



WAS THE EVOLUTION OF ANGIOSPERM-FRUGIVORE INTERACTIONS DRIVEN BY RECIPROCAL COEVOLUTION BETWEEN THEM?

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Abstract: The evolution of fruits contributed to the dominance of angiosperms and provided new ecological opportunities for frugivore vertebrates to diversify. However, it is not yet clear whether reciprocal coevolution between plants and frugivores drove the evolution of their mutualistic interactions. This review aimed at discussing major events of the evolution of fleshy-fruited angiosperms and their major seed dispersers, in order to elucidate if and how they responded to mutual selective pressures. Angiosperms evolved between the Mid and Late Cretaceous and they experienced a large diversification until the early Eocene. However, all main lineages of extant frugivores originated from the Eocene onward: frugivorous birds evolved in the Eocene but diversified in the Oligocene; primates evolved in the early Eocene and frugivorous bats diversified in the Oligocene-Miocene. This divergence in the times of the origins of angiosperm and their modern seed dispersers suggest that other animals interacted with early angiosperms. The most likely candidates are the rodent-like multituberculates. Several studies investigated how plant-frugivore mutualistic interactions contribute to the diversification in both plants and animals and we draw two main hypotheses from them: the plant-frugivore coevolutionary hypothesis and the neutral hypothesis. There are consistent evidences supporting each of these hypotheses, which suggest that they may not be mutually exclusives. An integrative approach is that plant-frugivore coevolution happens in pulses. Times of high environmental disturbances promote significant changes in mutualistic interactions and release new ecological opportunities for emerging species, which in turn exert stronger selective pressures and adaptive changes on fruit and frugivores traits. As evolving frugivores occupies those niches, interactions become more stable and coevolution is weaker and diffuse. We are currently undergoing a new period of unstable plant-frugivore interactions and we need more information on plant-frugivore coevolution in order to predict how species will respond to a changing world.

Keywords: coevolution; dispersal syndromes; fleshy fruits; mutualism; paleoecology.

INTRODUCTION

Frugivory is widespread in nature. Over 30% of the woody species in the forests of temperate zones and up to 90% in the tropical forests possess fleshy fruits that (Jordano 2017). These plants attract many vertebrates, including not only the three major extant frugivores, birds, bats and monkeys

(Jordano 2017), but also rodents (Sunyer *et al.* 2013), elephants (Bunney *et al.* 2017), ungulates (Albert *et al.* 2015), carnivores (Corlett 2017), fishes (Correa *et al.* 2018) and reptiles (Miranda 2017). For instance, a single plant genus, *Ficus*, is consumed by 10% of all bird species and 6% of all mammal species (Shanahan *et al.* 2001). Frugivory plays a pivotal role in sustaining and renewing biological populations

because many frugivores are seed dispersers and carry seeds away from parental plants, thus increasing seedling survival and promoting the colonization of new sites (Jordano 2017). Fruits and seed dispersal, together with flowers and their interactions with pollinators, were two of the most important features responsible for the evolutionary success of angiosperms (Gómez & Verdú 2012).

Seminal works on the evolution of plant-frugivore interactions were based on the framework developed for the study of pollination (Tewksbury 2002). They relied on the assumption that fleshy fruits evolved sets of traits, known as fruit syndromes (van der Pijl 1969), that match the biology of their respective frugivores, through coevolution (Gautier-Hion *et al.* 1985). For example, bird-dispersed fruits are often colorful because birds are visually-oriented, while many mammal-dispersed fruits are dull-colored since many species forage using olfactory cues (Lomáscolo & Schaefer 2010). The assumptions underlying the dispersal syndromes has allowed ecologists to test hypotheses on plant-frugivore coevolution, but findings are often controversial (Renoult *et al.* 2014). Some studies found correlations between the traits of frugivores and those of the fruits they eat which researchers attribute to coevolution (Schaefer *et al.* 2007, Lomáscolo *et al.* 2008, Lomáscolo & Schaefer 2010). On the other hand, many studies support that the evolution of dispersal syndromes would require strong directional selective pressure, but very few animals are obligate frugivores and most of them only consume fruits opportunistically (Correa *et al.* 2015, Jordano 2017, Nevo *et al.* 2018, Valenta *et al.* 2018). As a consequence, plant-frugivores interactions, are weak and diffuse, and tight coevolution between them is unlikely (Herrera 1985, Bascompte & Jordano 2007). Thus, such diffuse interactions would dilute the selective pressure of single consumers on plant traits and produce generalized sets of fruit traits (Valenta & Chapman 2018).

