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Plant Functional Traits of Plants Species Colonizing Forest Gaps

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Abstract: In this research, we analyzed functional plant traits and life forms of plant species growing on five forest gaps in the Dinaric fir–beech forest in Slovenia. The forest gaps were created as a result of natural disturbances. We selected 18 functional plant traits, whose values were obtained from the BiolFlor database. With the help of the JUICE program, we calculated the frequency of occurrence in individual forest gaps for each functional plant trait. Then, we calculated Spearman's correlation coefficient at $p < 0.05$ between the occurrence of individual functional plant traits and each forest gap. Individual locations differed statistically in 87 categories of plant functional traits. The forest gap Nad Drago differed statistically from the other forest gaps in 16 functional plant traits. Forest gaps are mainly colonized by perennials and herbaceous perennials and chamaephytes. These are plant species that begin to flower in June and July, bloom for two or three months, and are pollinated by insects, mainly hover flies and wild bees. This colonizing plant species reproduce via seeds or spores and vegetatively. Furthermore, birds and forest mammals are the vectors of fruit and seed dispersal.

Keywords: functional plant response; environmental changes; colonizing plants; Dinaric fir–beech forest

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1. Introduction

Plant species respond differently to environmental factors and the effects of ecosystem functioning. Their responses to environmental changes and contribution to ecosystem functions can be determined with the help of plant functional traits [1]. According to the definition of Violle et al. [2], functional traits are any morphological, physiological, or phenological characteristics at the individual level, from the cell to the whole organism, without reference to the environment or any other level of organization. Plant functional traits describe interactions between individual plant specimens and between individual plant specimens and their environment [3,4]. This is why they can be an effective tool for studying the response of plant species to changes in the environment. Today, they are mainly used to study the response of plant species to climate change, changes in land use either in agricultural landscapes or in more or less natural ecosystems, and natural processes of succession in the environment [5–9]. Forest gaps are also subject to continuous succession, either as a result of natural disturbances or as a result of human activity. Basically, the forest dynamics are the same in all forest gaps and take place in the direction of overgrowth with tree species. However, the difference is in the speed of overgrowth and in the plant species composition. Due to the changes in biotic and abiotic factors from the forest gap emergence to the final successional stage, forest gaps can, therefore, represent sites for studying functional plant traits of plant species characteristic of the individual successional stage of forest gap. With the occurrence of forest gaps, the illumination of the surface and the precipitation regime change, and temperature fluctuations are also greater. The exposure of forest gaps to radiation depends largely on the size of the forest gap and the size of the trees in the surrounding forest stand. Specifically, large trees shade the edges of the forest gap, and, if it is small, they can shade it almost entirely. The amount of light that reaches the floor of the forest gap also depends on the latitude at which the forest gap is located, the slope of the terrain, and the position on the adjacent or axial part. Both affect the angle of incidence of the sun's rays. The amount of incoming light also varies depending on the season and daily rhythm [10–12]. At the forest gap, the intensity of diffuse light decreases from the center to the edges [13]. The bigger the forest gap is, the more surface is exposed to light. The maximum light intensity in the forest gaps is reached between 10 a.m. and 2 p.m. and is greatest in the center of the forest gap. Soil temperature has a positive correlation with light intensity, and, in large forest gaps, it increases from morning to evening. In small and medium forest gaps, soil temperature is highest between 12:00 and 14:00 [12,14]. As for humidity, compared to the forest, it is more exposed to light, as it is directly exposed to precipitation. In addition, the retaining capacity of the soil and bed rock has a great influence on it. Humidity is also higher in the center and decreases toward the edges, where water is taken up from the soil by the roots of the surrounding trees [12,15,16].

The newly formed forest gaps represent a new living environment for both animals and plants. From the point of view of the flora, in the first phase after the formation of forest gap, the species composition of the forest gap depends on those tree species that stagnated in the understory until the forest gap occurred and did not have enough light for growth, on the seed bank in the soil of the forest gap, and on the plant colonization of species from nearby and distant surroundings [13]. The species that first colonize the forest gaps have a greater availability of resources than those that settle there later. Species heterogeneity is greater in bigger forest gaps [17,18]. Over time, when the herbaceous plants in the soil use up the available nutrients, their density begins to decrease, and forest gaps begin to populate with shrub species as well. As the abundance of shrub species increases, the abundance of herbaceous species decreases, and the forest gap gradually becomes overgrown with forest again [19]. Constantly changing abiotic and biotic factors over the years on the forest gap cause a change in species; some disappear or their coverage decreases, while the coverage of others increases [20,21].

In our research, we analyzed plant functional traits to research how they change according to the age of forest gap and thus to the individual successional stage. We were interested in the dominant plant functional traits of plants present at a certain age of the forest gap. Given that we studied naturally occurring forest gaps, they were of different sizes; therefore, the forest gap size also represented a factor influencing the occurrence of plant species with individual plant functional traits. The purpose of the research was to determine those common morphological characteristics (plant functional traits) of plant species that enable colonizing plant species to make optimal adaptations for survival in forest gaps. The aim was also to find out which plant life strategy is the most successful in forest gaps. We assumed that annuals and biennials would dominate the younger forest gaps, while perennials would dominate at the older ones. Considering the age of the forest gap, our hypothesis was also that plant species in younger forest gaps have plant functional traits of species growing in the forest understory, while older forest gaps are dominated by species whose plant functional traits enable efficient survival in open areas.

Furthermore, knowing the occurrence of plant species with certain plant functional traits in a certain successional stage can help us understand the wider ecological meaning of forest gaps in the forest ecosystem, especially regarding the connection between plants and animals. Some plant functional traits are also vital for some animal species and their population dynamics [22].

2. Materials and Methods

2.1. Selection of Sampling Locations

For the purposes of the research, we selected 5 forest gaps and one control plot—juvenile beech forest (location Kamen Zid) (Table 1). We chose the juvenile beech forest as the last successional stage of forest gap overgrowth with forest. All sample plots were selected in the Dinaric fir–beech forest (*Omphalodo-Fagetum sylvaticae*) in the south of Slovenia (Figure 1). We chose the Dinaric fir–beech forest because it represents the most widespread forest community in Slovenia. The geographical location itself was chosen because, in this part of Slovenia, it is the largest compact forest area constantly subjected to natural disturbances, which cause natural forest gaps. The selected forest gaps differed from each other in terms of time of occurrence and size. Their main characteristics are listed in Table 1. All forest gaps are results of natural disturbance (wind throw and ice snow) but we could not obtain exact data on their formation (Figure 2). Thus, we estimated the age of forest gaps on the basis of the state of bigger organic decomposing material (trunks and branches) and the annual growth of spruce saplings (faster growth on sunlight and habitus of a single plant) [23–25]. On selected forest gaps and the control plot (young beech forest), we first carried out an inventory of plant species in the subplots using the Braun–Blanquet method. We then performed an analysis of the changes in functional plant traits depending on the time of the gap formation.

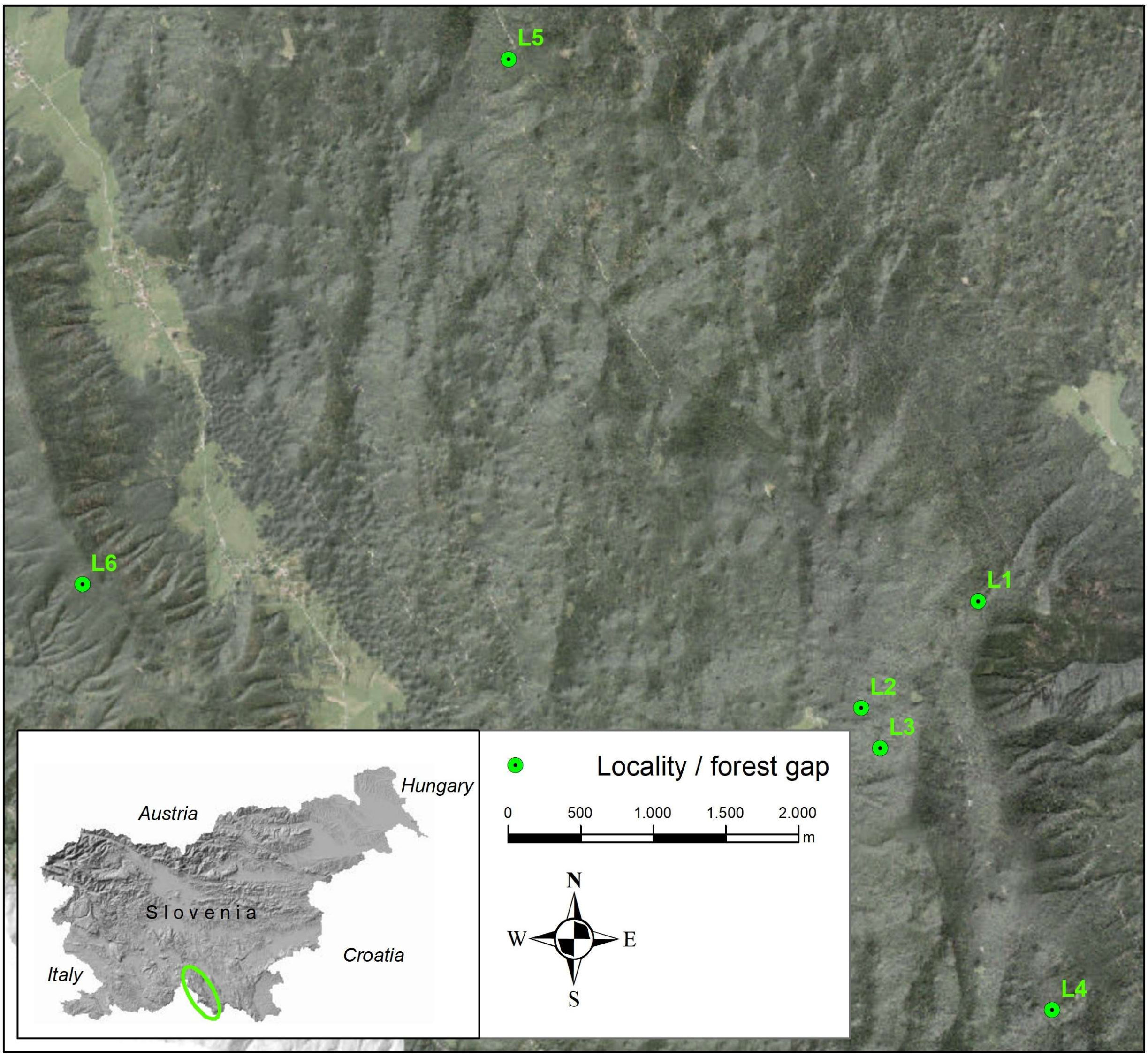


Figure 1. Locations of six sampling sites on map (1: Kamen Zid, 2: Pod Barnikom, 3: Nad Barnikom, 4: Goteniški Snežnik, 5: Goteniška Gora, 6: Nad Drago).

