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Pollination patterns of flora and vegetation in northern Croatia with reference to *Apis mellifera*

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Running title: POLLINATION PATTERNS IN NORTHERN CROATIA

Abstract – Pollination patterns i.e. the proportions of entomophilous, anemophilous, autogamous and hydrophilous plant species and those useful for the European honey bee (*Apis mellifera* L.) in the flora and vegetation of northern Croatia have been determined. The survey included 507 plant taxa, belonging to 95 plant families. The results show that most plant species depend on insect pollination (73.6%), followed by self-pollination (30%), wind (25%) and water pollination (0.6%). For some plant species there are one, two or more modes of pollination; the largest group consists of pure insect pollination (43%), followed by both insect and self-pollination (27%), pure wind pollination (22%), insect and wind pollination (2.6%), and so on. Overall, 54% of plant species useful to European honey bees were found, of which 51% provide pollen and 47% nectar. These results suggest that *A. mellifera* could be a potential pollinator for about half of the flora. Analysis shows significant differences in pollination patterns among habitat types and that most entomophilous plant taxa are found in grassland, forest and ruderal sites, indicating that these habitats are most important for pollinators. Other characteristics of plant species, such as flowering time, plant family, life form and origin, were also analysed to determine a possible relationship with pollination.

Keywords: European honey bee, insect pollinators, life forms, plant families

Introduction

Pollination is one of the key ecosystem services, enabling the reproduction of wild and cultivated plant species, i.e. the production of seeds and fruits. In Europe, in the area of temperate continental climate, various insects are pollinators. Most numerous are the hymenopterans (*Hymenoptera*), butterflies (*Lepidoptera*), flies (*Diptera*) and beetles (*Coleoptera*) (Kevan and Baker 1983, Ollerton et al. 2021). In addition to wild insects, European honey bees (*Apis mellifera* L.) play a very important role in pollination. Beekeeping is also used for the production of honey, pollen, propolis, royal jelly, bee venom, wax, queens and bee communities, as well as in apitherapy and apitourism.

Scientific studies have shown a declining trend in pollinator numbers (Potts et al. 2010, Goulson et al. 2015, Sánchez-Bayo and Wyckhuys 2019), mostly relating to habitat degradation and loss, urbanisation, agricultural intensification, pesticide and fertiliser use, pollution, pathogens, climate change, alien species and synergistic action of several factors. The most common declines involve specialists or species closely associated with a particular plant species or habitat, while a small number of generalists are increasing in number (Klein et al. 2007, Sánchez-Bayo and Wyckhuys 2019). However, some generalists are also declining, including the European honey bee. There are also other problems, e.g. competition between European honey bees and wild pollinators for forage (Goulson et al. 2015), a large knowledge gap about wild pollinators, etc. Along with the decline in pollinators, a decline in wild plant species pollinated by insects has been observed in some parts of the world (e.g., the UK) (Biesmeijer et al. 2006, Potts et al. 2010).

Ollerton et al. (2011) indicate that, in temperate regions of the world, about 78% of wild plant species are pollinated by animals, while Klein et al. (2007) have found that, of 107 leading crops worldwide, 91 species (85%) depend to varying degrees on animal pollination. According to Potts et al. (2010) pollination by insects, primarily bees, is necessary for 75% of all crops. However, there is relatively little literature on this topic. In Croatia, there are studies that deal with pollination from different aspects. One study refers to different taxonomic groups and species of insect pollinators in different habitats in north-eastern Croatia (Kovacic et al. 2016). A few papers present the results of melissopalynological analysis of honey samples from different areas of continental Croatia (Sabo et al. 2011, Štefanić et al. 2012, Špoljarić Maronić et al. 2017, Rašić et al. 2018), where the botanical origin (plant species used by European honey bees as nectar and pollen sources) was determined on the basis of pollen grains. Nevertheless, due to the economic importance of beekeeping in Croatia, several books and lists of plant species useful for *A. mellifera* have been published (e.g., Umeljić 2004, 2018, Bačić and Sabo 2007, Zima 2007, Bučar 2008, 2018, Zima and Štefanić 2018). There are several botanical studies that include an analysis of plant species useful for pollinators, especially European honey bees, according to specific habitat types (Martinis and Lovašen-Eberhart 1986, Dujmović Purgar and Hulina 2007, Britvec et al. 2013, Dujmović Purgar et al. 2015, Ljubičić et al. 2017, Štefanić et al. 2020). Franić (2019) provides an overview of the interaction between forestry and beekeeping in Croatia. However, none of the above papers includes an analysis of the proportion of insect-pollinated plant species and those useful to *A. mellifera* in the entire flora and all habitat types.

Given the lack of data on the proportion of plant species pollinated by insects in the total flora and in all habitat types, at both regional and global level, this paper presents such an analysis in Croatia for the first time. Given the aforementioned decline in pollinators and insect-pollinated plant species, such scientific research data is of utmost importance, as it can help in determining best practices for ecosystem management.

The objectives of this study were therefore (i) to determine the pollination patterns of the flora and vegetation in the continental part of Croatia, (ii) to determine the proportions of plant species useful to *A. mellifera* in the flora and by habitat type, and (iii) to analyse how pollination is related to by various characteristics of plant species, including flowering time, plant family, origin and life form.

Materials and methods

Study area

The study of flora and habitats was carried out in the area of the settlement Bedekovčina, with about 3400 inhabitants, in northern Croatia (On-line Suppl. Fig. 1). The study area is located partly in the valley of the River Krapina and partly in a hilly area at an altitude of 148 to 237 m a.s.l., on an area of about 30 km^2. The landscape consists of settlement, arable land with annual crops, traditional gardens, vineyards, orchards, forest, a small number of mown meadows, abandoned arable land and meadows in various stages of succession. Aquatic ecosystems include the River Krapina, numerous streams and canals, and five artificial lakes with an area of about 11.2 ha. The area is characterized by a temperate continental climate, belonging to the C_{fwbx} type according to the Köppen classification, and to humid climate according to the Thornthwaite classification, with average annual air temperature between 10 and 11 °C and average annual precipitation from 900 to 1000 mm (Zaninović et al. 2008).

Data collection

The field research of the flora and habitats was carried out in the period from 1992 to 2021. Plant species were identified using the Flora Europaea (Tutin et al. 1964-1980, 1993) and Exkursionsflora von Österreich (Adler et al. 1994). The nomenclature of the plant taxa and their taxonomic position follows Euro+Med PlantBase (2006-2021). Only for some taxa Flora Croatica Database (hereafter: FCD) (Nikolić, 2021) and Pladias (2021) were used, because they could not be found in the Euro+Med PlantBase (2006-2021). These include aggregate species, subspecies of the genus *Leontodon*, genus *Corydalis* and *Medicago x varia* Martyn.

Species were classified into habitat groups according to their affiliation to plant communities: (i) forest unaffected by flooding (ii) scrubland unaffected by flooding, (iii) floodplain forest and scrubland, (iv) forest-edge vegetation, (v) wet and mesic grassland, (vi) dry grassland, (vii) aquatic freshwater vegetation, (viii) marsh vegetation, (ix) ruderal vegetation, (x) weed vegetation and (xi) vegetation of walls. For each habitat group, the corresponding habitat types according to the National habitat classification of the Republic of Croatia (Anonymous, 2018) and vegetation classes according to the Classification system for European vegetation (EuroVeg CheckList, Mucina et al. 2016) were added (see On-line Suppl. Tab. 1).

Data on the mode of pollination (autogamy, entomophily, anemophily, hydrophily), flowering time, origin of taxa and life forms were taken from FCD (Nikolić 2021) and Pladias (2021).

Plant species useful to *A. mellifera* have been divided into the following categories of sources: nectar, pollen, honeydew and propolis. The data were taken from Maurizio and Grafl (1969), Bačić and Sabo (2007), and Bučar (2008, 2018).

All collected data are presented in On-line Suppl. Mat.

Data analysis

The data were treated statistically using Excel and Statistica v7. Contingency tables, displaying the multivariate frequency distribution of the variables, were constructed using Excel, while Pearson Chi-squares (χ^2) were calculated using Statistica v7 software.

