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Does Land Management Intensity Influence Pollinator Assemblages and Plant–Pollinator Interactions in the Lowlands of Terceira Island (Azores)?

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Abstract

Human-driven land use change and intensification is a major threat to global biodiversity. High levels of land management intensity may reduce species diversity, change the composition and structure of plant and animal communities and disrupt ecological processes. However, there is still scarce information on the impacts of land management intensity on island pollinator communities and their interactions with plants. Here, we aim to assess how different land use types (natural vegetation, semi-natural pastures, and intensive pastures), representing a gradient of grazing intensification, influence pollinator diversity and plant–pollinator interactions on Terceira Island (Azores). We surveyed 30 sites (10 per land use) and recorded 1453 visits by 41 pollinator species. Alpha diversity did not differ among land uses, but grazing intensification reduced the abundance of several native species while favoring some exotics, such as the honeybee. Network analyses showed changes in structural properties and declines in interactions between native species with increasing grazing disturbance. Introduced species, particularly the honeybee, dominated interactions in intensively managed habitats, replacing native species from key ecological roles. Our findings highlight the vulnerability of island ecosystems to grazing intensification and emphasize the need for conservation measures in the Azores, namely the reduction in grazing intensity, restoration of habitat connectivity, and implementation of pollinator-friendly agri-environmental schemes to enhance native biodiversity and sustain ecosystem services.

Keywords: biotic homogenization; flower visitors; island biodiversity; generalist pollinators; pastures; pollination networks

Academic Editor: Alexandru-Ionuţ Petrişor

Received: 16 August 2025
Revised: 1 October 2025
Accepted: 6 October 2025
Published: 10 October 2025

Citation: Boieiro, M.; Ceia-Hasse, A.; Oliveira, R.; Costa, R.; Borges, P.A.V. Does Land Management Intensity Influence Pollinator Assemblages and Plant–Pollinator Interactions in the Lowlands of Terceira Island (Azores)? *Land* **2025**, *14*, 2029. https://doi.org/10.3390/land14102029

1. Introduction

Human-driven land use changes and intensification are key drivers of global biodiversity loss, directly and indirectly changing species assemblages and influencing ecological processes through habitat destruction, fragmentation, and degradation [1–5]. The expansion of agricultural and urban areas, coupled with increasing land use intensity, threatens many species worldwide [1,6]. These factors also promote the introduction and spread of invasive alien species, thus influencing both native species interactions and the integrity of natural ecological processes [7]. This unprecedented biodiversity crisis is a major challenge that needs to be halted with the support of scientific knowledge to guide sustainable land use management at global, regional and local levels.

In oceanic islands, land use changes have led to species extinctions and extensive habitat loss [8–11], with profound yet often undocumented consequences. The higher vulnerability of island biota to biodiversity erosion processes stems from their inherent characteristics (i.e., island syndromes) and the small and isolated areas they occupy, but in recent centuries, human activities have dramatically increased the extinction risk for numerous island endemic species [8,10]. For example, in the Azores, nearly 95% of the native forest cover was lost following human colonization, being replaced by pastures, agricultural fields, forest plantations and urban areas [12–15]. Despite this extensive habitat loss, fossils of extinct endemic birds (whose disappearance matched with human arrival in the archipelago) were only recently discovered [16–18], highlighting the potentially devastating and long-lasting consequences of land use changes for the plant and invertebrate communities as well [19,20]. In fact, a recent study showed that half of the Azorean endemic arthropods are threatened by extinction and identified habitat transformation due to agriculture and climate change as the major direct menace [21].

Several studies from oceanic islands and archipelagos worldwide have shown that land use type is a key predictor of species richness and composition [22–24]. Often, natural habitats present higher values of endemic and non-endemic native species richness when compared to the human-created land uses (e.g., forest plantations, croplands, pastures, urban areas), where introduced species are usually dominant [24]. Therefore, the continuous expansion of human activities to natural habitats contributes to their destruction (when converted to human-created land uses) or deterioration as a result of human disturbance and alien species effects. Land use management in island ecosystems is a most challenging task due to the need to mitigate the conflicts between human activities and nature conservation in small-sized areas, often overpopulated and subjected to intense pressure from economic activities (many of which are related to tourism). Thus, gathering information on the effects of different land uses on island biodiversity and ecological interactions is of the utmost importance to support decision-making by the authorities responsible for island land use management.