Coevolutionary hypotheses are hard to test, because they rely on predictions that are often difficult to find in the fossil record (Althoff *et al.* 2014). However, a fundamental requirement of these hypotheses is temporal congruence in species evolution and diversification, because the time scales of plant and animal evolution can be quite different and species cannot coevolve if they are

temporally too far apart from each other (Valenta & Chapman 2018). Therefore, if the mechanism behind the changes in the diversity of plants and frugivores through time is coevolution, we might expect to find evolutionary convergence in the timing of phylogenetic and ecological radiation of fleshy-fruited angiosperms and frugivores (Eriksson 2014).

This review aims to discuss the evolution of the mutualism between fleshy-fruited angiosperms and frugivores. We addressed three major questions: 1) When did fleshy-fruited angiosperms originated and how did fruit traits evolved through time? 2) Was there congruence in the timing of the evolution and radiation of fleshy fruits and their major extant frugivores? 3) What role did mutualistic interactions play in the evolution of fleshy-fruited angiosperms and frugivores? We concentrate on the interactions between fleshy fruits and birds, bats and monkeys, the three major groups of vertebrates that have been the most important seed dispersers since the peak in the diversification of fruit types in the Eocene. Moreover, in this review we use the term “fruit” regarding its ecological and functional rather than its botanical definition, in order to include different kinds of diaspores that can be consumed by vertebrate frugivores.

MATERIAL AND METHODS

We conducted a literature review on the evolution of plant-frugivore interactions from articles available at Google Scholar, the Web of Science and *Portal de Periódicos CAPES*. We conducted the bibliographic search by combining a wide array of search terms, such as “evolution”, “plant-frugivore interactions”, “frugivores”, “angiosperms”, “paleoclimate”, among others. For example, in order to acquire data on the origins of frugivorous primates, we started by applying the combination of terms evolution, primates and frugivory. Then, if needed, we refined the search with new, more specific terms. We did not apply any time filters to our results, in order to include important seminal researches on the topic as well as recent findings that contributed to the understanding of plant-frugivore interactions. Altogether, these searching methods allowed us to include a large number of papers in our review.

ORIGIN AND EVOLUTION OF FLESHY FRUITS AND FRUGIVORES

Fleshy fruits

Defining the exact origins of fleshy-fruited angiosperms is not an easy task because fruits are hardly well preserved in the fossil record (Colinvaux & Oliveira 2001). Therefore, the endeavor of gathering evidences on angiosperm evolution and the traits of ancient fleshy fruits relies largely on records of fossil seeds, because they are often better preserved than soft tissues, and correlations with traits of extant lineages (Eriksson 2008). This is a trustworthy approach because in modern angiosperms there is a strong positive correlation between seed size and fruit complexity and, thus, paleobotanists use seed size as a surrogate of plant diversity (Bolmgren & Eriksson 2010).

The fossil record indicates that the origin of angiosperms happened somewhere around 130 Mya, between the Mid and Late Cretaceous (Soltis & Soltis 2004, Butler *et al.* 2009). Although fleshy tissue around the seeds is even older and can be found in some old lineages of gymnosperms (e.g., cycads, Ginkgo spp.) (Tiffney 2004), it was in angiosperms that fruit diversity met its evolutionary success, expressed as the vast number of extinct and extant families that possess fleshy fruits and depended, or depends, on biotic seed dispersal. Fruits did not have had a single origin and they evolved independently and convergently many times throughout the history of angiosperms (Bolmgren & Eriksson 2010). For instance, in Rubiaceae fruits have evolved at least 12 times independently (Kainulainen *et al.* 2010) and in Solanaceae capsular fruits and berries evolved independently in different lineages (Särkinen *et al.* 2013). Arguably, the mainstream hypothesis of the evolution of fruits assumes that they are adapted to attract seed dispersers, even if originally they had other functions (Mack 2000, Tiffney 2004).