Results

Flora

In the Bedekovčina area, a total of 507 plant taxa (On-line Suppl. Mat.) were identified, belonging to 95 plant families (On-line Suppl. Tab. 2), of which *Compositae* are the most numerous (54 taxa), followed by *Poaceae* (51), *Fabaceae* (28), *Lamiaceae* (26), *Cyperaceae* (23), etc. According to the affiliation to higher taxonomic groups, the class *Magnoliopsida* prevailed (496 taxa), followed by *Polypodiopsida* (10) and *Pinopsida* (1).

A relatively small number of threatened species were found: one endangered (EN), seven vulnerable (VU) and five near-threatened species (NT) (On-line Suppl. Mat.).

Habitat types

Regarding habitat types, most plant taxa were recorded in ruderal vegetation (30%), followed by wet and mesic grassland (28%), forest unaffected by flooding (28%), weed vegetation (12%), marsh vegetation (9%), floodplain forest and scrubland (5%), scrubland unaffected by flooding (5%), forest-edge vegetation (4%), dry grassland (2%), freshwater aquatic vegetation (2%) and vegetation of walls (0.2%). Some plant species occur in two or more habitat types.

Pollination patterns

Among the pollination modes, expressed in absolute percentages in relation to the total number of plant species, insect pollination (entomophily) is the most widespread, with 73.6%, followed by self-pollination (autogamy) with 30%, wind pollination (anemophily) with 25%, and water pollination (hydrophily) with 0.6% (Fig. 1a). There are also ferns whose fertilisation requires water (2%). The sum of the percentages exceeds 100% because some plant species have more than one mode of pollination.

The largest proportion of species is pollinated exclusively by insects (43%) (Fig. 1b). Both insect and self-pollination occur in 27% of plant species, followed by wind pollination (22%), insect and wind pollination (2.6%), etc. (Fig. 1b). The values are expressed in relative percentages.

Certain modes of pollination are associated with specific plant families. Among the families with the largest number of species, *Compositae*, *Fabaceae*, *Lamiaceae*, *Apiaceae*, *Rosaceae*, *Caryophyllaceae* and *Plantaginaceae* are predominantly insect-pollinated and to a lesser extent self-pollinated, while *Poaceae* and *Cyperaceae* are wind-pollinated (On-line Suppl. Fig. 2).

Insect pollination is prevalent in all habitat types, shown in absolute percentages (Fig. 2a), with the highest proportion in ruderal (24%), forest (22%) and grassland habitats (20%). As can be seen from Tab. 1, for the grassland, forest and ruderal habitats, the calculated Chi-square (χ^2 = 14.5, P < 0.05) indicates their statistically significant difference, with insect pollination as the dominant mode. The proportion of wind- and self-pollinated plant species varies by habitat group (Fig. 2a). The largest proportion of wind-pollinated plant species (9%) is found in open habitats, such as grassland. No wind-pollinated species were found in forest-edge vegetation, probably because these habitats are sheltered from the wind. Self-pollinated plant taxa make up a significant proportion in ruderal (11%) and weed habitats (6%), because there are many annual species with a short life cycle, thus ensuring survival. Pollination by water is represented only in aquatic vegetation. Representation of pollination modes by habitat type in relative percentages and with an overlap of pollination modes (Fig. 2b) shows that pollination patterns vary considerably among habitat types (χ^2 = 39.8, P < 0.001). Obtained variability of pollination modes (Fig. 2b): insect pollination ranging 26–60%, both insect and self-pollination ranging 6-45%, wind pollination ranging 0–38%, self-pollination ranging 0–9%, and both insect and wind pollination ranging 0-6%. Pure insect pollination is most prevalent in forest-edge vegetation, followed by forest, grassland and ruderal vegetation. Both insect- and self-pollination are best repesented in weed, scrub, forest-edge and ruderal vegetation. Pure wind pollination is most prevalent in marsh and grassland vegetation.

Plant species useful for *Apis mellifera*

The European honey bee plays a very important role in the pollination of plant species. In this study, a total of 54% of plant taxa useful to *A. mellifera* were identified: 47% as a nectar source, 51% as a pollen source, 4% as a honeydew source, and 1% as a propolis source (On-line Suppl. Tab. 3). Of the plant species that depend only on insect pollination (43% of total species), 67% (29% of total species) can be used by European honey bees as a nectar source and 63% (27% of total species) as a pollen source (Fig. 3). Of the plant species with both insect and self-pollination (27% of total species), European honey bees can potentially use 63% (17% of total species) each as a nectar and/or pollen source. Of the wind-pollinated plant species (22% of total species), European honey bees can use 18% (4% of total species) as a pollen source.

The distribution of plant species useful to *A. mellifera* per habitat type is shown in Fig. 4. As can be seen from the figure, most plant species providing nectar to *A. mellifera* were found in ruderal (16%), grassland (15%) and forest habitats (14%), while there were fewer in other habitat types. A similar trend was observed for plant species serving as a source of pollen: the highest numbers were found in ruderal (17%), forest (16%) and grassland habitats (16%). Relatively few species are known to be a source of honeydew (up to 2%) and propolis (< 1%), and they grow in forest and scrub vegetation.

Flowering time

Most plant species flower in June (66%), and fewest in December (0.6%) and January (0.8%). During the ten months of flowering period, from February to November, pollinators and *A. mellifera* could use nectar and pollen (Fig. 5).

Life forms

With regard to life forms in the flora, herbaceous perennials or hemicryptophytes predominate (53%), followed by annual plant species or therophytes (21%), geophytes (17%), woody plants or phanerophytes (11%), hydrophytes and chamaephytes (4% each), with some species associated with two life forms.

By habitat type, hemicryptophytes predominate in grassland, ruderal and forest habitats; therophytes have a high proportion in ruderal and weed habitats; geophytes are most numerous in forest habitats; phanerophytes in forest and scrub vegetation; chamaephytes in forest, and hydrophytes in marsh and aquatic vegetation (On-line Suppl. Fig. 3).

All life forms are dominated by insect pollination (Tab. 2, On-line Suppl. Fig. 4), while wind and self-pollination are less well represented. Theorophytes also have a considerable amount of self-pollination, whereas aquatic pollination occurs only in hydrophytes (On-line Suppl. Fig. 4).

Origin of plant species

By origin, indigenous or native plant species are most abundant (79.1%), followed by archaeophytes (11.8%), neophytes (8.5%) and three taxa (0.6%) of uncertain origin. Indigenous plant species dominate in all habitat types except weed vegetation, where archaeophytes have a higher proportion (On-line Suppl. Fig. 5). Furthermore, ruderal and weed vegetation contains a considerable proportion of archaeophytes and neophytes.

Analysis of pollination modes by origin of plant species shows that, in all three groups (indigenous plant species, archaeophytes and neophytes), plant species pollinated by insects dominate, while wind pollination and self-pollination are less well represented (On-line Suppl. Fig. 6). Only among the archaeophytes are there slightly more plant species with self-pollination than with wind pollination. The importance of insect pollination for plants of different origins can also be seen in Tab. 3, which shows that this mode of pollination is particularly prevalent in native plant species and neophytes ($\chi^2 = 19.6$, $P < 0.01$).

Discussion

The flora studied depends mostly on insect pollination. Our results are in agreement with Ollerton et al. (2011) and Potts et al. (2010), who state that about 78–80% of wild plant species in temperate zones are pollinated by insects. A similar percentage was obtained in a study by Štefanić et al. (2020) in NE Croatia, which found that 72.6% of plant species on field margins are beneficial to pollinators, although not all habitat types were included. For the flora of the Czech Republic, Chytrý et al. (2021) show only maps with the proportions of pollination modes influenced by relief and climate. Melendo et al. (2003) indicate, for the endemic flora in the south of the Iberian Peninsula with a Mediterranean climate, that 91% of the plant species are biotically pollinated, mainly by insects.

