

Article

Short- and Mid-Term Spatiotemporal Diversity Patterns of Post-Fire Insect-Pollinated Plant Communities in the Mediterranean

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Abstract: In the Mediterranean, one of the most fire-prone regions in the world, wildfires are considered a key factor in vegetation distribution, structure, and function. Severe or frequent fires can lead to homogenized plant communities and habitat fragmentation with significant consequences for the ecosystem and plant-dependent animals such as pollinators. Herein, we present the results of a 10-year post-fire study (2013–2022) conducted on Chios Island, Greece. We explored the effects of a large-scale fire on beta diversity patterns of the flowering insect-pollinated plant communities and its turnover and nestedness components in both burned and unburned sites. In addition, we investigated whether the recorded differences in the burned and unburned plant communities were a result of species gains or losses in the post-fire years. Burned communities display higher post-fire beta diversity compared to the unburned ones, due to higher species turnover across all years of reference. Species turnover was highest overall in the burned sites during the second post-fire year and decreased a decade later. In conclusion, Mediterranean flowering insect-pollinated plant communities are rather fire-resilient, implying positive impacts on pollinator diversity and plant-pollinator interactions during regeneration after a wildfire.

Keywords: beta diversity; fire ecology; post-fire succession; entomophilous plants; plant ecology



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1. Introduction

Fire influences ecosystem patterns and processes worldwide [1]. Over half of the land surface of Earth is considered to be fire-prone [2], with perhaps a third of the land mass experiencing frequent intensive burning [3]. In the Mediterranean, one of the most fire-prone regions in the world [2], wildfires are considered a key factor that shaped vegetation structure and function [4,5]. As a consequence, Mediterranean ecosystems are generally fire-resilient, a phenomenon responsible for the majority of the observed plant adaptations and functional traits [6–9].

Regions where fires regularly occur have exceptionally high levels of species richness and endemism [10]. Indeed, in such areas, wildfires are amongst the major drivers of species diversity, along with climate, resource availability, palaeogeographical history, and environmental heterogeneity [5,10]. The Mediterranean Basin is the second largest global biodiversity “hotspot” that has been shaped by its rugged topography, insularity, and naturally occurring wildfires [11]. As a result, the flora of the Mediterranean area is one of the richest in the world concerning its area size [5]. The European part of the Mediterranean Basin which is rich in islands is especially one of the world’s major centers of plant diversity, as 10% of all known higher plants occur there [5,12].

The effects of fire on vegetation and the post-fire regeneration and succession are well-studied in the Mediterranean (e.g., [13–18]). There is a consensus that regeneration in

the Mediterranean follows a pattern of autosuccession [17,19,20]. However, regeneration patterns may vary due to fire severity [21,22], seasonality [23], frequency [24,25], and the vegetation type before the fire [26]. For instance, frequent or high-severity fires possibly have important implications on plant communities by homogenizing species composition, as they create landscapes dominated by disturbance-tolerant or rapidly colonizing species [27,28]. In contrast, low to moderate severity fires promote biodiversity by creating novel conditions that promote spatial heterogeneity and species turnover in plant communities and subsequently in pollinator communities as well [29,30].

Fires can indirectly affect floral rewards [31] and in specific environments, especially in the Mediterranean, they can stimulate flowering (for a review see [8]). In turn, plant community composition, the quantity and quality of forage resources present, and the geographic locality are important factors in shaping and organizing pollinator communities [32]. Recently, LaManna, et al. [33] showed that wildfires increased the importance of mutualism in structuring plant and pollinator communities and mediated the importance of biotic associations between pollinators and flowering plants to beta diversity of each trophic level. In addition, they showed that the biotic associations between pollinator and plant species explained substantial variation in beta diversity beyond what could be explained by abiotic factors, such as wildfire severity, indicating the importance of plant communities for pollinator communities and vice versa in structuring post-fire communities [33]. Pollination is a fundamental mutualistic ecosystem service [34,35]. In fact, 85% of plants are insect-pollinated and several insect (also other) species depend on flowers for their survival [36]. Studying the effects of fire on flowering plants' diversity and community structure is important in view of its profound implications for pollinators, especially in the context of the global pollinator crisis [37–39].

