

The Role of Pollinators in Maintaining the Biodiversity of Some Exotic Cultures

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Abstract

The fertilization process and the production of seeds are due to pollination, where every pollen grain from the male part of a plant is transferred to a female part of the plant. Most often, cross-pollination is carried out zoophilous, anemophilous or hydrophilous. The subject of the present paper is pollination, which has the following subtypes: entomophily, chiropterophily and ornithophily. The main entomophilous pollinators are: bees, bumblebees, butterflies, wasps, flies and moths. Entomophily pollination is the most wide-spread and significant sub branch for agricultural and horticultural crops. It's analyzed the importance of pollinators within the agave (*Agave tequilana* F.A.C Weber) crop, durian (*Durio zibethinus* Murray), banana (*Musa spp.*), cocoa (*Theobroma cacao* L.) and vanilla (*Vanilla spp.*). Looking at different aspects such as the morphology and biology of the bloom or the particularities of adaptation to the environment, it can be concluded that for each of these cultivated species, the particularities of the pollination mechanism, evolved depending on the geographic area and the ecosystem. The aim of this work is to present the importance of pollinators, their role in maintaining genetic diversity in these exotic cultures of great economic and food importance, and the means by which they are protected for the benefits in plantations and industry.

Keywords: biodiversity, exotic cultures, food production, pollination

1. INTRODUCTION

The fertilization process and the production of seeds are possible through pollination mechanism, where every pollen grain from the male part of a plant is transferred to the female part of the plant. Pollen is either transferred by wind, by water or by animal pollinators (invertebrates and vertebrates). Self-pollination can be done by the transfer from anthers to the stigma of the same or different flower, while cross-pollination is between different genotypes of the same species. However, self-pollination can seldom be considered a dominant fertilization mechanism, due to long-term risks of inbreeding and loss of genetic diversity. Multiple advantages of insect pollination compared to wind pollination can be given, such as increased efficiency and maximized number of plant species, due to successful pollination [1,2].

A recent global estimate suggests that almost 90% of angiosperms depend on invertebrates or vertebrates pollination [3] while a significant part of gymnosperms are

likely biotically pollinated [4].

In this review, firstly we introduce data of pollinators' diversity, followed by the importance of zoophilous pollinators, especially invertebrates. Finally, focuses on animal pollinators are investigated, particularly on pollinators of exotic cultures.

2. THE DIVERSITY OF POLLINATORS

Estimating the current diversity of pollinators is a subject to several disputes and is without a doubt problematic, considering the fact that public awareness concerning environmental issues is neglected and mostly giving false reports. The possibility of providing accurate estimates regarding the overall phylogenetic diversity and the number of species (mainly birds, mammals and bees) involved is achievable [5-7].

In Table 1 recent estimates of pollinator diversity on the basis of the cited reviews and studies are exemplified.

Table 1. Estimated pollinator classes for the world's wild flowering plants

Order	Categories of pollinators	Estimated taxa in the major groups	Estimated taxa of subgroups	References
<i>Lepidoptera</i>	Butterflies and moths	141.600		[7]
<i>Heterocera</i>	Moths		123.100	[8,9]
<i>Rhopalocera</i>	Butterflies		18.500	[8,9]
<i>Coleoptera</i>	Beetles	77.300		[7]
<i>Cetoniinae</i>	Flower chafers		4.000	[10]
<i>Hymenoptera</i>	Bees, wasps, ants	70.000		[7]
<i>Anthophila</i>	Bees		17.000	[8,9,11,12]
<i>Pompilidae</i>	Spider wasps		5.000	[13]
<i>Vespoidea</i>	Social wasps		5.000	[2,8]
<i>Diptera</i>	Flies	55.000		[7]
<i>Syrphidae</i>	Hoverflies		6.000	[8,9]
<i>Bombyliidae</i>	Bee flies		4.500	[8,9]
<i>Thysanoptera</i>	Thrips	1.500		[7,8]
<i>Aves</i>	Birds	1.089		[6,8]
<i>Trochilidae</i>	Hummingbirds		365	[8,9]
<i>Meliphagidae</i>	Honeyeaters		177	[8,9]
<i>Nectariniidae</i>	Sunbirds		124	[8,9]
<i>Zosteropidae</i>	White-eyes		100	[8,9]
<i>Psittacidae</i>	Lorikeets		53	[14]
<i>Mammalia</i>	Mammals	344		[6]
<i>Chiroptera</i>	Bats		236	[8]
<i>Pteropus</i>	Flying foxes		63	[15]
Nonflying mammals	Others		108	[8]
Total of major groups		346.833		

As described above, the most abundant group of pollinators is the *Lepidoptera* (particularly the moths), with more than 140,000 species which are likely to visit flowers, due to the functional mouthparts of the adult form. These pollinators are followed by the butterflies group as described by Wardhaugh (2015), which mostly feed on plant and flower exudates.

The next diverse group is occupied by *Coleoptera* and *Hymenoptera*, which comprises more than half of the above-described group pollinators. In the *Hymenoptera* group the bees are the most abundant subgroup. In terms of existing species, Kristensen et al. (2007) suggested that nearly half a million of lepidopteran species exist, primarily moths followed by butterflies. This suggests the lack of existing studies of these pollinator types.