There is great concern that land use reshaping in island environments due to anthropogenic changes may hamper essential ecosystem services, such as pollination. Pollination is one of the most crucial ecosystem services, being fundamental for plant reproduction and biodiversity, and supporting global food production and nutrition security for humanity [25,26]. Nevertheless, there is increasing evidence that pollinator populations have been declining in many countries, jeopardizing ecosystem sustainability, food security, and economic stability [27,28]. Island pollinator communities are considered more vulnerable than their mainland counterparts since they are poorer in species, and have lower population sizes and lower redundancy in species functional roles [8,29]. During the last few decades, several studies reported the impacts of land use change and disturbance on island pollinator communities, emphasizing both the direct and indirect effects (e.g., mediated by invasive alien species). In the Maldives, Biella et al. [30] found that pollinator communities are well segregated by land use as a response to human activities, with several species occurring exclusively in natural, agricultural or urban areas. However, the spread of generalist invasive exotic plants from anthropogenic habitats is threatening native pollination interactions and may lead to biotic homogenization. Similarly, several invasive pollinators (such as the honeybee *Apis mellifera* and the buff-tailed bumblebee *Bombus terrestris*) that benefit from land use conversion by humans, were found to disrupt native pollination networks across multiple island ecosystems [31–33]. In the Azores, a study across the major land use types found that pollinator communities are species-poor and remarkably similar between land uses, largely due to the expansion of native generalist pollinators into human-modified environments [34]. The study also highlighted the influence of plant species composition on pollinator communities, alerting for potential significant changes as a consequence of alien species invasion. In fact, Boieiro et al. [35] recently showed that human disturbance altered species composition and pollination interactions in native forest areas with an increasing presence of alien plants and pollinators in disturbed sites, some of which already playing important roles in local pollination networks. Measuring the impact of human-driven environmental changes on biodiversity and pollination networks is key to better understanding the dynamics of species interactions. This information may then guide land management strategies to mitigate potential negative impacts on pollination services.

This work aims to evaluate the influence of land use type on pollinator diversity and plant–pollinator interactions along a disturbance gradient spanning from natural vegetation areas to intensive pastures in the lowlands of Terceira island (Azores). Here, we address the following questions: (1) Do pollinator species richness, abundance and composition differ along the disturbance gradient? (2) Is there a change in plant–pollinator network structure and on species roles along the disturbance gradient? (3) Does grazing intensification favor the replacement of the main plant and pollinator interactors with introduced species prevailing in human-created land uses (pastures)?

2. Materials and Methods

2.1. Study Area

The study was carried out on Terceira, the third largest island (402 km^2) of the Azores archipelago. This island is situated in the north Atlantic Ocean (between 38°37′–38°48′ N and 27°02′–27°22′ W) being distanced from mainland by over 1500 km. Azorean landscapes had several different natural habitat types prior to human colonization, but since the 15th century human activities started changing the landscape by using land for agriculture, forestry and urbanization [13,14]. In the lowlands of the Azorean islands, but particularly in Terceira, a large fraction of the land is now devoted to pastures since dairy production is one of the most important economic activities [36], with several products (milk, butter and cheese) being recognized internationally. Consequently, the landscape is now dominated by three land use types—natural vegetation, semi-natural pastures and intensive pastures—which correspond to an ecological gradient with increasing intensity of use by cattle. Along this gradient there are apparent changes in vegetation structure and soil trampling between the different land uses [22,34] (Figure 1). The areas of natural vegetation have no livestock and low or no human presence. The vegetation is more complex than in pastures, with the presence of trees and shrubs, and many plant species are native, including some Azorean endemics (Figure 1a). The semi-natural pastures are occasionally used for livestock feeding. In terms of management, semi-natural pastures are long-established, have little or no yearly reseeding, no regular tillage and minimal or no use of fertilizers [37]. They are often dominated by a few grass species (*Holcus lanatus*, *Agrostis* spp.) being characterized by having greater richness of native plant species and higher structural complexity compared to intensive pastures (Figure 1b). Intensive pastures are frequently grazed by dairy cattle and managed for high forage output. Management involves rotational grazing, frequent cuts for silage, denser fencing, raceways, and permanent water points. These pastures are typically sown with ryegrass–clover, being re-seeded after summer, thus pasture renovation and drainage works are more frequent than in semi-natural pastures. Consequently, vegetation structure is simplified, with low forb cover during peak production and dominance by grasses (e.g., *Lolium* spp., *Holcus lanatus*), alongside the occurrence of several introduced plants [37,38] (Figure 1c). There is still insufficient information on the plant and pollinator diversity in the study area, but previous studies reported species-poor communities dominated by generalist species and the occurrence of several exotics [34,35].

Figure 1. General view of the three land uses studied—areas of natural vegetation (**a**), semi-natural pastures (**b**) and intensive pastures (**c**)—which represent a gradient of land management intensity.

2.2. Sampling Design and Techniques

Pollinators and their interactions with plants were studied in ten replicate sites of each land use type during summer 2023 (from August 1st to September 10th), matching the flowering period and peak of insect activity [39,40], as rainfall is frequent in the other seasons. Overall, 30 sites were studied across the island (Table S1) following the spatial sampling design of a previous study [34]. In each study site, we set a linear 50m transect (with 2 m width) to record all the pollinators observed (flying, resting or visiting flowers), taking about 20 min to complete. In Azores, many pollinator species can be easily identified on the spot since this archipelago is young and remote, thus having lower species richness than the other Macaronesian archipelagos [41–45]. Nevertheless, whenever necessary, the pollinators were collected with a sweeping net to confirm species identity. Pollinator sampling was carried out between 10 a.m. and 4 p.m. on sunny days or with only a few clouds, without rain, and with little or no wind, as these are the most suitable conditions for observing diurnal pollinators [46]. For the pollinators observed on flowers, the plant species being visited was also recorded. In each site, we identified all plant species in bloom and counted the number of flowers along the study transect as these variables may influence pollinator diversity and visitation. We also recorded vegetation height at six different points along the transect, separated from each other by approximately 10 m.

