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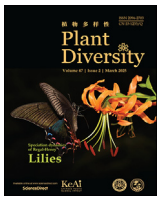

Review article

Seed dispersal by deception: A game between mimetic seeds and their bird dispersers

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ABSTRACT

Mimetic seeds attract birds to disperse seeds mainly by mimicking fleshy fruits or arillate seeds, however, they provide little nutritive reward for bird dispersers. The key characteristics of mimetic seeds are conspicuous seed color, hard seed coat, certain toxic secondary metabolites, and perhaps smooth waxy layer. In this review, we discuss the global distribution of mimetic seeds, the interaction of mimetic seeds with bird dispersers, and secondary metabolites that underlie key characteristics of mimetic seeds. Mimetic-seed species mainly occur in the tropics, with large numbers distributed along coastal areas. The interaction between mimetic-seed species and bird dispersers can be antagonistic, mutualistic, or both. These interactions are generally established by conspicuous visual cues and hard tactile cues from mimetic seeds. The formation and variation of key characteristics of mimetic seeds may contribute to the metabolism of several kind of secondary compounds. Here, we also discuss mimetic-seed dispersal in the context of an evolutionary game, and propose several aspects of mimetic-seed dispersal that remain unstudied. While this review is based on preliminary findings and does not account for other potential influencing factors such as climate, it is expected to contribute to an improved understanding of mimetic-seed dispersal.

1. Introduction

Plant-animal interactions are formed and maintained by signals and the transmission of energy (Schaefer et al., 2004; Sinnott-Armstrong et al., 2020; Neu et al., 2023). In mutualistic interactions, plants generally offer nutritive reward (e.g., nectar, fruit pulp, elaiosome) to attract potential pollinators or seed dispersers, and in some cases, plants signal their reward through visual or olfactory cues (Schaefer et al., 2008; Cazetta et al., 2012; Nevo et al., 2019; Stephens et al., 2020). Plants have evolved to exploit deceptive signals that attract potential pollinators or seed dispersers but provided little reward, which is common in mimicry systems (Schaefer and Ruxton, 2009; Pfeiffer et al., 2010; Midgley et al., 2015). In these mimicry systems, plant–animal interactions usually involve a tripartite of players: the mimic, the model, and the dupe (Pasteur, 1982).

Mimetic-seed dispersal involves a tripartite interaction between the mimetic seeds (the mimic), the fleshy fruits, arillate seeds or perhaps insects (the model), and frugivorous birds (the dupe). Mimetic seeds (or imitative seeds), a group of highly conspicuous seeds with little nutritive reward (e.g., fleshy aril, pulpy testa), have been proposed to mimic fleshy fruits or arillate seeds consumed by frugivorous birds (van der Pijl, 1982). They usually have a glossy appearance with contrasting red, black, or red-black seed color, smooth but hard seed coat, are retained on the mother plant for prolonged time, and contain certain toxic secondary metabolites (van der Pijl, 1982; Peres and van Roosmalen, 1996; Galetti, 2002, Tables 1 and 3). Previous research has identified at least 46 mimetic-seed species in 24 genera and 10 families, with most cases occurring within the Fabaceae, and has shown that mimetic-seed species are predominantly found in tropical regions (Table 1 and Fig. 1). Additionally, we define potential mimetic-seed species as those that produce seeds sharing similar characteristic of mimetic

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Table 1
The key characteristics of mimetic-seed species in angiosperm.

