according to the latest available European Red Lists of Hoverflies and Butterflies (Vujić et al. 2022; Van Swaay et al. 2025). These included six Endangered (EN) species and two Vulnerable (VU) butterfly species. Most threatened species were hoverflies, particularly species of the genus *Cheilosia*. Mires hosted three threatened hoverflies exclusively, namely *Cheilosia alpestris*, *C. faucis* and *C. impudens*, all classified as Endangered as well as the Vulnerable butterfly *Thymelicus lineola*. Grasslands hosted only one exclusive threatened species, the Endangered hoverfly *Pipizella nigriana*. Three threatened species were shared between habitats: the Endangered hoverflies *Cheilosia nivalis* and *C. pedemontana*, and the Vulnerable butterfly *Thymelicus sylvestris*. Overall, threatened pollinator species were more numerous in mires and among species shared by both habitats than among species exclusive to grasslands. No new floristic records for Piedmont were identified. Among pollinators, several species were new records for the region: the hoverflies *Platycheirus discimanus*, *Cheilosia psilophthalma*, *C. faucis*, *C. sahlbergi*, *C. semifasciata* and *Neoascia geniculata*, all recorded in mires, and

the bee *Hylaeus gracilicornis*, recorded in grasslands. *N. geniculata* and *H. gracilicornis* were also new records for Italy. Two rare pollen beetles (Nitidulidae, Meligethinae) were also recorded. *Brassicogethes humerosus* was collected in a mire, whereas several specimens of *Clypeogethes chlorocyaneus* were collected exclusively in grassland habitats. Both species are known from very few localities in Europe and represent noteworthy records for the study area.

3.2 Community composition

The NMDS ordinations of plant and pollinator communities (Fig. 3) showed a clear differentiation between both plant and pollinator communities of grassland and mire habitats, together with significantly fitted environmental vectors. Stress values were 0.096 for vegetation and 0.160 for pollinators, indicating a good and acceptable fit.

The NMDS ordination of the plant communities showed a separation between mires and grasslands, with environmental fitting indicating that higher open water cover was significantly associated with mire plant communities, as expected. In contrast, higher rock and flower cover was significantly associated with grassland plant communities. The PERMANOVA analysis confirmed that plant community composition differed significantly between habitat types ($F = 4.566$, $p = 0.007$), with habitat explaining approximately 36% of the variation ($R^2 = 0.365$).

The NMDS ordination of the pollinator communities showed that they also differed significantly between habitats, with fitted environmental vectors suggesting that open water availability was associated with mire plots (Fig. 3). The PERMANOVA analysis showed a significant separation of pollinator communities between habitats ($F = 1.471$, $p = 0.034$), with habitat explaining approximately 15% of the variation ($R^2 = 0.155$).

The test for homogeneity of multivariate dispersion confirmed that the observed differences were not driven by unequal within-group dispersion, both for pollinator and plant communities.

Fig. 3

The Procrustes randomization test revealed a significant and strong concordance between plant and pollinator community composition (r = 0.681, $p = 0.018$). Macroplots with more similar plant communities tended to support more similar pollinator communities.

3.3 Bipartite network metrics

Pollinator networks were reconstructed for each of the five study sites in both habitat types (10 macroplot-level networks), aggregating the six replicates for each habitat within each site. The graphical representation of the bipartite networks revealed structural differences between mire and grassland habitats (Fig. 4). Mire networks were generally smaller, with fewer plants, pollinators and interactions. They were also largely dominated by hoverflies, which represented the main pollinator group in most mire networks. By contrast, grassland networks showed a more heterogeneous taxonomic composition of pollinators, being mainly characterized by bees, followed by hoverflies. Beetles and butterflies also contributed visibly to grassland interaction networks, whereas their role appeared much more limited in mire networks.

Fig. 4

These visual patterns were supported by the quantitative network metrics, which differed significantly between habitats (Fig. 5; Table S6). Mire networks had significantly lower network size ($p = 0.012$), pollinator richness ($p = 0.022$), plant richness ($p = 0.012$), and total interaction abundance ($p = 0.036$) than grassland networks. Despite their smaller size and lower interaction abundance, null-model standardized metrics revealed that the number of links was higher in mire networks than expected given their marginal totals compared to grassland networks ($p = 0.037$). Similarly, interaction evenness was higher in mires, indicating that interactions were significantly more evenly distributed relative to null expectations ($p = 0.012$). By contrast, H2′ was higher in grassland networks ($p = 0.012$), suggesting greater network-level specialization. Grassland networks were therefore not only larger and richer, but also more structured in

terms of interaction exclusiveness. Mean species-level specialization of plants and pollinators (d'pl and d'poll) did not differ clearly between habitats, indicating that the main differences between mire and grassland networks emerged at the whole-network level rather than through consistent changes in the mean specialization of individual species (p = 1.000 and p =0.403, respectively).

Fig. 5

Considering observed robustness values, which include the previously mentioned differences in species richness and interaction abundance, mire networks appeared more vulnerable than grassland networks to the loss of habitat-exclusive plant species (Fig. 6, Table S6). In particular, pollinator robustness after the preferential removal of habitat-exclusive plants was significantly lower in mires than in grasslands (p = 0.012), indicating that pollinator communities in mire habitats were less able to persist when exclusive plant species were removed first. By contrast, no significant differences between habitats emerged under random species-loss scenarios, either for plant robustness (p = 1.000) or for pollinator robustness (p = 0.060). No significant differences emerged in plant robustness for the removal of habitat-exclusive pollinators either (p = 0.403).