These major orders are followed by *Diptera* which comprise the flies. The diversity of these pollinators might change in the future by the multiple studies conducted until now [18-20]. In the studies conducted by Orford et al. (2015) and Ollerton et al. (2009), they suggested the integration of non-syrphid *Diptera* in further research along with multiple studies regarding the diversity of this order, due to the fact that the knowledge in dipterans changed greatly in the course of 30 years of research. Further studies will provide significant insights into the mechanisms by which pollinators are attracted and trapped [19]. Larson et al. (2001) also stated that these syrphid flies are the most important flower pollinators. There are little studies regarding the relationship between the response to land-use change and species-level traits of vertebrate pollinators. In fact, feeding association to land use is an important trait in bird and bat land changes [20]. It has been demonstrated that nectarivorous bats respond positively to moderate levels of forest exploitation, compared to the insectivorous pollinators. A botanical survey conducted by Hodgkison revealed that in 1 ha of old-growth forest, 13.7% of the trees were partly dependent upon fruit bats pollination and seed dispersal [21].

Even though the remaining groups exhibit rather low diversity, this will most likely change in the future due to the fact that in certain regions they are ecologically important for diverse plants.

Diversity in the vertebrate groups is rather low compared to the invertebrates. The most diverse group is occupied by the order *Aves*, followed by *Chiroptera*. The latter is significantly important in terms of pollination, especially in tropical forests.

In the following section, we will detail recent studies on the pollination mode and the pollinated species.

1.1. Zoophilous pollination

Among insects, main anthophilous taxa comprise: butterflies, moths (*Lepidoptera*), beetles (*Coleoptera*), flies (*Diptera*), ants, bees (*Hymenoptera*), and thrips (*Thysanoptera*).

Cantharophily is considered to be the oldest type of pollination. The beetle-pollinated flowers are usually off-white or greenish in color, large, with a dulled texture and a heavy scent similar to *Malus spp.* [22]. Beetles usually visit flowers for pollen, even though easily accessible nectar or nutritive tissues may be also consumed, considering the fact that ovaries usually are well protected from pollinators' biting mouthparts [1].

Beetles have been abundant since at least the Mesozoic, and it is likely that some of them have been flower visitors since the origin of the earliest angiosperms. For example, the current association of beetle pollination (cantharophily) with primitive woody angiosperms (*Magnolia*) probably dates back to the evolutionary origins of both groups. Beetle

pollination is considered to be the most primitive type of pollination by animals, and is not very important in cool temperate regions. It is most common in the moist tropics, and to a lesser degree in arid areas. Beetles constitute the largest order of insects, and some of this diversity is thought to have arisen through the same evolutionary radiation of flowers and insects during the Tertiary that led to the origin of the other major orders of flower-visiting insects. They are significantly important because they can deposit larger quantities of pollen on the stigmas and can travel for longer period, compared to their conspecifics [23].

The major beetle families that commonly or exclusively contain anthophilous species are the *Buprestidae* (jewel beetles), *Cantharidae* (soldier beetles), *Cerambycidae* (longicorn or longhorn beetles), *Cleridae* (checkered beetles), *Dermestidae*, *Lycidae* (net-winged beetles), *Melyridae* (soft-winged flower beetles), *Mordellidae* (tumbling flower beetles), *Nitidulidae* (sap beetles), and *Scarabaeidae* (scarabs) [1].

Myophily is the pollination made by flies which visit nectar-producing flowers, except for the hover flies (*Syrphidae*) which mainly feed on pollen rather than nectar. The flowers are radial or lantern shaped, with a dull texture and a greenish, purple or dark colored. The reproductive organs are usually hidden and the pollen grain shape similar to that of myophilous taxa [1,22].

As described in the previous section, there are two groups in order *Lepidoptera*, the butterflies and the moths. It is known that butterflies are diurnal and most moths are nocturnal. These pollinators are the most visible and recognized. Pollen is often involuntarily stuck to the proboscis or other body parts, such as the head, antennae, legs etc. [22].

Phalaenophily (moth pollination) is mostly associated with nocturnal light-colored flowers that have anthesis at night, whereas butterfly pollination (psychophily) is related to diurnal anthesis, but with more colored spectra, such as yellow, red and blue flowers [1]. Flowers pollinated by butterflies are usually open during the day and closed at night. They have a light scent and are brightly colored. The species included in this description are *Aster spp.*, *Buddleia spp.*, *Lonicera spp.*, *Rubus spp.*, *Silene* and *Solidago spp.*. These species' flowers are tube-like shaped with hidden nectarines [22].

As described in the previous section, the members of order *Hymenoptera* visit flowers for nectar and pollen. Here, the *Agonidae* (fig wasps) are highly specialized pollinators of figs [24], whether ants are rather poor pollinators, known to visit on average only 20 plant species and rarely pollinating them [1,22,25].

While invertebrates are the most widespread pollinators, mammals, birds, and lizards have also been documented as pollinators [2]. These include pollinators like bats, which primarily visit flowers for nectar and pollen, as well as nonflying species like the Australian marsupials.

Although chiropterophily is geographically widespread, the other mammalian pollinators are more restricted and less known, together with lemurs in Madagascar and some species of Australian marsupials (sugar gliders, honey possums, marsupial mice).