Fruits and seeds of the first angiosperms of the Cretaceous were very small and lacked adaptations to seed dispersers, which remained relatively unchanged for the next 50 Myr (McLoughlin & Pott 2018). In this geologic period, constant habitat disturbances greatly influenced early angiosperm evolution. Dinosaurs, the largest herbivores of the Cretaceous, inflicted strong

disturbances in the vegetation (Bakker 1978), just as modern large herbivores do (Omeja *et al.* 2014) and wildfires also had a significant impact on Earth's ecosystems (Brown *et al.* 2012). These disturbances most likely set the evolutionary stage for primitive angiosperms, selecting for small, fast-growing plants with corresponding small fruits, more suited for disturbed habitats (Brodrigg & Feild 2010). However, at approximately 80 Mya, angiosperm seed size, fruit size and fruit types started to diversify (Bolmgren & Eriksson 2010). This radiation accelerated following the largest mass extinction event on Earth's history, which wiped out all nonavian dinosaurs at the end of the Cretaceous-Paleogene Boundary (KPB) around 65 Mya. Vegetation structure changed drastically and angiosperms experienced a diversification burst until the early Eocene, around 50 Mya, when fruit diversity reached its peak (Brown *et al.* 2012) and all modern fruit types (i.e., dehiscent/indehiscent, dry/fleshy, apocarpous/syncarpous) were already set (Eriksson 2014). The transition between the Paleocene and the Eocene (~55 Mya), as well as the early Eocene, were marked by increases in Earth's temperature (Paleocene Eocene Thermal Maximum and early Eocene Climatic Optimum, respectively) (Smith *et al.* 2012). Consequently, during most of this phase the global landscape changed and highly diverse subtropical to warm temperate angiosperm-dominated forests extended as far as the high latitudes in the northern hemisphere (Townsend *et al.* 2010). This changing environment provided new, unexplored niches for evolving organisms and marked the first stage of the evolution of plant-frugivore interactions.

The diversification of angiosperms during the late Cretaceous can be explained by, at least, three different processes (Eriksson 2014). The coevolution between new plants and animals (especially small mammals) emerging at the early Eocene could somehow have favored large seeds. Alternatively, the vegetation transition from open habitats to closed forests in the early Tertiary increased competition for light in the understory and larger seeds were probably better competitors in these environments due to their larger reserves (Tiffney 2004). Or the angiosperms evolving in the forests of the early Tertiary could have been taller and, consequently, had larger seeds than their ancestors of the late Cretaceous (Moles 2005). It is

not yet clear which of these processes was the main driver of angiosperms diversification (Fleming & Kress 2011), but it seems that plant size, seed size and biotic dispersal are coadapted traits that evolved together in the early Tertiary (Eriksson 2008).

This scenario remained until the Eocene-Oligocene transition (EOT, between ca. 34–33.5 Mya), when Earth's environment suffered another drastic change, followed by the most significant mass extinction event since the end of the Cretaceous (Pound & Salzmann 2017). Earth became much cooler and the southern hemisphere became drier (Bowen 2007). Lower temperatures, associated with strong tectonics and sea-level fall (Pound & Salzmann 2017), changed plant diversity and forests distribution worldwide, with a pronounced contraction of tropical forests to low latitudes and the emergence of temperate forests in the northern hemisphere and grasslands at higher latitudes (Jaramillo *et al.* 2006). The large rainforests from the Tertiary were replaced by more open woodlands and savannas, with lower vegetation (Abello *et al.* 2018). As a consequence of such massive changes in Earth ecosystems and the subsequent turnover in flora diversity, animal communities experienced a significant transformation (Lindow & Dyke 2006, Buerki *et al.* 2013, Pound & Salzmann 2017). The most prominent frugivores of the late-to-mid Eocene, which included small browsers and arboreal forest-dwelling mammals, went extinct, thereby releasing niche space for another species to exploit, such as flying frugivores (Eriksson 2014).