Fig. 6

4. DISCUSSION

Our study provides the first description of plant–pollinator networks in mires, showing that these habitats support pollinator communities that are compositionally distinct from those of adjacent grasslands. Despite their small size and fragmentation, mires hosted numerous habitat-exclusive and conservation-relevant species, with hoverflies particularly well represented, whereas grasslands supported richer and more abundant pollinator communities, with a stronger contribution from bees, butterflies and beetles. Mire networks were smaller and contained fewer interactions, but their main vulnerability emerged under the preferential loss of habitat-exclusive plants, which caused a stronger decline in pollinator persistence than

in grasslands. These findings show that the ecological distinctiveness of alpine mires extends beyond vegetation, while also highlighting the complementary biodiversity value of adjacent grasslands, and suggest that ongoing plant-community change may affect associated pollinator communities and interaction-network stability.

4.1 Alpine mires support distinct plant and pollinator communities compared to grasslands

The lower plant species richness observed in mires compared with grasslands is consistent with the literature, as these habitats are subject to strong environmental filtering associated with soil water saturation, low nutrient availability and, in many cases, acidic conditions (Wheeler and Proctor 2000; Rydin and Jeglum 2013). These factors restrict the number of species able to colonize and persist, favoring communities composed of taxa ecologically adapted to extreme and relatively stable conditions (Rydin and Barber 2001; Rydin and Jeglum 2013). More than half of the plant species recorded in our mire sites were absent from grasslands, and these mire-exclusive species accounted for 85.5% of the total vegetation cover in mires. Vegetation structure was therefore largely determined by habitat-specific species, such as *Carex nigra*, *C. rostrata*, *C. limosa*, *Eriophorum angustifolium*, *Menyanthes trifoliata*, *Parnassia palustris*, *Trichophorum cespitosum* and *Viola palustris*. The differences between mire and grassland plant communities were accompanied by a significant differentiation also in pollinator communities. The concordance between the configurations of the two communities, revealed by the Procrustes analysis, indicates that macroplots with similar vegetation tended to host similar pollinator communities. This result suggests that plant community composition could represent an important ecological filter through which habitat influences the animal component, likely related to the diversity and abundance of floral resources (Gillespie et al. 2024). However, the association between vegetation and pollinators is unlikely to be mediated solely by the resources available to adult pollinators. In fact, plant community composition also reflects the environmental conditions, *in primis* microclimatic and hydrological, which may directly affect pollinators and, particularly, their larval stages (Lucas et al. 2017; Piccini et al. 2022; Oldham et al. 2025). Conversely, grassland vegetation was richer and characterized by a broader pool of flowering species,

consistent with the high plant diversity typically associated with alpine and subalpine grasslands. Higher flower cover was also associated with grassland communities, suggesting a greater availability and diversity of floral resources for pollinators. This richer and more heterogeneous vegetation likely contributed to the larger and more taxonomically diverse pollinator communities observed in grasslands. The higher explanatory power of habitat for plant community composition than for pollinator community composition, as revealed by the PERMANOVA, is consistent with differences in the mobility of the two groups. Plants are constrained by local soil, hydrological and microclimatic conditions, whereas adult pollinators are less directly dependent on the local environmental conditions of each macroplot. This greater insect mobility may explain why pollinator communities showed a less pronounced differentiation between mires and grasslands than plant communities.

Although mires support a lower number of species, nearly half of the pollinator species recorded in mires were not recorded in the grasslands, suggesting the presence of a distinct faunal component associated with these habitats. Mire-exclusive species occurred in all the taxonomic groups analyzed, with beetles and hoverflies making a particularly substantial contribution (55.6% of beetle richness, 48.1% of hoverfly richness, 45.5% of butterfly richness, and 39.1% of bee richness). Overall, these findings are consistent with Rydin and Jeglum (2013), who reported Diptera, Hymenoptera and Coleoptera as by far the most species-rich insect orders in peatlands. Among pollinator groups, hoverflies represented the main exception to the general lower richness and abundance observed in mires compared to grasslands. Indeed, their species richness and overall abundance were nearly identical in the two habitats, whereas bees, beetles and butterflies were markedly more species-rich and abundant in grasslands. The dominance of hoverflies in mires can also be interpreted in light of the ecological conditions of these habitats. Many species are adapted to relatively cool local conditions and are therefore often associated with high elevations (Sommaggio et al. 2022), conditions that are also typical of mire habitats (Słowińska et al. 2022). In addition, the larvae of numerous species are associated with water-saturated soils, shallow water, decomposing organic matter or wetland plants (Hayes et al. 2016; Moquet et al. 2018). Mires may therefore provide complementary

resources across different stages of the life cycle: floral resources for adults and suitable substrates for larval development. The larval ecology of hoverflies found exclusively in mires further reinforces this interpretation. Larvae of *Melanogaster nuda*, *Sericomyia lappona*, *Sphegina clunipes* and *Sphegina cornifera* show a strong preference for submerged sediments and water saturated ground that includes sodden plant debris, whereas those of *Neoascia geniculata*, *Neoascia tenur* and *Platycheirus angustipes* develop feeding on mire associated aquatic plants (Speight et al. 2026). This finding is consistent with Koch et al. (2021), who highlighted the importance of wetlands for rare hoverfly species. Moreover, these data extend the available knowledge for the alpine mires, where research has so far focused primarily on other groups of aquatic or semi-aquatic insects, such as Odonata and Heteroptera (Sindaco et al. 2007; Montagna et al. 2008; Bionda et al. 2013). By contrast, grasslands supported richer and more abundant communities of bees, beetles and butterflies, with a large proportion of species recorded exclusively in this habitat. Although hoverflies remained the richest group, bees were the most abundant pollinators in grasslands. This pattern is consistent with the higher plant richness and flower cover observed in grasslands, which provided a larger and more heterogeneous pool of floral resources.