Regarding ornithophily, multiple bird families are significantly important and primarily nectarivorous. There are six major families that include the hummingbirds (*Trochilidae*), honeyeaters (*Meliphagidae*), sunbirds (*Nectariniidae*), sugarbirds (*Promeropidae*), flowerpeckers (*Dicaeidae*), and Hawaiian honeycreepers (*Drepanididae*). Other families that include lower estimated taxa are *Thraupidae* (honeycreepers), *Zosteropidae* (whiteeyes), and *Psittacidae* (lorikeets) [2,26].

The last group is occupied by two families of bats

which contain flower-visiting species: the leaf-nosed bats (*Phyllostomidae*) and the fruit bats (*Pteropidae*). The flowers that they visit are usually night-blooming and solely dependent on bat pollination [26].

Measuring pollinators' importance is time-consuming and difficult, especially in terms of global perspective [27,28]. All of the species presented above have the potential to be useful pollinators, each for their distinctive plant group.

2. TARGETED CROPS POLLINATORS

In this section we will discuss the pollinators' importance in pollinating the most cultivated crops, as well as the importance of exotic cultivated species in terms of industry, propagation and future perspectives. The main discussed species are represented by agave (*Agave tequilana* F.A.C Weber), durian (*Durio zibethinus* Murray), banana (*Musa spp.*), cocoa (*Theobroma cacao* L.) and vanilla (*Vanilla spp.*) (Figure 1).



Figure 1. Localization of the targeted crops on the world map; *Agave tequilana* F.A.C. Weber - Mexic; *Vanilla spp.* - South America /Mexico; *Theobroma cacao* L. - Africa; *Durio zibethinus* Murray - South Asia

2.1. *Agave tequilana* pollinators

The genus *Agave* is the most richest and diverse group of plants in Mexico. The locals developed several technologies in order to produce Agave-derived alcoholic beverages. Until now they produced different beverages, such as: tequila, bacanora, mezcal, pulque and raicilla. The evolution of *Agave* species is related to nectar-feeding bats, which play main roles as functional pollinators. Nowadays, the increasing demand of agave-derived products led to a reduction in species' genetic diversity and bat food availability. Management practices reduced their dependence on bat pollination focusing on replanting the fields with clonal shoots and harvesting the plants before flowering. This negatively affected both agaves and bats. In the study conducted by Trejo-Salazar et al. they collected data of the amount of Agave pollinated bats in order to evaluate their importance in plant diversity and bat nectar supply [29]. They concluded that allowing 5% of the plants in 1 ha to flower (222 individuals), then at least 89 bats could feed every night during flowering period. This means that if producers allow 5-10% of *A. tequilana* F.A.C. Weber. to flower, more than 2 million bats could feed every month.

Three main nectarivorous bats are known to pollinate the *Agave* species: *Choeronycteris mexicana* Tschudi, *Leptonycteris nivalis* Saussure and *L. yerbabuenae* Martínez & Villa-R. Multiple studies were conducted in order to describe and record the relationship between agaves and bats [29-33]. The nectarivorous pollinators are also integrated in the protection list by Mexican and US as Threatened and Endangered and in US Fish and Wildlife Service 2006,

Diario Oficial de la Federación 2012 and IUCN 2016 [34-36].

Multiple publications include reports of bats visiting flowers of additional agave species through the presence of agave pollen on the body or feces of bats [32,37]. Successful pollination occurs at night due to the reduced time (few hours after dehiscence) of pollen germination [38]. Bats' nectar consumption changes in response to energy requirements and Agaves' sugar concentration [39]. Almost 50% of Mexico is covered in semiarid and dry zones and almost 6000 species (20%) of the Mexican flora are found. This highlights the importance of bats' conservation and plants' genetic diversity.

2.2. *Theobroma cacao* pollinators

The genus *Theobroma* is exclusively pollinated by ceratopogonid midges, such as *Forcipomyia spp.* Alongside, other insects from the order *Diptera* have been documented to visit the flowers of cocoa, such as *Cecidomyiidae* (gall midges), *Chironomidae* (non-biting midges), *Drosophilidae* (fruit flies), and *Psychodidae* (moth flies). Unfortunately, their contribution to pollination is scarce, studies confirming that microscopic observations of pollen grains were noted only on *Forcipomyia spp.* [40].

Overall, Cocoa (*Theobroma cacao* L.) is the third agricultural export commodity, after coffee and sugar. In terms of production, Côte d'Ivoire occupies the first position with 1000 t of raw cocoa beans/year [41]. From a total of 4 million tons globally produced cocoa dry beans, 60% are obtained in Africa [42].

Nowadays multiple inadequate systems endanger cocoa

yield. These comprise unshaded monocultures, which lead to soil erosion, increased disease and pest occurrence, water shortages and weed development [43-46]. Even though multiple studies demonstrated that cocoa is a shade-tolerant tree, increased productions have been observed in full sun-lest plants [47].

In multiple studies, researchers observed that along with sun exposure, precipitation was the main driver initiating flowering in the rainy season (April), compared to the dry season [48-50]. This aspect is in opposition to the weather conditions that affect *Forcipomyia*'s visiting activity: rainy or cloudy weather decrease their activity compared to sunny weather [40].