In this study, we examine the post-fire regeneration of a Mediterranean plant community focusing on insect-pollinated plants beyond any changes in α -diversity. We monitored 13 post-fire communities by comparing composition or beta diversity of burned and unburned communities in the course of ten years after a wildfire. To do so, we used data collected systematically after a large-scale wildfire event in Chios Island, Greece, rather than the commonly applied “space-for-time” method (e.g., [13,40,41]). By detecting spatial patterns (incl. turnover and nestedness components) of beta diversity in burned and unburned communities, our main goal was to explore whether fire acts as a filter by creating more homogenized (with decreased beta diversity) flowering insect-pollinated plant communities [40]. Such homogenized conditions are typical after severe or frequent fires and result in species loss for plants and pollinators [21,28,30]. In this study, we address specifically the following questions regarding insect-pollinated flowering plants in the course of the first ten post-fire years: (1) What are the differences between burned and unburned communities considering the spatiotemporal patterns of beta diversity and its nestedness and turnover components? (2) How did species composition change in terms of species loss and gain?

2. Materials and Methods

2.1. Study Area

Chios Island is located in the north-eastern part of the Aegean Sea in the country of Greece. The vegetation of this island is typical of a Mediterranean island (dominated by maquis, phrygana, and pine forests) and the flora is well-studied (e.g., [42–44]). Biogeographically, the island belongs to the North-Eastern Aegean module along with other islands like Lesbos, Samos, and Ikaria [45,46]. Having a low degree of endemism, Chios shows many phytogeographical similarities with neighboring Anatolia [44,47,48]. The most widespread forest species is Calabrian pine (*Pinus brutia* Ten.). Historical and more recent frequent fires have created a rather patchy distribution of this species, at least in some parts, resulting in a sub-climax vegetation, where the pine co-exists with high shrubs (e.g., *Arbutus* spp., *Pistacia lentiscus* L., and *Quercus* spp., mainly *Q. coccifera* L.), low shrubs, mostly entomophilous [e.g., *Salvia fruticosa* Mill., *Cistus* spp., *Satureja thymbra* L., *Genista*

acanthoclada DC., *Thymbra capitata* (L.) Cav., and *Sarcopoterium spinosum* (L.) Spach]. The main cultivations are olive groves (*Olea europaea* L.) and the mastic tree (*P. lentiscus* var. *chia*).

One of the largest fires in Chios' history occurred in August 2012 and ravaged the island for approximately ten days (18 August 2012 to 28 August 2012). The fire started from the central part of the island, and due to the strong north winds, it soon moved towards the south and burned approximately 148 km² of coniferous forests, maquis, phrygana, and cultivations, and all-in-all 17.5% of the entire island. The fire did not burn the area homogeneously, which was probably because of the habitat and landscape heterogeneity, the prevailing meteorological conditions, and the tactics applied during fire suppression. As a result, several diverse-in-size patches remained unburned within the burned area.

2.2. Study Sites and Field Sampling

Three months after the fire, in November 2012, following a thorough in situ survey, we selected 13 sampling sites, nine burned and four unburned (Table S1, Supplementary). Study sites covered at least 0.4 ha with a minimal distance of 1.5 km from each other (see also [49]). The unburned sites had not been affected by the fire and were dominated by typical entomophilous shrubs (*S. fruticosa*, *Cistus* spp., *S. thymbra*, *G. acanthoclada*, and *T. capitata*, amongst others). As burned sites, we considered those almost completely burned with few sporadic unburned patches containing about the same plants occurring in the unburned sites; the site habitat types were of diverse origin, viz. phrygana, pine forests, maquis, and cultivations (Figure 1, Table S1, Supplementary). Most burned sites comprised more than one dominant habitat type (Table S1, Supplementary) as boundaries of different vegetation types were difficult to discriminate.