Figure 2. Photographs of all sampling locations (**L1**—Kamen Zid, **L2**—Pod Barnikom, **L3**—Nad Barnikom, **L4**—Goteniški Snežnik, **L5**—Goteniška Gora, **L6**—Nad Drago).

Table 1. Forest gaps and their features (coordinates, UTM quadrant, altitude, aspect, substrate, soil, year of origin). The location marked * is the control site with the juvenile phase of beech forest.

Locality/Forest Gap	Coordinates	Altit.	Ex.	Surface	Substrate	Year
L1 (Kamen Zid) *	Lat: 45°36′50″ Lon: 14°44′0″	1068 m a.s.l.	SE	175 m^2	Limestone	2000
L2 (Pod Barnikom)	Lat: 45°36′26″ Lon: 14°43′23″	1132 m a.s.l.	SW	600 m^2	Dolomite	2007

Table 1. *Cont.*

Locality/Forest Gap	Coordinates	Altit.	Ex.	Surface	Substrate	Year
L3 (Nad Barnikom)	Lat: 45°36′17″ Lon: 14°43′29″	1161 m a.s.l.	SE	1400 m^2	Limestone, dolomite	2007
L4 (Goteniški Snežnik)	Lat: 45°35′19″ Lon: 14°44′24″	1205 m a.s.l.	E	1300 m^2	Limestone, dolomite	2013
L5 (Goteniška Gora)	Lat: 45°38′51″ Lon: 14°41′30″	1100 m a.s.l.	SE	3200 m^2	Limestone, dolomite	2011
L6 (Nad Drago)	Lat: 45°36′53″ Lon: 14°39′15″	954 m a.s.l.	E	1480 m^2	Dolomite	2014

2.2. Selection of Plant Functional Traits

We selected the 18 most used plant functional traits (Table 2). Data on the values of plant functional traits were obtained from the BIOLFLOR database [26]. The BIOLFLOR database mostly contains data on Central European plant species. However, the database does not contain species that are widespread only in Slovenia or in the southern part of Europe. For these species, we subsequently assigned the value of the functional trait to the plant species according to the description of the functional trait in BIOLFLOR or data collected from other literature sources [27–29]. For some species, we could not determine the value of the plant functional trait either from the descriptions in the BIOLFLOR database or from the literature sources. In such cases, we assigned the value ‘no data’ to the functional trait.

Table 2. Selected plant functional traits with single categories.

Plant Functional Traits	Categories
Life form	Megaphanerophyte, nanophanerophyte, chamaephyte, hemicryptophyte, geophyte, therophyte
Life span	Annual, biennial, plurennial
Vegetative propagation	Bulb, fragmentation, rhizome, runner, runner-like pleiocorm, runner-like rhizome, runner with tuberous, shoot tuber, turion
Storage organs	Root tuber, rhizome, runner, runner-like pleiocorm, runner-like rhizome, runner with tuberous, shoot tuber, trunk, tuft
Leaf persistence	Overwintering green, persistent green, spring green, summer green, without leaves
Leaf anatomy	Helomorphic, hygromorphic, mesomorphic, scleromorphic, without leaves
Leaf form	Acicular, bipinnate, digitate, full, grass like, lobate, long leaf, no leaves, palmate, pinnate, pinnatifid, simple,
Beginning of flowering	March, April, May, June, July, August
Duration of flowering	1 month, 2 months, 3 months
Type of reproduction	By seed/by spore, by seed and vegetatively, by spore and vegetatively, mostly by seed, mostly by spore, mostly vegetatively
Pollen vector	Insects, wind, self-pollination, abiotic factors
Breeding system	Allogamous, autogamous, automixis, facultative allogamous, facultative autogamous, mixed mating, xenogamous
Flower color	Blue, brown, green, lilac, pink, purple, red, violet, white, yellow
Floral rewards	Nectar (none, present, plenty, little), pollen (present, plenty, little), none, deceit
Flower class after Mueller *	For bees, bumble bees, butterflies, moths, flies, Hymenoptera, wasps, Syrphidae, wind flowers, flowers with hidden nectar, flowers with partly hidden nectar, nasty flowers, deceptive flowers, flowers with open nectar, flowers with pollen, flowers with open nectar, true lip flowers, trap flowers

Table 2. *Cont.*

Plant Functional Traits	Categories
Flower type after Kugler **	Bell-shaped flower, brush flowers, disc flowers, flag flowers, head flowers, funnel flowers, lip flowers, flowers with pollen, stalk disc flowers, true lip flowers, trap flowers
Fruit type	Aggregate drupelets, aggregate nutlets, berry, capsule, legume, nut, lomentum, drupe, schizocarp, siliqua
Diaspore type	Aggregate fruit, fruit with appendage, fruit, fruitlet, infructescence, mericarp, seed, spore

* Müller (1881) categorized the flowers pollinated by insects into nine basic classes according to the type of pollinator. According to some morphological special traits of some flowers, he divided the basic classes into several smaller classes. ** Kugler (1970) categorized the flowers according to their shape into 10 basic classes with subclasses based on their intermediate shapes.

2.3. Statistics

Using the JUICE software, we calculated the frequency of its occurrence in sub-plots at individual sampling locations for each plant trait. Using the Statistica 8.0 software (Statsoft Inc., Tulsa, OK, USA, 2007), we then calculated the Spearman correlation coefficient at $p < 0.05$ between the occurrence of individual plant traits and the sampling location [30]. Additionally, we calculated statistical differences between individual locations for each category of plant functional traits at $p < 0.05$ using the same software. For each category of plant functional trait, we first tested whether or not the distribution of the trait in the locations was normal using the statistical software Statistica 8.0. In our case, all distributions were normal, which is why we subsequently used one-way ANOVA and a post hoc Bonferroni test [31] to analyze the differences between locations, as the frequency of occurrence of plant species with a specific functional trait at a particular location represented the statistical variable in our research. The overall results for categories of plant functional traits where the analysis showed statistically significant differences between locations were shown using medians in joint frequency diagrams. We used the median as the middle value because it is used as such for numerical data and it is easier to show in diagrams, since it represents the middle value, with one half of the data having smaller or equal values and one half having greater or equal values. We used an asterisk to mark the category of plant functional traits for which an individual location showed statistically significant differences from at least three other locations. We decided to use differentiation from at least three other locations because we wanted to point out the locations that differed the most in terms of the presence of plants with a specific functional trait.

3. Results

A total of 186 different plant species were recorded in the understory in all forest gaps and control plot. The largest number of species (106) was found in the forest gap Goteniška Gora. The fewest species (58) were found in the beech forest (Kamen Zid). For all plant species in total, we recorded 144 different categories within 18 plant functional traits. According to life form (Figure 3a) and life span (Figure 3b), most of the plants found in forest gaps were geophytes or hemicryptophytes and had a plurennial life span. They reproduced vegetatively (Figure 3c,d)) mostly with rhizomes or were described as runners. The largest percentage of plant species found in forest gaps had mesomorphic, scleromorphic, or hygromorphic leaves (Figure 3e), which are persistent green or summer green (Figure 3f). Their leaf form belonged mostly to three groups: simple leaves, full leaves, and pinnate leaves (Figure 3g).

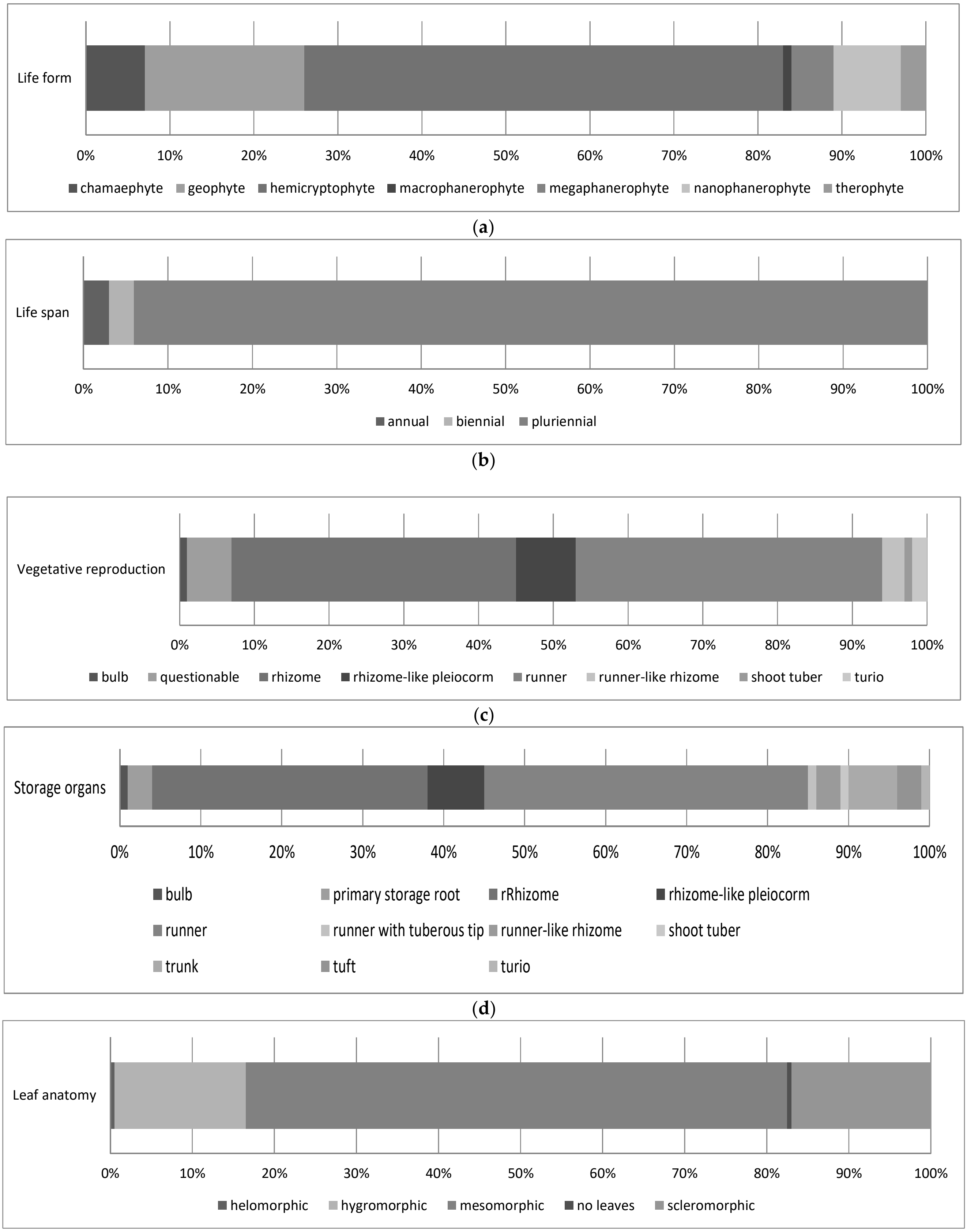
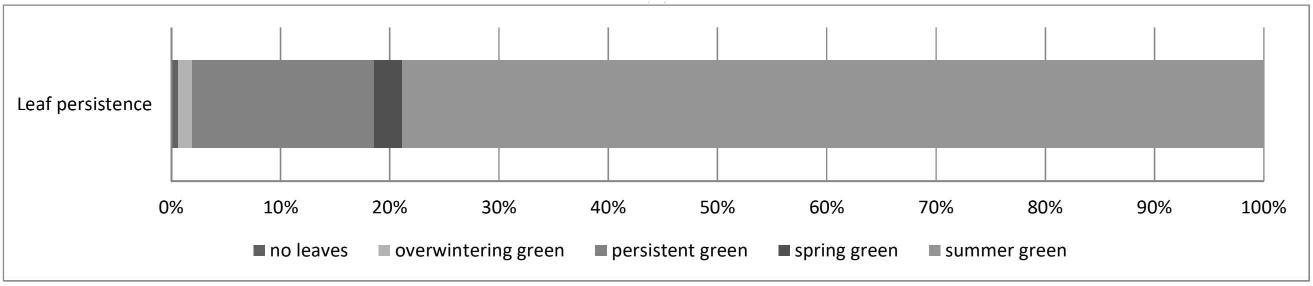
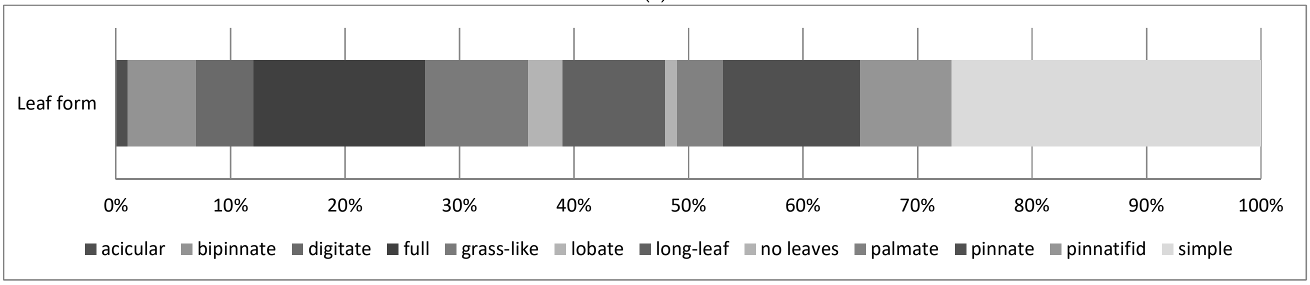