According to the data collected, about two thirds of plant species depend on only one mode of pollination, while about one third of plant species have two or, less frequently, several pollination modes. Durka (2002) determined exactly the same proportion of insect pollination (43%) for the flora of Germany as in N Croatia, slightly less for both insect and self-pollination (21%), much more for self-pollination (22%), less for wind pollination (18.5%), and almost the same for water pollination (0.5%). The data are not fully comparable, as Durka (2002) used, for plant species with several pollination modes, only the dominant one. Somewhat later, Kühn et al. (2006) mapped the distribution of pollination modes across the whole of Germany, with the help of modelling. Altitude and wind speed were strongly correlated with the proportions of pollination modes. Remarkable spatial differences were obtained: insect pollination ranging 41.9–63.1%, wind pollination ranging 15.5–32.7%, and self-pollination ranging 16.1–29.9%. A coarse spatial resolution was used with a cell size of about 130 km^2 and a different method for calculating the proportion of pollination modes than in this paper.

To our knowledge, an approach combining multiple pollination modes of the whole flora and all habitat types, as used in this study, was not found in the available literature, so further comparison is not possible.

The proportion of certain pollination modes in a given area is influenced by ecology and evolution. The dominance of insect pollinated plant species on the global level is explained by the high rate of diversification during evolution (Givnish 2010). Wind pollination of angiosperms probably evolved from insect pollination in response to unfavourable weather conditions in some areas (strong wind, heavy rain and low temperatures) and the associated lack of insect pollinators (Culley et al. 2002, Friedman and Barrett 2008). In some plant species, a transitional stage between wind and insect pollination i.e. ambophily is still present (Culley et al. 2002). In the flora studied, plant species with both wind and insect pollination are relatively rare. Self-pollination is a typical feature of annual species (Lloyd 1992) or therophytes. Such plant species are not dependent on the availability of pollinators, weather conditions and pollen transmitters (animals, wind and water), which is particularly important when a species is rare in its habitat (Lloyd 1992). According to Pyšek et al. (2011), self-pollination is a crucial feature for the invasion process of alien plant species. In the flora studied, there are very few plant species that are only self-pollinated, but a considerable proportion that are both insect- and self-pollinated. To ensure their survival, some plant species exhibit multiple pollination modes.

On a broad spatial scale, according to Givnish (2010), 202 out of 379 plant families are animal-pollinated, and only 39 are wind- or water-pollinated. The same trend, with the largest number of insect-pollinated plant families, has been found in N Croatia, and a small number are wind pollinated. Most wind-pollinated species belong to herbaceous families of open habitats such as marsh and grassland vegetation (*Poaceae, Cyperaceae, Juncaceae*) and woody species (*Betulaceae, Corylaceae, Fagaceae, Moraceae*) which are tall and exposed to the wind and flower before they form leaves.

The results of this study revealed that insect pollination is the predominant mode of pollination for most life forms as well as for plant species of different origins. However, the analyses showed that the distribution pattern of life forms and plant species by origin is mainly influenced by habitat types rather than pollination modes. In fact, it has been found that habitat types, and then affiliation to plant families, have the greatest influence on the distribution of pollination modes.

Different plant species have different flowering times, thus occupying different temporal niches and providing food for different species of pollinators during the vegetation season (Fenster et al. 2004). Depending on the species, the duration of the flowering period varies. There are also rare species that bloom all year, and even in December and January, but due to low temperatures, short daylight and lack of dormant insects, it is hard to speak of pollination. From February, the number of flowering species and active pollinators increases until June, and then the number decreases until November.

Recently, the phenology of plant species has been significantly affected by climate change (Tylianakis et al. 2008, Gordo and Sanz 2009). That is, climate change is causing plant species to begin flowering much earlier than usual, which can affect the temporal matching of pollinators and plant species (Tylianakis et al. 2008).

Among pollinators, *A. mellifera* could be a potential pollinator for about half of the flora, according to the research results of this study. The actual number is probably even higher, because there are no data for each wild plant species on whether it is visited by European honey bees. As already mentioned, for bees the most important group is that of insect-pollinated plant species, and somewhat less the group of insect- and self-pollinated plant species. In these groups, about two thirds of the plant species can be used by *A. mellifera* as a source of nectar and pollen. In addition, bees use less than one fifth of the wind-pollinated plant species as a pollen source. Comparison with the literature is not possible, as no comparable data are available, which underlines the need for further studies in this field.

Potts et al. (2010) also highlight the fact that the contribution of European honey bees to the pollination of wild plant species is not well supported by empirical data. For example, regarding *A. mellifera*, the entomophilous plant species are relatively well known. They all produce pollen in greater or lesser amounts, and most nectar, but not all (nectarless species: *Chelidonium majus* L., *Clematis vitalba* L., *Papaver rhoeas* L., *Rosa canina* L., and others) (Maurizio and Grafl 1969). Anemophilous plant species produce large amounts of pollen through wind pollination, which is a very important food for many insect pollinators and the European honey bee. These include many widespread tree species (e.g., *Alnus glutinosa* (L.) Gaertn., *Betula pendula* Roth, *Corylus avellana* L., *Fagus sylvatica* L., *Populus tremula* L., *Quercus petraea* (Matt.) Liebl., *Q. robur* L., etc.), and also common herbaceous plant species (e.g. *Plantago lanceolata* L., *P. major* L., *Rumex* spp., etc.) (Maurizio and Grafl 1969). Of the other anemophilous plant species, *A. mellifera* is known to use plant taxa from *Poaceae* (total annual pollen yield may be as high as 1–10%), *Cyperaceae* (Maurizio and Grafl 1969), and probably many others. However, it is not completely known which species are involved. Thus, the number of anemophilous species used by *A. mellifera* is probably much higher than presented in this paper.

It is known that bees use the most suitable species among those available (Maurizio and Grafl 1969). Which plant species are used by European honey bees can be determined by melissopalynological analysis. Several such studies have been published for the continental part of Croatia (Sabo et al. 2011, Štefanić et al. 2012, Špoljarić Maronić et al. 2017, Rašić et al. 2018). In the papers cited, pollen grains from 4 to 33 plant taxes were found in honey samples. However, the final number of plant species visited by the bees is certainly much higher, since in the cited works not all honey samples were analysed during the vegetation season, and pollen samples collected separately by the bees were not analysed at all.

As *A. mellifera* is the best-studied insect pollinator, many findings from this study can be applied to wild pollinators, especially from the *Hymenoptera* group, which have similar foraging behaviour.

Which pollinators are associated with particular plant species can be found, in part, in the CrypTra database (Ellis and Ellis-Adam 1993), whose analysis shows that relationships are not characterised by specialisation. In the plant pollination system, Johnson and Steiner (2000) point out that, in Europe, generalists among pollinators prevail over specialists.

The study area is characterised by a diverse relief and a mosaic landscape. The great diversity of habitats is enhanced by the very small areas of land ownership characteristic of this part of N Croatia. As some plant species only grow in certain habitats, habitat diversity is a prerequisite for flora biodiversity. The results show that habitat types differ significantly in terms of pollination patterns. In this study, three groups of habitats were identified where most insect-pollinated plant species occur, and which are also useful for *A. mellifera*. These habitats include grassland, forest and ruderal sites.

Grassland habitats belong mostly to the wet and mesic meadows of the class *Molinio-Arrhenatheretea* Tx. 1937. These are still very species-rich habitats, although much of the former meadows have been abandoned and are in various stages of succession. The reason for this is the change in the way of life of the local residents in the last 30 years. People have abandoned traditional agriculture and livestock breeding (mainly cows). Significantly reduced grassland areas result in a reduced food source for pollinators. The importance of such habitats for *A. mellifera* in the continental part of Croatia is highlighted by Ljubičić et al. (2017), and in the Mediterranean part of Croatia by Britvec et al. (2013). Comprehensive research in several European countries has also shown that semi-natural habitats (grassland) are very rich in bee pollinators (*Hymenoptera: Apiformes*) (Westphal et al. 2008). Restoration of grassland habitats is possible and involves the reintroduction of traditional extensive management, e.g. mowing two to three times a year.