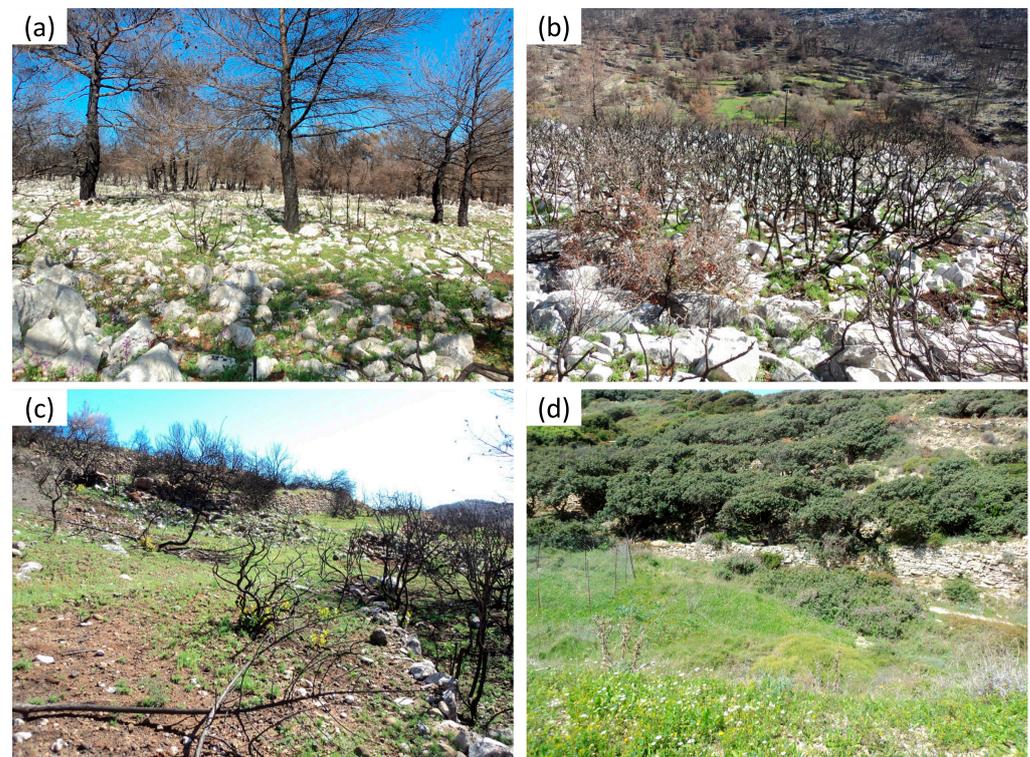


Figure 1. Four sampling sites in Chios in April 2013 (year 1 after the fire). (a) burned pine forest (site S9), (b) burned maquis (site S8), (c) burned mastic trees adjacent to a pine forest (site S10), (d) unburned site with mastic tree cultivations (site S6). For site details, see Table S1 Supplementary.

Samplings, always by the same collector (i.e., the first author), took place between 2013 (1st post-fire year) and 2022 (10th post-fire year), namely during the years 2013, 2014, 2015, 2021, and 2022 (hereafter referred as year 1, year 2, year 3, year 9, and year 10, respectively).

In each year, all entomophilous plants in flower (thus excluding wind-pollinated ones) were recorded from late March to early July during three rounds separated by 3–5 weeks. Plants were recorded in 25 randomly selected squares of 1 m² each at each site and round. By employing this method, some rare plant species might have been excluded, but we have made sampling efforts comparable across sites and years. The identification of most plants was performed in situ. Species unidentified in situ were collected and identified in the lab. All plant specimens were identified to species level except *Taraxacum* spp. which was identified as morphospecies (hereafter referred to as species). Collected plant specimens have been deposited in the Herbarium of the Laboratory of Biogeography and Ecology of the University of the Aegean.

2.3. Beta Diversity Patterns and Statistical Analysis

We computed total multiple site beta diversity (MBD) and its constituent components (i.e., nestedness and turnover; n-MBD and t-MBD, respectively) using the `beta.multi` and `beta.sample` (setting the ‘sample’ argument to 1000) functions from the ‘betapart’ R package [50,51] based on presence/absence data. MBD can provide valuable insight regarding the overall spatial heterogeneity of community assemblages [52]. Then, using the `mded` function from the homonymous R package (‘mded’ 0.1-2 R package) [53], we evaluated the dissimilarity (Sorensen’s dissimilarity) of the distributions for the total MBD and its components for every year and sampling site category included in our analyses.

We also computed the temporal beta diversity between the years from 2013 to 2014, and respectively from 2013 to 2022, as we wanted to test the initial (two years after the fire) and the intermediate (ten years after the fire) temporal effects of fire on community composition based on presence/absence data. Based on the ‘adespatial’ 0.3.19 R package [54], we estimated the temporal beta diversity index (TBI), which measures the change in community composition between two time periods and can be decomposed into species gains and losses [55], assuming that species assemblages at our sampling sites did not change between the baseline period (i.e., 2013) and the future periods (i.e., 2014 and 2022). Subsequently, TBI was randomly re-estimated ($n = 9999$) via bootstrapping and thus, a p -value was obtained for the TBI difference between 2013–2014 and 2013–2022 for all sampling sites.

3. Results

3.1. Floristic Composition

We recorded a total of 203 plant species across sites and years belonging to 41 families (Table S2, Supplementary). The most common families were Fabaceae (40 species), Asteraceae (33 species), Lamiaceae (16 species), Apiaceae (11 species), and Orchidaceae (10 species). The genus *Trifolium* (10 species) was the most common. Among all species, one was a Greek endemic (*Allium exile* Boiss. and Orph.) and another one was alien (*Oxalis pes-caprae* L.). The total number of species per site varied from 29 to 75 and from 13 to 42 yearly and among sites (Table 1).