The insect specimens collected were stored in vials with ethanol (70%) for laboratorial study. In the lab, the specimens were identified using a Leica S9i stereomicroscope and specific taxonomic literature (e.g., [47–50]). The insect specimens were later deposited in the *Dalberto Teixeira Pombo* entomological collection (DTP) at the University of the Azores (Angra do Heroísmo, Azores, Portugal). All species, both from flowering plants and pollinators, were categorized into distributional groups as endemic, native (indigenous species excluding the endemics) or introduced in the Azores following Borges et al. [42,45].

2.3. Data Analysis

We calculated alpha diversity metrics for pollinators in each land use type following the Hill numbers since they provide complementary information on species richness, rarity, and dominance [51,52]. Hill diversities are a mathematically family of indices that differ in their calculation only by an exponent q that determines their sensitivity to species relative abundances. We computed a diversity profile for each habitat type by estimating Hill numbers for a range of q values, namely observed species richness ($q = 0$), the exponential of Shannon–Wiener diversity index ($q = 1$), the reciprocal of Simpson's diversity index ($q = 2$), and the reciprocal of the Berger–Parker index ($q = \infty$). We also present data on pollinator abundance in the different land use types and calculated evenness using the Pielou index. To assess sampling completeness, we first estimated species richness using the non-parametric estimator Chao1 and then calculated the ratio of observed to estimated species richness for each land use. The differences in alpha diversity metric values between land use types were assessed using non-parametric Kruskal–Wallis tests. These analyses were carried out using packages *vegan* and *BAT* [53,54]. To assess differences in species composition between sites and land uses, we performed a non-metric multidimensional scaling (NMDS) ordination using the pollinator abundance data. To test if the pollinator communities differed significantly between land use types, we followed the GLM framework, which is more robust to overdispersion than PERMANOVA or ANOSIM, using package *mvabund* [55,56].

During fieldwork, we collected several environmental variables in each study site, namely flowering plant species richness, flower abundance and vegetation height, since they often play a role on driving pollinator abundance, diversity and composition at local scale (e.g., [33–35]). We tested the influence of these variables on pollinator species richness and abundance between land uses using generalized linear mixed models (GLMMs) with a negative binomial distribution and a log link [57], which is considered to model count data appropriately without the need for data transformation [57–60]. We used the sites as random factors and the remaining variables (land use intensity, plant richness, flower abundance and vegetation height) as fixed factors. In addition, we incorporated pollinator species as a fixed factor in the GLMM to assess differences in pollinator abundance between land-use types. We used Akaike's information criterion (AIC) to select the explanatory variables in each model. Only the variables whose removal would result in a worse model fit and that were significant at a 0.05 level were kept in the final model [58,60]. These statistical analyses were performed using package *glmmTMB* [61].

The plant–pollinator interaction data recorded at the 30 study sites were used to create bipartite networks using the bipartite package [62], with a separate network created for each study site. Bipartite networks are a powerful tool to visualize and interpret pollination interactions by displaying the associations between pollinators and plants using flower visitation data. Several network metrics (links per species, connectance, nestedness, Shannon diversity, interaction evenness, specialization asymmetry, generality) were computed to characterize the pollination networks of each land use type and to search for differences that may relate with the disturbance gradient. These metrics were selected on the basis of evidence from previous studies demonstrating their utility as indicators of environmental quality ([63] and references therein). To evaluate differences in the selected network metrics across land uses, we applied Kruskal–Wallis tests followed by post hoc Dunn's tests using the *stats* and *dunn.test* packages [64].

All statistical analyses were carried out using R software version 4.5.1 [65].

3. Results

3.1. Alpha Diversity and Environmental Drivers

We recorded 1453 flower visitors from 41 species in the 30 study sites (Table S2). Most flower visitors were insects, but we also detected the introduced Madeiran lizard (*Teira dugesii*) visiting flowers. The most abundant groups of insect pollinators were dipterans (48.2%; mostly hoverflies and blowflies) and hymenopterans (29.2%, mostly bees). A considerable number of species is exotic to the Azores and only three endemic taxa were found (the hoverflies *Sphaerophoria nigra* and *Xanthandrus azorensis*, and the butterfly *Pieris brassicae azorensis*). The lists of plants and pollinators identified in this study are shown in the Supplementary Materials (Tables S2 and S3) and were made publicly available through the Global Biodiversity Information Facility platform (GBIF) [66,67].

Sampling completeness was relatively high and similar between the study habitat-types, averaging 0.81, 0.85 and 0.86, on natural vegetation, semi-natural and intensive pastures, respectively. The three study land use types showed no significant differences in pollinator abundance, evenness and species richness, nor in any of the other alpha diversity metrics (all $p > 0.05$) (Table 1, Figure 2). Interestingly, we found that pollinator species richness and abundance are positively associated with plant species richness (respectively, $p < 0.01$ and $p < 0.05$), but land use type, vegetation height and the number of flowers per site do not seem to influence pollinator species richness and abundance at the local scale (all $p > 0.05$).

Table 1. Alpha diversity metrics following Hill numbers of pollinators in the study habitat-types of Terceira lowlands. The following Hill numbers were computed: species richness, exponential of Shannon diversity index (Shannon), reciprocal of Simpson's diversity index (Simpson) and reciprocal of Berger–Parker index (Berger–Parker). Data presented as mean ± SD and range.