Even though fluctuations of *Forcipomyia* population synchronizes with cocoa flowering peaks, only about 5-10% of flowers are pollinated [44]. Kaufmann (1975) reported that out of the 70 ceratopogonid species only eight are attracted to flowers and even fewer succeed in carrying pollen grains to ensure pollination. Regarding their breeding conditions in Côte d'Ivoire, they require moist and decaying organic material [52], but massive landscape degradation led to decreased breeding opportunities, excepting the vicinity of natural forests [51,53,54]. Cribbs' laboratory experiments showed that *F. townsvillensis* eggs did not develop without complete blood meals [55]. As future requirements, *Forcipomyia* spp. mass breeding and release is an important aspect considering that no attempts have been undertaken up to date. Also, many research gaps must be completed, such as improving pollination efficiency [56], pesticide control, enhancing ant pollination and improving crop systems (soil mulching, agroforestry).

2.3. *Durio zibethinus* pollinators

The genus *Durio* display floral characteristics that specifically attract large, nocturnal pollinators. Pollination is mainly realized by flying foxes (*Pteropus* spp., *Acerodon* spp., *Desmalopex* spp.) the largest worldwide-known pteropodids. Investigations into pollination [57] are scarce compared to seed dispersal [58-60]. Rather than flying foxes, the former focused on the relationship between smaller, nectarivorous pteropodids and fruit economic importance [61,62].

As described above, chiropterophilous plants exhibit bat-flower syndrome, the best example being *Durio zibethinus* Murray, an economically and culturally important crop [62].

Pollination made by flying foxes or other pteropodids (*Eonycteris spelaea* Dobson) led farmers to have a negatively perception that they cause damage (flower consumption or destruction) and negatively affect fruit production [63,64]. Recent experiments contradicted these perceptions, cave nectar bats being major pollinators of *Durio* spp. In a study conducted in Sulawesi (Indonesia), Sheherazade et al. (2019) presented the first evidence that durian flowers are pollinated by bats. In his research the most frequent pollinator with the longest visits was *Eonycteris spelaea* Dobson, followed by *Pteropus alecto* Temminck (black flying fox) and *Acerodon celebensis* Petters (Sulawesi flying fox) [65]. Furthermore, they estimated that bat pollination services are valued at around ~\$ 117/ha/fruiting season, signaling the importance of bat conservation in order to increase the production of durian. *A. celebensis* Petters is listed by the International Union for Conservation of Nature (IUCN) as vulnerable due to excessive hunting [36].

Until recently, no attempt has been made to assess the specific role of flying foxes in durian reproductive ecology [57]. Using camera traps, Aziz et al. (2017), demonstrated that flying foxes primarily visit durian flowers to feed on nectar, without causing damage.

As future requirements, the relationship between flying

foxes and plant productivity is an important aspect to improve peoples' perception of why plant productivity and bat populations decline. The former aspect has been pointed out by few studies on bat hunting or legal killing as pests, as well as habitat changes [66-69].

2.4. *Musa* spp. pollinators

The genus *Musa* comprises all edible cultivars and is divided into four sections, *Australimusa*, *Callimusa*, *Eumusa* and *Rhodochlamys*. *Musa acuminata* Colla and *Musa balbisiana* Colla, comprised in the *Eumusa* section, are the main ancestors of the modern edible banana cultivars, [70].

Flower characteristics displayed by genus *Musa* attract nocturnal visitors [71-73]. As described in section 3.3 about *Durio* species, pollination is mainly realized by flying foxes, such as *Pteropus vampyrus* Linnaeus. Upright banana inflorescences are visited by birds, whereas pendant inflorescences are visited by bats [72]. Due to excessive hunting, the population decreased and it is listed by IUCN as near threatened [74]. Also, future habitat loss (increased deforestation rates) may be responsible for the extinction of 24% of *Pteropodidae* species. This situation determined the bat populations to relocate, which usually occurs due to food shortage and roosting sites [75,76]. For instance, influx of *P. scapulatus* Petters populations in eastern areas of Australia led to public health concerns.

In order to evaluate their foraging patterns and behavioral ecology, Hengjan et al. (2018) recorded two individuals of *Pteropus vampyrus* Linnaeus and several *Pteropus* spp. via satellite telemetry. The maximum distance between the bats' location release and their furthest roost was \square 100 km. Also, the number of bat-visits corresponded with the number of fruit dropping [77].

Pedrozo et al. (2018) studied the multiple approaching strategies of phyllostomid bat species on *Musa paradisiaca* L. inflorescences [78]. They discovered a novel feeding behavior in *Glossophaga* spp. Furthermore, the activity pattern of nectarivorous bats differed greatly compared to omnivorous bats. The former species' visiting peaks were at 21:00 and 23:30 hs and the latter species visiting peaks were at 23:45 and 02:30 hs.

The understanding of *Pteropodidae* foraging behavior and movement patterns is crucial for species' conservation, landscape management, disease prevention and minimized conflict between humans and flying foxes.

2.5. *Vanilla* spp. pollinators

Up to the 19th century it was believed that the genus *Vanilla* was pollinated by *Melipona beecheii* Bennet [79] and later by *Euglossa* spp. and *Eulaema* spp [80]. The smaller bee species *Euglossa* are pollinators of *Vanilla planifolia* Jacks. ex Andrews and *V. trigonocarpa* Hoehne, whereas the larger bee species *Eulaema* pollinate *V. bahiana* Hoehne (Brazil), *V. pompon* Schiede and *V. insignis* Ames (Mexico). A diversity of bees in genera *Euglossa*, *Exeretes* and *Melipona*, as well as hummingbirds were observed visiting *V. planifolia* Jacks. ex Andrews and *V. hartii* Rolfe (Mexico) [80,81].