The vast majority of the plant species occurred on only a small fraction of the sites. Only three species were present in all 13 sites. These species were two annuals (the cosmopolitan species *Anagallis arvensis* and the Mediterranean-European species *Centaurium tenuiflorum*) and one perennial which was the Mediterranean *Helichrysum stoechas*. In addition, 6 species occurred in 12 out of the 13 sampling sites (Table 2).

3.2. Multiple Site Beta Diversity

Spatiotemporal heterogeneity was elevated in our study system, as evidenced by the statistically significant high turnover in the sampled multiple site beta diversity values for the baseline period (2013) compared to all future periods (2014, 2015, 2021, and 2022) for both the burned and unburned sampling sites ($p < 0.01$) (Figure 2).

Table 1. Number of plant species in flower (#) per site, fire category (B: burned, U: unburned), and year. For site details, see Table S1, Supplementary.

Site	Fire	# of Plant Species					
		Total	2013	2014	2015	2021	2022
S1	B	45	21	30	33	23	21
S3	B	75	34	35	37	36	33
S5	B	66	30	39	39	24	28
S8	B	45	22	23	23	21	24
S9	B	72	23	42	30	40	40
S10	B	56	21	41	29	28	27
S11	B	59	34	37	26	28	19
S12	B	60	26	32	28	21	29
S13	B	71	37	30	29	37	34
S2	U	29	19	13	16	19	26
S4	U	49	25	23	22	29	31
S6	U	68	37	33	42	28	30
S7	U	65	26	34	42	36	35

Table 2. Most common species in the study sites across all study years.

Species Name	Family	Life Cycle	Chorology	# of Sites
<i>Anagallis arvensis</i>	Primulaceae	Annual	Cosmopolitan	13
<i>Centaurium tenuiflorum</i>	Gentianaceae	Annual	Mediterranean-European	13
<i>Cistus creticus</i>	Cistaceae	Perennial	Mediterranean	12
<i>Crepis commutata</i>	Asteraceae	Perennial	E-Mediterranean	12
<i>Helichrysum stoechas</i>	Asteraceae	Perennial	Mediterranean	13
<i>Hypochaeris achyrophorus</i>	Asteraceae	Annual	Mediterranean	12
<i>Leontodon tuberosus</i>	Asteraceae	Perennial	Mediterranean	12
<i>Teucrium divaricatum</i>	Lamiaceae	Perennial	E-Mediterranean	12
<i>Thymra capitata</i>	Lamiaceae	Perennial	Mediterranean	12

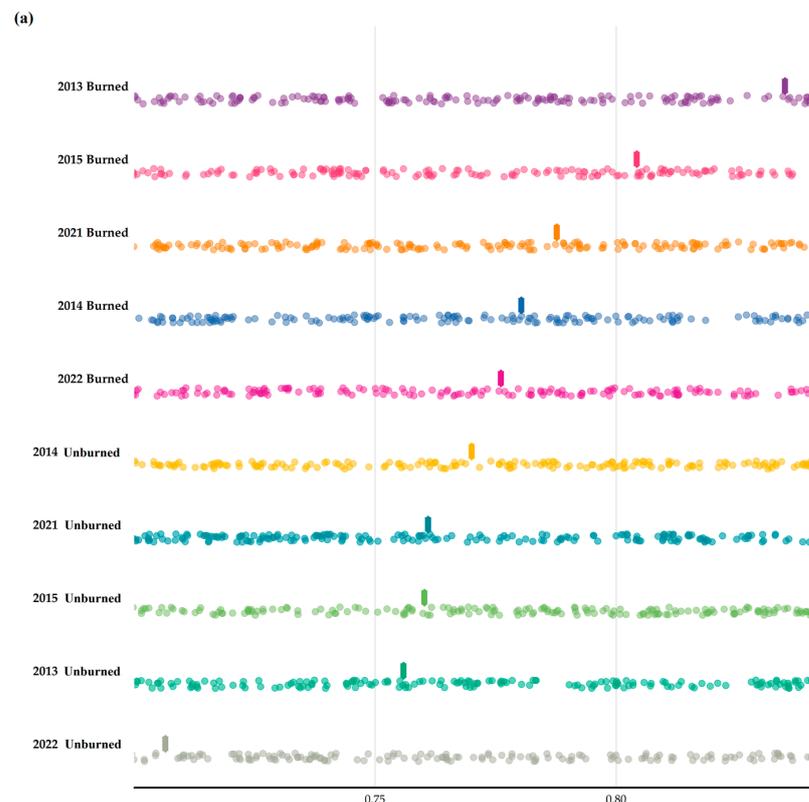


Figure 2. Cont.