Forest habitats belong mainly to beech (*Fagus sylvatica* L.) communities of the class *Carpino-Fagetea sylvaticae* Jakucs ex Passarge 1968. They are located in the hills, outside the influence of flood waters. Other types of woody vegetation (scrubland unaffected by flooding, floodplain forest and scrubland) cover relatively small areas. Compared to other habitat types, forest is the least changed. However, it is highly fragmented which negatively affects insect pollination (Kolb and Diekmann 2005), mostly privately owned, and affected by frequent and unplanned logging. Wind-pollinated plant species predominate among woody species. Herbaceous plant species develop in the ground layer and usually flower in the spring before tree leaves form.

Ruderal habitats are a very heterogeneous group of plant communities in phytosociological terms (Mucina et al. 2016). In the study area, these are places alongside buildings, roads, railway lines and ditches, on construction sites, yards, landfills, composting sites, and filled and trampled areas. In general, these are habitats where humans prevent the development of natural vegetation through various disturbances. In addition to typical ruderal species, those of weed, grassland and, to a lesser extent, other habitat types grow in these stands. A large part of these habitats is mown and is replacement habitat for grassland species, namely those that are resistant to frequent mowing. For pollinating insects, such habitats can be a food source, but only if mowing is not too frequent and if the plants have enough time to form flowers. The results of other studies (Dujmović Purgar and Hulina 2007, Dujmović Purgar et al. 2015) in the continental part of Croatia show the importance of ruderal habitats for *A. mellifera*. Studies in urban areas in the UK have also confirmed the importance of such habitats for flower-visiting insects (Baldock et al. 2015).

The entire study area in N Croatia is under significant anthropogenic influence. This is evident not only from the large areas covered with ruderal and weed vegetation, but also from a significant proportion of archaeophytes and neophytes in the composition of the flora, as well as from a small number of threatened species. Although neophytes pose a threat to native plant species and habitat diversity, some neophytes (*Robinia pseudoacacia* L., *Amorpha fruticosa* L., *Solidago gigantea* Aiton, etc.) can also serve as an additional nectar and pollen source for *A. mellifera* (Zima and Štefanić 2018). Even a common invasive alien species that is allergenic to humans, *Ambrosia artemisiifolia* L., serves as a pollen source for European honey bees (Špoljarić Maronić et al. 2017). Similarly, entomophilous neophytes serve as a food source for many wild pollinators (Suni et al. 2022). Visitation of alien plant species by entomofauna demonstrates their integration into the network of native pollinators, but there are controversial views on whether this is a positive or negative phenomenon (Potts et al. 2010). On the positive side, alien plant species, including many ornamental plants, provide food for pollinators; and, on the negative side, native plant species may be deprived of pollinators (Tylianakis et al. 2008). Suni et al. (2022) have shown that pollinators in urban areas have a preference for invasive alien plant species over native ones.

Various anthropogenic activities are known to cause declines in biodiversity at all levels of biological organization, including declines in insect pollinators (Potts et al. 2010, Goulson et al. 2015, Sánchez-Bayo and Wyckhuys 2019), which can lead to declines in plant species (Biesmeijer et al. 2006), and vice versa. Of all pollination modes, only insect pollination is threatened.

To preserve the biodiversity of pollinators, it is necessary to preserve the biodiversity of flora and natural and semi-natural habitats. Dennis et al. (2003, 2007), Garibaldi et al. (2014), Goulson et al. (2015) and Bretagnolle and Gaba (2015) suggest implementing various practices: providing nesting opportunities for pollinators, increasing heterogeneity of agricultural land (smaller fields), leaving or restoring areas of natural or semi-natural vegetation between or near crops, leaving weeds between crops (which can reduce crop yields but promote pollinator biodiversity), sustainable and/or organic agriculture, reducing the use of pesticides and machinery, no-tillage farming, seeding (wild) flower strips between and along crops and roads, planting hedgerows, seeding flowering crops, managing plant phenology (sowing plants that flower at different times), introducing pollinator monitoring, preventing the introduction of non-native bees, prohibiting the keeping of European honey bees in some natural areas to stimulate wild pollinators, enforcing effective quarantine measures for the movements of European honey bees to prevent the spread of pathogens and parasites, etc.

Some scientists point to the importance of cultivated plant species in maintaining wild pollinator biodiversity and providing food for *A. mellifera* (Garbuzov and Ratnieks 2014a, b, Salisbury et al. 2015). However, cultivated plant species can only be considered as an additional food source when a particular crop is sown or planted and for only a certain period of year. It is unlikely that a diversity of cultivated plant species in a given area will provide food for pollinators throughout the vegetation season. From the mid-twentieth century to the present, various pesticides used in crop production have had lethal or sublethal effects on pollinators (Goulson et al. 2015), which is difficult to reconcile with pollinator stimulation. In addition, studies of insect foraging show that some commonly planted non-native ornamental species are unused or rarely used by pollinators (Garbuzov and Ratnieks 2014b, Lowenstein et al. 2019).

In Croatia, the food source for insect pollinators is still dominated by wild plant species. In wild plant and insect species, there is an evolutionary specialization of individual functional groups of insect pollinators to specific plant functional groups, which are linked in so-called pollination syndromes (Fenster et al. 2004).

Conclusions

The pollination pattern of the flora studied shows that insect pollination predominates, followed by self-, wind and water pollination. About two-thirds of the plant species depend on only one mode of pollination (mostly insect and wind pollination), while about one-third of the plant species depend on two (mostly both insect and self-pollination) and less frequently on several modes of pollination.

The distribution of pollination patterns is mainly influenced by habitat types. Detailed studies on this topic are needed in the future. Most insect pollinated plant species are found in grassland, forest, and ruderal habitats, highlighting their importance to pollinators. Among habitats, semi-natural grassland is most threatened because of the cessation of mowing.

In addition to habitat types, plant family affiliation also has a considerable influence on the distribution of pollination modes.

The European honey bee can potentially participate in the pollination of about half of the flora.

Given the predominance of wild plant species in N Croatia as a food source for pollinators in terms of the number of species, the area they cover, and their various temporal niches, it is crucial to preserve the biodiversity of wild flora and associated habitats.

The results of this work, with minor variations, can most likely be generalized to most of inland Croatia and to other temperate regions with similar relief, climatic conditions and habitats.

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This work is dedicated to Zvjezdana’s dear friend Janko (24/01/2022).

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Tab. 1. Contingency table showing number of plant species in certain habitat type in relation to pollination modes.

Habitat type	Insect pollination	Insect and self-pollination	Wind pollination	Other modes of pollination	Total
Grass veg.*	**48**	22	37	3	**110**
Forest veg.*	**62**	36	23	11	**132**
Ruderal veg.*	**54**	37	22	8	**121**
Other habitats	55	44	29	16	**144**
Total	**219**	**139**	**111**	**38**	**507**

* $\chi2$: 14.5; $p < 0.05$

Tab. 2. Contingency table showing number of plant species by life form in relation to pollination modes. Life form abbreviations: H – hemicryptophytes, T – therophytes, G – geophytes, Ch – chamaephytes, P – phanerophytes, Hy – hydrophytes.

Life forms	Insect pollination	Insect and self-pollination	Wind pollination	Other forms of pollination	Total
H	112	53	48	9	222
T	27	38	17	9	91
G	28	11	16	10	65
P	25	12	14	2	53
Ch	6	7		1	14
Hy	5		2	6	13
Combinations	16	18	14	1	49
Total	**219**	**139**	**111**	**38**	**507**

Tab. 3. Contingency table showing number of plant species by origin in relation to pollination modes. A – archaeophytes; I – indigenous; N – neophytes.