Therefore, three major evolutionary moments summarizes the history of angiosperms and fruits from the Cretaceous up to the EOT (Table 1). The first comprehends an initial phase from the origins of angiosperms ca. 130 Mya to approximately 80 Mya, when fruits and seeds were small and lacked adaptations for seed dispersers. Then, angiosperms experienced a radiation phase from 80 Mya until the early Eocene (ca. 50 Mya) when seed size and fruit diversity increased and reached its peak, rainforests covered much of the Earth's land surface and the first groups of modern frugivores appeared. Finally, a turnover phase took place following the EOT, when temperate forests replaced tropical forests in the higher latitudes and the major lineages of extant frugivores evolved and diversified. In the next sections, we will discuss the evolution of

frugivores in each of these three moments and, finally, if they played any role at all in the evolution and diversification of fruit traits.

Frugivores

Vertebrate seed-dispersal is much older than the rise of fleshy-fruited angiosperms, going back 300 Myr (Tiffney 2004). For instance, herbivorous dinosaurs possibly dispersed the seeds of cycads and conifers in the early Cretaceous (Fleming & Kress 2011). However, these associations were rather fortuitous (Tiffney 2004) and until the late Cretaceous fruits and seeds lacked adaptations for vertebrate seed dispersal, which only evolved during the radiation phase of angiosperms between 80 Mya and the early Eocene (Eriksson 2008). Therefore, the evolution of legitimate frugivory occurred only after the end of the first phase of angiosperm diversification (80–50 Mya) (Eriksson 2014). Therefore, frugivores only began to interact with plants long after these had already evolved (Fleming & Kress 2011). For instance, birds, monkeys and bats are arguably the most important extant frugivores (Jordano 2017) and they only became legitimate seed dispersers long after the peak in angiosperm diversification (i.e., early Eocene), especially during the Oligocene and the Miocene (34–10 Mya), when most of the modern lineages of frugivores evolved (Fleming & Kress 2011).

Birds, are the main consumers of fleshy-fruits and they interact with twice as many plant families than bats and monkeys (Fleming & Kress 2011). Frugivory can be found in all major clades of birds (Palaeognathae, Galloanserae and Neoaves) and it is supposed to have evolved multiple times in the group (Cracraft *et al.* 2003). Considering the representativeness of birds in the extant frugivore fauna, they were suggested to have laid the basis for the evolution of frugivory in other groups, especially euprimates (Fleming & Kress, 2011), but this hypothesis does not find much support (Eriksson 2014). The first records of bird evolution date back to the Late Jurassic (Xu *et al.* 2014), but the major orders that include extant frugivores evolved much later, in the rapid diversification of the group following the mass extinction of the KPBB (Jarvis *et al.* 2014). Nonetheless, clear evidences of frugivory in birds just appeared in trogons of the early Eocene (Kristoffersen 2002). Furthermore, passerines, the most speciose order of birds which

Table 1: Characteristics of the main phases of angiosperm evolution from the Early Cretaceous up to the Eocene-Oligocene Transition.

	FIRST PHASE	DIVERSIFICATION PHASE	TURNOVER PHASE
Period	Early - Mid Cretaceous (~130 Mya to ~80 Mya)	Late Cretaceous – Eocene (~80 Mya to ~50 Mya)	Following the EOT (~34 Mya)
Global climate	Warm	Warm	Cool
Major events	Origin of angiosperms Largest mass extinction in Earth's history (during KPB)	Burst of angiosperm diversification Liberation of new niches for evolving frugivores	Global cooling Second largest mass extinction in Earth's history Origin and diversification of extant frugivores
Vegetation	Dominion of ferns, conifers and extinct Bennettitales. Open woodlands.	Large angiosperm-dominated tropical and warm-temperate forests from the Equator to the highest latitudes Closed rainforests Taller trees	Replacement of tropical forests by temperate forests and grasslands in higher latitudes Replacement of large rainforests by savannas and open woodlands
Angiosperms traits	Small and fast-growing plants Small fruits and seeds Abiotic seed dispersal	Increase in fruit and seed size Establishment of all modern fruit types Abiotic and biotic seed dispersal	Slight decrease in fruit and seed size Mainly biotic seed dispersal
Major frugivores	Ocasional frugivores and the Multituberculata	Multituberculata and plesiadapiforms	Birds, monkeys and bats