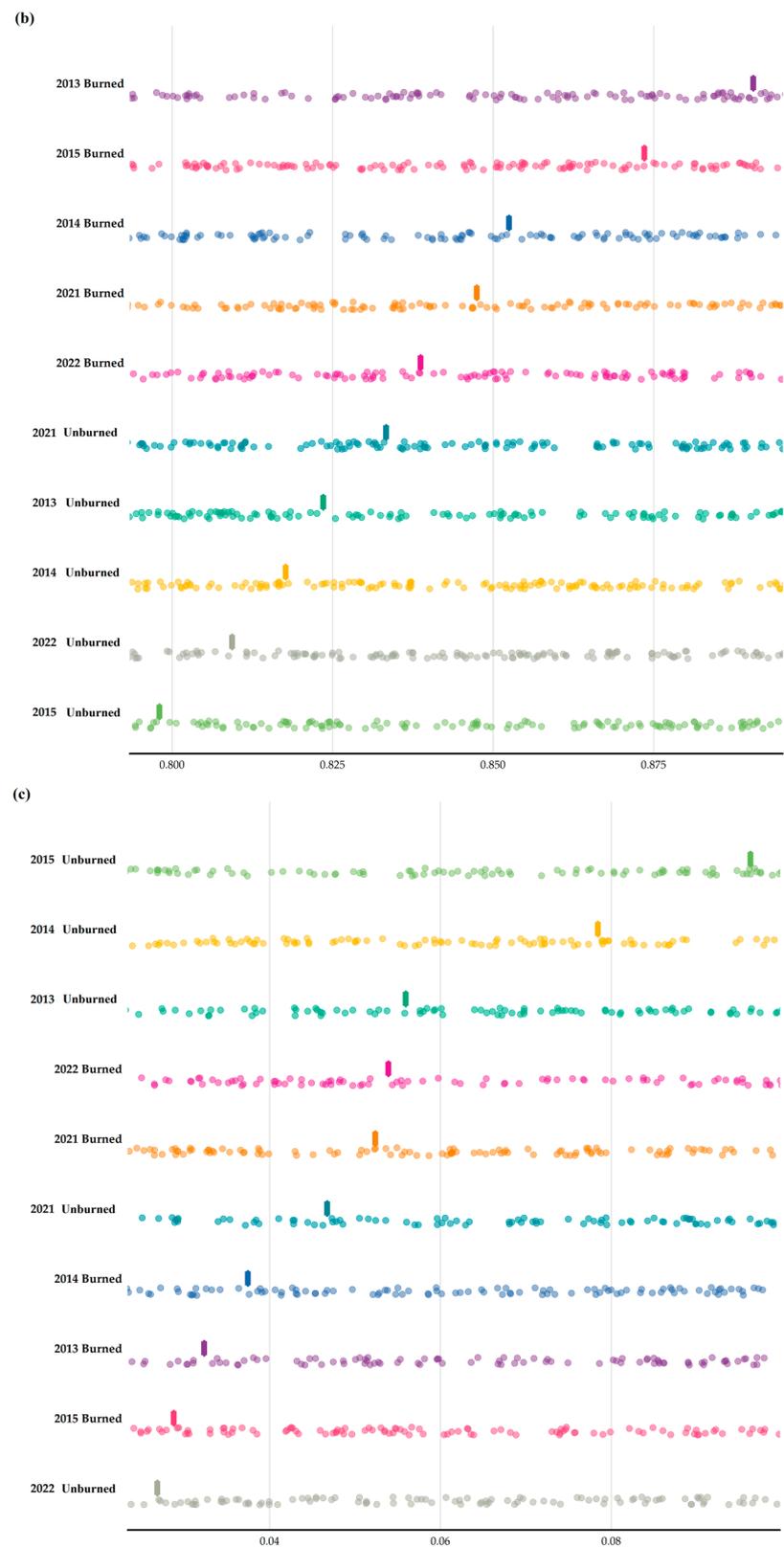


Figure 2. Raincloud plot of the (a) total multiple site beta diversity (MBD), as measured by Sorensen's dissimilarity, and its two components: (b) turnover and (c) nestedness, based on the resampled values obtained from the beta.sample function with the 'sample' argument set to 1000.