	Natural Vegetation	Semi-Natural Pastures	Intensive Pastures
Species richness	9.9 ± 6.2 (4–21)	10.6 ± 6.3 (4–21)	9.3 ± 4.5 (4–16)
Shannon	6.6 ± 3.7 (2.2–12.4)	7.2 ± 4.4 (2.7–16.1)	6.2 ± 2.6 (3.1–9.8)
Simpson	5.2 ± 3.0 (1.7–10.6)	5.6 ± 3.6 (2.3–12.9)	4.9 ± 1.9 (2.4–8.5)
Berger-Parker	2.6 ± 5.2 (1.3–6.7)	2.7 ± 6.9 (1.7–6.2)	2.8 ± 9.3 (1.7–4.9)

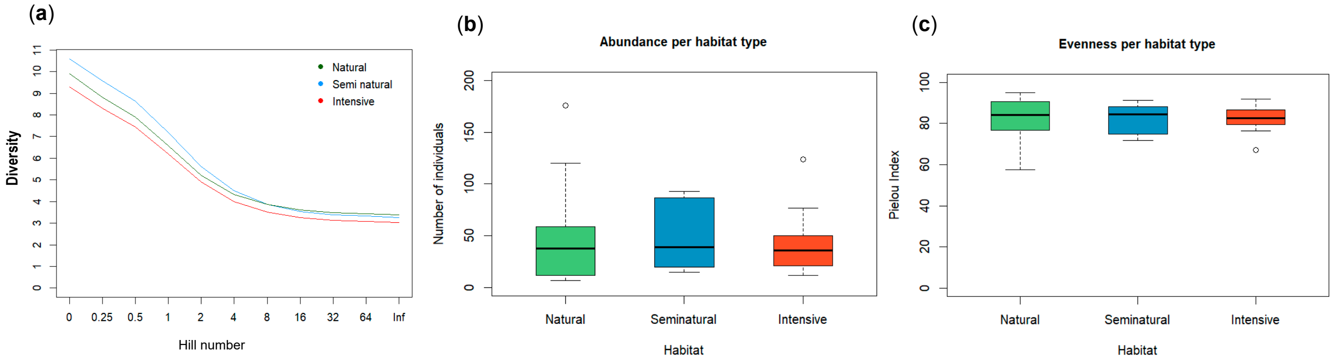

Figure 2. Alpha diversity profiles of flower visitors following Hill numbers in the different land use types of Terceira lowlands (**a**). Differences in pollinator abundance (**b**) and evenness (**c**) between land uses are also shown using boxplots.

3.2. Differences in Species Composition Between Land Uses

A visual analysis of the NMDS ordination shows that pollinator assemblages in pastures are relatively homogeneous while natural vegetation areas have much more heterogeneous pollinator assemblages, some being similar to those from pastures while others are much different (Figure 3). Nevertheless, no significant differences were found in species composition ($p < 0.05$) as many pollinator species were common to the three study land use types. However, we found changes in the abundance of several pollinator species that seem to be related to the degree of land management intensity. For example, the introduced blowflies *Calliphora vicina* and *C. vomitoria*, and the honeybee were more abundant in pastures than in areas of natural vegetation (GLMM: p = 0.007, p = 0.04, $p < 0.001$, respectively) while the native flies *Stomorhina lunata* and *Sphaerophoria scripta* were more abundant in the natural vegetation sites (GLMM: $p = 0.02$, $p < 0.001$, respectively).

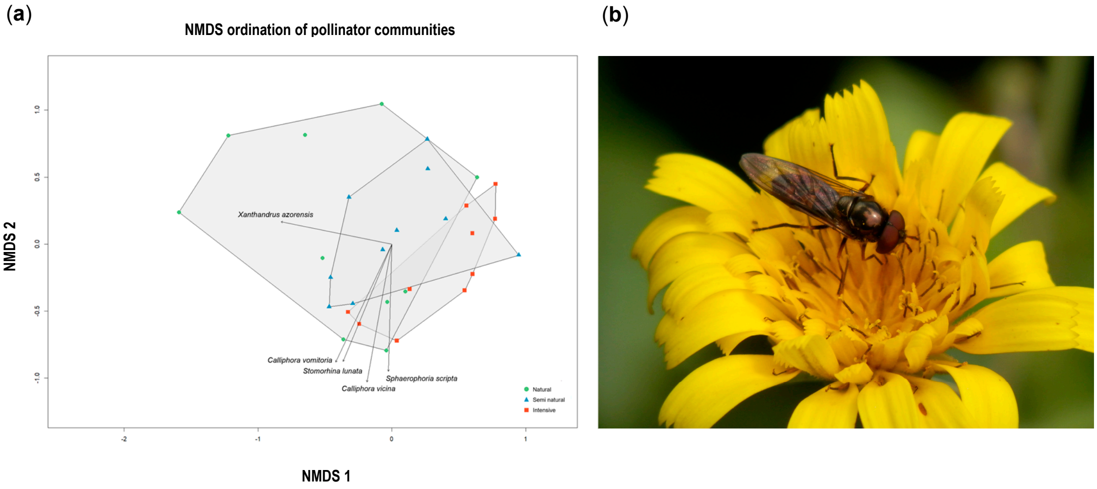

Figure 3. Visual analysis (following a NMDS ordination) of the compositional differences in pollinator assemblages from the three land uses studied in Terceira island (stress = 0.128). The names of pollinator species that contributed most to differences between land uses (species scores with $p < 0.01$) are indicated (**a**). The endemic hoverfly *Xanthandrus azorensis* was almost exclusively recorded from natural vegetation sites (**b**).