includes ca. of 60% of all living avian species and most of the frugivorous species, are even younger, dating back to the late Oligocene (Lindow & Dyke 2006, but see Ericson et al. 2003 for a discussion on an earlier origin of passerines in Australia). Birds were the first frugivorous group to exploit the flying niche, which they would later share with bats, and it clearly provided them with many advantages, specially the ability to easily access a resource that became more patchily distributed in the late Eocene (Eriksson 2014).

The second most important seed dispersers are primates. More than 90% of all living primate species consume fruits (Lambert 2011). In tropical forests, primates may represent 25% to 40% of all frugivore assemblages (Chaves et al. 2018). According to Sussman et al. (2013), euprimates (i.e., “primates of modern aspect”) evolved in the Paleocene-Eocene transition (~55 Mya), roughly at the same time of the first frugivorous birds.

They were considerably fruit eaters, which can be attributed to morphological adaptations (grasping feet, low-crowned molar teeth, orbital convergence) to a frugivorous diet (Bloch *et al.* 2002). Euprimates evolved in a very close relationship with fleshy-fruited angiosperms, because speciation and diversification rates were higher and extinction rates were lower in those lineages that established mutualistic interactions with fleshy-fruits (Gómez & Verdú 2012). The importance of these interactions for the evolution and diversification of euprimates is deeply expressed in the prevalence of fruits in the diets of most extant primates (Chapman & Dunham 2018).

Finally, bats belong to the second most diverse order of mammals, with ca. of 20% of all living mammal species. The two families in which frugivory evolved as the main feeding habit are the Pteropodidae (Old-World fruit bats), with 171 frugivorous species, and Phyllostomidae (leaf-

nosed bats), with approximately 96 frugivorous species (Dumont 2003). Together, these two families account for over 350 species and nearly a third of all bat species (Rojas *et al.* 2012). The evolutionary history of bats is poorly understood because their fragile bones are hardly preserved in the fossil record and their phylogenies are conflicting (Jones *et al.* 2005). Nevertheless, the oldest known fossil bat (*Icaronycteris index*) is supposed to be at least 53 million years old (Simmons & Geisler 1998) and, thus, their origins can be traced back to the early Eocene. Many bat lineages were already established by the middle Eocene, suggesting a rapid diversification of the group (Simmons 2005). However, unlike birds and primates, which already displayed frugivory by the early Eocene, the first bats were small and insectivorous (Simmons & Geisler 1998, Simmons & Conway 2003). Pteropodids diverged from this primitive ancestral lineage at sometime around 28 to 18 Mya, in the Oligocene (Teeling 2005). Phyllostomid bats evolved in the early Oligocene (30.8–33.3 Mya) (Rojas *et al.* 2016), but frugivorous lineages evolved later, during the late Oligocene and early Miocene (~20 Mya) (Rojas *et al.* 2012, Baker *et al.* 2016). The congruence in the origins of frugivory in phyllostomids and pteropodids supports the hypothesis that global shifts in the distribution of tropical forests facilitated the evolution of frugivory in these two lineages (Baker *et al.* 2012). As for primates, the evolution of frugivory in bats opened new ecological opportunities for the evolution of the group and has driven accelerated diversification within both phyllostomids and pteropodids (Dumont *et al.* 2012, Shi & Rabosky 2015).