3.3. Temporal Beta Diversity Index

Regarding the unburned sites, species losses prevailed in beta diversity patterns in year 2 (bottom-left panel; Figure 3), but this trend reversed by year 10 (bottom-right panel; Figure 3). In both cases, these patterns were not significantly different, even though in one site (S2) plant composition between year 1 and year 10 differed significantly (bottom-right panel; Figure 3). As for the burned sites, temporal beta diversity was driven by species gains which were more pronounced and differed significantly among each other (TBI = 0.137; $p < 0.05$) in year 2. The same trend was observed in year 10 (top-left and top-right panel; Figure 3), but species gains were not significantly different (TBI = 0.018; $p > 0.05$).

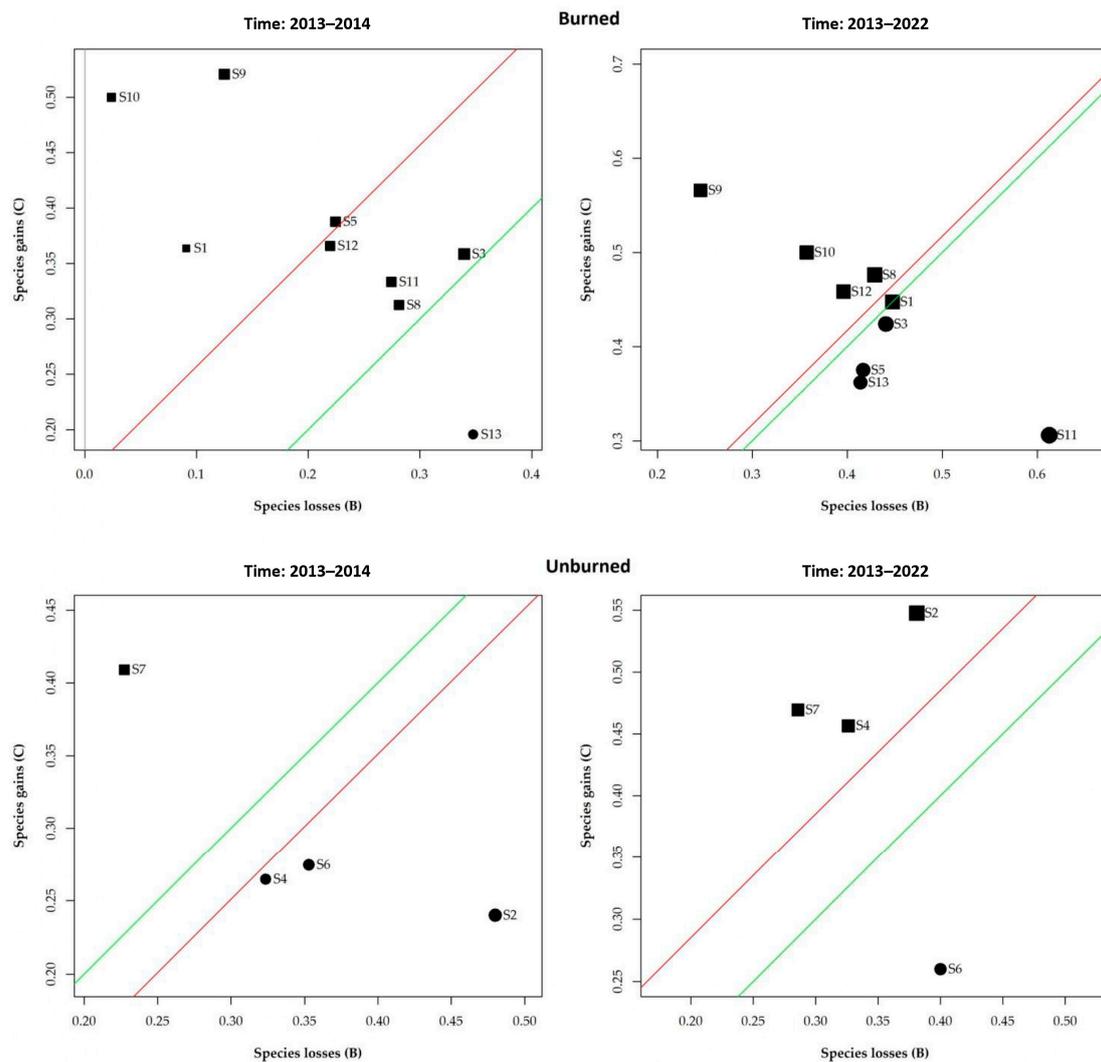


Figure 3. B–C plot comparing the burned sites (**top part**) and the unburned sites (**bottom part**) of year 1 (2013) with year 2 (2014) (**left part**) and year 1 (2013) with year 10 (2022) (**right part**). The nine burned and four unburned sites are plotted using the losses (B) and gains (C) computed from the species richness data. The green line: line with a slope of 1 where gains equal losses. The red line was drawn parallel to the green line and passing through the centroid of the points. If positioned above the green line species gains, on average, dominate losses; if positioned under the green line, the opposite. Points, representing sites, are drawn as squares when species gains dominate losses and as circles when losses prevail. The size of the points indicates the number of species at each site.