Mires hosted several pollinator species of conservation concern that were recorded exclusively in this habitat. These included the hoverflies *Cheilosia alpestris*, *C. faucis* and *C. impudens*, all classified as Endangered. Moreover, five hoverfly species recorded in mires (*Cheilosia faucis*, *C. psilophthalma*, *C. sahlbergi*, *C. semifasciata* and *Platycheirus discimanus*) represented new records for Piedmont, while *Neoascia geniculata*, also recorded in mires, represented a new record for Italy. Grasslands also hosted species of conservation interest, including the Annex IV butterflies *Parnassius apollo* and *Phengaris arion* and the Endangered hoverfly *Pipizella nigriana*. *Hylaeus gracilicornis*, a new record for Italy, was also sampled in grassland. Notably, some conservation-relevant grassland species were already covered by protection, whereas species recorded exclusively in mires were more frequently classified as threatened but lacked legal protection. The occurrence of the two relict pollen beetles further reinforces the conservation relevance of both habitats. *Brassicogethes humerosus* is a relict species characterized by a highly

fragmented distributional pattern, restricted to a few wet and cold localities in central-western Europe and, in Italy, was previously known only from two sites in the Stura d'Ala Valley (Audisio and De Biase 2005; Jelínek and Audisio 2007). Our mire record therefore adds a further locality within this highly restricted Italian range. *Clypeogethes chlorocyaneus* is similarly known from only a few localities in the Balkans and Piedmont (Audisio and De Biase 2005; Avgin et al. 2015). Its occurrence exclusively in grasslands during our surveys further illustrates the complementary conservation value of the two adjacent habitats.

4.2 Mire networks: smaller and more generalized compared to grassland

Floristic and faunal differences between the two habitats were also reflected in the size and structure of the interaction networks. Mire networks were characterized not only by lower plant and pollinator species richness, but also by a reduced number of interactions compared with grassland networks. Standardization using Patefield null models allowed us to assess how interactions were distributed relative to expectations based on these constraints (Blüthgen et al. 2006; Kaiser-Bunbury and Blüthgen 2015; Blüthgen and Staab 2024). Results showed that mire networks had a relatively higher number of links and greater interaction evenness than grassland networks: for a given set of matrix marginal totals (plant and pollinator richness and total interaction number), interactions in mires were distributed across a relatively large number of plant–pollinator pairs and were less concentrated in a few dominant links compared to grassland. Indeed, in mires, where floral resources are poorer overall, visitors may tend to exploit a relatively large proportion of the available plant species. The predominance of hoverflies, many of which display relatively generalist visitation behavior (Branquart and Hemptinne 2000; Lucas et al. 2018), may also have contributed to this pattern.

Grassland networks exhibited higher standardized H2′ values, indicating greater specialization at the whole-network level. Although this pattern may appear inconsistent with the strong ecological distinctiveness of mire communities, species and interaction specialization describe different properties. Species may occur predominantly in mire habitats while still interacting with multiple locally available partners. The lower

H2′ values observed in mire networks may instead reflect greater overlap in resource use, potentially associated with the predominance of hoverflies and the more limited pool of flowering plant species. The absence of significant differences in mean plant and pollinator d′ further indicates that individual species were, on average, not more specialized in either habitat. Therefore, the higher H2′ values of grassland networks likely arose from differences in the collective configuration and relative weighting of interactions across the network, rather than from a consistent increase in species-level specialization within either guild.

4.3 Dependence on habitat-exclusive plants increases network vulnerability

Mire robustness of pollinator communities when habitat-exclusive plant species were removed was significantly lower than that of grassland robustness. No differences between mires and grasslands emerged under random-removal scenarios, nor did plant robustness differ following the preferential loss of habitat-exclusive pollinators. Network vulnerability therefore appeared to be specifically associated with the loss of the habitat-exclusive plant species. This pattern is consistent with the dominant contribution of habitat-exclusive species to mire vegetation. Mire-exclusive plants accounted for most of the vegetation cover and included species that occupied central positions within the interaction networks, such as *Menyanthes trifoliata*, *Potentilla erecta*, *Parnassia palustris*, *Carex nigra* and *Dactylorhiza maculata*. Their removal therefore rapidly reduced the number of interaction pathways available to pollinators. This finding is particularly relevant in the context of the vegetation changes already documented in alpine mires (Pollo et al. 2026). Declines in specialist species and increases in generalists, including woody species, may maintain or even increase total plant richness while profoundly altering the functional identity of the community. Although many of the taxa currently declining or disappearing are bryophytes, losses are already evident among vascular flowering plants. Our results therefore suggest that further degradation of alpine mires could also affect pollinator communities by reducing the availability of characteristic floral resources and the redundancy of their interactions.