Species	Fruit type	The color of seed (or fruit)	The color of other parts	Type of seed nutriment	References
Allium tricoccum	Capsule	Black	Pale brown capsule	0	van der Pijl (1982), p.41; Galetti (2002), Table 12.1
Pollia condensata	Capsule	Metallic blue (fruit)	Green capsule	0	Vignolini et al. (2012)
Gahnia beecheyi	Nutlet	Bicolored, black and red (nut)	Black glumes	0	van der Pijl (1982), p.45
Gahnia sieberiana	Nutlet	Red or red-brown, shiny (nut)	Black glumes	0[a]	Galetti (2002), Table 12.1
Abarema spp.	Pod	Bicolored, blue-white	Orange pod	0[a]	Galetti (2002), Table 12.1
Abrus precatorius	Pod	Bicolored, red and black, shiny	Pale brownish pod	0	Ridley (1930), p.430; van der Pijl (1982), p.40; Galetti (2002), Table 12.1; Brancalion et al. (2010), fig. 1
Adenanthera aglaosperma	Pod	Bicolored, scarlet red with a black dot at the tip	Dark brown pod	0	Ridley (1930), p.430
Adenanthera pavonina	Pod	Bright red	Brownish black outside, light brown inside pod	0	Ridley (1930), p.430; van der Pijl (1982), p.40; Brancalion et al. (2010), fig. 1; Jaganathan et al. (2018)
Adenanthera	Pod	Red; bicolored, black and red	Orange pod	0	Galetti (2002), Table 12.1
Archidendron clypearia	Pod	Black	Orange outside and red inside pod	0[a]	Ridley (1930), p.430; van der Pijl (1982), p.43
Archidendron ellipticum	Pod	Black seed with a pale bluish bloom	Dull red pod	0[a]	Ridley (1930), p.430
Archidendron hendersonii	Pod	Black	Red pod	0[a]	van der Pijl (1982), p.43
Archidendron microcarpum	Pod	Black	Very conspicuous orange pod	0[a]	Ridley (1930), p.430
Archidendron spp.	Pod	Black	Orange to red pod	0[a]	Galetti (2002), Table 12.1
Batesia floribunda	Pod	Red	Brown pod	0	van der Pijl (1982), p.43; Galetti (2002), Table 12.1
Dermatophyllum secundiflorum	Pod	Red	Brown pod	0	Galetti (2002), Table 12.1
Erythrina spp.	Pod	Red; bicolored, red and black	Black pod	0	Ridley (1930), p.430; Galetti (2002), Table 12.1
Erythrina velutina	Pod	Red	Black pod	0	Brancalion et al. (2010), fig. 1
Jupunba brachystachya	Pod	Bicolored, white and bluish-black	Brown inside valves	0	van der Pijl (1982), p.43
Jupunba langsdorffii	Pod	Bicolored, bluish black and white	Red inside valves	0	Brancalion et al. (2010), fig. 1
Ormosia arborea	Pod	Bicolored, red and black	Dark brown valves	0	Galetti (2002); Guimarães et al. (2003); Brancalion et al. (2010), fig.1
Ormosia bopiensis	Pod	Bicolored, orangish red and black	Brown pod	0	Foster and Delay (1998); Foster (2008)
Ormosia isthmensis	Pod	Bright rosy red, glossy	Brown pod	0	Foster and Delay (1998)
Ormosia lignivalvis	Pod	Bicolored, scarlet and black	Brown pod	0	Peres and van Roosmalen (1996)
Ormosia macrocalyx	Pod	Bright orangish red	Light brown pod	0	Foster and Delay (1998); Foster (2008)
Ormosia monosperma	Pod	Bicolored, red and black	Brown pod	0	van der Pijl (1982), p.40
Ormosia spp.	Pod	Red; bicolored, black and red	Brown pod	0	Galetti (2002), Table 12.1
Pararchidendron pruinosum	Pod	Shiny black	Reddish orange pod	0	Galetti (2002), Table 12.1
Pithecellobium spp.	Pod	Black	Pink pod	–	Galetti (2002), Table 12.1
Rhynchosia mannii	Pod	Bluish black	Reddish brown inside, light brown outside pod	0	van der Pijl (1982), p.44
Rhynchosia melanocarpa	Pod	Bicolored, red and black	Red pod	0	Pizo et al. (2020)
Rhynchosia phaseoloides	Pod	Bicolored, red and black	Brown pod	0	van der Pijl (1982), p.44
Rhynchosia pyramidalis	Pod	Bicolored, red and black	Dark brown pod	0	van der Pijl (1982), p.44; Garwood and Lighton (1990)
Rhynchosia spp.	Pod	Bicolored, black and red	Brown pod	0	Galetti (2002), Table 12.1
Sterculia brevissima	Follicle	Black	Red follicle	1	Schaefer and Ruxton (2009)
Sterculia spp.	Follicle	Blue to black	Bright scarlet follicle	1	Ridley (1930)
Brackenridgea nitida	Drupe	Black	Red calyx	1[a]	Galetti (2002), Table 12.1
Campylospermum elongatum	Drupe	Black	Red calyx	1[a]	Galetti (2002), Table 12.1
Ochna atropurpurea	Drupe	Black, glossy	Red calyx	1[a]	Galetti (2002), Table 12.1
Paeonia spp.	Follicle	Black	Red follicle	0[a]	Galetti (2002), Table 12.1
Glochidion spp.	Capsule	Orange or pink	Brown capsule	1	Ridley (1930), p.429
Glochidion zeylanicum var. *zeylanicum*	Capsule	Orangish red	Brown capsule	1[a]	Galetti (2002), Table 12.1
Margaritaria nobilis	Capsule	Metallic blue	Green capsule	1	van der Pijl (1982), p.43; Cazetta et al. (2008)
Margaritaria spp.	Capsule	Metallic blue	Green capsule	1[a]	Galetti (2002), Table 12.1
Melicope ternata	Follicle	Black	Brown follicle	0[a]	Burns (2005)
Harpullia arborea	Capsule	Black	Yellow capsule	0[a]	Galetti (2002), Table 12.1