Figure 3. *Cont.*



(**f**)



(**g**)

Figure 3. Percentages of individual categories that appeared within *life form* (**a**), *life span* (**b**), *vegetative reproduction* (**c**), *storage organs* (**d**), *leaf anatomy* (**e**), *leaf persistence* (**f**), and *leaf form* (**g**) plant functional traits.

Most of the plant species that we detected on the forest gaps bloom in August, July or June, for one, two, or up to six months (Figure 4a,b). Their flower colors fell into 10 different color categories, with white and yellow flower colors predominating (Figure 4c). Among the recorded plant species, there was a great variety of flower shapes according to both the Mueller and the Kugler classifications. We classified their flowers into 13 categories according to Muller and 11 according to Kugler, whereby the plant species most often had flowers with hidden or open nectar and were in the form of disc flowers or flower heads (Figure 4d,e).

The flowers of plant species present at forest gaps had mostly nectar as a flower reward and plenty of pollen, which is why they were mostly pollinated with insects (Figure 5a,b). Their dominant type of reproduction was a combination of seeds and vegetatively or just by seeds (Figure 5c). Almost 40% of them were allogamous, and one-quarter of them were facultative allogamous or have mixed mating (Figure 5d). According to fruit type plant functional traits (Figure 5e,f), most of the plant species belonged to the category of plants with capsule or nut and of plants with diaspore types such as seeds, whole fruits, or fruits with appendages.

On the basis of the Spearman correlation coefficient (Table 3), we found that only chamaephytes were statistically strongly correlated with forest gaps. Furthermore, perennials and herbaceous perennials were characteristic for forest gaps. In terms of plant morphology, there was a statistically significant positive correlation between forest gaps and plant species whose storage organs were stolons in the case of "runners" and cluster roots, and with summer-green, mesomorphic leaves (intermediate stage between scleromorphic and hydromorphic leaves). Species that had palmately lobed, linear, or simple leaves were also characteristic. There was a typical positive correlation between forest gaps and plant species with red and white labiate flowers with hidden nectaries, which were pollinated mainly by bees, flies, and especially hover flies. Pollinators were primarily attracted by the nectar, but there was a significant positive correlation with plant species without any 'reward' in the flower. Species without flowers (ferns) were also positively correlated with forest gaps. A statistically significant positive correlation with forest gaps was shown for species that began flowering in June and July and species that flowered for two or three months. In terms of reproduction, there was a positive correlation between forest gaps and species that could reproduce simultaneously by seeds and vegetatively or simultaneously by spores and vegetatively, and whose pollen vectors were wind and abiotic factors. These species were also allogamic, facultatively allogamic, or characterized by automixis. Species that spread with stone fruits or clusters of stone fruits, aggregate fruits, and loments were characteristic for the surveyed forest gaps. In this regard, there was a significant positive correlation of species whose unit of seed dispersal was represented by a fruit with an appendage and a cluster of fruits.

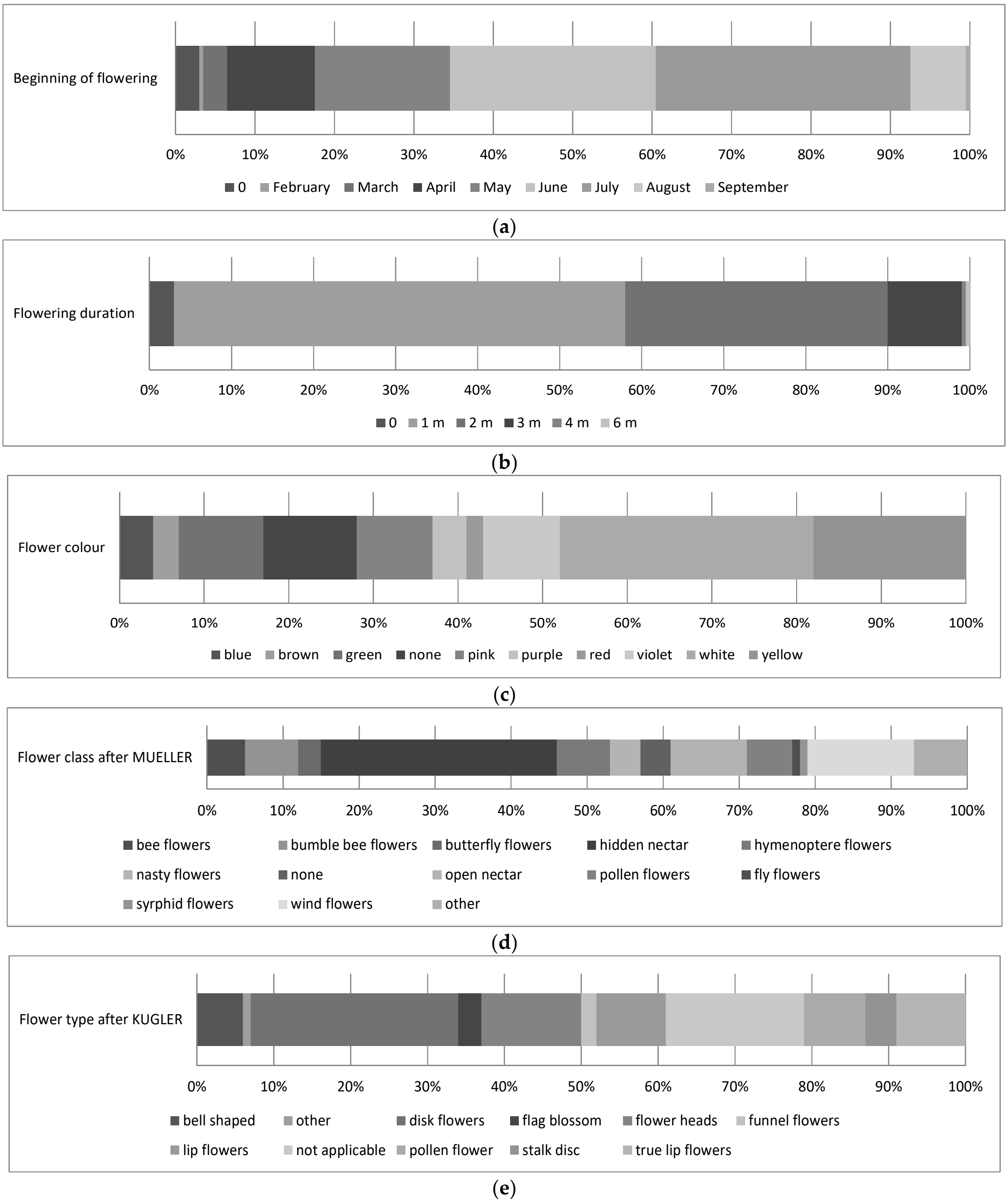


Figure 4. Percentages of individual categories that appeared within *beginning of flowering* (**a**), *flowering duration* (**b**), *flower color* (**c**), *flower class after Mueller* (**d**), and *flower class after Kugler* (**e**) plant functional traits.