4. Discussion

This study explores the effects of fire on the composition of the flowering plant community within ten years after a wildfire. Insect-pollinated plant communities followed

different beta diversity patterns in the burned compared with the unburned sites. Burned communities displayed higher heterogeneity in species composition compared to the unburned ones in all years after the fire. The higher values of spatial beta diversity were observed during the first post-fire year (i.e., 2013), mainly because of high species turnover (Figure 2). Even though these values are reduced with time after the fire, they remain higher compared with the unburned sites over the same years (Figure 2). In addition, burned communities tend to gain species during the second post-fire year, but this effect is already lost 10 years after the fire (Figure 3).

4.1. Beta Diversity Patterns

Fire affects the community composition of plant species and, consequently, beta diversity [13,28,40]. We observed significant differences and a clear trend in beta diversity. More specifically, early post-fire burned plant communities were highly dissimilar to the unburned ones. This was mainly due to rapid plant turnover [52], as burned communities were virtually unnested and in disequilibrium. Moreover, beta diversity in the burned plant communities decreased over time, being lowest a decade after the wildfire but still being higher compared with the unburned ones.

Frequent burning and/or severe fires can lead to community homogenization in the burned communities [21,24,28]. We did not observe this pattern in the freshly burned plant communities immediately after the fire, which indicates an increased heterogeneity that might have been caused by a low or a moderate fire severity [22,29]. The burned communities seem to reach a state of equilibrium and increased homogeneity a decade later (Figures 2 and 3). The elevated beta diversity we observed one year after the fire may be attributed to the non-uniformity of fire intensity that led to a variegated mosaic, with unburned patches within the burned areas. Chios, like most of the Mediterranean areas, has been shaped by frequent fires along with grazing [5,43,56]. This has resulted in a habitat matrix with different burned histories and vegetation types across space and time. These spatiotemporal variations in fire-related patches are called pyrodiversity and can produce the biotic and environmental heterogeneity that drives biodiversity across local and regional scales [10]. Pyrodiversity can, in turn, create favorable conditions for other organisms, as it is positively related to the richness of the pollinators, flowering plants, and plant–pollinator interactions [29,57].

Regarding flowering plant species composition, we found that only a small number of species were present in all or almost all sites across years. On the contrary, most of the species were present in a small number of sites. Probably the plants that flowered during the first post-fire years depended on the vegetation of the site before the fire [26] and on random dispersal and colonization of new species [58,59]. For instance, Arnan, Rodrigo, and Retana [26] highlighted the fact that the pattern of change of mature plant communities after a fire is a complex phenomenon that depends on the characteristics of the plant community before the fire. They showed that post-fire regeneration of plant communities depends on the dominant tree or shrub species characterizing the community type before the fire and on the proportion of obligate seeders that allow for a quicker regeneration of the original community.

4.2. Temporal Beta Diversity

Considering the temporal scale, we observed that most of the burned sites gained plant species during the second post-fire year in contrast with the unburned sites that mostly experienced species losses (Figure 3). On the contrary, the number of species was reduced in the burned sites ten years after the fire, as they had a similar number of species as the communities of the first post-fire year. Our results are in line with previous studies displaying that species richness is higher soon after a fire with a maximum of two years after [31,60,61]. This increased diversity has positive implications for the pollinators as floral community composition and diversity are important factors shaping the diversity and community structure of pollinators such as bees and hoverflies [31,62]. Our data