Origin of plant species	Insect pollination	Insect and self pollination	Wind pollination	Other modes of pollination	Total
I	172	104	91	34	**401**
A	19	28	10	3	**60**
N	27	7	8	1	**43**
Total	**218**	**139**	**109**	**38**	**504**

$\chi2$: 19.6; $p < 0.01$

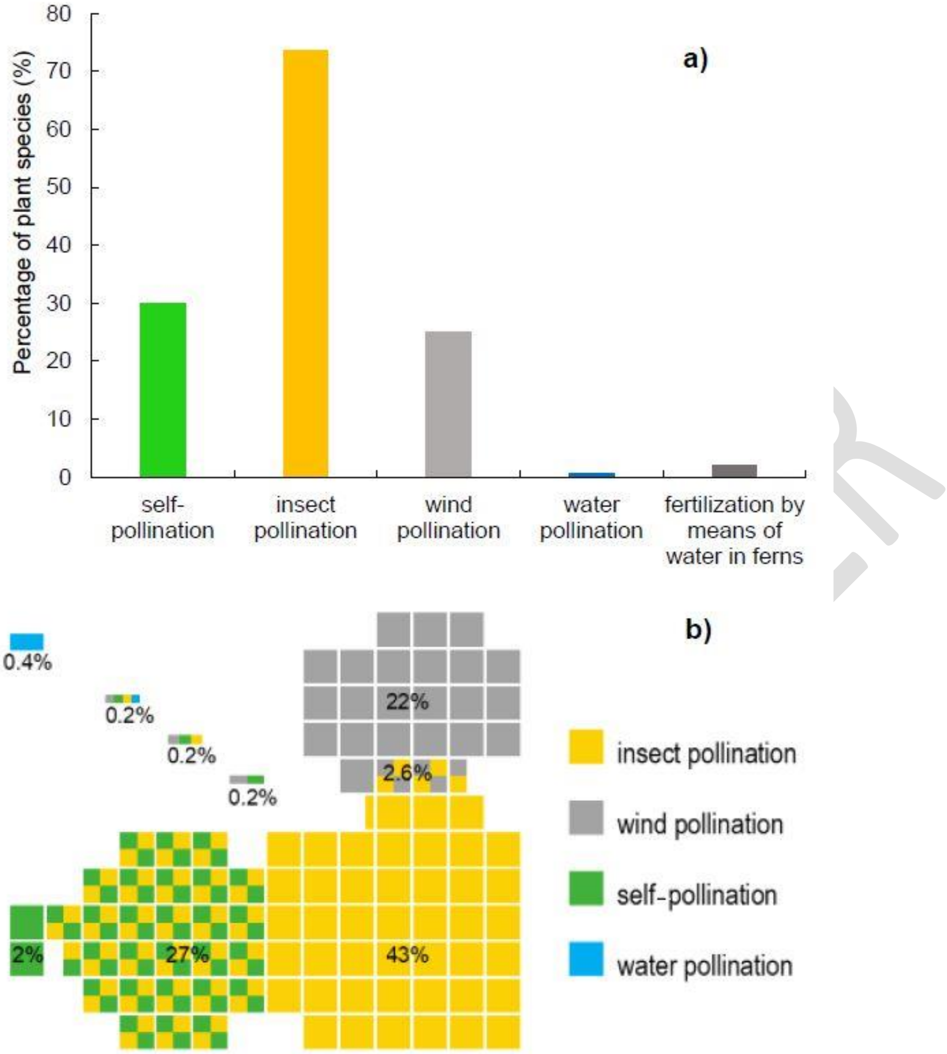


Fig. 1. Contributions of the different modes of pollination in the flora studied in the northern Croatia: a – representation of individual modes of pollination in absolute percentages (where the sum exceeds 100% because some plant species have more than one mode of pollination), b – contribution and overlap of specific modes of pollination in relative percentages.

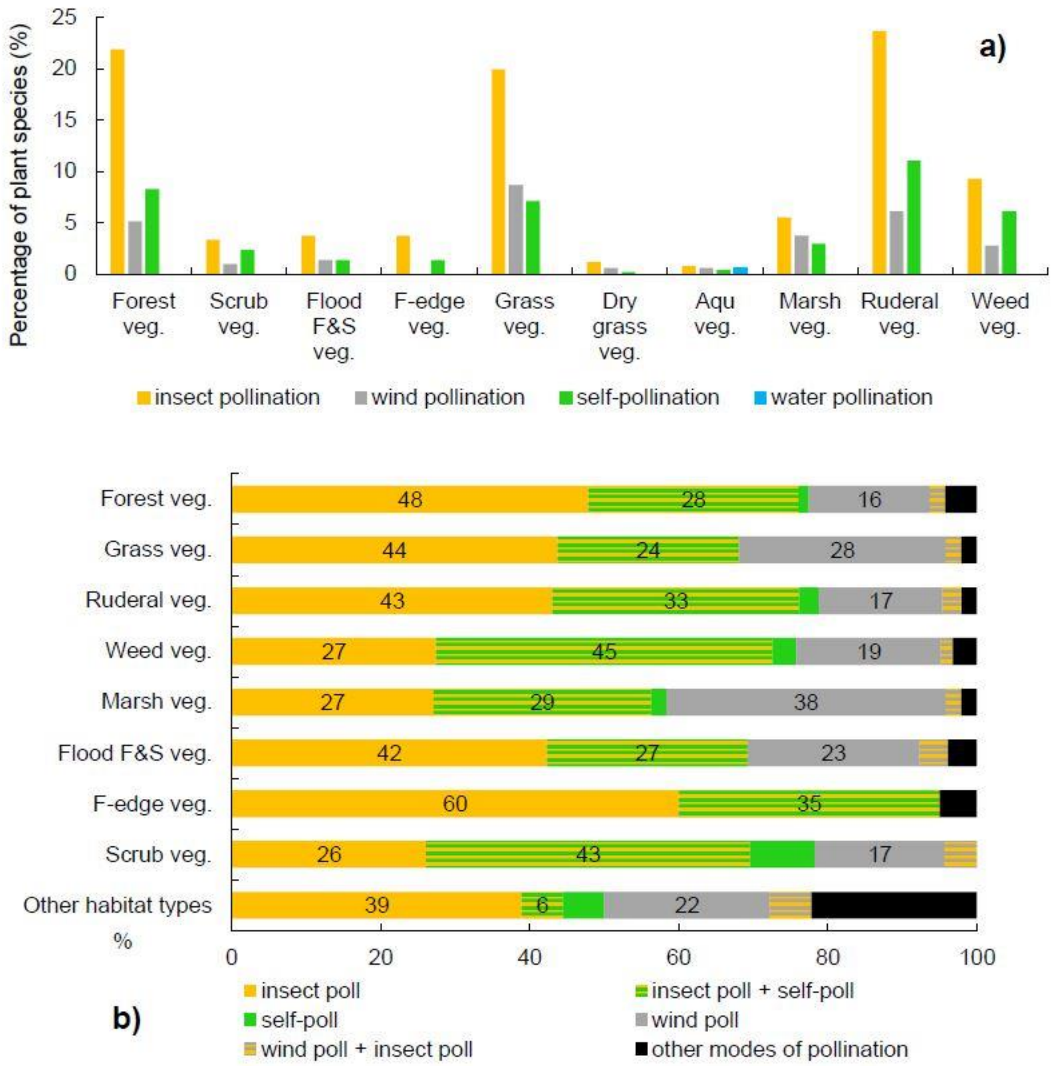


Fig. 2. Percentages of different pollination modes in different habitat groups: a – representation of individual modes of pollination by habitat in absolute percentages (sum exceeding 100% because some plant species have more than one mode of pollination), b – representation of the proportion and overlap of specific modes of pollination by habitat type in relative percentages (where the groups differ significantly with respect to pollination mode: Chi-square = 39.8, $P < 0.001$). Abbreviations: Forest veg. – forest vegetation unaffected by flooding, scrub veg. – scrub vegetation unaffected by flooding, flood F&S veg. – floodplain forest and scrub vegetation, F-edge veg. – forest-edge vegetation, grass veg. – wet and mesic grassland vegetation, dry grass veg. – dry grassland vegetation, aqu. veg. – aquatic freshwater vegetation, marsh veg. – marsh vegetation, ruderal veg. – ruderal vegetation, weed veg. – weed vegetation, wall veg. – wall vegetation.