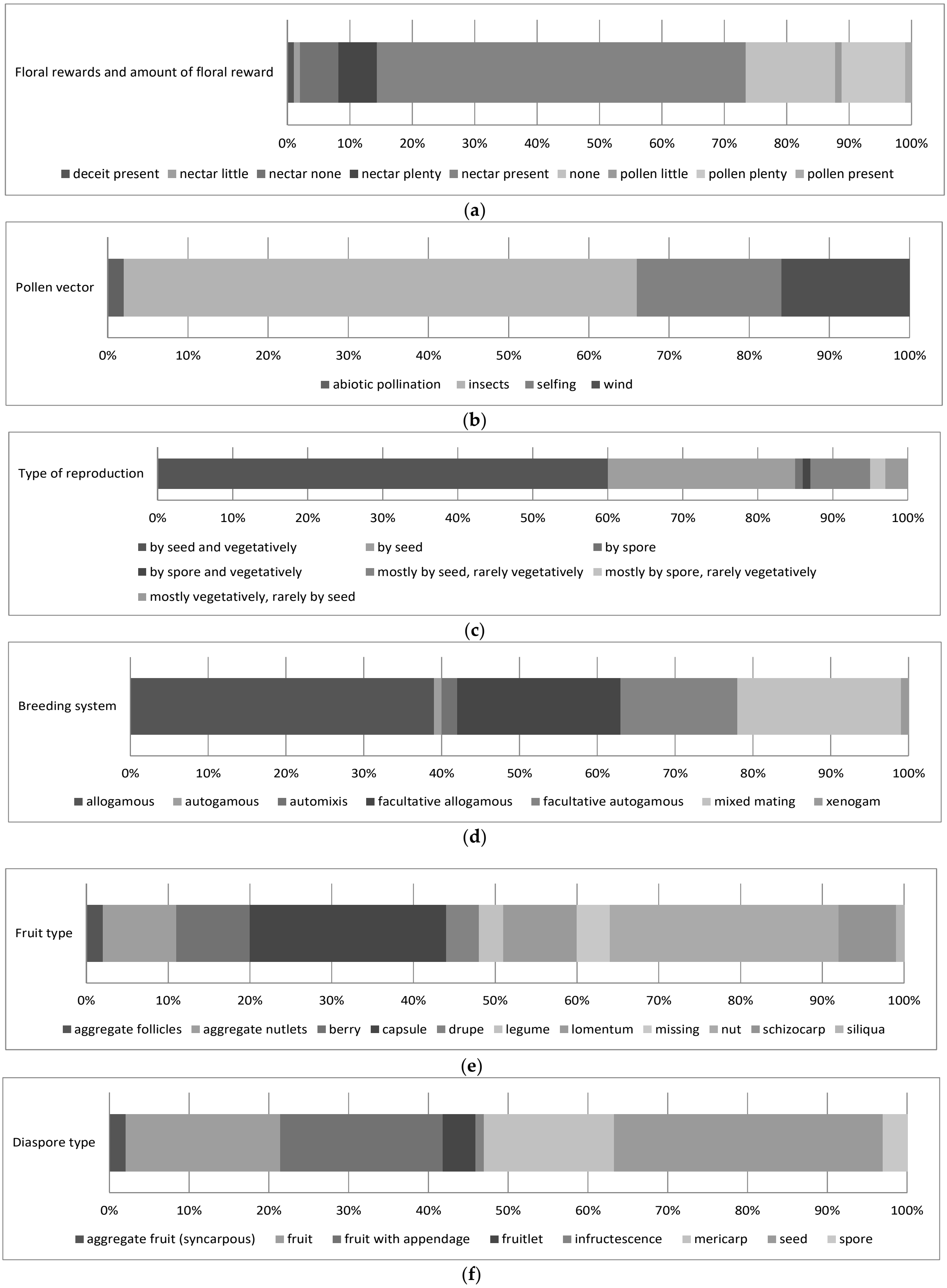


Figure 5. Percentages of individual categories that appeared within *flower rewards* (**a**), *pollen vector* (**b**), *type of reproduction* (**c**), *type of breeding system* (**d**), *fruit type* (**e**) and *diaspore type* (**f**) plant functional traits.

Table 3. Plant functional traits and its single categories, showing statistically significant correlations with forest gaps at $p < 0.05$ (bold values exhibited a statistically significant positive correlation).

Plant Functional Traits	Categories	Spearman's Coef. Corel.
Life form	Chamaephyte	0.74
Life span	Biennial	−0.27
	Plurennial	0.28
Vegetative propagation	Runner-like rhizome	−0.64
Storage organs	Runner	0.68
	Root tuber	−0.29
	Runner-like rhizome	−0.64
	Tuft	0.43
Leaf persistence	Summer green	0.23
Leaf anatomy	Mesomorphic	0.26
Leaf form	Long leaf	0.46
	Lobate	−0.57
	Palmate	0.67
	Simple	0.28
Beginning of flowering	May	−0.25
	June	0.37
	July	0.39
Duration of flowering	2 months	0.23
	3 months	0.23
Type of reproduction	By seed and vegetatively	0.44
	By spore and vegetatively	0.52
Pollen vector	Wind	0.41
	Abiotic factors	0.34
Breeding system	Allogamous	0.54
	Automixis	0.35
	Facultative autogamous	0.40
	Mixed mating	−0.40
Flower color	Green	−0.30
	Red	0.29
	White	0.28
Floral rewards	None—nectar	−0.35
	Nectar—present	0.27
	Pollen—plenty	−0.30
	Pollen—little	−0.27
	No reward	0.63
Flower class after Müller	For bees	0.31
	For bumble bees	−0.28
	For flies	0.50
	For Syrphidae	0.44
	Flowers with hidden nectar	0.55
	Flowers with open nectar	−0.43
	Flowers with pollen	−0.42
	Trap flowers	−0.39
	Without flowers	0.30
Flower type after Kugler	Bell-shaped flower	−0.55
	Flag flowers	−0.50
	Lip flowers	**0.31**
	True lip flowers	**0.42**

Table 3. *Cont.*

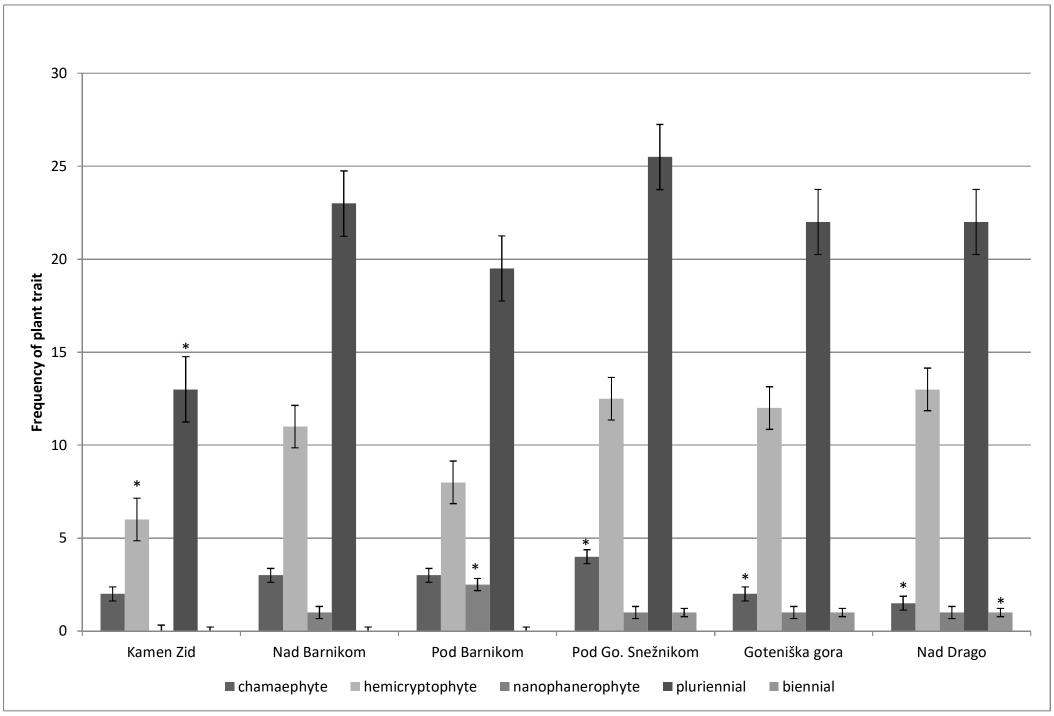
Plant Functional Traits	Categories	Spearman's Coef. Corel.
Fruit type	Aggregate nutlets	**0.38**
	Aggregate drupelets	**0.51**
	Berry	−0.40
	Drupe	**0.24**
	Legume	−0.50
	Siliqua	**0.41**
Diaspore type	Aggregate fruit	**0.50**
	Mericarp	**0.50**
	Spore	**0.43**

There was a statistically significant negative correlation between forest gaps and plant species that were biennial and stored nutrients in the primary storage root and in the tubers in the case of runners. There was also a negative correlation with species with lobed leaves and green-colored, bell-shaped, or papilionaceous flowers with open nectaries, pollen, or traps. Furthermore, a negative correlation was also found for species which began flowering in May and for species pollinated by bumblebees. In terms of dissemination, however, there was a negative correlation between forest gaps and species with berries and legumes.

Individual locations differed statistically in 87 categories of plant functional traits. In terms of life forms of plant species and their life cycle, the location Kamen Zid differed the most, with the statistically significantly lowest presence of hemicryptophytes and statistically significantly lowest presence of perennials in the undergrowth. The location Pod Barnikom also differed from others, as it had the highest presence of nanerophytes compared to the other five locations. Of the five locations, the location Pod Goteniškim Snežnikom differed because of the highest presence of chamaephytes, while the locations Goteniška Gora and Nad Drago differed from the other three in terms of the presence of chamaephytes. The location Nad Drago differed statistically from the other three locations because of the presence of biennial plants. There were no biennial plants at the locations Kamen Zid, Nad Barnikom, and Pod Barnikom (Figure 6a).

In terms of type of vegetative reproduction, the locations Kamen Zid and Nad Drago statistically differed the most from the other locations (Figure 6b). Compared to other locations, these locations had the lowest number of plant species that reproduced with stolons. The same applies to the method of storing energy. Both locations had the fewest species that stored their energy in the creeping parts of the plant. Additionally, the forest gap Nad Drago differed from three locations because of the highest presence of species that stored their energy in the primary storage root and the fact that it had no plant species that stored their energy in the cluster roots, unlike in other locations.

In terms of leaf anatomy and leaf persistence, the location Kamen Zid differed yet again (Figure 6c). Specifically, compared to the other five locations, the location Kamen Zid had the statistically significantly lowest number of species with mesomorphic leaves and summer green leaves; compared to three other locations (Nad Barnikom, Pod Goteniškim Snežnikom, Nad Drago), it had the lowest number of species with scleromorphic and evergreen leaves (compared to Goteniški Snežnik, Goteniška Gora, and Nad Drago). In terms of leaf form (Figure 6d), the location Nad Drago stood out, differing statistically from the other locations in that we did not find any species with linear or palmately lobed leaves. The most common species were those with lobed leaves. Together with the location Pod Goteniškim Snežnikom, they differed from the other locations in that they were the only two locations with plant species with bipinnate leaves. The locations Kamen Zid and Pod Barnikom stood out from the other three locations with the lowest presence of species with pinnate leaves. The location Kamen Zid also had statistically significant differences from three locations (Nad Barnikom, Pod Barnikom, Nad Drago), as it had the lowest presence of species with pinnate leaves. Compared to the other four locations (except for Nad Drago), the location Pod Barnikom had the lowest occurrence of species with palmately compound leaves.