follow the common pattern of regeneration in the Mediterranean with herbaceous, mainly annual, plants dominating the first years after the fire [17,18,61]. The majority of these plants are obligate seeders that germinate fast after a fire [26,61,63]. Fire can even trigger fire-stimulating flowering, viz. flowering that occurs in the first post-fire year on resprouts from bulbs or rhizomes, followed by abundant seedling recruitment in the second post-fire year [8,64]. Most of the species in the burned sites during the first post-fire years belonged to Asteraceae and Fabaceae, a commonly observed phenomenon in the Mediterranean [15,61]. All these herbaceous species contribute to the increased species richness during the first years but tend to disappear over time [60,61]. In particular, in the burned sites we recorded many losses of Fabaceae species even from the second post-fire year, while the number of Asteraceae species increased. Many of these Asteraceae species have been linked with increased numbers of pollinators in the early post-fire years [49,65]. For instance, in a previous study in the same area, we found that plants like *Crepis commutata*, *Sonchus asper*, *Leontodon tuberosus*, and *Scorzonera elata* are among the key species for the hoverfly communities and contribute to increased populations of syrphids soon after the fire [49]. Moreover, we also have found that the Asteraceae yellow-flowered plants are closely related with bee species like the social Halictidae bee *Lasioglossum malachurum*, whose populations are increased during the first post-fire years [65].

At the same time, we observed differences in the flowering of many short-shrub perennial species. These differences mostly depend on the severity of the fire as it has a major role in affecting species diversity and composition [21,22]. For instance, during the first year after the fire, we only recorded flowers of certain species (i.e., *Cistus* spp.) in sites with lower fire severity in which some individuals survived the fire. At the same time, we recorded many seedlings and young plants of the *Cistus* spp. plants in all our burned sites. These plants reach reproductive maturity two years after a fire [66]. As a result, during the second year, we recorded many young plants in flower for many of these obligate seeders (e.g., *Cistus* spp., *G. acanthoclada*), even though they only had a small number of flowers compared to more mature plants in the unburned sites. The *Cistus* species (*C. creticus*, *C. parviflorus*, *C. salviifolius*) are among the most important species for pollinators, as they provide substantial amounts of pollen [31] and are closely linked to many pollinators such as hoverflies, many *Lasioglossum* bees, and several other species of pollinators that include bees, flies, beetles, and butterflies [49,65]. At the same time, there are some plants (e.g., *T. capitata*, *H. stoechas*, *Phagnalon graecum*, *Stachys cretica*) that are characterized as “delayed seeders” because their seedlings are produced by seeds that remain in the burned soil and for some reason they do not germinate until the second post-fire year [18]. Among them, thyme (*T. capitata*) is probably the most important plant for pollinators during the summer when the flowering season has finished for most of the other plant species (Georgios Nakas, personal observations).

The low-scrub perennial species dominated the landscape nine and ten years after the fire as they were the major vegetation type replacing the grasslands and the bare ground that dominated the landscape soon after the fire [17,18]. At the same time, some phanerophytes also became very dominant in most of the burned sites. Plants like *A. andrachne* and *Myrtus communis* may have large populations and occupy a large percentage of the burned sites nine and ten years after the fire together with other wind-pollinated shrubs (e.g., *Quercus* spp., *P. lentiscus*). Most of these plants were present since the first year after the fire as they are resprouters [63]. However, we did not find them in flower during the first three years, but they were in full flower a decade after the fire, thus providing resources mainly for larger pollinators like the bumblebee *Bombus terrestris* (Georgios Nakas, personal observation).

5. Conclusions

The fire in Chios did not lead to habitat degradation and homogenous plant communities, as has been shown for other communities after severe or frequent fires in Mediterranean-type ecosystems [24,28]. On the contrary, the fire initially led to increased

heterogeneity, a rather positive result, since this diversity has been linked to increased diversity of pollinators and increased plant-pollinator interactions [29,33,67]. In terms of species losses and gains, the post-fire burned communities during the second year gained many different species, mostly herbaceous, which is typical for post-fire regeneration in the Mediterranean [31,60,61]. However, the flowering plant communities a decade after the fire had a similar number of species with the freshly burned of year 1, but their composition was different since some annual herbaceous species had been replaced with perennials. These results firmly suggest that flowering plant communities are rather resilient to fire in the Mediterranean, suggesting that the same will stand for pollinator communities and plant-pollinator interactions during regeneration after a wildfire [33,49,65]. However, caution is needed, since fires tend to become more frequent and more severe [68,69] with unpredictable consequences even in fire-prone systems like the Mediterranean region.

Supplementary Materials: The following supporting information can be downloaded at <https://www.mdpi.com/article/10.3390/land12122109/s1>. Table S1: Study sites in Chios Island, categorized as burned (B) and unburned (U); Table S2: Plant species as recorded during each of the sampling years and in different fire categories (burned—B and unburned—U). Grey color indicates presence.

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Data Availability Statement: The data presented in this study are available on request from the corresponding author. The data are not publicly available due to ongoing Project.

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