Importantly, the relatively generalized organization of mire networks did not prevent them from being vulnerable to the loss of habitat-exclusive plant species. The removal of habitat-exclusive plant species could eliminate a large proportion of the crucial foraging opportunities. This result is consistent with studies showing that network responses to species extinctions depend not only on the distribution of interactions, but also on overall species richness, partner redundancy, the order in which species are lost and the identity and ecological role of the lost species (Memmott et al. 2004; Thébault and Fontaine 2010; Traveset et al. 2017). From an applied perspective, this composite measure may be particularly relevant for conservation because it reflects the realized capacity of mire pollinator communities to persist following plant loss, rather than a size-corrected network property that would not, in itself, buffer communities against actual extinction cascades. The greater observed vulnerability of mire networks should nevertheless be interpreted alongside their smaller size and lower species richness.

Robustness should be regarded as an indicator of the structural tolerance of the network rather than as a direct prediction of actual coextinction. The simulations assume that a species becomes extinct once all its observed partners have been lost and do not account for the possibility that pollinators may exploit resources outside the sampled macroplot, shift their preferences or establish novel interactions. Nevertheless, the result remains informative from a conservation perspective.

5. CONCLUSIONS

To our knowledge, this study provides the first characterization of plant–pollinator interaction networks in mires. These threatened habitats supported pollinator communities that differed in species composition from those of adjacent grasslands and were dominated by hoverflies, with smaller contributions from bees, butterflies and beetles. The occurrence of several Endangered *Cheilosia* species recorded exclusively in mires further underscores the conservation value of these habitats. Although mire networks were smaller and contained fewer species and interactions than grassland networks, they supported a distinctive component of alpine pollinator diversity and were particularly vulnerable to the loss of plant species

recorded exclusively in mires and already known to be declining. Ongoing changes in mire vegetation may therefore have cascading effects on pollinator communities and their interactions. These findings strengthen the need to conserve and restore alpine mires by safeguarding their hydrological integrity and specialist vegetation through measures that limit drainage, alterations to water flow and overgrazing. Adjacent alpine grasslands supported higher plant and pollinator species richness and larger interaction networks, but remain vulnerable to land-use abandonment and subsequent vegetation encroachment. Conservation strategies should therefore prioritize the maintenance of mire–grassland mosaics to preserve habitat complementarity in species composition and sustain plant–pollinator interactions across the alpine landscape.

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Figure captions

Fig. 1 Location of the 10 study macroplots in the five areas in the Western Italian Alps: (a) regional location of the study area; (b) distribution of the five sites that include the study macroplots: Laghi di Bellagarda (1); Alpe Saulera (2); Alpe Paschiet (3); Laghi Falin (4); Col Blegier (5); (c) detailed view of Laghi Falin site, showing the macroplots established in the grassland (d) and mire (e).

Fig. 2 Gamma diversity of plants (a), of pollinators (b), and of pollinator taxa across habitat types (c). Mean cover of plants (d), total abundance of pollinators (e) and relative abundance of pollinator taxa across habitat types (f).

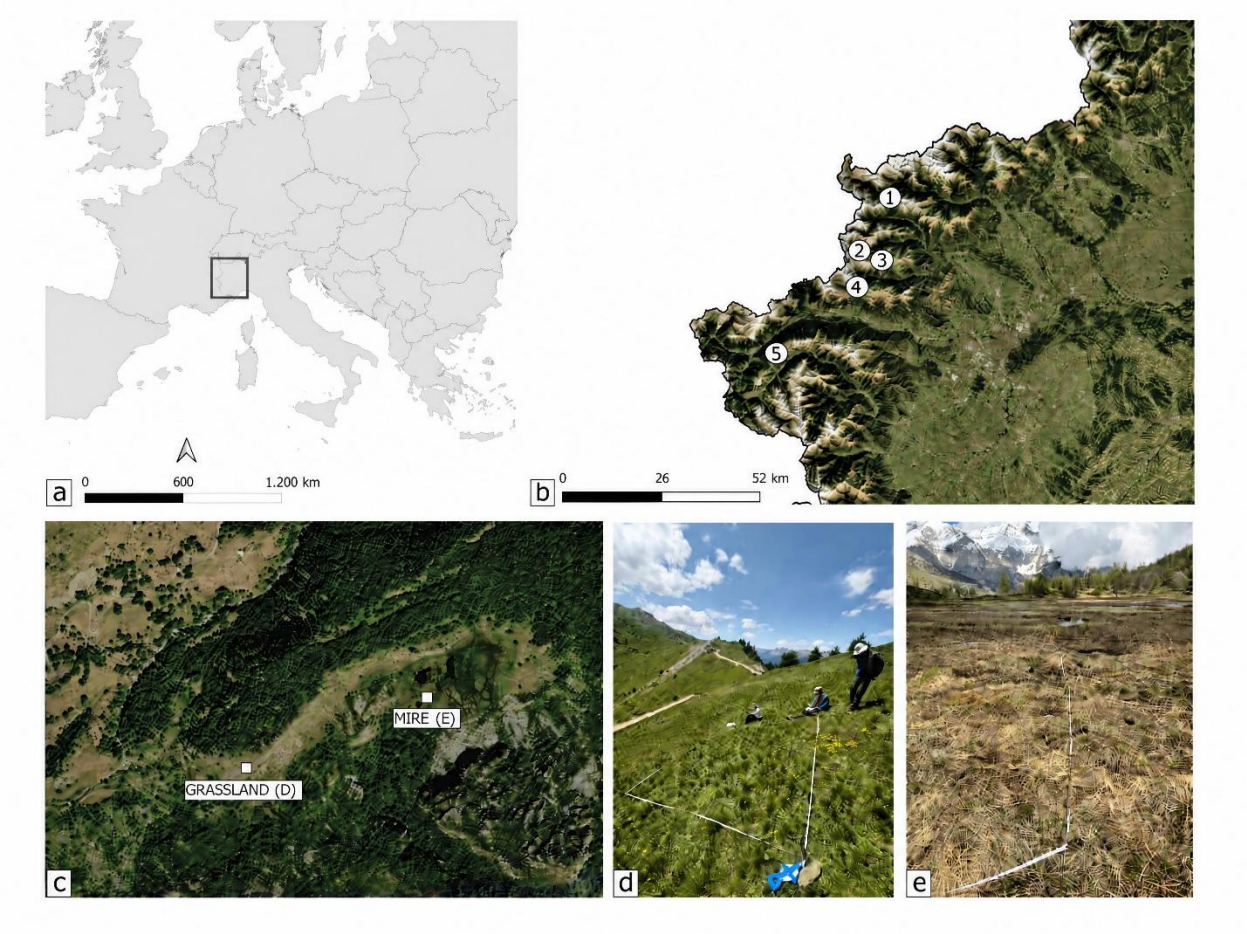
Fig. 3 Non-metric multidimensional scaling (NMDS) ordination of plant communities (left) and pollinator communities (right). Each point represents one macroplot; colors indicate habitat type and symbols indicate sites. Ellipses represent the 80% confidence region for each habitat. Significant environmental vectors ($p < 0.05$) fitted onto the ordination are shown as arrows. "Cov" stands for cover, expressed as a percentage.