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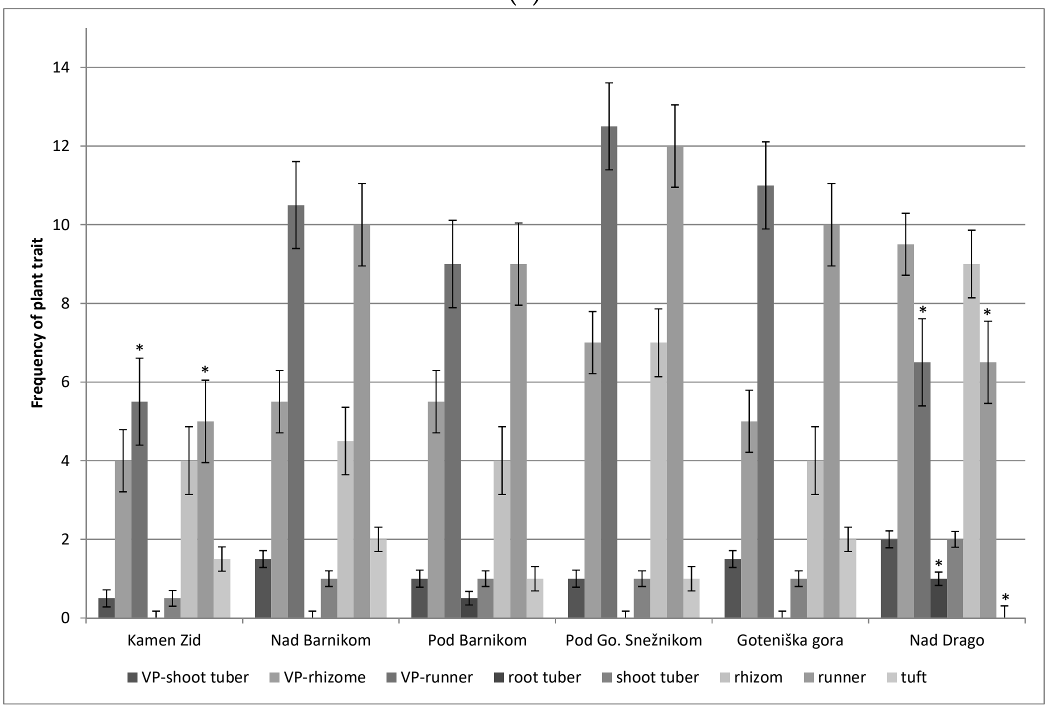

(**b**)

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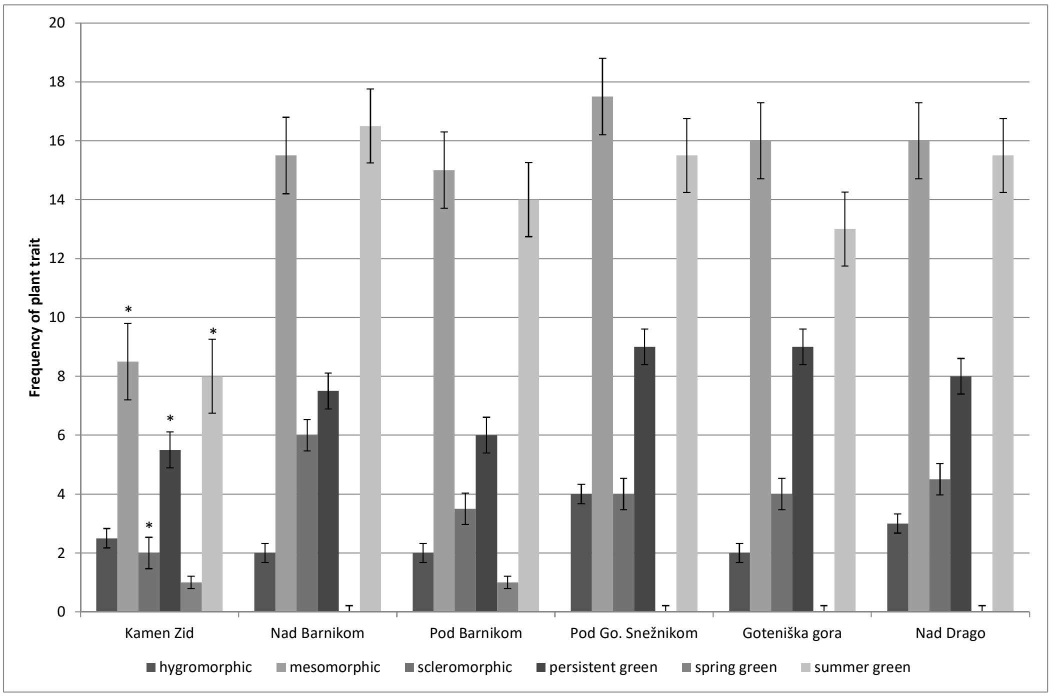

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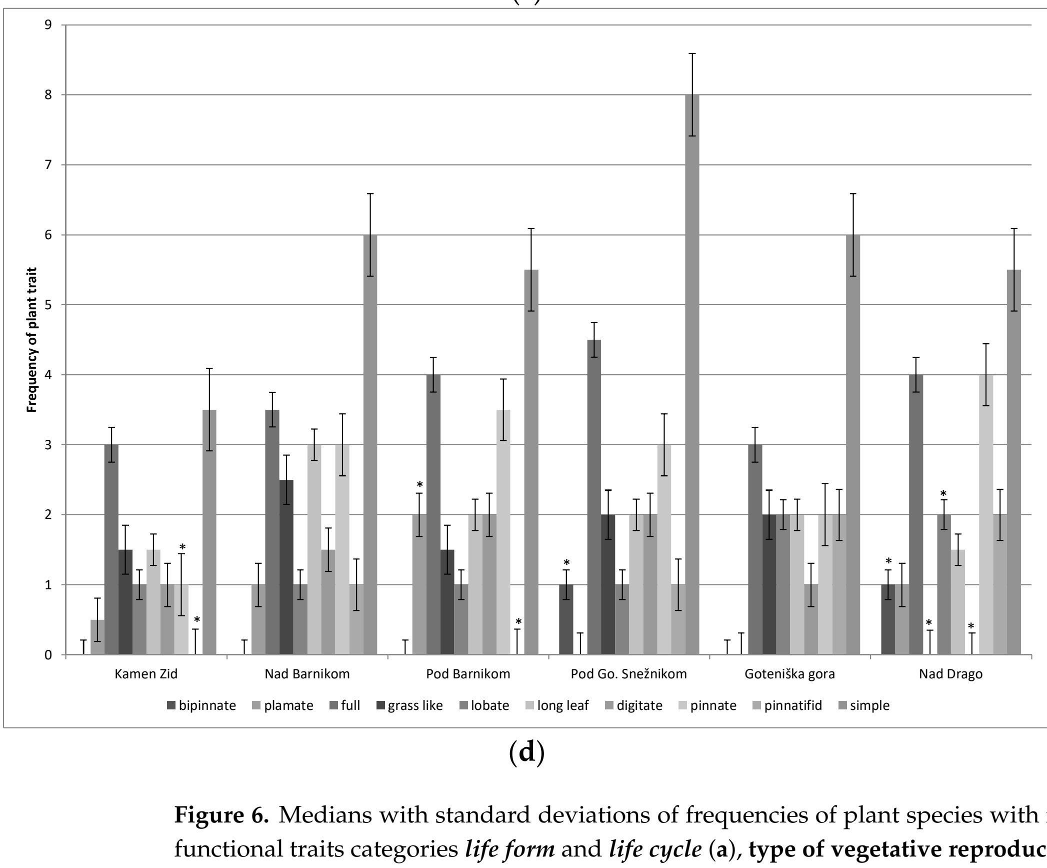
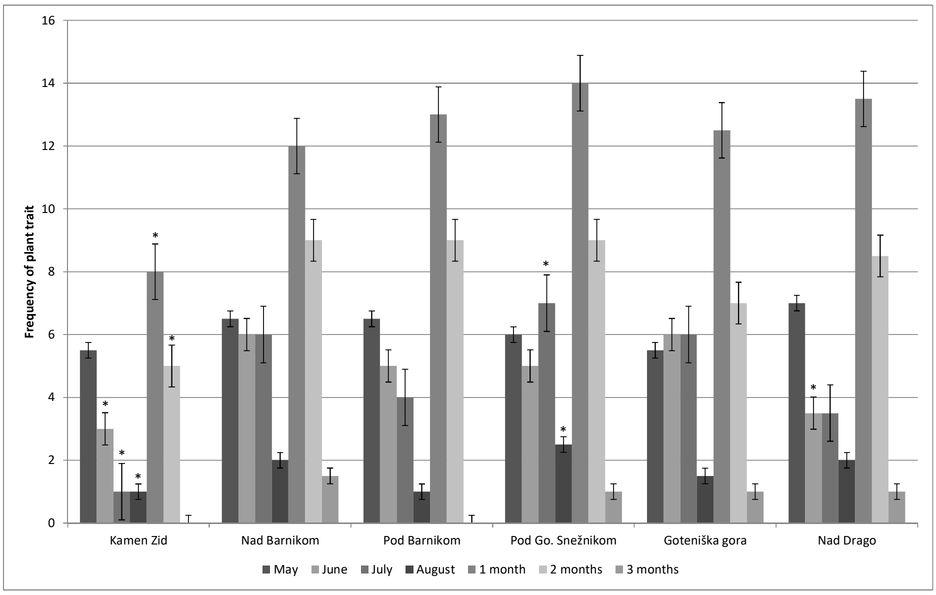


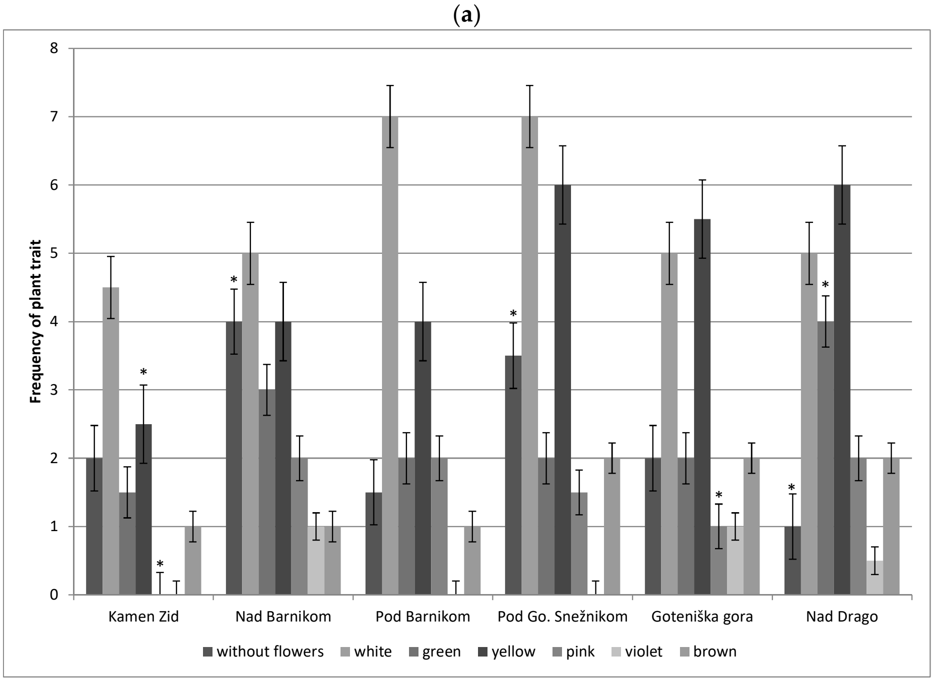
(**d**)

Figure 6. Medians with standard deviations of frequencies of plant species with individual plant functional traits categories ***life form*** and ***life cycle*** (**a**), **type of vegetative reproduction** and **storage organs** (**b**), **leaf anatomy** and **leaf persistence** (**c**), and **leaf form** (**d**) are represented. Statistical differences with Bonferroni test between individual localities were calculated. Asterisks mark those categories in which a single location was statistically significantly different from at least three others.