CONVERGENCE IN THE TIMING OF THE ORIGINS OF FLESHY-FRUITED ANGIOSPERMS AND THEIR SEED DISPERSERS

All major extant frugivores, birds, monkeys and bats, evolved throughout the Eocene (55–34 Mya) and later in the Oligocene/Miocene (34–10 Mya), when angiosperm diversity was already high. However, seed size, fruit size and plant diversity started to increase much earlier, in the late Cretaceous, and continued to increase into the transition with the Tertiary (Bolmgren & Eriksson 2010, Eriksson 2014). This evidence suggests a mismatch of tens of millions of years in the timing of the evolution

of modern seed dispersers and their core food plants (Fleming & Kress 2013). For example, the bat subfamily Stenodermatini is largely recognized as a specialist on fruits of Moraceae, especially *Ficus* (Sánchez & Giannini 2018). However, Stenodermatini evolved at 16.8 Mya (Rojas *et al.* 2016), while *Ficus* is nearly 75 millions of years old (Särkinen *et al.* 2013). Altogether, these evidences imply that other groups of frugivores participated in the early phase of interactions with fleshy-fruited angiosperms.

Dinosaurs have been suggested as such frugivores (Bakker 1978, Barrett 2014), but there is considerable debate on this assumption, mainly because it is unlikely that these large animals relied strongly on the small fruits of early angiosperms (Butler *et al.* 2009). Fishes were among the first frugivorous of the Late Cretaceous, but their role on the evolution of fleshy fruits is still largely conjectural and, if at all, it was obviously restricted to wetland plants (Correa *et al.* 2015, 2018). Some other animals, like small lizards (Olesen & Valido 2003) and marsupials (Tiffney 2004), were potential frugivores and dispersal agents of early angiosperms until the KPB, but these animals were omnivorous and probably consumed fruits occasionally (Tiffney 2004).

Notwithstanding, compelling evidences indicate that the most important early frugivores of fleshy fruits were the extinct plesiadapiforms and mainly the multituberculates (Eriksson 2014). Plesiadapiforms were primate-like arboreal mammals of the Paleocene (Bloch *et al.* 2007). Their fossil morphology suggest that they were omnivorous, but that they occasionally included fruits in their diet (Boyer *et al.* 2010, Chester & Beard 2012). Given that they were an abundant and highly diversified clade, they were probably casual seed dispersers of early angiosperms fleshy fruits. Likewise, multituberculates were small, rodent-like mammals that evolved in the middle Jurassic (~165 Mya) and were the most successful lineage of mammals in the Mesozoic (Wilson *et al.* 2012, Yuan *et al.* 2013). Their unique dental complexity indicates that they had a high range of feeding habits, including carnivory, insectivory, omnivory, granivory and also frugivory (Wilson *et al.* 2012). This group started to diversify around 20 Mya before the KPB, which coincides with the growing diversification of angiosperms and

fruits, and they shifted toward a plant-dominated diet throughout the end of the Cretaceous and in the early Paleocene, at least partially due to the growing availability of new and unexplored plant-feeding niches (Wilson *et al.* 2012). The demise of plesiadapiforms and multituberculates by the Eocene released ecological opportunities that were gradually occupied by the evolving lineages of modern frugivores (Boyer *et al.* 2012).

WHAT IS THE ROLE OF MUTUALISTIC INTERACTIONS IN THE (CO)EVOLUTION OF FLESHY-FRUITED ANGIOSPERMS AND FRUGIVORES?

Species coevolution are driven by one of the most powerful forces in the nature: ecological interactions (Thompson 1999, Hembry *et al.* 2014). For instance, interspecific competition is supposed to be one of the main causes of coevolutionary divergence among species (Connell 1980, Schluter 2010) and predation promote evolutionary diversification of both predator and prey species (Zu *et al.* 2016, Pontarp & Petchey 2018). On the other hand, mutualistic interactions between animals and plants comprise some of the putative examples of species coevolution, such as yucca and yucca moths (Pellmyr & Leebens-Mack 1999), figs and fig wasps (Wiebes 1979), ants and myrmecophytes (Brouat *et al.* 2001) and many others. Despite being tightly related to coevolutionary processes, obligate mutualisms are relatively uncommon in nature and, therefore, the role of facultative mutualisms (*e.g.*, plant-frugivore interactions) on species evolution is not so clear (Rojas *et al.* 2016). Several studies investigated how plant-frugivore mutualistic interactions contribute to the diversification in both plants and animals, but their findings are highly controversial (Eriksson 2008, Lomáscolo & Schaefer 2010, Lotan & Izhaki 2013, Nevo & Valenta 2018, Ramos-Robles *et al.* 2018). From these divergent results, we draw to main hypotheses concerning the evolutionary relationship between angiosperms and frugivores: the plant-frugivore coevolutionary hypothesis and the neutral hypothesis.