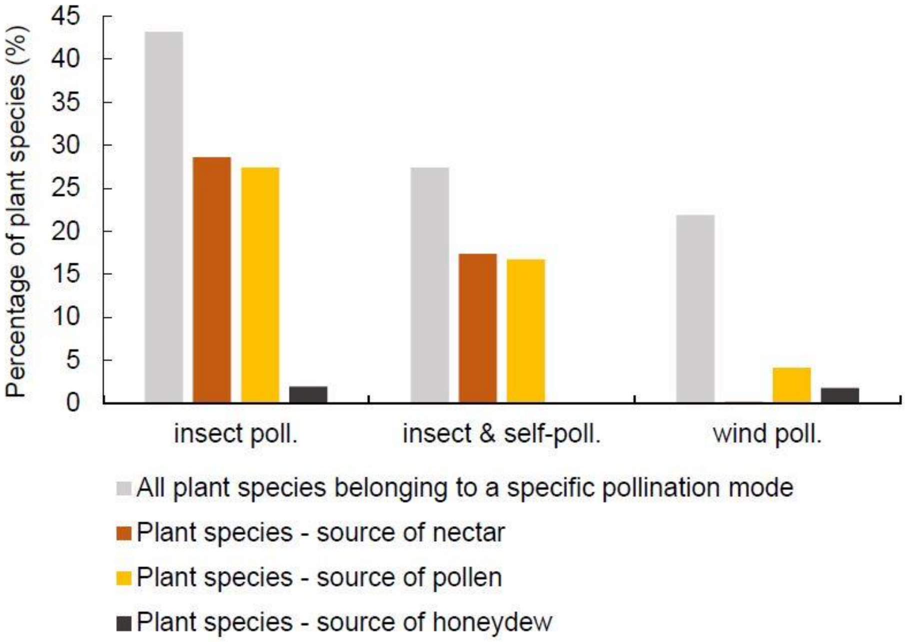


Fig. 3. Percentages of plant species useful for *Apis mellifera* (as a source of nectar, pollen and honeydew) by pollination mode.

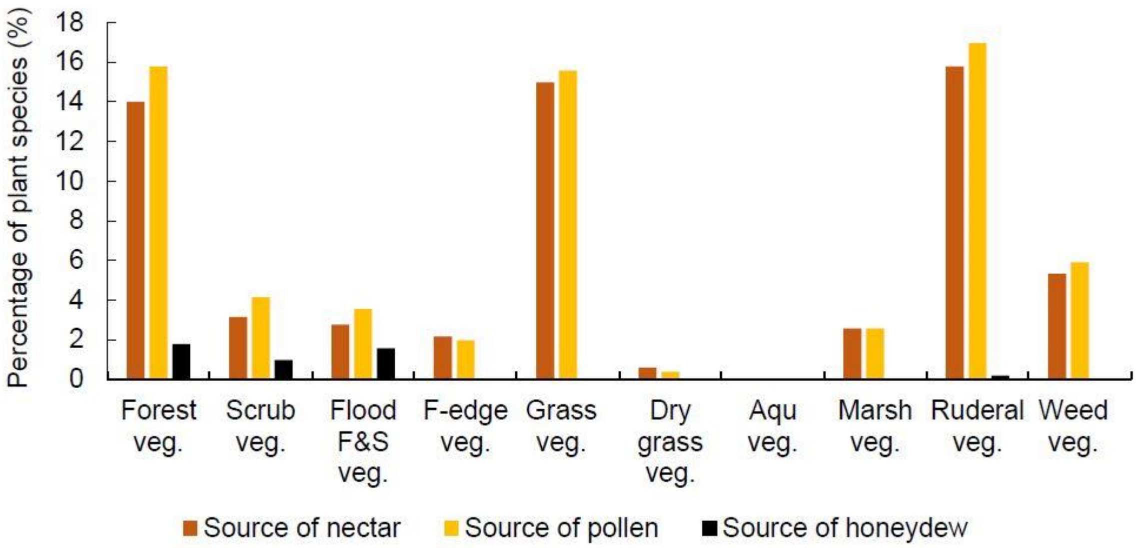


Fig. 4. Percentage contribution of plant species that are a source of nectar, pollen and honeydew for *Apis mellifera* by habitat group. (For habitat abbreviations see caption of Fig. 2).

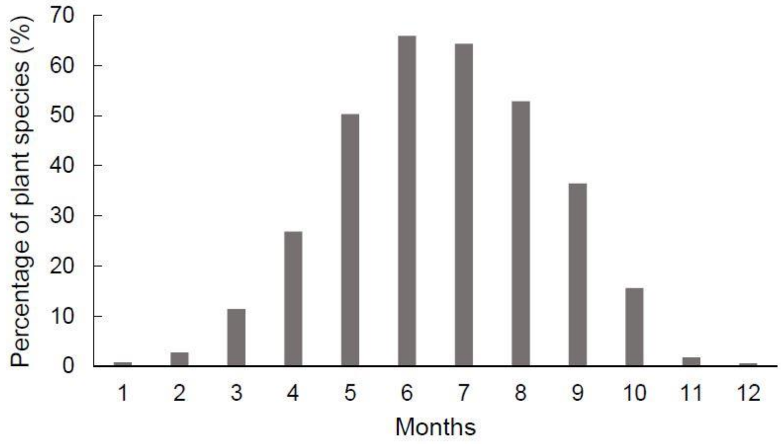


Fig. 5. Percentage contribution of plant species in Bedekovčina flora according to flowering time

On-line Supplementary material

On-line Suppl. Tab. 1. Habitat groups associated with habitat types according to the National Habitat Classification of the Republic of Croatia (Anonymous, 2018) and phytosociological affiliation according to Mucina et al. (2016).

Habitat abbreviation	Habitat group	NKS (Anonymous, 2018) code/s	Code/s and syntaxon/syntaxa name/s according to Mucina et al. (2016)
Forest veg.	forest unaffected by flooding	E.3., E.4., E.9.	FAG *Carpino-Fagetea sylvaticae* Jakucs ex Passarge 1968 QUE *Quercetea robori-petraeae* Br.-Bl. et Tx. ex Oberd.1957 ROB *Robinietea* Jurko ex Hadač et Sofron1980
Scrub veg.	scrubland unaffected by flooding	D.1.	RHA *Crataego-Prunetea* Tx. 1962
Flood F&S veg.	floodplain forest and scrubland	E.1., E.2.	PUR *Salicetea purpureae* Moor 1958 ALN *Alnetea glutinosae* Br.-Bl. et Tx. ex Westhoff et al. 1946 FRA *Franguletea* Doing ex Westhoff in Westhoff et Den Held 1969
F-edge veg.	forest-edge vegetation	I.1.5., C.5.1.	EPI *Epilobietea angustifolii* Tx. et Preising ex von Rochow 1951 GER *Trifolio-Geranietea sanguinei* T. Müller 1962
Grass veg.	wet and mesic grassland	C.2.	MOL *Molinio-Arrhenatheretea* Tx. 1937
Dry grass veg.	dry grassland	C.3.	FES *Festuco-Brometea* Br.-Bl. et Tx. ex Soó 1947
Aqu veg.	aquatic freshwater vegetation	A.3.	LEM *Lemnetea* O. de Bolòs et Masclans 1955 POT *Potamogetonetea* Klika in Klika et Novák 1941
Marsh veg.	marsh vegetation	A.4.	PHR *Phragmito-Magnocaricetea* Klika in Klika et Novák 1941
Ruderal veg.	ruderal vegetation	I.1.3., I.1.4., I.1.7.	POL *Polygono-Poetea annuae* Rivas-Mart. 1975 ART *Artemisietea vulgaris* Lohmeyer et al. in Tx. Ex von Rochow1951 BID *Bidentetea* Tx. et al. ex von Rochow1951 SIS *Sisymbrietea* Gutte et Hilbig 1975
Weed veg.	weed vegetation	I.1.6.	PAR *Papaveretea rhoeadis* S. Brullo et al. 2001 CHE *Chenopodietea* Br.-Bl. in Br.-Bl. et al. 1952 DIG *Digitario sanguinalis-Eragrostietea minor*is Mucina, Lososová et Šilc 2016
Wall veg.	vegetation of walls	B.1.	ASP *Asplenietea trichomani*s (Br.-Bl. In Meier et Br.-Bl. 1934) Oberd. 1977