We also observed statistically significant differences between locations in terms of the beginning of flowering and flowering duration. Once again, the location Kamen Zid differed the most from the other locations, as it had the lowest occurrence of species that start flowering in June, July or August (Figure 7a). Furthermore, it also had the fewest species that flower for one or two months. While the location Pod Goteniškim Snežnikom differed from the four other locations in that it had the highest presence of plant species that begin flowering in July, the same location also differed from three other in that it had a lower presence of species flowering in August. The location Nad Drago, like the location Kamen zid, also differed from the same three locations because it had a lower presence of species that begin flowering in June. We also observed statistically significant differences between locations in the presence of plant species with a specific flower color. The most species without flowers were present at the locations Nad Barnikom and Pod Goteniškim Snežnikom, while the location Nad Drago had the fewest species. The location Kamen Zid had the fewest plant species with yellow and pink flowers. There were also significantly less of the latter at the location Goteniška gora. The most species with green flowers were at the location Nad Drago (Figure 7b).

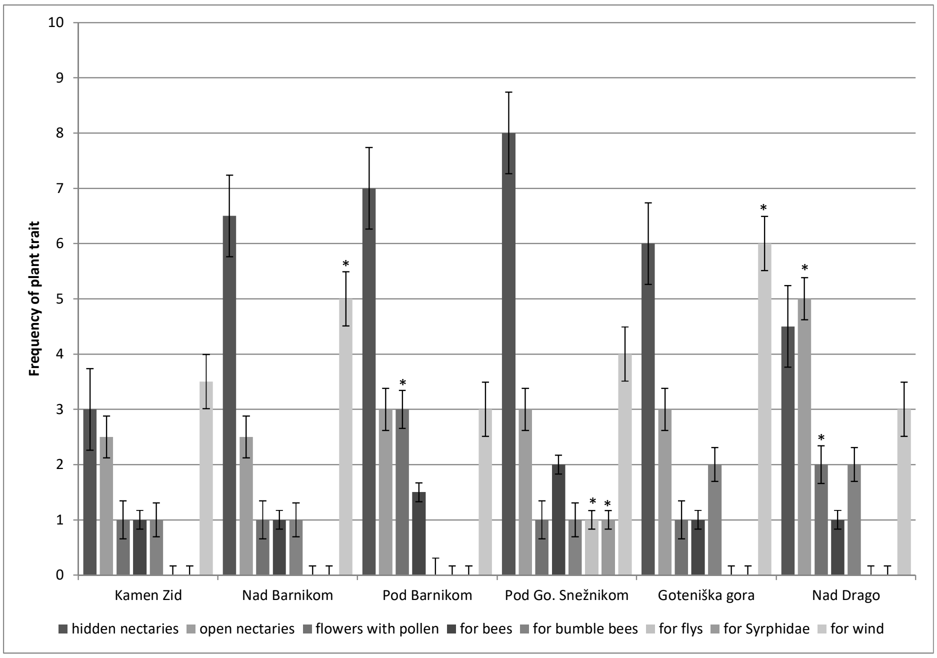


(**a**)

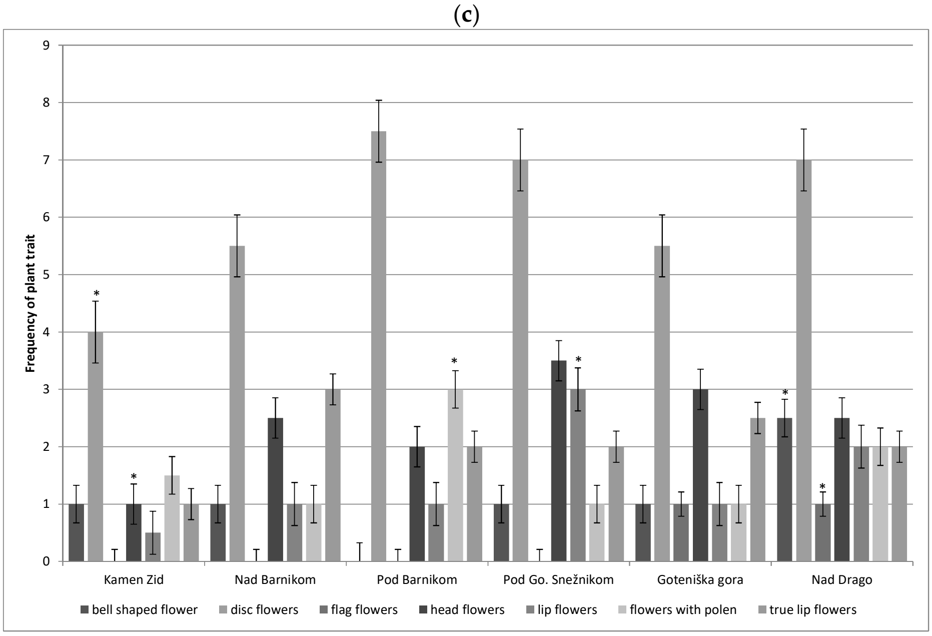


(**b**)

Figure 7. *Cont.*



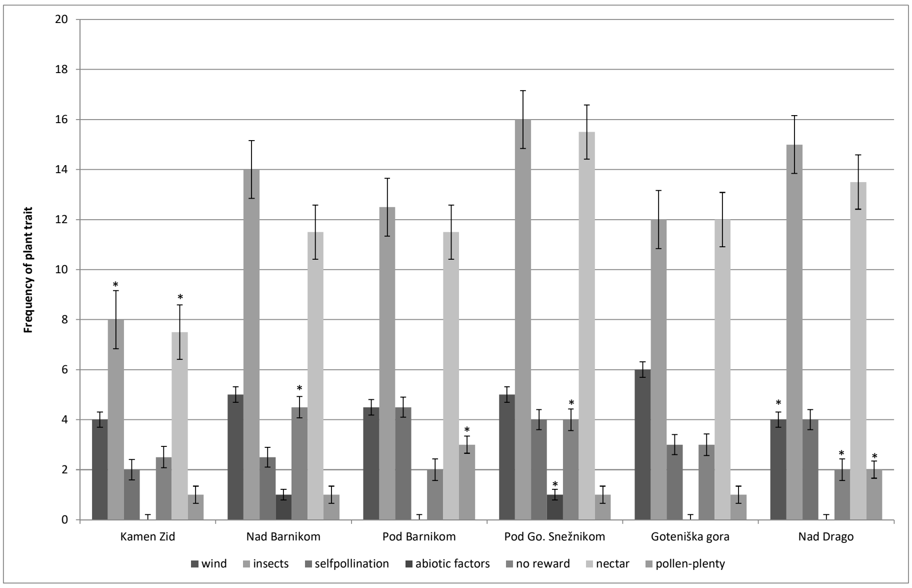
(**c**)



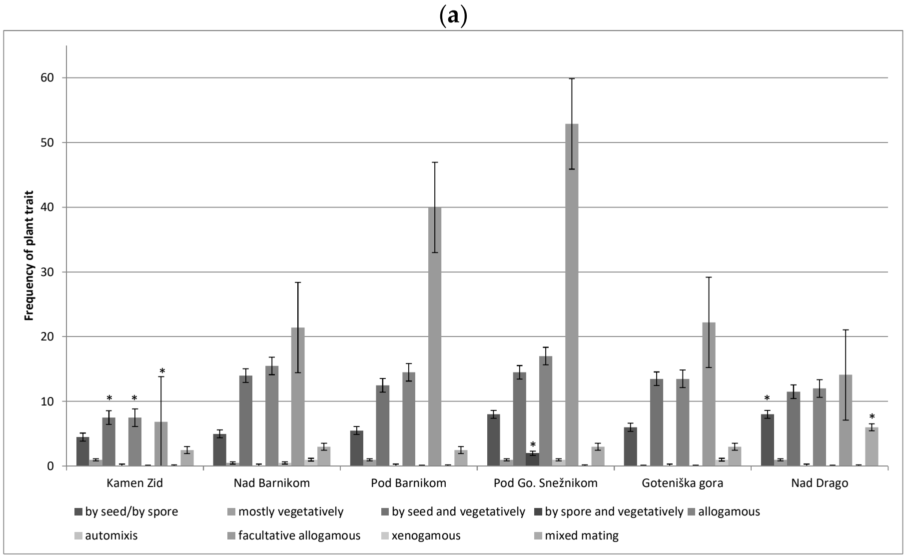
(**d**)

Figure 7. Medians with standard deviations of frequencies of plant species with individual plant functional traits categories ***beginning of flowering*** and ***flowering duration*** (**a**), ***flower color*** (**b**), ***flower typeafter Müller*** (**c**), and ***flower type after Kugler*** (**d**) are represented. Statistical differences with Bonferroni test between individual localities were calculated. Asterisks mark those categories, in which a single location was statistically significantly different from at least three others.