The neutral hypothesis is based on Hubbell's (2001) Neutral Theory, which assumes that species are functionally equivalents and, for that reason, ecological and evolutionary process are established

randomly. It arose as the assumptions underlying the dispersal syndromes were rarely confirmed in the field (Valenta & Chapman 2018). Early studies on plant-frugivore coevolution hypothesized that dispersal syndromes would be a widespread phenomenon in nature (Tewksbury 2002), but they failed to support this hypothesis because tight associations between frugivores and fleshy-fruits are not common (Herrera 1985). In fact, most plant-frugivore interactions are weak and diffuse (Bascompte & Jordano 2007), *i.e.* plant and frugivores do not depend highly on each other and interact in a group-wise manner (Eriksson 2014). Consequently, any singular directional selective pressure exerted by a frugivore on a plant trait would be attenuated by other frugivores, which in turn would make paired coevolution between them unlikely (Bascompte & Jordano 2007). Diffuse coevolution is advantageous for fruiting plants because relying on multiple partners provides functional redundancy of seed dispersal services and promote its continuity even after the loss of one frugivore species (Rother *et al.* 2015).

There are considerable evidences supporting the neutral hypothesis of plant-frugivore evolution. For example, the first phase of angiosperm diversification (80~50 Mya) happened before, not rarely by a great amount of time, the origins of many modern frugivores (Fleming & Kress 2011), and, thus, they can be excluded from any potential coevolution with early angiosperms (Eriksson 2014). Moreover, the astonishing diversity of fruit traits may be attributed to phylogeny (Valenta *et al.* 2018), climate (Buerki *et al.* 2013) and geographic distribution (Hampe 2003). Also, transformations of fruit types may not depend on strong selective pressure by frugivores because their ontogenies are very similar and can happen without major changes in their genetic structure (Seymour *et al.* 2013, Eriksson 2014). Furthermore, recent studies on ecological network demonstrated that many plant-frugivore interactions are randomly established, *i.e.* the probability of interaction between species is a product of their relative abundances (Fort *et al.* 2016).

Regarding the plant-frugivore coevolution hypothesis, despite the scarcity of evidences supporting strong correlations among fruit traits, many studies found that frugivores may influence at least some of them (Herrera 1985, 1998, Yoder

& Nuismer 2010, Day & Kokko 2015, Brodie 2017). Fruit size is probably the example that stands out, because there is a significant trend towards a positive correlation between frugivores body size and fruit size, suggesting that the latter is an important feature mediating plant-frugivore interactions (Wheelwright 1985, Bach & Kelly 2004, Lord 2004, Burns 2013, Pires & Melo unpublished data). For instance, Galetti *et al.* (2013) demonstrated that the loss of large-bodied frugivorous birds (*i.e.*, toucans) led to a reduction of seed size of a keystone palm species in less than 100 years, suggesting that human-induced defaunation of large frugivores may cause changes in the evolutionary trajectories of animals and plants. Other fruit traits, such as coloration, odor and display evolved as a response to the sensorial biology of frugivores (Lomáscolo *et al.* 2008, Lomáscolo & Schaefer 2010, Baker *et al.* 2012, Valenta *et al.* 2013, Stournaras & Schaefer 2017, Nevo & Valenta 2018). From the animal's perspective, the evolution of specialized structures such as teeth morphology in mammals (Corlett 2017) and some bill shapes in birds (Jordano 2017) are also the outcome of directional selection towards frugivory. Moreover, despite that extant frugivores only appeared after the origins of their plant resources, plant-frugivore interactions may have prompted diversification of bats (Rojas *et al.* 2012), primates (Gómez & Verdú 2012), birds (Kissling *et al.* 2009) and crown lineages of plants (Fleming & Kress 2011, Sánchez & Giannini 2018).