3.3. Plant–Pollinator Networks in the Different Land Uses

The pollination networks from the ecological gradient spanning from natural vegetation to intensive pastures showed some differences in the richness and composition of interacting species and in their structural properties (Figure 4, Table 2, Figure S1). Overall, there is a simplification of plant communities in pasture areas and a few introduced plants (*Trifolium repens, Mentha suaveolens* and *Lotus pedunculatus*) concentrate most of the pollinator visits. These species, along with *Mentha pulegium*, are common in pastures, showing higher tolerance to the disturbance by cattle. In areas of natural vegetation, several native plants (including *Leontodon taraxacoides* and *Daucus carota*) received most visits by pollinators and the few endemic plants found in this study (*Erica azorica, Hypericum foliosum*) were recorded exclusively in this land use type. Regarding pollinators, two species, the honeybee *A. mellifera* and the fly *S. lunata*, dominated interactions in pasture areas, reflecting their high abundance and pollination generalism. Although these species were also important in areas of natural vegetation, a considerable number of visits there were made by *Lasioglossum* bees and by the hoverfly *Episyrphus balteatus*, both of which interacted with a wide range of plant species.

There was a marked difference in web asymmetry between intensive pastures and the other land uses since the former had a much lower ratio of plant to pollinator species (Table 2). Generality, the mean effective number of flowering plant species per pollinator species, also decreased along the disturbance gradient, having its highest score in the natural vegetation. Shannon's diversity of interactions decreased along the disturbance gradient, being lowest in intensive pastures (a nearly significant trend, p = 0.07) while the mean number of links per interactor remained similar across land uses. Interestingly, connectance (the realised proportion of possible links) and nestedness (a measure of the tendency for specialist species to interact with subsets of the species that generalists use) differed significantly between land uses, with higher values recorded in intensive pastures compared to the other two land use types. Despite this study having a reasonable replication (with 10 sites per land use), the biological interpretation of our results needs caution since network metrics may be influenced by sampling issues and the number of interactors [68–70].

Interestingly, the proportion of plant–pollinator interactions involving just native species was highest in natural vegetation areas (44.2%), decreased in semi-natural pastures (26.1%), and was lowest in intensive pastures (20.8%). This pattern reflects the changes in species composition and dominance along the disturbance gradient, with introduced species becoming more prevalent in human disturbed habitat types (pastures).