In "Type of seed nutriment", "0" indicates hard seeds without an edible part, whereas "1" indicates seeds with a thin fleshy testa or other eatable parts.
[a] Characteristic is uncertain.

Table 2
Several mimetic-seed species and their bird dispersers.

Species	Bird dispersers	Family; Genus	Size	Key characteristics	References
Pollia condensata	Birds	–	–	–	Vignolini et al. (2012)
Gahnia beecheyi	*Pycnonotus bimaculatus*	Pycnonotidae; *Pycnontus*	20 cm; 30 g	Resident; Frugivorous	van der Pijl (1982), p. 41; AV; DN; IN
Abrus precatorius	Cockatoos	Cacatuidae	–	–	van der Pijl (1982), p. 41
Adenanthera pavonina	Barbets	Capitonidae	–	–	van der Pijl (1982), p. 41
Ormosia arborea	*Ramphastos toco*	Ramphastidae; *Ramphastos*	61 cm; 592–760 g	Resident; Arboreal; Frugivorous	Galetti (2002); ADW; DN
	Pipile jacutinga	Cracidae; *Pipile*	63.5–74 cm; 1100–1400 g	Resident; Arboreal; Frugivorous	Galetti (2002); AV; DN; EB
	Penelope obscura	Cracidae; *Penelope*	68–75 cm; 960–2100 g	Resident; Frugivorous	Galetti (2002); AV; DN; IN
	Psophia viridis	Psophiidae; *Psophia*	45–52 cm; 1071 g	Resident; Terrestrial; Frugivorous	Galetti (2002); AV; DN
Ormosia isthmensis	*Eucometis penicillata*[a]	Thraupidae; *Eucometis*	16–17 cm; 27–19 g	Resident; Arboreal; Invertivorous	Foster and Delay (1998); AV; DN
	Myiodynastes luteiventris[a]	Tyrannidae; *Myiodynastes*	8.5–21.6 cm; 45.4 g	Migratory; Arboreal; Omnivorous	Foster and Delay (1998); AV; CCNAB; DN; IN
	Empidonax minimus[a]	Tyrannidae; *Empidonax*	12.5–14 cm; 8–13 g	Migratory; Arboreal; Invertivorous	Foster and Delay (1998); AV; DN; IN
Ormosia lignivalvis	*Tinamus major*	Tinamidae; *Tinamus*	40–46 cm; ♂700–1142 g, ♀945–1249 g	Resident; Terrestrial; Omnivorous	Peres and van Roosmalen (1996); AV; DN
	Mitu tuberosum	Cracidae; *Mitu*	83–89 cm; 3860 g	Resident; Terrestrial; Frugivorous	Peres and van Roosmalen (1996); AV; DN
	Psophia leucoptera	Psophiidae; *Psophia*	45–52 cm; 1280–1440 g	Resident; Terrestrial; Frugivorous	Peres and van Roosmalen (1996); AV; DN
	Mitu mitu	Cracidae; *Mitu*	83–89 cm; ♂2960 g, ♀2745 g	Resident; Terrestrial; Frugivorous	Peres and van Roosmalen (1996); AV; DN
	Penelope jacquacu	Cracidae; *Penelope*	66–76 cm; ♂1242–1360 g, ♀1142 g	Resident; Terrestrial; Frugivorous	Peres and van Roosmalen (1996); AV; DN
	Psophia crepitans	Psophiidae; *Psophia*	45–52 cm; 985–1058 g	Resident; Terrestrial; Frugivorous	Peres and van Roosmalen (1996); AV; DN
Ormosia macrocalyx	Unidentified passerines	Passeriformes	–	–	Foster and Delay (1998)
Paeonia officinalis	*Sylvia atricapilla*	Sylviidae; *Sylvia*	14 cm; 8.5–31 g	Migratory; Omnivorous	Andrieu and Debussche (2007); AV; DN