The location Pod Goteniškim Snežnikom had statistically significant differences in terms of the flower type after Müller (Figure 7c). This location had the lowest occurrence of plant species pollinated by various types of wasps and flies. The statistically significantly highest number of plant species whose flowers contained primarily pollen was at the location Pod Barnikom, with the lowest at the location Nad Drago. The latter locations also stood out with the highest occurrence of species with exposed nectaries in the flower. The statistically significantly highest number of wind-pollinated plants was at the locations Nad Barnikom and Goteniška Gora. The analysis of the flower form after Kugler also showed a statistically significant highest number of plant species with flowers rich in pollen at the location Pod Barnikom. In terms of representation of other categories, the location Kamen Zid stood out again with the lowest occurrence of plant species with bell-shaped flowers or capitula. While the location Pod Goteniškim Snežnikom had the most species with labiate flowers, the locations Goteniška Gora and Nad Drago had the most species with papilionaceous flowers. Additionally, the location Nad Drago had the statistically significant highest presence of bell-shaped flower species (Figure 7d). The location Nad Drago location also differed in most categories in terms of flower award and pollen vector. Compared to three other locations (Nad Barnikom, Pod Goteniškim Snežnikom, Goteniška Gora), it had fewer species whose pollen vector was wind and whose flowers had no award for pollinators. The locations Nad Barnikom and Pod Goteniškim Snežnikom differed from the others in terms of the greatest presence of species without a flower award, with the latter also differing from the four other locations by the greater presence of species that had the ability to self-pollinate. The location Kamen Zid differed from the others with the lowest presence of species whose pollen was transferred by insects and species whose method of attracting pollinators was the nectar in the flower (Figure 8a).

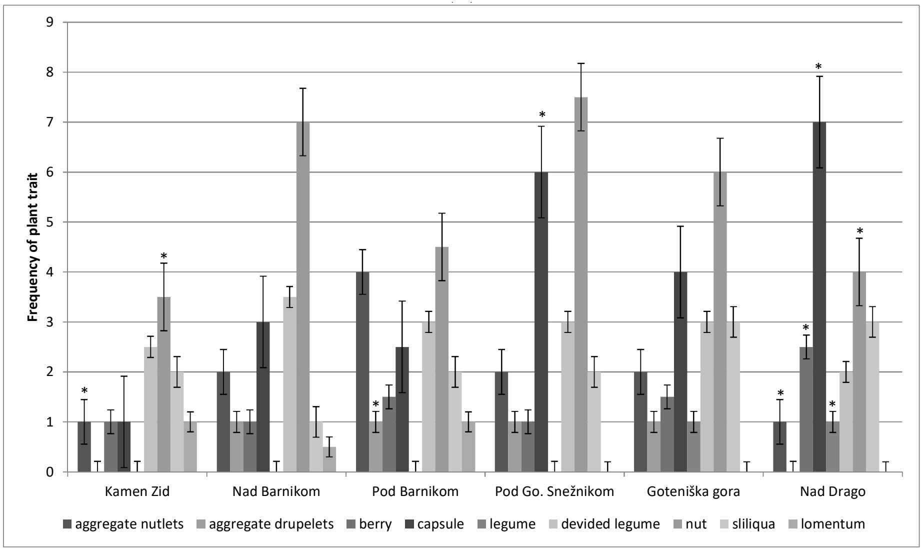


(**a**)

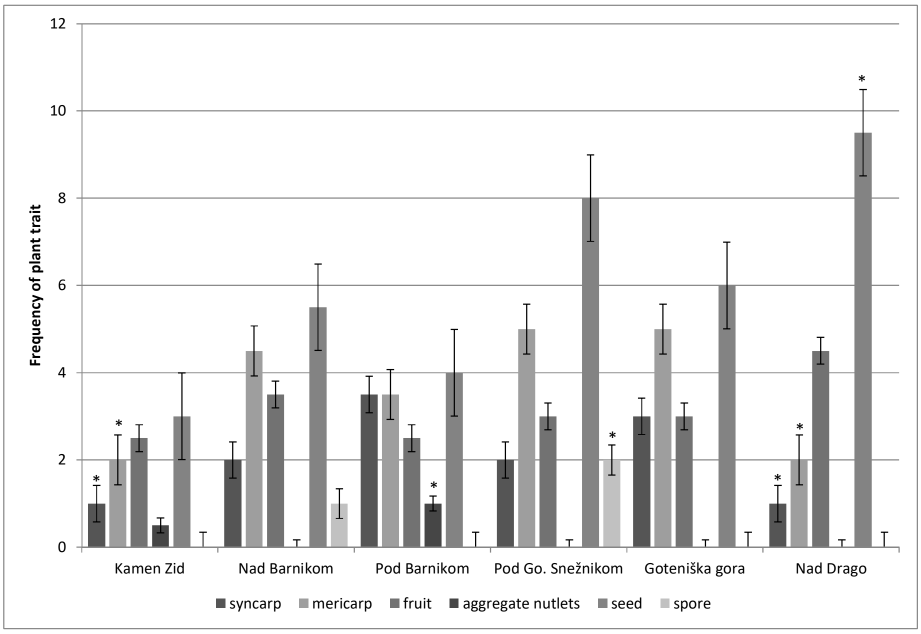


(**b**)

Figure 8. *Cont.*



(**c**)



(**d**)

Figure 8. Medians and standard deviations of frequencies of plant species with individual plant functional traits categories ***flower award*** and ***pollen vector*** (**a**), ***type of reproduction*** and ***type of breeding system*** (**b**), ***fruit type*** (**c**), and ***diaspore type*** (**d**) are represented. Statistical differences with the Bonferroni test between individual localities were calculated. Asterisks mark those categories in which a single location was statistically significantly different from at least three others.

From the type of reproduction and type of breeding system point of view, compared to the other locations, the Kamen Zid location had the least number of species that reproduced mainly by seeds and vegetatively, and that were characterized by allogamy and facultative allogamy (Figure 8b). Compared to the four other locations, the Nad Drago location had the most species with seed or spore reproduction and mixed mating. In one of the categories, Pod Goteniškim Snežnikom also differed from the other locations, as there were the most species present that reproduced by spores and vegetatively. According to the fruit type, both the Nad Drago location and the Kamen Zid location had the fewest species, whose fruit types were berry and nut. Together with the location Pod Goteniškim Snežnikom, Nad Drago had the most species whose fruit was a capsule. At the same time, compared to the others, this location also had the statistically significantly highest number of species with berry as the fruit type. The Nad Drago location also differed from the other locations except Goteniška Gora in that it contained the most species whose fruit was a legume. The one Pod Barnikom differed from all the other locations, as there were the most species with aggregate drupelets (Figure 8c). Plant species with seeds as the diaspore type were statistically most frequently represented at the Nad Drago location. The same applied to the Kamen Zid location. Species with spores as a diaspore type were the most common at the location Pod Goteniškim Snežnikom, and those with aggregate nutlets were the most common at the location Pod Barnikom (Figure 8d).

4. Discussion

According to the analysis of plant functional traits in the comparison of forest gaps, the forest gap Nad Drago showed the largest deviations amongst all locations. Its deviation can be explained by the fact that this forest gap is the youngest and represents the beginning of the succession. As a newly exposed area, it represents a settlement area for pioneer plant species, most of which are biennials. Moore and Vankat [32] reached similar conclusions, except that they found a higher percentage of annual plants for one or two year old forest gaps. On older forest gaps, their percentage was minimal, as found in our study. The statistically significantly higher percentage of species with roots as the primary storage organ can be explained by the fact that there are still many early spring species of forest understory in the forest gap Nad Drago, whose rapid growth in spring is facilitated by the energy stored in the root [33,34]. It should be noted that the forest understory was better developed in the nearby old-growth-stage beech forest than that in the juvenile-phase beech forest. In an old-growth-stage forest, more light reaches the ground than in a juvenile-stage forest. The presence of early spring plants is also indicated by the analysis of flowering, showing the statistically significant lowest number of plants flowering in summer compared to other forest gaps. A comparison within the forest gaps showed that most species on the forest gap flower in May. However, we should not forget that all studied forest gaps are located in an area that may still be under the cover of snow in April. In terms of flowering, there should be the fewest species without flowers in this forest gap. The result is because of the fact that the BiolFlor database lists grasses and sedges, in addition to ferns, as non-flowering plants. It is also true that the coverage of grasses and sedges is the lowest at the location Nad Drago. Considering that we observed the occurrence of species such as *B. sylvaticum* in larger populations during our study, primarily in forest gaps and not in the forest, we can conclude that overgrowth with grasses has not yet started, as the forest gap is the youngest. Among other flowering species, there was a statistically higher occurrence of species with bell-shaped flowers at this location compared to others. A statistically significant higher occurrence of species with exposed nectaries is also correlated with this flower form. Bell-shaped flowers and exposed nectaries define simpler flowers, in which nectar is more easily accessible and, thus, available to different pollinators [35]. At this location, we also found statistically more plant species with green flowers. Considering that green-colored flowers are predominantly pollinated by hover flies and that there was no statistically significant correlation with other types of pollinators, the higher occurrence of bell-shaped flowers and flowers with exposed nectaries is more likely the result of the species composition in the forest gap. The same explanation could be applied to the result that the location Nad Drago had the statistically highest number of species that were simultaneously allogamous and autogamous, compared to other species. Several species with this trait were found only in this location. Although this location has the highest number of species that reproduce by seeds and spores, when viewed as a whole, reproduction by seeds and vegetatively still prevails in this forest gap (as in other forest gaps).

According to some statistically significant differences between plant functional traits, the forest gap Pod Barnikom is somewhat similar to the juvenile-stage beech forest at the location Kamen Zid. It has the same statistically significant lower number of plant species with pinnate and palmately lobed leaves as on the other forest gaps. As already mentioned, plants with lobed leaves are characteristic of more open and wind-exposed areas [36], and the mentioned forest gap is less exposed to wind because it is the smallest, and it is shaded and protected from the sides by tall trees. As a result, it has fewer plant species with a leaf form that is adapted to efficiently bear mechanical pressures [36]. In fact, small, long, and narrow forest gaps have less influence on the understory [17,18]. The characteristic of overgrowing forest gap is the result of the statistically significantly higher presence of nanophanerophytes. However, we should emphasize the influence of its size on the results. As it is the smallest, the percentage of overgrowing surface is greater than that of the other forest gaps, although there is already noticeable overgrowth at the edges of other forest gaps; however, because of their sizes, it will take longer for other forest gaps to become overgrown compared to the forest gap Pod Barnikom. Here, again compared to the other forest gaps, there is a statistically significantly higher number of plant species that predominantly provide pollinators with pollen. However, this is probably primarily because of the species composition, since species with hidden nectaries still dominate, as in all other forest gaps. The same could be said for the statistical differences among locations in terms of fruit type and diaspore type. However, at the location Nad Barnikom, most statistically significant differences that separate the forest gaps from all others are the result of the greater coverage of grasses and sedges on this forest gap. Specifically, grasses are pollinated by wind, and they are defined in the BiolFlor database as plants without flowers; moreover, considering that they are pollinated by wind, they also represent the percentage of plant species that do not provide a pollinator with an award in the flower. Statistically significant differences in plant functional traits, therefore, define the forest gap Nad Barnikom as a forest gap with more grasses and sedges compared to the other forest gaps.