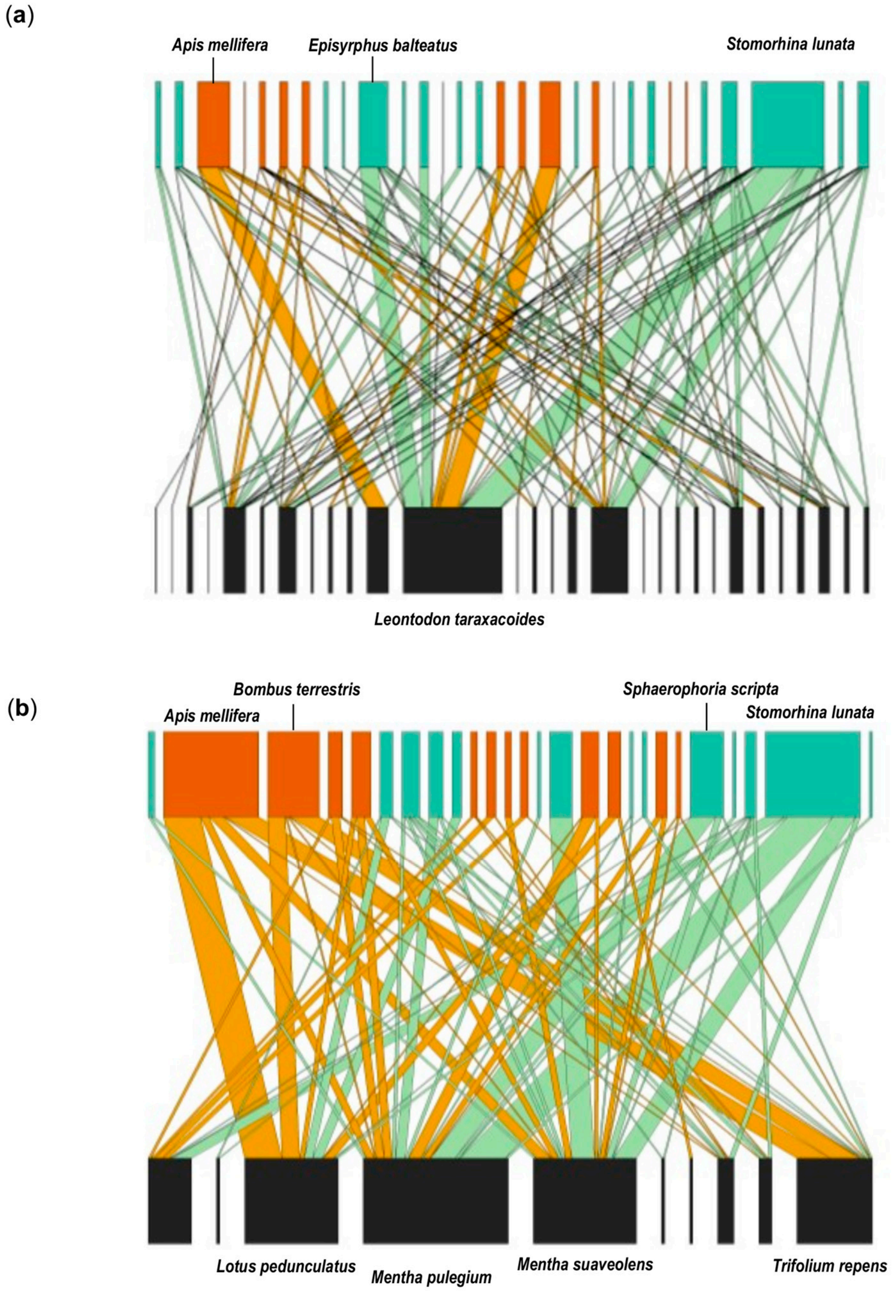

Figure 4. *Cont.*

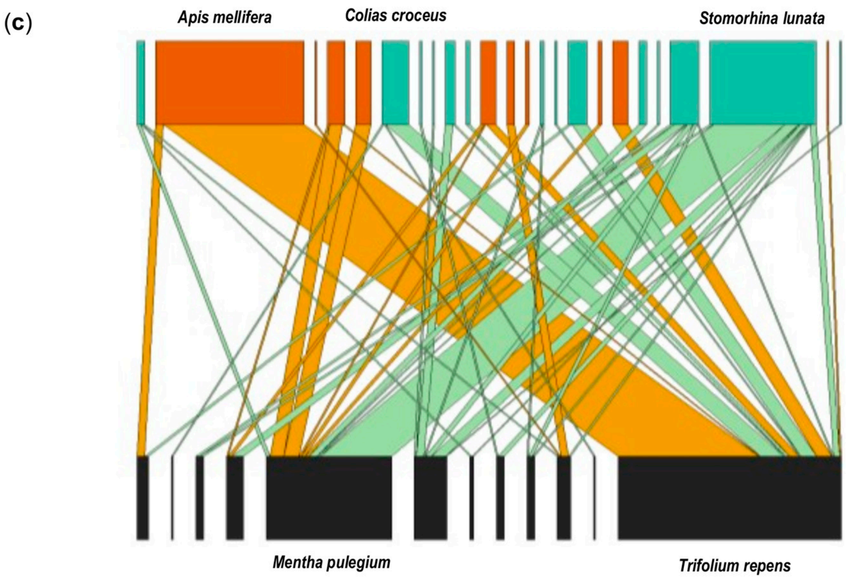

Figure 4. Pollination networks from the three dominant land uses—natural vegetation (**a**), semi-natural (**b**) and intensive pastures (**c**)—in the lowlands of Terceira island. The data from 10 study sites per land use type were pooled. Plant and pollinator species names with higher interaction frequency are highlighted and pollinator species are categorized as native (green) or introduced (orange).

Table 2. Pollination network metrics from the three dominant land uses (natural vegetation, semi-natural and intensive pastures) in the lowlands of Terceira island. Data are the mean ± SE from 10 replicate sites per land use type. The results of post hoc tests are shown (as superscript letters) when significant differences ($p < 0.05$) were found between land use types for a specific network metric.

	Land Use Types		
Network Metrics	**Natural Vegetation**	**Semi-Natural Pasture**	**Intensive Pasture**
Number of flowering plant species	5.7 ± 1.3 ^{a}	4.7 ± 0.8 ^{a}	2.3 ± 0.2 ^{b}
Number of pollinator species	7.6 ± 1.6 ^{ab}	8.4 ± 1.6 ^{a}	5.5 ± 1.1 ^{b}
Links per species	0.92 ± 0.10	0.92 ± 0.07	0.80 ± 0.06
Connectance	0.30 ± 0.04 ^{a}	0.37 ± 0.04 ^{a}	0.52 ± 0.04 ^{b}
Nestedness	28.2 ± 3.8 ^{a}	28.2 ± 4.1 ^{a}	40.8 ± 3.3 ^{b}
Shannon diversity	2.0 ± 0.3	2.0 ± 0.2	1.4 ± 0.1
Interaction evenness	0.54 ± 0.03	0.59 ± 0.03	0.57 ± 0.03
Specialisation asymmetry	−0.08 ± 0.06	−0.20 ± 0.08	−0.30 ± 0.09
Generality	1.8 ± 0.3 ^{a}	1.7 ± 0.1 ^{a}	1.2 ± 0.1 ^{b}

4. Discussion

Land management intensity is an important driver of pollinator species richness, composition and ecological interactions in many continental areas, but there is still scarce data concerning its effects on island ecosystems [34,71–75]. In this study, we found that different levels of land management intensity (matching a gradient of grazing intensity) did not influence local pollinator species richness, but had a significant impact on pollinator community structure and plant–pollinator interactions. This supports the recent claim that species richness is a poor indicator in conservation, being key to analyze the patterns of individual species dynamics [63,76]. Indeed, introduced pollinator species (particularly the honeybee) were more abundant in pastures than in natural areas and played a dominant role as pollinator in both intensive and semi-natural pastures. These changes in pollinator communities and pollination interactions seem to result both from direct and indirect effects of grazing, with particularly significant impacts being mediated through alterations in local plant communities.