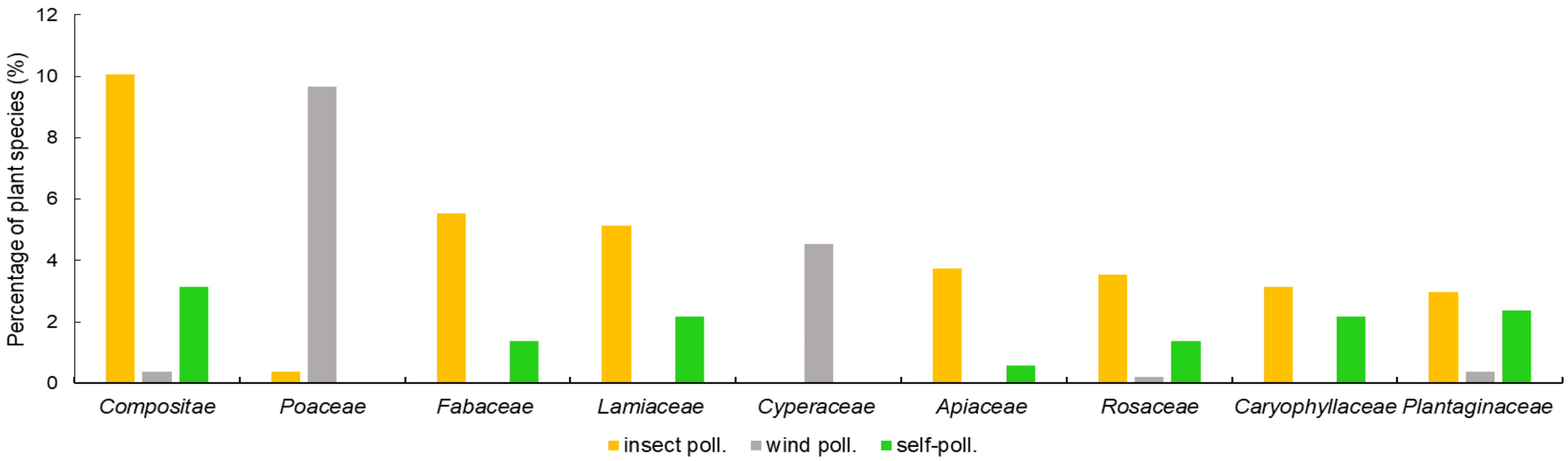
On-line Suppl. Tab. 2. Representation of plant families in the flora of Bedekovčina.

No.	Family	Number of species	No.	Family	Number of species
1	*Compositae*	54	51	*Corylaceae*	2
2	*Poaceae*	51	52	*Crassulaceae*	2
3	*Fabaceae*	28	53	*Cucurbitaceae*	2
4	*Lamiaceae*	26	54	*Dryopteridaceae*	2
5	*Cyperaceae*	23	55	*Ericaceae*	2
6	*Apiaceae*	19	56	*Gentianaceae*	2
7	*Rosaceae*	18	57	*Iridaceae*	2
8	*Caryophyllaceae*	17	58	*Moraceae*	2
9	*Plantaginaceae*	17	59	*Oleaceae*	2
10	*Brassicaceae*	16	60	*Orchidaceae*	2
11	*Ranunculaceae*	16	61	*Solanaceae*	2
12	*Juncaceae*	11	62	*Vitaceae*	2
13	*Polygonaceae*	11	63	*Anacardiaceae*	1
14	*Euphorbiaceae*	8	64	*Araceae*	1
15	*Rubiaceae*	8	65	*Araliaceae*	1
16	*Salicaceae*	8	66	*Athyriaceae*	1
17	*Boraginaceae*	7	67	*Berberidaceae*	1
18	*Primulaceae*	7	68	*Butomaceae*	1
19	*Geraniaceae*	6	69	*Cannabaceae*	1
20	*Amaryllidaceae*	5	70	*Celastraceae*	1
21	*Liliaceae*	5	71	*Ceratophyllaceae*	1
22	*Onagraceae*	5	72	*Colchicaceae*	1
23	*Asparagaceae*	4	73	*Commelinaceae*	1
24	*Dipsacaceae*	4	74	*Dennstaedtiaceae*	1
25	*Fagaceae*	4	75	*Haloragaceae*	1
26	*Malvaceae*	4	76	*Juglandaceae*	1
27	*Oxalidaceae*	4	77	*Lentibulariaceae*	1
28	*Papaveraceae*	4	78	*Loranthaceae*	1
29	*Sapindaceae*	4	79	*Lythraceae*	1
30	*Scrophulariaceae*	4	80	*Melanthiaceae*	1
31	*Viburnaceae*	4	81	*Montiaceae*	1
32	*Violaceae*	4	82	*Phytolaccaceae*	1
33	*Apocynaceae*	3	83	*Pinaceae*	1
34	*Campanulaceae*	3	84	*Polygalaceae*	1
35	*Chenopodiaceae*	3	85	*Polypodiaceae*	1
36	*Equisetaceae*	3	86	*Portulacaceae*	1
37	*Lemnaceae*	3	87	*Potamogetonaceae*	1
38	*Orobanchaceae*	3	88	*Resedaceae*	1
39	*Typhaceae*	3	89	*Rhamnaceae*	1
40	*Valerianaceae*	3	90	*Saxifragaceae*	1
41	*Alismataceae*	2	91	*Simaroubaceae*	1
42	*Amaranthaceae*	2	92	*Staphyleaceae*	1
43	*Aristolochiaceae*	2	93	*Ulmaceae*	1
44	*Aspleniaceae*	2	94	*Urticaceae*	1
45	*Balsaminaceae*	2	95	*Verbenaceae*	1
46	*Betulaceae*	2			
47	*Caprifoliaceae*	2			
48	*Clusiaceae*	2			
49	*Convolvulaceae*	2			

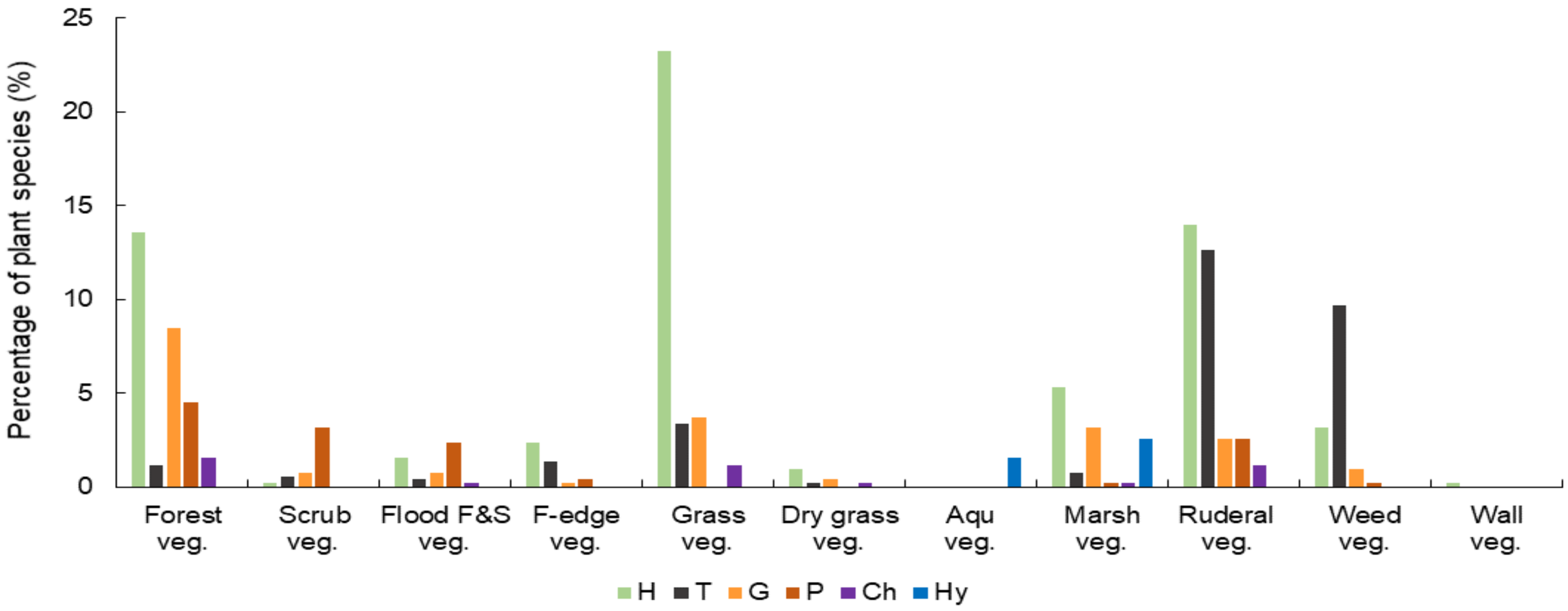
On-line Suppl. Tab. 3. Percentages of plant species in the flora of Bedekovčina useful for *Apis mellifera*.