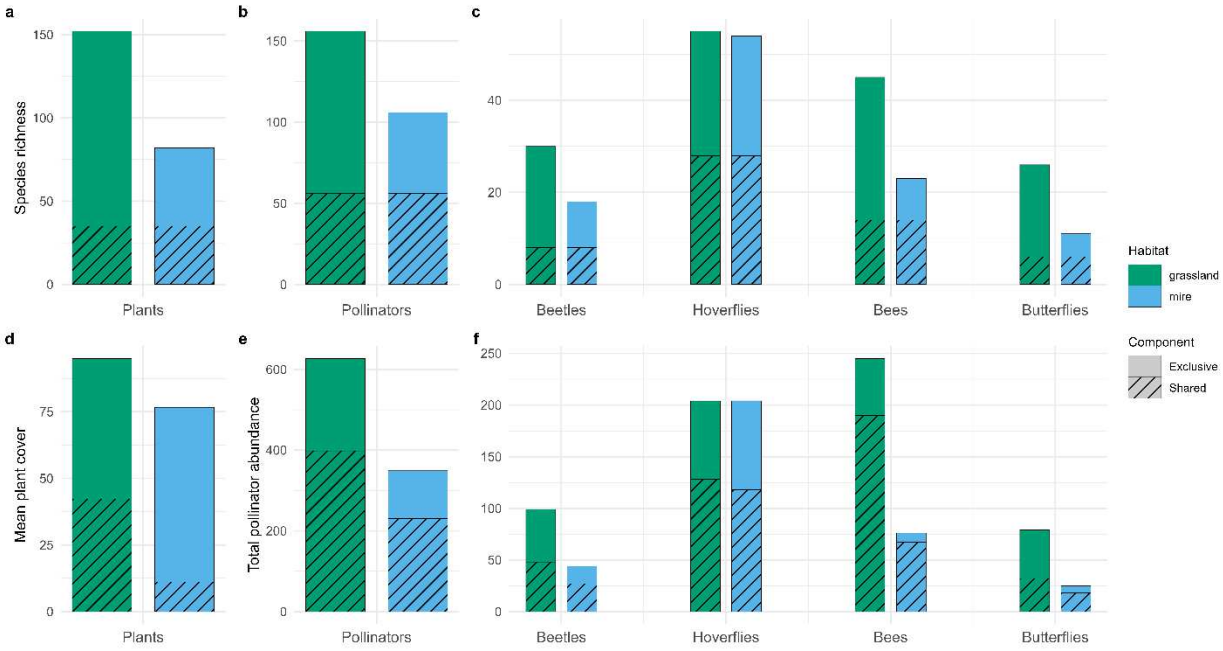
Fig. 4 Plant–pollinator interaction networks in mire (left) and grassland (right) habitats across the five study sites (AP: Alpe Paschiet; AS: Alpe Saulera; BE: Laghi di Bellagarda; CB: Col Blegier; LF: Laghi Falin). Plant species are shown in the upper level and pollinator species in the lower level. Link width is proportional to the frequency of each plant–pollinator interaction. Pollinators are colored by taxonomic group, using blue shades for mires and green shades for grasslands; from darkest to lightest, colors indicate Beetles, Bees, Butterflies, and Hoverflies. Species are labeled with abbreviated codes; full species names are provided in Tables S4 and S5.