The large amount of credible evidence supporting either the plant-frugivore coevolutionary hypothesis or the neutral hypothesis may indicate that they are not mutually exclusive and advocate for the need of an integrative theoretical framework of the dynamics of angiosperm-frugivore evolution. In this sense, Eriksson (2014) proposed that the coevolution between fleshy-fruited angiosperms and frugivores occurs in pulses. According to this proposal, coevolutionary plant-frugivore interactions are stronger in periods of high environmental disturbances, such as climate change, orogeny, tectonics, species turnover, etc. These disturbances often promote significant changes in mutualistic interactions and release ecological opportunities for emerging species, which in turn exert stronger selective pressures and adaptive changes on fruit and frugivores

traits (Eriksson 2014). This in accordance with paleontological evidence, because the phylogenetic radiation of modern frugivores happened after the mass extinction of the KPBB and converged with the peak of angiosperm diversification in the Eocene (Fleming & Kress 2011), and their ecological radiation happened throughout the drastic changes in the Eocene-Oligocene (Pound & Salzmann 2017) and the Oligocene-Miocene (Beddow *et al.* 2016). Moreover, considering that we are facing times of strong human-induced environmental changes and unparalleled rates of species loss (Barnosky *et al.* 2011), the hypothesis of pulses in coevolution can also explain why the evolutionary response of seed size to defaunation happened in such a short time (Galetti *et al.* 2013, Brodie 2017). These periods of strong coevolution between frugivores and fleshy-fruited angiosperms are interspersed by periods of more stable and weaker interactions, as the previously opened niches become saturated by evolving frugivores, decreasing subsequent co-diversification (Eriksson 2014, Price *et al.* 2016). The stability of plant-frugivore interactions undermines the strength of directional selective pressures, thus promoting diffuse, group-wise coevolution, rather than pairwise coevolution (Costa *et al.* 2018).

Eriksson (2014) argued that angiosperm diversification from the Late Cretaceous to the Eocene (80~55 Mya) may represent a long pulse of strong reciprocal coevolution between fleshy-fruits and the multituberculates and that since then coevolutionary pulses became weaker and more localized in space and time. He also suggests that we are currently undergoing a new period of unstable plant-frugivore interactions, which started with the extinction of large-bodied mammals in the Late Quaternary (Lorenzen *et al.* 2011). If this holds true, evolutionary information on plant-frugivore interactions can be used for conservational purposes as we can predict that fruit and animal traits will rapidly respond to the loss of interacting partners (Galetti *et al.* 2013). Therefore, future research will benefit as more refined phylogenies of fleshy-fruited angiosperms and frugivores become available, which will allow us to test for taxon-specific patterns and identify more accurately when coevolution drives plant-frugivore interactions (Eriksson 2014).

CONCLUSIONS

The evolution of fleshy-fruited angiosperms marked a novel time in the history of life on Earth and understanding the dynamics of plant-frugivore evolution is fundamental for the conservation of these mutualistic interactions in face of the severe environmental changes that threatens biodiversity worldwide. The dispersal syndromes hypothesis states that tight associations between the morphologies of plants and frugivores are evidences of their coevolution. Nonetheless, field studies only rarely find strong trait matching between them, casting doubt on coevolutionary interpretations of plant-frugivore interactions. Although birds, monkeys and bats, the three major extant frugivores, only evolved after angiosperm diversity was already high, there is considerable congruence on the radiation of many modern frugivore lineages and that of the core plants they consume. These evidences suggest that angiosperm-frugivore coevolution may happen in pulses and that it is stronger in times when interaction networks face strong disturbances. This is of particular interest for biological conservation, because human activities are greatly influencing species interactions around the world, which can result in profound evolutionary consequences for biodiversity.

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