	Total number of plant species useful to *Apis mellifera*	Source of nectar	Source of pollen	Source of honeydew	Source of propolis
Number of plant species	276	240	259	21	7
%	54	47	51	4	1

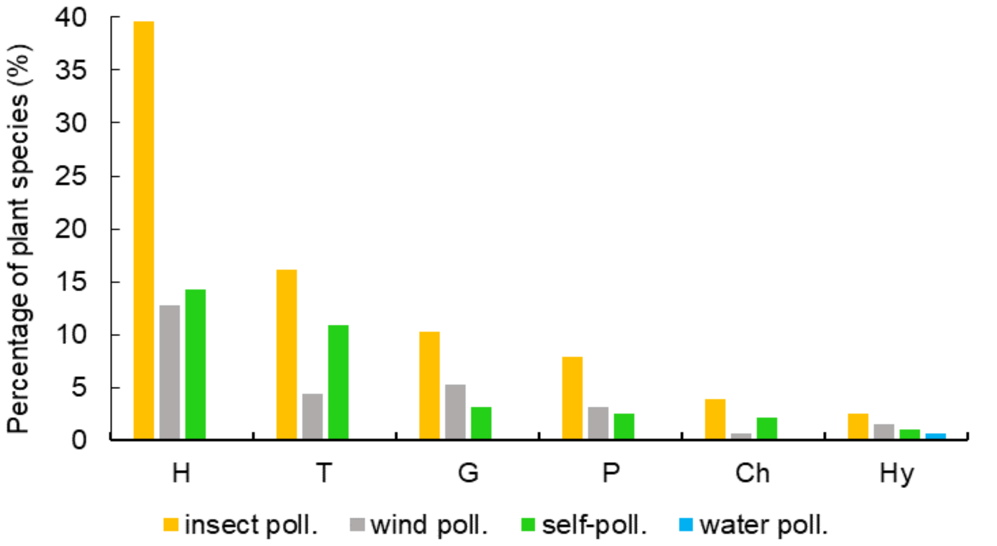
On-line Suppl. Fig. 1. Map of the position of the investigated area of Bedekovčina in the northern Croatia.



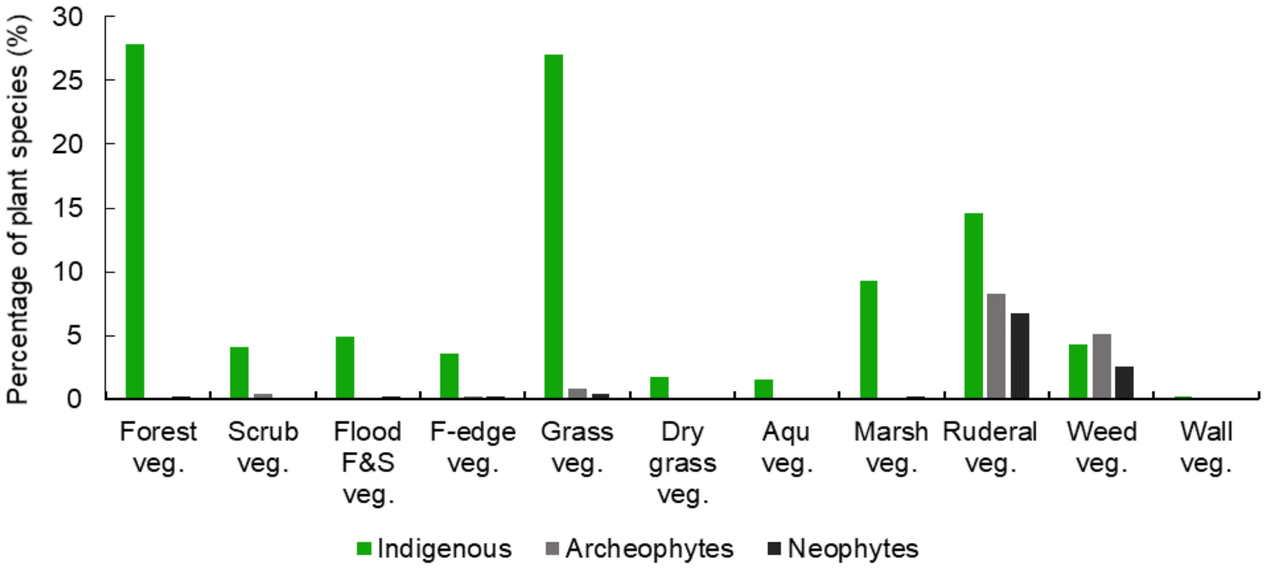
On-line Suppl. Fig. 2. Percentages of pollination modes by plant family. Only plant families with 17 or more plant species are shown.



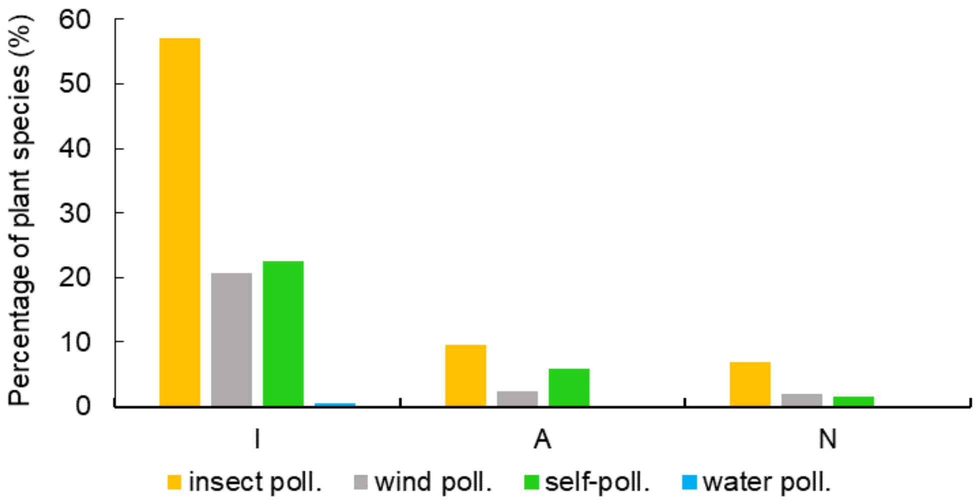
On-line Suppl. Fig. 3. Percentages of life forms by habitat group. Abbreviations: H - hemicryptophytes; T - therophytes; G - geophytes; P - phanerophytes; Ch - chamaephytes; Hy - hydrophytes. Abbreviations of habitat groups are explained in On-line Suppl. Tab. 1.



On-line Suppl. Fig. 4. Proportion of pollination modes as dependent on life form. Abbreviations: H - hemicryptophytes; T - therophytes; G - geophytes; P - phanerophytes; Ch - chamaephytes; Hy - hydrophytes.



On-line Suppl. Fig. 5. Distribution of plant species depending on their origin and habitat type. Abbreviations of habitat groups are explained in On-line Suppl. Tab. 1.



On-line Suppl. Fig. 6. Percentage contribution of pollination modes by origin. Abbreviations: I - indigenous plant species; A - archaeophytes; N - neophytes.