	Erithacus rubecula	Muscicapidae; *Erithacus*	14 cm; 14–25 g	Migratory; Omnivorous	Andrieu and Debussche (2007); AV; DN
	Turdus merula	Turdidae; *Turdus*	24–27 cm; 94.6–97.1 g	Migratory; Arboreal; Omnivorous	Andrieu and Debussche (2007); AV; ADW; DN
	Turdus philomelos	Turdidae; *Turdus*	20–23 cm; 50–107 g	Migratory; Terrestrial; Omnivorous	Andrieu and Debussche (2007); AV; DN
Margaritaria nobilis	*Turdus leucomelas*	Turdidae; *Turdus*	23–27 cm; 47–78 g	Migratory; Omnivorous	Cazetta et al. (2008); AV; DN

[a] Indicates effective bird dispersers of mimetic-seed species; other dispersers may be effective, but they have not been confirmed yet. Data on animal size and life history were obtained from Animal Diversity Web (ADW); Avibase (AV); Classic Collection of North American Birds Website (CCNAB); DongNiao App (DN); eBird Website (EB); iNaturalist Website (IN); Other references are listed following the description.

seeds, most of which are within the same genus as reported mimetic-seed species (Appendix A).

Four non-exclusive hypotheses have been proposed to elucidate the phenomenon of mimetic-seed dispersal: deception (mimetism or parasitism), mutualism, aposematism, and exaptation. The deception hypothesis suggests that mimetic seeds mimic fleshy fruits to attract birds for seed dispersal while providing little reward in return (van der Pijl, 1982; Galetti, 2002; Pizo et al., 2020). The mutualism hypothesis, proposed by Peres and van Roosmalen (1996), also referred to as the “hard-seed for grit” hypothesis, posits that mimetic-seed dispersal is mutually beneficial for both birds and mimetic seeds. For birds, especially those terrestrial omnivorous birds, the hard mimetic seed may function as mineral grit to enhance digestive efficiency. For mimetic seeds, the digestive process in the bird gut breaks seed dormancy without causing damage, resulting in a higher seedling germination rate. The aposematism hypothesis suggests that the red seeds (e.g., seeds of *Ormosia* species) may act as a deterrent to seed predators by signaling the presence of toxic alkaloids, thus serving as an aposematic cue (Foster and Delay, 1998). The exaptation hypothesis argues that conspicuous color of mimetic seeds sharing similar seed coat characteristics with non-mimetic-seed species (e.g., plant species within the same genera) but not dispersed by birds could be considered exaptation (Galetti, 2002). The exaptation hypothesis also suggests that dormancy protects mimetic seeds against deterioration before dispersal (Brancalion et al., 2010). Although each

Table 3
Secondary metabolites in mimetic seeds of different species and their biological functions.