Although Colombia is the most *Euglossa*-rich country, no definite registration for *Vanilla* pollinators has been made [82].

Even though *Vanilla* flowers present a physical-barrier to self-pollination, in several species (*V. bicolor* Lindl., *V. palmarum* (Salzm. ex Lindl.) Lindl. and *V. planifolia* Jacks. ex Andrews) the abundance of stigmatic fluid is able to reach

the pollinia, facilitating pollination [80,83]. The decrease in euglossine bee populations is linked to *Vanilla* plantations, resulting in a loss of natural pollination.

Further analysis of pollination syndromes and floral anatomy are essential in order to develop more commercial cultivars and reduce the cultivation costs. Furthermore, effective cross-pollination is vital to maintain genetic variation and pollinator conservation.

3. CONCLUSIONS

Pollinator diversity and the role of pollination greatly progressed by the years, but further studies need to be conducted. Understanding the evolution of pollination system and ecology requires additional experimental and observational data, field monitoring and surveying on larger groups in order to overview pollinators' declines and diversity.

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REFERENCES

- [1] Gullan, P.J. and Cranston, P.S. 2014. The insects: an outline of entomology. John Wiley & Sons, pp.298-302.
- [2] Inouye D.W., Pollinators, Role of, 2007. Ed.: Simon Asher Levin, Encyclopedia of Biodiversity. pp. 1-9, ISBN 9780122268656.
- [3] Ollerton J, Winfree R, Tarrant S. 2011. How many flowering plants are pollinated by animals? *Oikos*, 120; 321–26.
- [4] Kato, M., Inoue, T., and Nagamitsu, T. 1995. Pollination biology of *Gnetum* (Gnetaceae) in a lowland mixed dipterocarp forest in Sarawak. *American Journal of Botany*, 82(7); 862-868.
- [5] Ollerton J. 1999. The evolution of pollinator-plant relationships within the arthropods. In *Evolution and Phylogeny of the Arthropoda*, pp.741–58. Zaragoza, Spain: Entomol. Soc. Aragon.
- [6] Regan E.C., Santini L., Ingwall-King L, Hoffmann M, Rondinini C, et al. 2015. Global trends in the status of bird and mammal pollinators. *Conserv. Lett.* 8; 397–403.
- [7] Wardhaugh, C. W. 2015. How many species of arthropods visit flowers? *Arthropod-Plant Interactions*, 9(6); 547–565.
- [8] Roubik, D.W. (Ed.) 1995. Pollination of cultivated plants in the tropics (No. 118). Food & Agriculture Org.
- [9] Ollerton, J. 2017. Pollinator Diversity: Distribution, Ecological Function, and Conservation. *Annual Review of Ecology, Evolution, and Systematics*, 48(1); 353–376.
- [10] Sakai K. and Nagai S. 1998: The Cetoniine beetles of the World. In: Fujita H. (ed.): *Mushi-Sha's iconographic series of insects 3*. Mushi-Sha, Tokyo.
- [11] Danforth B.N., Sipes S., Fang F., Brady S.G. 2006. The history of early bee diversification based on five genes plus morphology. *PNAS* 103:15118–23.
- [12] Michener C.D. 2007. *The Bees of the World*. Baltimore, MD: Johns Hopkins Univ. Press
- [13] Pitts J.P., Wasbauer M.S., von Dohlen C.D. 2005. Preliminary morphological analysis of relationships between the spider wasp subfamilies (*Hymenoptera: Pompilidae*): revisiting an old problem. *Zool. Scr.* 35:63–84.
- [14] Winfree, R., Bartomeus, I., Cariveau, D. P. (2011). Native pollinators in anthropogenic habitats. *Annual Review of Ecology, Evolution, and Systematics*, 42; 1-22.
- [15] Almeida, F. C., Giannini, N. P., Simmons, N. B., and Helgen, K. M. 2014. Each flying fox on its own branch: a phylogenetic tree for *Pteropus* and related genera (*Chiroptera: Pteropodidae*). *Molecular Phylogenetics and Evolution*, 77; 83-95.
- [16] Kristensen N.P., Scoble M.J., Karsholt O. 2007. Lepidoptera phylogeny and systematics: the state of inventorying moth and butterfly diversity. *Zootaxa*, 1668; 699–747.
- [17] Larson B.M.H., Kevan P.G., Inouye D.W. 2001. Flies and flowers: taxonomic diversity of anthophiles and pollinators. *Can. Entomol.* 133; 439–65.
- [18] Ollerton J., Masinde S., Meve U., Picker M., Whittington A. 2009. Fly pollination in *Ceropegia* (*Apocynaceae: Asclepiadoideae*): biogeographic and phylogenetic perspectives. *Ann. Bot.* 103; 1501–1514.
- [19] Orford K.A., Vaughan I.P., Memmott J. 2015. The forgotten flies: the importance of non-syrphid *Diptera* as pollinators. *Proc. R. Soc. B* 282; 20142934.
- [20] Tschamtkke, T., Sekercioglu, C.H., Dietsch, T.V., Sodhi, N.S., Hoehn, P., Tylianakis, J.M. 2008. Landscape constraints on functional diversity of birds and insects in tropical agroecosystems. *Ecology*, 89; 944–51.
- [21] Hodgkison, R., Balding, S. T., Zubaid, A., Kunz, T. H. 2003. Fruit Bats (*Chiroptera: Pteropodidae*) as seed dispersers and pollinators in a lowland malaysian rain Forest1. *Biotropica*, 35(4); 491-502.
- [22] Jones, G.D., and Jones, S.D. 2001. The uses of pollen and its implication for entomology. *Neotropical Entomology*, 30(3); 314-349.
- [23] Willmer, P.G. and Finlayson, K. 2014. Big bees do a better job: intraspecific size variation influences pollination effectiveness. *J. Pollinat. Ecol.* 14; 244–54.
- [24] Weiblen, G.D. 2002. How to be a fig wasp. *Annu. Rev. Entomol.* 47; 299–30
- [25] Rico-Gray, V. and Oliveira, P.S. 2007. The ecology and evolution of ant-plant interactions. University of Chicago Press. pp: 85-93.
- [26] Fleming, T.H., Geiselman, C. and Kress, W.J. 2009. The evolution of bat pollination: a phylogenetic perspective. *Annals of botany*, 104(6); 1017-1043.
- [27] Ballantyne, G.A., Baldock, K.C.R. and Willmer P.G. 2015. Constructing more informative plant–pollinator networks: visitation and pollen deposition networks in a heathland plant community. *Proc. R. Soc. B* 282; 20151130.
- [28] Ballantyne, G., Baldock, K.C.R., Rendell, L. and Willmer, P.G. 2017. Pollinator importance networks illustrate the crucial value of bees in a highly speciose plant community. *Sci. Rep.* 7; 83-89.
- [29] Trejo-Salazar, R.E., Eguiarte, L.E., Suro-Piñera, D. and Medellín, R.A. 2016. Save our bats, save our tequila: industry and science join forces to help bats and agaves. *Natural Areas Journal*, 36(4); 523-531.
- [30] Arizaga, S., Ezcurra, E., Peters, E., Ramírez, F. and Vega E. 2000. Pollination ecology of *Agave macroacantha* (Agavaceae) in a Mexican tropical desert. I. Floral biology and pollination mechanisms. *American Journal of Botany* 87; 1004-1010.
- [31] Silva-Montellano, A., and L.E. Eguiarte. 2003. Geographic patterns in the reproductive ecology of *Agave lechuguilla* (Agavaceae) in the Chihuahuan Desert. I. Floral characteristics, visitors, and fecundity. *American Journal of Botany*, 90; 377-387.
- [32] Rocha, M., Valera, A. and Eguiarte, L.E. 2005. Reproductive ecology of five sympatric *Agave* littea