Grazing is considered a strong ecological filter for plant communities, often reducing plant diversity, changing plant community structure and composition, and leading to the dominance of a few plant species that tolerate grazing, trampling and elevated nutrient input (e.g., nitrogen) (e.g., [73–75] and references therein). Similar findings were recorded in the Azores, where pastures support lower flowering plant species richness than the neighboring natural areas, while a few introduced species (e.g., *Trifolium repens*, *Mentha suaveolens*, *Lotus pedunculatus*) thrive under grazing conditions. These changes in plant communities due to grazing may have consequences for higher trophic levels, particularly for pollinators, since these animals depend on plants for food, shelter and habitat. Several studies have shown that pollinators may tolerate or even benefit from low intensity grazing (as predicted by the Intermediate Disturbance Hypothesis), but intensive grazing often leads to pollinator species loss [72,74,75]. However, to better understand the consequences of grazing on pollinator diversity and pollination interactions, it is key to consider the plant functional traits related to pollination since they determine the attractiveness, accessibility, and availability of floral resources, thereby directly affecting pollinator visitation patterns. In our study, despite the decline in plant diversity along the grazing gradient, pastures retained several species characterized by generalist floral functional traits (e.g., disk and lip-type flowers), like *Leontodon taraxacoides* and *Mentha* spp. These plants provide food resources (i.e., nectar and pollen) that are easily accessible to a wide range of pollinators, thereby maintaining functional trait matching between plants and pollinators in pastures and contributing to the stability of pollination networks under grazing pressure. This is not the case in Central European grasslands, where intensive pastures are dominated by a single plant species (*Trifolium repens*) with a specialized flower structure (flag-type flower) that is only accessible to a few pollinator groups (e.g., bees, butterflies and moths with medium-long proboscis) [74,75]. Consequently, overgrazing has triggered marked alterations in plant and pollinator communities, disrupting pollination interactions and potentially compromising the long-term stability of these grassland ecosystems.

The absence of significant differences in species richness between the three land use types can also be attributed, at least in part, to the particularities of the Azorean pollinator fauna. The Azorean pollinator communities are considered to be species poor, taxonomically disharmonic (when compared to mainland) and dominated by generalist pollinator species [34,35,77,78]. This is not only due to the biogeography of the Azores, since the archipelago is young and remote, but also a consequence of the six centuries of human colonization that led to extensive native habitat destruction, species extinctions and widespread anthropogenic disturbance [11,13,14]. Thus, particularly in the lowlands, the extant native pollinator species may be now adapted to sustain low to moderate levels of disturbance. The introduction of generalist commercial pollinators, which are now widespread in the archipelago, further contributed to the faunal homogenization of pollinator communities between different land uses. In recent years, the number of apiaries has doubled, and this rapid growth is expected to continue following the goals of the strategic plan for beekeeping in the Azores [79]. Nevertheless, there are still differences in the structure of pollinator communities and in plant–pollinator interaction networks between the land uses studied (Table 2, Figures 3 and 4).

The increasing importance of introduced species along the disturbance gradient jointly with the replacement of native species from key ecological roles is a matter of great concern that needs further research to assess its consequences on pollination and ecosystem stability. In Azores, we have witnessed a dramatic increase in the arrival and spread of alien species, but (with a few exceptions) the consequences to native biodiversity and ecological processes remain to be studied [80–84]. One introduced species that clearly benefits from pastureland is the honeybee, being one of the pollinators responsible for high number of visits to flowers in these anthropogenic land uses. The spread of this species in Azores is human-assisted and is favored by the conversion of natural areas into pastures, benefiting from ample food resources (provided by introduced plants with specialized flower structures) that are less explored by the generalist native pollinators. Due to its wide feeding spectra, high dispersal capability and tendency to form large, densely populated colonies, the honeybee has become ecologically dominant in many terrestrial ecosystems, particularly in human modified landscapes [31,85]. In several island ecosystems, it is considered a problematic species since outcompetes native pollinators, influences plant–pollinator interactions and negatively affects plant reproductive success [33,86,87]. A recent study has even shown that the negative impacts of honeybees on native pollinators and plant reproduction may begin at low beehive densities [88]. Due to the vulnerability of the Azorean biota to alien species introductions, it is necessary to implement a monitoring program to assess the impacts of the introduced honeybee on native biodiversity and pollination interactions, but also set mandatory impact assessments for beehive placement and revise beehive density guidelines for the archipelago. These measures are necessary if we aim to balance food production needs with nature conservation goals in biodiversity hotspot areas with high levels of endemism.