According to the analysis of plant functional traits, the forest gap Goteniška Gora differs the least from the other forest gaps. It has a statistically significant higher number of anemophilous plants than other forest gaps, but this is again caused by the representation of grasses. Statistically significant differences in flower color and form are probably only the result of species composition and do not represent a specific characteristic of the forest gap. With the help of plant functional traits, we can recognize the specific characteristic of the forest gap Pod Goteniškim Snežnikom. The statistically significantly higher presence of plant species that are without flowers, are without a flower award for the pollinator, and are reproducing simultaneously with spores and vegetatively indicates a higher proportion of ferns compared to the other forest gaps. Ferns prefer humid areas, with the aforementioned forest gap having the highest Ellenberg's humidity value of all forest gaps. It also differs from other forest gaps by the higher presence of plant species flowering in July. The reason for this difference could be its altitude. It is the highest-lying forest gap of all studied forest gaps, as a result of which the growing season starts later, and most species flower in July. Differences in other functional traits are also probably the result of species composition.

5. Conclusions

A characteristic of forest gaps colonizing plant species is vegetative propagation together with seeds or spores. These are species that prefer habitats with more sunlight, prefer medium wet to dry soil, and are tolerant to high daily and seasonal temperature fluctuations. In the Dinaric fir–beech forests, colonizing plant species are primarily those that start flowering in June and July, and flower at least two months. This increases the likelihood of pollination and population growth. Seeds of species that populate gaps are distributed by birds and other wild animals. That is why they have juicy pitted or aggregate fruits and fruits (seeds) with appendages. In gaps, the dominant community of plant species has a competitive strategy. In the research, we confirmed that the appearance of plant species with certain plant functional traits is influenced by both the age of the forest gap and the size of the forest gap, which are naturally related to changes in abiotic factors. Furthermore, on the basis of the occurrence and frequency of selected plant functional traits on forest gaps, we can roughly determine the successional stage of the forest gap.

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References

1. Lavorel, S.; Garnier, E. Predicting changes in community composition and ecosystem functioning from traits: Revisiting the Holy Grail. *Funct. Ecol.* **2002**, *16*, 545–556. [CrossRef]
2. Violle, C.; Navas, M.L.; Vile, D.; Kazakou, E.; Fortunel, C.; Hummel, I.; Garnier, E. Let the concept of trait be functional. *Oikos* **2007**, *116*, 882–892. [CrossRef]
3. McGill, J.B.; Enquist, B.J.; Weiher, E.; Westoby, M. Rebuilding community ecology from functional traits. *Trends Ecol. Evol.* **2006**, *21*, 178–185. [CrossRef] [PubMed]
4. Garnier, E.; Navas, M.L. A trait-based approach to comparative functional plant ecology: Concepts, methods and applications for agroecology. A review. *Agron. Sustain. Dev.* **2012**, *32*, 365–399. [CrossRef]
5. Malézieux, E.; Lamanda, N.; Laurans, M.; Tassin, J.; Gourlet Fleury, S. Plant Functional Traits and Types: Their relevance for a better understanding of the functioning and properties of agroforestry systems. In Proceedings of the 2nd International Symposium on Multi-Strata Agroforestry Systems with Perennial Crops, CATIE, Turrialba, Costa-Rica, 17–21 September 2007.
6. Garnier, E.; Lavorel, S.; Ansquer, P.; Castro, H.; Cruz, P.; Dolezal, J.; Eriksson, O.; Fortunel, C.; Freitas, H.; Kigel, J.; et al. Assessing the Effects of Land-use Change on Plant Traits, Communities and Ecosystem Functioning in Grasslands: A Standardized Methodology and Lessons from an Application to 11 European Sites. *Ann. Bot.* **2007**, *99*, 967–985. [CrossRef] [PubMed]
7. Castro, H.; Lehsten, V.; Lavorel, S.; Freitas, H. Functional response traits in relation to land use change in the Montado. *Agric. Ecosyst. Environ.* **2010**, *137*, 183–191. [CrossRef]
8. Chelli, S. Plant Functional Traits and Environmental Variations. Ph.D. Thesis, University of Camerino, Camerino, Italy, 2013; 112p.
9. Garnier, E.; Vile, D.; Roumet, C.; Lavorel, S.; Grigulis, K.; Navas, M.L.; Lloret, F. Inter- and intra-specific trait shifts among sites differing in drought conditions at the north western edge of the Mediterranean Region. *Flora* **2018**, *254*, 147–160. [CrossRef]
10. Turton, S.M. Solar Radiation Regimes in Rainforest Understoreys, Gaps and Clearings, with Specieal Referene to Northeast Queensland. Ph.D. Thesis, Department of Geography, James Cook University of North Queensland, North Queensland, Australia, 1991; 203p.
11. Brown, M.J.; Parker, G.G.; Posner, N.E. A survey of ultraviolet-B radiation in forest. *J. Ecol.* **1994**, *82*, 843–854. [CrossRef]
12. O'Hara, K. *Multiaged Silviculture: Managing for Complex Forest Stand Structures*; Published to Oxford Scholarship Online: Oxford, UK, 2014; 262p.
13. Peterken, G.F. *Natural Woodland, Ecology and Conservation in Northern Temperate Regions*; Cambridge University Press: New York, NY, USA, 1996; 522p.
14. Buajan, S.; Liu, J.; He, Z.; Feng, X.; Muhammad, A.; Farooq, T.H. Effect of Gap Size on The Dynamic of Micro Environments during the Daytime at *Castanopsis kawakamii* Natural Reserve Forest, Sanming City, China. *Environ. Nat. Resour. J.* **2016**, *14*, 30–34.
15. Gálhidy, L.; Mihok, B.; Hagyo, A.; Rajkai, K.; Standovár, T. Effects of gap size and associated changes in light and soil moisture on the understorey vegetation of a Hungarian beech forest. *Plant Ecol.* **2006**, *183*, 133–145. [CrossRef]
16. Kollár, T. Light Conditions, Soil Moisture, and Vegetation Cover in Artificial Forest Gaps in Western Hungary. *Acta Silv. Et Lignaria Hung.* **2017**, *13*, 25–40. [CrossRef]
17. Collins, B.S.; Dunne, K.P.; Pickett, S.T.A. Reponses of Forest Herbs to Canopy Gaps. In *The Ecology of Natural Disturbance and patch Dynamics*; Picket, S.T.A., White, P.S., Eds.; Academic Press: London, UK, 1985; pp. 217–234.
18. Fahey, R.T.; Puettmann, K.J. Ground-layer disturbance and initial conditions influence gap partitioning of understorey vegetation. *J. Ecol.* **2007**, *95*, 1098–1109. [CrossRef]
19. Čarni, A.; Hrovat, T. Vegetacija gozdnih posek na nekarbonatni podlagi na območju Ratitovca. *Hladnikia* **2002**, *14*, 5–11.
20. Kelemen, K.; Mihók, B.; Gálhidy, L. Dynamic response of herbaceous vegetation to gap opening in a central European beech stand. *Silva Fenn.* **2012**, *46*, 53–65. [CrossRef]

21. Ravnjak, B.; Bavcon, J.; Carni, A. Plant Species Turnover on Forest Gaps after Natural Disturbances in the Dinaric Fir Beech Forests (*Omphalodo-Fagetum sylvaticae*). *Diversity* **2022**, *14*, 209. [CrossRef]
22. Forrest, J.; Thomson, J.D. Pollinator experience, neophobia and the evolution of flowering time. *Proc. R. Soc. B* **2009**, *276*, 935–943. [CrossRef]
23. Fraver, S.; Wagner, R.G.; Day, M. Dynamics od coarse woody debris following gap harvesting in the Acadian forests of central Maine, U.S.A. *Can. J. For. Res.* **2002**, *32*, 2094–2105. [CrossRef]
24. Müller-Using, S.; Bartsch, N. Decay dynamic of coarse and fine woody debris of a beech (*Fagus sylvatica* L.) forest in Central Germany. *Eur. J. For. Res.* **2009**, *128*, 287–296. [CrossRef]
25. Sefidi, K.; Marvie Mohadjer, M.R. 2010: Characteristics of coarse woody debris in successional stages of natural beech forests (*Fagus orientalis*) of Northern Iran. *J. For. Sci.* **2010**, *56*, 7–17. [CrossRef]
26. Klotz, S.; Kühn, I.; Durka, W. *BIOLFLOR—Eine Datenbank zu Biologisch-Ökologischen Merkmalen der Gefässpflanzen in Deutschland—Schriftenreihe für Vegetationskunde 38*; Bundesamt für Naturschutz: Bonn, Germany, 2002.
27. Šilić, Č. *Šumske Zeljaste Biljke*; Zavod za Udžbenike i Nastavna Sredstva: Belgrade, Serbia, 1988; 271p.
28. Martinčič, A.; Wraber, T.; Jogan, N.; Podobnik, A.; Turk, B.; Vreš, B.; Ravnik, V.; Frajman, B.; Stergulc Krajšek, S.; Trčak, B.; et al. *Mala Flora Slovenije. Ključ za Določanje Praprotnic in Semenk*; Tehniška Založba Slovenije: Slovenia, Ljubljana, 2007; 967p.
29. Pierce, S.; Negreiros, D.; Cerabolini, B.E.L.; Kattge, J.; Diaz, S.; Kleyer, M.; Shipley, B.; Wright, S.J.; Soudzilovskaia, N.A. A field-portable list of CSR strategies. *Funct. Ecol.* **2017**, *31*, 444–457. [CrossRef]
30. Paušič, A.; Čarni, A. Functional response traits and plant community strategy indicate the stage of secondary succesion. *Hacquetia* **2012**, *11*, 209–225.
31. Tripathi, A.; Pandey, A. Post-Hoc Comparison in Survival Analysis: An Easy Approach. *J. Biosci. Med.* **2017**, *5*, 112–119. [CrossRef]
32. Moore, M.R.; Vankat, J.L. Response of the herb layer to the gap dynamics of a mature beech-maple forest. *Am. Midl. Nat. J.* **1986**, *115*, 336–347. [CrossRef]
33. Smith, R.L.; Smith, T.M. *Ecology & Field Biology*; Benjamin Cummings: San Francisco, CA, USA, 2001; 771p.
34. Whigham, D.F. Ecology of Woodland Herbs in Temperate Deciduous Forests. *Annu. Rev. Ecol. Evol. Syst.* **2004**, *35*, 583–621. [CrossRef]
35. Knuth, P. *Handbook of Flower Pollination Based upon Herman's Müller's Work 'The Fertilisation of Flowers by Insects'*; The Clarendon Press: Oxford, UK, 1906; 383p.
36. Nikolić, T. *Morfologija Biljaka*; ALFA, d.d.: Zagreb, Croatia, 2017; 569p.