(Agavaceae) species in central Mexico. American Journal of Botany, 92; 1330-1341.

[33] Sánchez, R., and Medellín, R.A. 2007. Food habits of the threatened bat *Leptonycteris nivalis* (Chiroptera: Phyllostomidae) in a mating roost in Mexico. Journal of Natural History, 41; 1753-1764.

[34] Diario Oficial de la Federación. 2012. Modificación a la Declaración General de Protección de la Denominación de Origen Mezcal. Primera Sección. Mexico, D.F.

[35] US Fish and Wildlife Service (USFWS). 2006. Lesser long-nosed bat (*Leptonycteris curasoae yerbabuena*) 5-year review: Summary and evaluation. US Fish and Wildlife Service, Phoenix, AZ.

[36] Tsang, S.M. and Sheherazade (2016). *Acerodon celebensis*. IUCN Red List Threat. Species. Retrieved from <https://doi.org/10.2305/iucn.uk.2016-2.rlts.t137a21988719.en> (accessed on: 18.11.2019)

[37] Eguiarte, L.E., Aguirre-Planter, E., Aguirre, X., Colín, R., González, A., Rocha, M., Scheinvar, E., Trejo, L. and Souza, V. 2013. From isozymes to genomics: Population genetics and conservation of Agave in México. The Botanical Review, 79; 483-506.

[38] Shivanna K.R., Linskens, H.E. and Cresti, M. 1991. Pollen viability and pollen vigor. Theoretical and Applied Genetics, 81; 38-42.

[39] Ayala-Berdon, J., Galicia, R., Flores-Ortiz, C., Medellín, R.A. and Schondube, J.E. 2013. Digestive capacities allow the Mexican long-nosed bat (*Leptonycteris nivalis*) to live in cold environments. Comparative Biochemistry and Physiology Part A, 164; 622-628.

[40] Winder, J.A. 1977. Recent research on insect pollination of cocoa. Cocoa Growers Bulletin, 25; 11-19.

[41] Donald, P.F. (2004). Biodiversity impacts of some agricultural commodity production systems. Conservation biology, 18(1); 17-38.

[42] FAOSTAT. Food and Agriculture Organization of the United Regions. Crops. <http://www.fao.org/faostat/en/#data/QC>. (accessed on: 15.11.2019)

[43] Sonwa, D.J. 2004. Biomass management and diversification within cocoa agroforests in the humid forest zone of southern Cameroon. Cuvillier Verlag.