The effects of grazing on plant and pollinator communities and their interactions are evident from a comparative analysis of the pollination networks across the three land-use types, which represent a gradient of grazing intensity. Overall, grazing intensification led to a loss of plant diversity, the replacement of native plant and pollinator species by introduced ones in key ecological roles, a simplification of the interaction network and a marked decrease in interactions involving only native species. In fact, the increases in connectance and nestedness along the gradient seem to result from network simplification as a result of losses of specialist interactions with native plant species and a centralization of interactions by generalist introduced species in intensive pastures [63,89].

The lowest values of links per species and interaction diversity recorded in intensive pastures, together with the high proportion of interactions involving introduced species, highlight the need to define and implement conservation measures to improve habitat quality for native plants and pollinators. An important step for pollinator conservation in Azores is the progressive conversion of intensive pastures into semi-natural pastures, taking into consideration the landscape configuration context. Pastures are the dominant land use in the Azores (in Terceira they occupy nearly 42% of the island surface) and it will be crucial to reduce grazing pressure from the most environmentally vulnerable areas, thus promoting biodiversity conservation, nutrient cycling, carbon sequestration and soil and water quality. Furthermore, the habitat quality of pastures should be improved by enhancing connectivity with adjacent natural areas through ecological corridors or by creating/maintaining patches with native plants within or alongside pasture margins, ensuring conditions for pollinator feeding, nesting and overwintering [90,91]. These actions should cover multiple spatial scales, from local patches to the landscape matrix, aiming to improve their effectiveness in fostering the recovery of native pollinator populations as well as their diversity in anthropogenic habitats. The sustainability of these measures will largely depend on the long-term commitment of stakeholders, being crucial to initiate the development of an agri-environmental scheme, funded by the regional government, to promote pollinator-friendly practices in Azorean pastures.

This study aims to advance our understanding of the effects of land use management intensity (particularly grazing effects) on pollinator diversity and plant–pollinator interactions in oceanic islands, but we are aware of some limitations of this research. Extending the study over a few years would have provided valuable insights into the consistency of our findings by accounting for temporal variation in floral resources and insect activity and their influence on plant–pollinator interactions [92]. Additionally, sampling during other seasons (when both floral resources and insect activity are lower) could offer complementary information to our conclusions. It would also have been important to assess how the differences observed in the visitation networks translate into changes on the reproductive success of the study plants. It is well known that pollinator visitation rates are not always correlated with seed production by plants since pollination effectiveness varies across species/groups of pollinators [93–95]. Nevertheless, the high number of visits by a diverse array of pollinators to several exotic plants found in the Azorean pastures seems to favor their spread and ecological dominance, posing a nature conservation challenge. The situation could deteriorate further if, in addition to the loss of native plant species in pasture areas, there is an increase in the ecological dominance of exotic plants with specialized floral traits (such as *Trifolium repens*). In these plants, the nectar is concealed within the floral tube, making it inaccessible to pollinators with short proboscises. These changes may lead to the loss of local pollinator species, and the resulting simplification of interaction networks could weaken their resilience to ecological disturbances [72,74].

Effective land use management in oceanic islands is a complex and delicate challenge, requiring the integration of multidisciplinary scientific knowledge to promote sustainable human development while safeguarding the natural heritage of these unique ecosystems. This study offers some insights into the mechanisms and consequences of land use intensification and aims to foster research on this important topic.

Supplementary Materials: The following are available online at https://www.mdpi.com/article/10.3390/land14102029/s1, Table S1: List of the study sites with indication of their name, geographical location and land use, Table S2: List of the pollinators sampled in the different land uses, Table S3: List of the flowering plant species visited by pollinators in the different land uses, Figure S1: Pollination networks from the study land uses.

Author Contributions: Conceptualization, M.B. and P.A.V.B.; methodology, M.B. and P.A.V.B.; formal analysis, A.C.-H., M.B. and R.O.; investigation, M.B., R.C. and R.O.; resources, M.B. and P.A.V.B.; data curation, M.B. and P.A.V.B.; writing—original draft preparation, M.B. and R.O.; writing—review and editing, A.C.-H., M.B., P.A.V.B., R.C. and R.O.; visualization, A.C.-H., M.B. and R.O.; supervision, M.B. and P.A.V.B.; project administration, M.B. and P.A.V.B.; funding acquisition, M.B. and P.A.V.B. All authors have read and agreed to the published version of the manuscript.

Funding: M.B. was supported by contract DL57/2016/CP1375/CT0001 (https://doi.org/10.54499/DL57/2016/CP1375/CT0004 (accessed on 2 May 2025)) financed by Fundação para a Ciência e a Tecnologia at the University of the Azores.

Data Availability Statement: All relevant data are within the paper, in Supplementary Materials and was made publicly available from GBIF (http://ipt.gbif.pt/ipt/resource?r=pollinators_terceira, accessed on 2 May 2025).

Acknowledgments: We thank Rui Elias for helping with the identification of several plant specimens. Abrão Leite and Laurine Parmentier kindly supported laboratorial work. We are also grateful to the reviewers for their constructive comments which significantly improved the manuscript.

Conflicts of Interest: The authors declare no conflicts of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, or in the decision to publish the results.

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