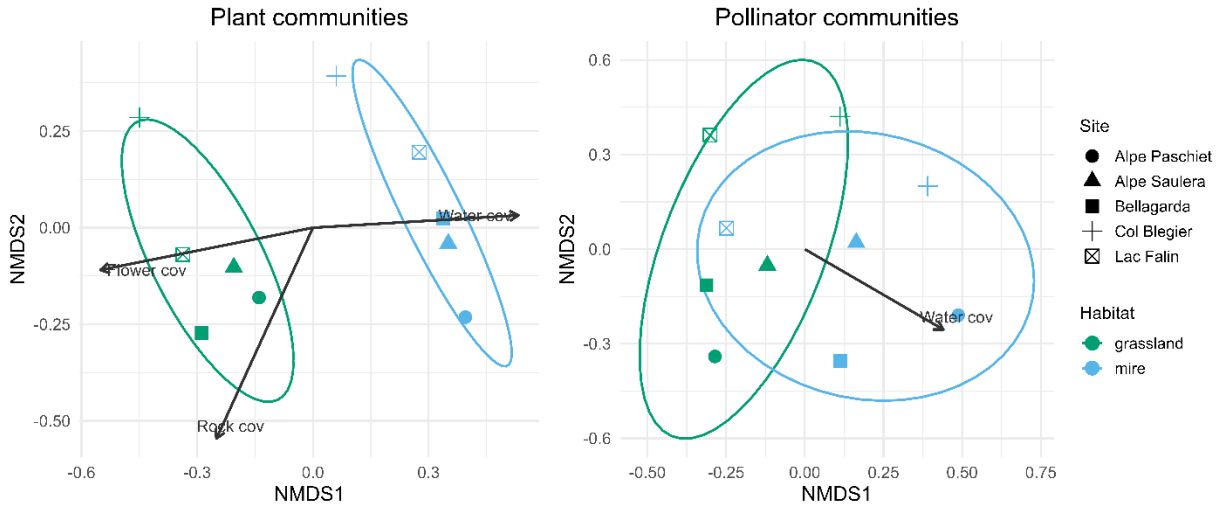
Fig. 5 Macroplot-level network metrics for grassland and mire habitats. Observed network values are reported for the network size, the plant richness, the pollinator richness and the number of interactions. Z-scores calculated using Patefield null models preserving matrix marginal totals are reported for the number of links, the interaction evenness (E_2), the standardized network-level specialization (H_2'), and the plant

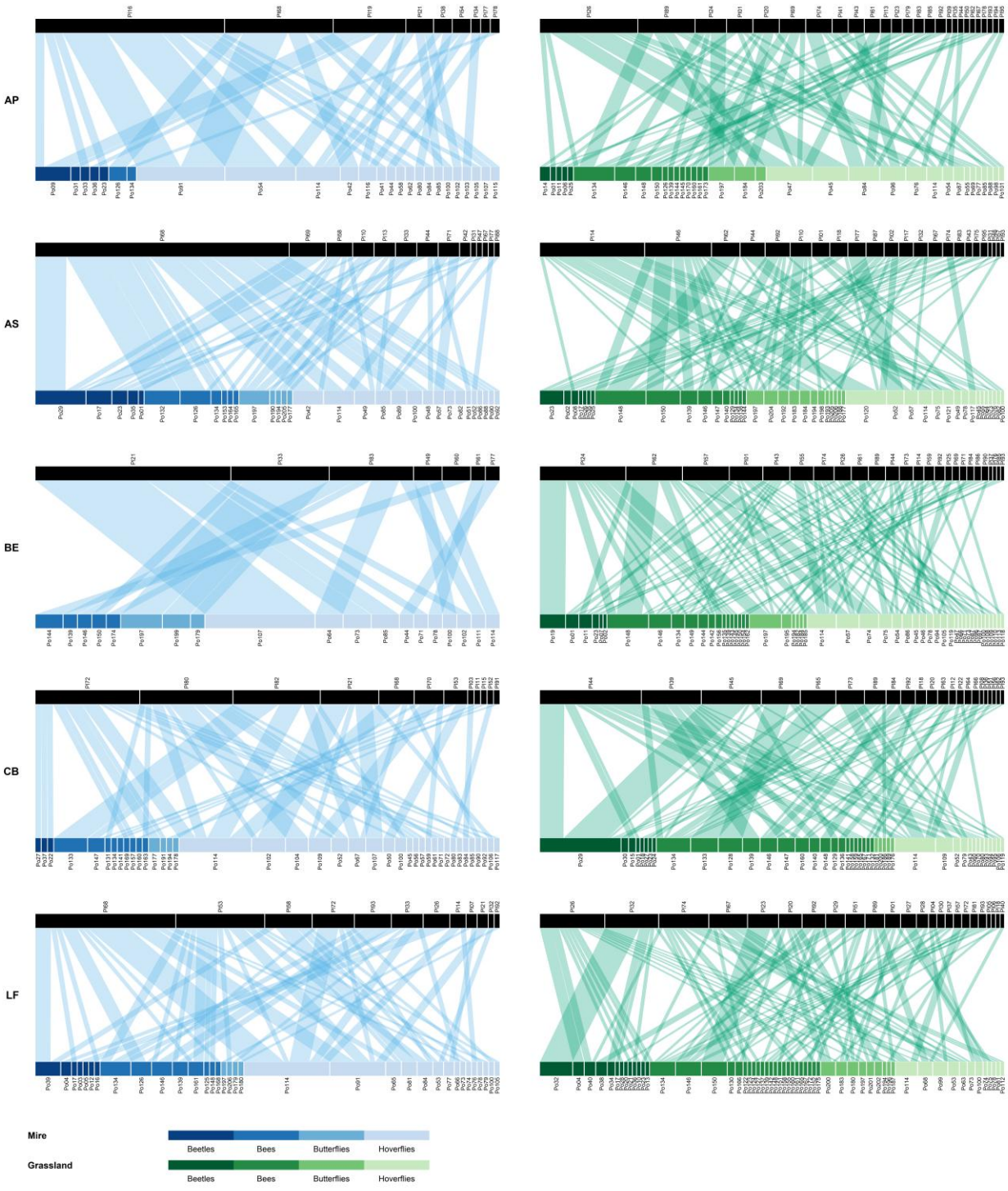
723 and the pollinator standardized species-level specialization (d' pl. and d' poll., respectively). The
724 significance of the differences was tested using the Wilcoxon test (***: $p < 0.001$; **: $p < 0.01$; *: $p < 0.05$).
725
726 **Fig. 6** Robustness of macroplot-level pollinator networks in grasslands and mires under different simulated
727 species-loss scenarios. Robustness was assessed by simulating random and habitat-exclusive species loss,
728 evaluating plant persistence after pollinator removal and pollinator persistence after plant removal.
729 Differences between habitats were tested using Wilcoxon tests (***: $p < 0.001$; **: $p < 0.01$; *: $p < 0.05$).
730