[44] Bos, M.M., Steffan-Dewenter, I. and Tscharntke, T. 2007. Shade tree management affects fruit abortion, insect pests and pathogens of cacao. Agriculture, Ecosystems & Environment, 120(2); 201-205.

[45] Clough, Y., Faust, H. and Tscharntke, T. 2009. Cacao boom and bust: Sustainability of agroforests and opportunities for biodiversity conservation. Conservation Letters, 2(5); 197-205.

[46] Schroth, P., Läderach, A.I., Martinez-Valle, C. and Bunn, L. 2016. Jassogne Vulnerability to climate change of cocoa in West Africa: patterns, opportunities and limits to adaptation. Sci. Total Environ., 556; 231-241.

[47] Asare, R., Asare, R.A., Asante, W.A., Markussen, B.O. and Ræbild, A. 2017. Influences of shading and fertilization on on-farm yields of cocoa in Ghana. Experimental Agriculture, 53(3); 416-431.

[48] Omolaja, S.S., Aikpokpodion, P., Oyediji, S., and Vwioko, D.E. (2009). Rainfall and temperature effects on flowering and pollen productions in cocoa. African Crop Science Journal, 17(1).

[49] Chumacero de Schawe, C., Durka, W., Tscharntke, T., Hensen, I., and Kessler, M. 2013. Gene flow and genetic diversity in cultivated and wild cacao (*Theobroma cacao*) in Bolivia. American journal of botany, 100(11); 2271-2279.

[50] Tondoh, J.E., Kouamé, F.N.G., Guéi, A.M., Sey, B., Koné, A.W. and Gnessougou, N. 2015. Ecological changes induced by full-sun cocoa farming in Côte d'Ivoire. Global Ecology and Conservation, 3; 575-595.

[51] Kaufmann, T. 1975. Studies on the ecology and

biology of a cocoa pollinator, *Forcipomyia squamipennis* I. & M. (Diptera, Ceratopogonidae), in Ghana. Bulletin of Entomological Research, 65(2); 263-268.

[52] Forbes, S.J. and Northfield, T.D. 2017. Increased pollinator habitat enhances cacao fruit set and predator conservation. Ecological applications, 27(3); 887-899.

[53] Adjaloo, M.K., Banful, B.K.B. and Oduro, W. 2013. Evaluation of breeding substrates for cocoa pollinator, *Forcipomyia* spp. and subsequent implications for yield in a tropical cocoa production system. American Journal of Plant Sciences, 4(2); 203-210.

[54] Perry, J., Lojka, B., Quinones Ruiz, L.G., Van Damme, P., Houška, J. and Fernandez Cusimamani, E. 2016. How natural forest conversion affects insect biodiversity in the Peruvian Amazon: Can agroforestry help? Forests, 7(4); 82.

[55] Cribb, B.W. 2000. Oviposition and maintenance of *Forcipomyia (Lasiohelea) townsvillensis* (Diptera: Ceratopogonidae) in the laboratory. Journal of Medical Entomology, 37(3); 316-318.

[56] Toledo-Hernández, M., Wanger, T.C. and Tscharntke, T. 2017. Neglected pollinators: Can enhanced pollination services improve cocoa yields? A review. Agriculture, ecosystems & environment, 247; 137-148.

[57] Aziz, S.A., Clements, G.R., McConkey, K.R., Sritongchuay, T., Pathil, S., Abu Yazid, M. N.H. and Bumrungsri, S. 2017. Pollination by the locally endangered island flying fox (*Pteropus hypomelanus*) enhances fruit production of the economically important durian (*Durio zibethinus*). Ecology and evolution, 7(21); 8670-8684.

[58] Deshpande, K., and Kelkar, N. 2015. How do fruit bat seed shadows benefit agroforestry? Insights from local perceptions in Kerala, India. Biotropica, 47; 654-659.

[59] Nakamoto, A., Kinjo, K. and Izawa, M. 2009. The role of Orii's flying-fox (*Pteropus dasymallus inopinatus*) as a pollinator and a seed disperser on Okinawa-jima Island, the Ryukyu Archipelago, Japan. Ecological Research, 24; 405-414.

[60] Oleksy, R., Racey, P.A. and Jones, G. 2015. High-resolution GPS tracking reveals habitat selection and the potential for long-distance seed dispersal by Madagascan flying foxes *Pteropus rufus*. Global Ecology and Conservation, 3; 678-692.

[61] Acharya, P.R., Racey, P.A., Sothibandhu, S. and Bumrungsri, S. 2015. Feeding behaviour of the dawn bat (*Eonycteris spelaea*) promotes cross-pollination of economically important plants in Southeast Asia. Journal of Pollination Ecology, 15; 44-50.

[62] Bumrungsri, S., Sriparaya, E., Chongsiri, T., Sridith, K. and Racey, P.A. 2009. The pollination ecology of durian (*Durio zibethinus*, *Bombacaceae*) in southern Thailand. Journal of Tropical Ecology, 25(1); 85-92.

[63] Lee, S.S., Yaakob, N.S., Boon, K.S. and Chua, L.S.L. 2002. The role of selected animals in pollination and dispersal of trees in the forest: implications for conservation and management. Journal of Tropical Forest Science, 234-263.

[64] Aziz, S.A., Olival, K.J., Bumrungsri, S., Richards, G.C. and Racey, P.A. 2016. The conflict between pteropodid bats and fruit growers: species, legislation and mitigation. In Bats in the Anthropocene: Conservation of bats in a changing world, pp. 377-426. Springer, Cham.

[65] Sheherazade, Ober, H.K. and Tsang, S.M. 2019. Contributions of bats to the local economy through durian pollination in Sulawesi, Indonesia. Biotropica.

[66] Mildenstein, T., Tanshi, I. and Racey, P.A. 2016. Exploitation of bats for bushmeat and medicine. In C. Voigt & T. Kingston (Eds.), Bats in the Anthropocene: Conservation of bats in a changing world, pp. 325-376. Springer Open.

- [67] Epstein, J.H., Olival, K.J., Pulliam, J.R., Smith, C., Westrum, J., Hughes, T. and Field, H.E. 2009. *Pteropus vampyrus*, a hunted migratory species with a multinational home-range and a need for regional management. *Journal of Applied Ecology*, 46(5); 991-1002.
- [68] O'shea, T.J., Cryan, P.M., Hayman, D.T., Plowright, R.K. and Streicker, D.G. 2016. Multiple mortality events in bats: a global review. *Mammal Review*, 46(3); 175-190.
- [69] Sritongchuay, T., Hughes, A.C. and Bumrungsri, S. 2019. The role of bats in pollination networks is influenced by landscape structure. *Global Ecology and Conservation*, 20, e00702.
- [70] Stover, R.H. and Simmonds, N.W. 1987. Classification of banana cultivars. In: Stover RH and Simmonds NW (ed.) *Bananas*, 3rd edn. Wiley, New York, pp. 97-103.
- [71] Itino, T.; Kato, M. and Hotta, M. 1991. Pollination ecology of the two wild bananas, *Musa acuminata* subsp. *halabanensis* and *M. salaccensis*: chiropterophily and ornithophily. *Biotropica*, 23(2); 151-158.
- [72] Liu, A.; Li, D.; Wang, H. and Kress, W.J. 2002. Ornithophilous and chiropterophilous pollination in *Musa itinerans* (*Musaceae*), a pioneer species in tropical rain forests of Yunnan, southwestern China. *Biotropica*, 34(2); 254-260.
- [73] Murphy, M.; Clare, E.L.; Rydell, J.; Yovel, Y.; Bar-On, Y.; Oelbaum, P. and Fenton, M. B. 2016. Opportunistic use of banana flower bracts by *Glossophaga soricina*. *Acta Chiropterologica*, 18(1); 209-213.
- [74] Bates, P., Francis, C., Gumal, M., Bumrungsri, S., Walston, J., Heaney, L. and Mildenstein, T. 2008. *Pteropus vampyrus*. The IUCN Red List of Threatened Species 2008:e.T18766A8593657. <http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T18766A8593657.en> (accessed on: 14.11.2019).
- [75] Eby, P. 1991. Seasonal movements of grey-headed flying-foxes, *Pteropus poliocephalus* (*Chiroptera: Pteropodidae*), from two maternity camps in northern New South Wales. *Wildlife Research*, 18(5); 547-559.
- [76] Kung, N.Y., Field, H.E., McLaughlin, A., Edson, D. and Taylor, M. 2015. Flying-foxes in the Australian urban environment—community attitudes and opinions. *One Health*, 1; 24-30.
- [77] Hengjan, Y., Saputra, V., Pramono, D., Basri, C., Ando, T., Ohmori, Y. and Hondo, E. 2018. Nighttime behavioral study of flying foxes on the southern coast of West Java, Indonesia. *Journal of Veterinary Medical Science*, 17; 0665.
- [78] Pedrozo, A.R., Gomes, L.A. and Uieda, W. 2018. Feeding behavior and activity period of three Neotropical bat species (*Chiroptera: Phyllostomidae*) on *Musa paradisiaca* inflorescences (*Zingiberales: Musaceae*). *Iheringia. Série Zoologia*, 108.
- [79] Dressler R.L. 1981. *The Orchids: Natural History and Classification*. Harvard University Press, Cambridge, MA.
- [80] Soto-Arenas, M.A. and Dressler, R.L. 2010. A revision of the Mexican and Central American species of *Vanilla Plumier ex Miller* with a characterization of their ITS region of the nuclear ribosomal DNA. *Lankesteriana*, 9(3); 285-354.
- [81] Anjos, A.M., Barberena, F.F.V.A. and Pigozzo, C.M. 2017. Biologia reprodutiva de *Vanilla bahiana* Hoehne (*Orchidaceae*). *Orquidário*, 30(3/4); 67-79.
- [82] Ramirez, S., Dressler, R.L. and Ospina, M. 2002. Abejas euglosinas (*Hymenoptera: Apidae*) de la Región Neotropical: Listado de especies con notas sobre su biología. *Biota colombiana*, 3(1).
- [83] Gigant, R.L., Rakotomanga, N., Goulié, C., Da Silva, D., Barre, N., Citadelle, G., and Besse, P. 2016. Microsatellite markers confirm self-pollination and autogamy in wild populations of *Vanilla mexicana* Mill. (syn. *V. inodora*) (*Orchidaceae*) in the Island of Guadeloupe in. *Microsatellite Markers*, 10, 64674.