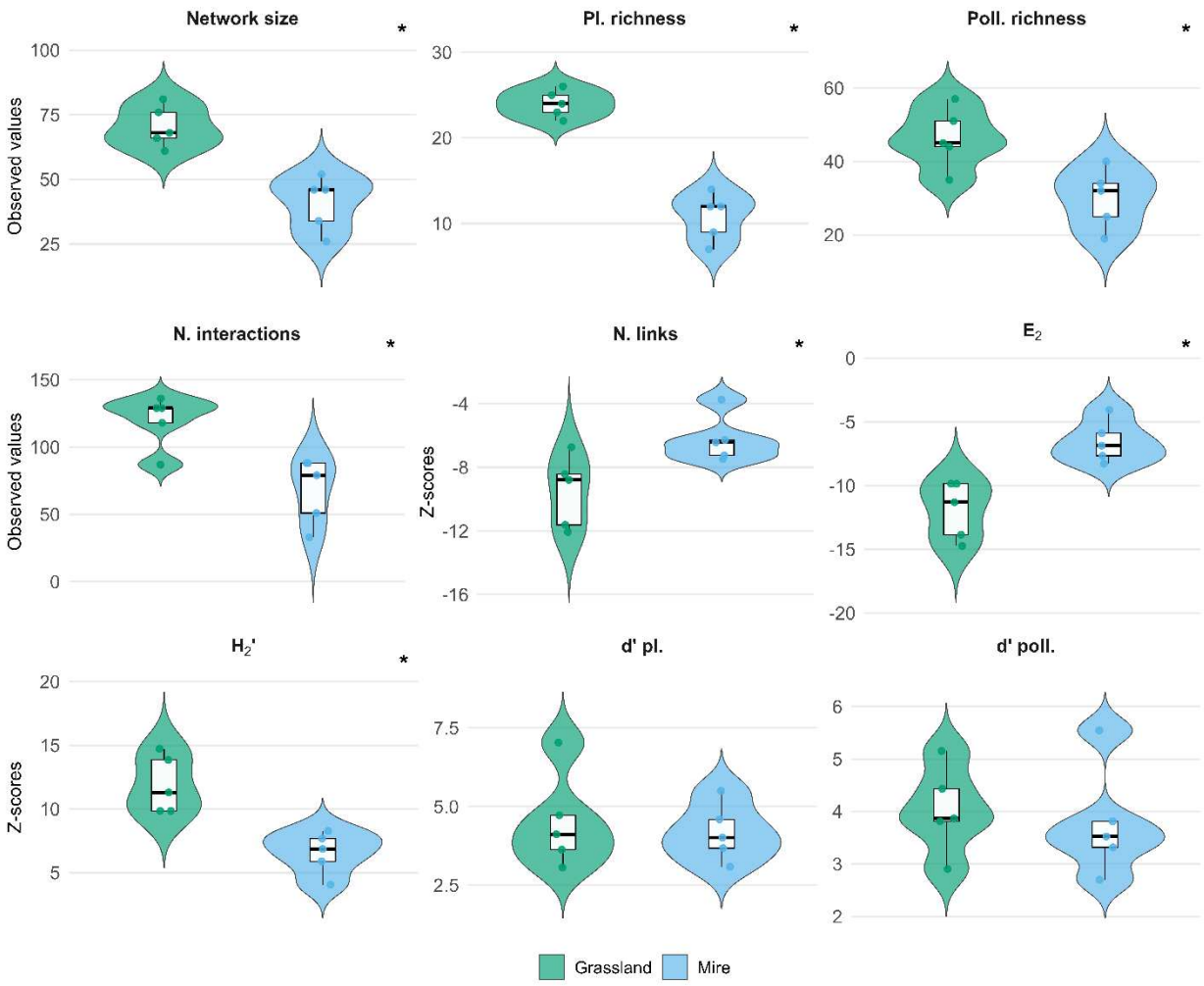
731 **Figures**

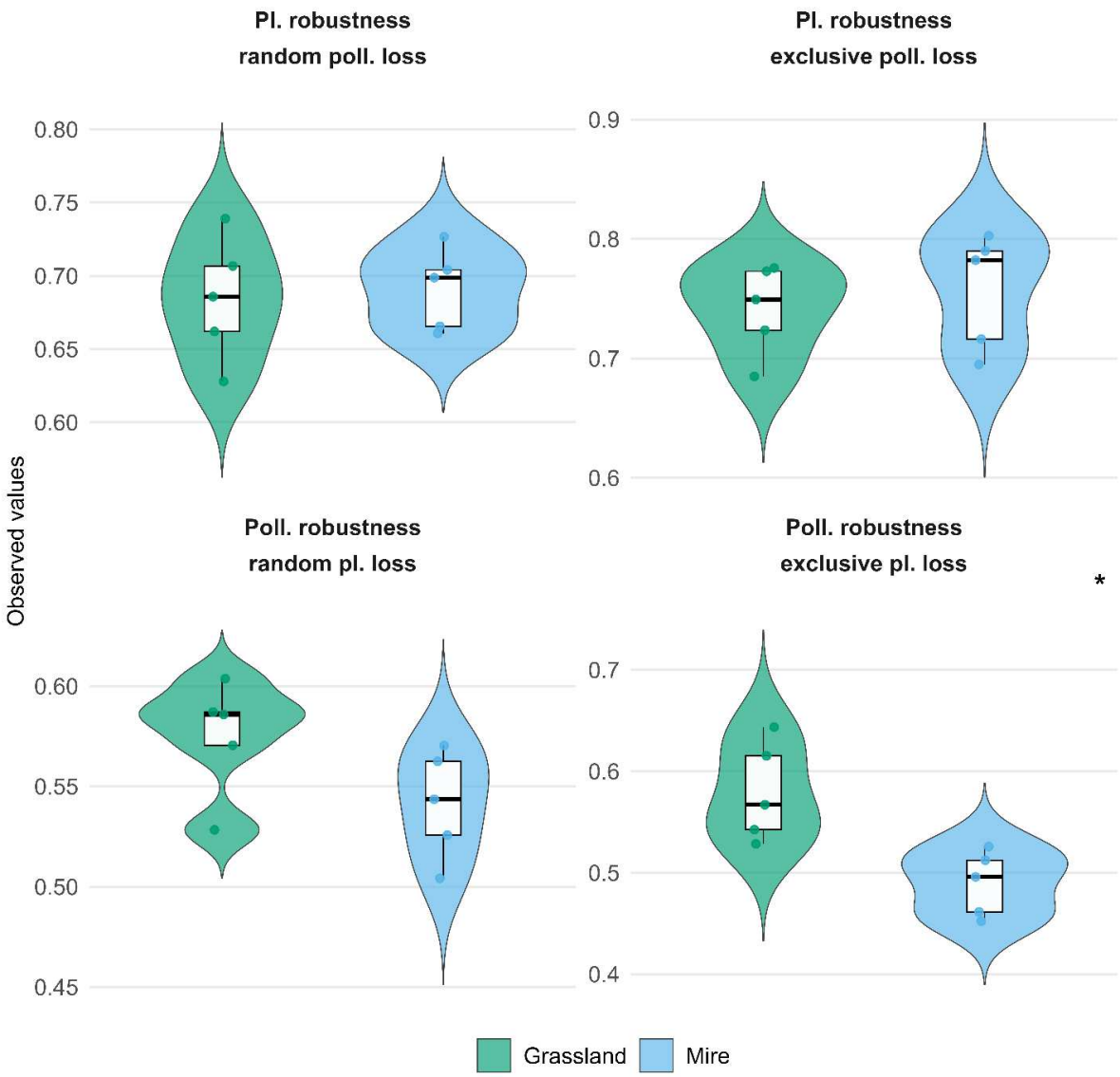



a
b
c
d
e
f
Species richness
Mean plant cover
Total pollinator abundance
Plants
Pollinators
Beetles
Hoverflies
Bees
Butterflies
Habitat
grassland
mire
Component
Exclusive
Shared


Plant communities
Pollinator communities
NMDS1
NMDS2
Water cov
Flower cov
Rock cov
Site
Alpe Paschiet
Alpe Saulera
Bellagarda
Col Blegier
Lac Falin
Habitat
grassland
mire


AP
AS
BE
CB
LF
Mire
Beetles
Bees
Butterflies
Hoverflies
Grassland
Beetles
Bees
Butterflies
Hoverflies


Network size
*
Observed values
100
75
50
25
Pl. richness
*
30
20
10
Poll. richness
*
60
40
20
N. interactions
*
Observed values
150
100
50
0
N. links
*
Z-scores
-4
-8
-12
-16
E2
*
0
-5
-10
-15
-20
H2'
*
Z-scores
20
15
10
5
d' pl.
7.5
5.0
2.5
d' poll.
6
5
4
3
2
Grassland
Mire


Pl. robustness
random poll. loss
Pl. robustness
exclusive poll. loss
Poll. robustness
random pl. loss
Poll. robustness
exclusive pl. loss
*
Observed values
0.80
0.75
0.70
0.65
0.60
0.9
0.8
0.7
0.6
0.60
0.55
0.50
0.45
0.7
0.6
0.5
0.4
Grassland
Mire

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- SupplementaryMaterials.docx