Mimetic-Seed Species	Chemical Contents	Biological Function	References
Allium tricoccum	Total alkaloids	–	Galetti (2002)
Abrus precatorius	Hypaphorine; Choline; Trigonelline	Reduce the fecundity of female spider (*Tetranychus urticae*), most effectively	Dimetry et al. (1992)
	Arbine; L-arbine	Biomarker of abrin	Owens & Koester (2008); Johnson et al. (2009)
	N, N-dimethyltryptophan metho cation; Precatorine; Indoles; Isoquinolines; Piperidines	–	Ghosal and Dutta (1971); Qian et al. (2022)
Adenanthera pavonina	Total alkaloids	–	Adedapo et al. (2009)
Erythrina velutina	Erysodine; Erysovine	Cyto-toxicity	Ozawa et al. (2009)
	8-oxo-erythraline; Erysotrine; Glycoerysodine	Promising cyto-toxicity, act synergistically when combined with TRAIL	Ozawa et al. (2009)
	Hypaphorine	Sleep-inducing effect in mice	Ozawa et al. (2009)
	Erymelanthine; Erysodine N-oxide (colorless); Erysopine 15-O-Sulfate (colorless); Sodium Erysovine 15-O-Sulfate (brown); Erysovine N-Oxy-15-O-Sulfate (colorless); 16-O-β-D-Glucopyranosyl Coccoline (colorless); (3 R)-16-O-β-D-glucopyranosyl erysodine N-oxide (colorless); (3 R)-16-O-β-D-glucopyranosyl-10,11-dehydro-coccoline (colorless)	–	Ozawa et al. (2009); Ozawa et al. (2011); Todoroki et al. (2021)
Ormosia arborea	Quinolizidine alkaloids: Panamine (or its isomers); Ormosanine (or its isomers); Angustifoline; Sparteine; Lupanine, etc.	Inhibit seed predation by agoutis	Guimarães et al. (2003)
Ormosia isthmensis	Acosmine; Aloperine; Ammodendrine; Angustifoline; Dehydropanamine; Dihydroaloperine; Homoormosanine; Homopodopetaline; Homoxyormosanine; Lupanine; N-formylallylcytisine; Ormosanine; Ormosinine; Panamine; Podopetaline; Sparteine; 5,6-dehydrolupanine; 10,17-dioxosparteine; l l,12-dehydrosparteine; 4β-hydroxylupanine; 13β-hydroxylupanine	–	Ricker et al. (1999)
Ormosia lignivalvis	Ammodendrine; Dehydropanamine; Ormosanine; Ormosinine; Panamine; 5,6-dehydrolupanine; 13β-hydroxylupanine	–	Ricker et al. (1999)
Ormosia macrocalyx	Aloperine; Ammodendrine; Angustifoline; Dihydroaloperine; Homoormosanine; Homopodopetaline; Homoxy-6-epipodopetaline; Homoxyormosanine; Lupanine; N-formyldihydroallylcytisine; Ormosanine; Ormosinine; Panamine; Podopetaline; Sparteine; 5,6-dehydrolupanine; 10-oxosparteine; l l,12-dehydrosparteine; 17-oxolupanine; α-isoangustifoline; β-isosparteine; 3β-hydroxylupanine (nuttalline); 4β-hydroxylupanine; 13α-(angeloyloxy) lupanine; 13α-O-(4′-hydroxytigloyloxy) lupanine; 13α-tiglyoxylupanine	–	Kinghorn et al. (1988); Ricker et al. (1999)
Sophora secundiflora	Cytisine series (N-methylcytisine, anagyrine)	–	Izaddoost (1975)
Brackenridgea nitida	Terpenoids; Flavonoids	–	Galetti (2002)
Ochna atropurpurea	Isoflavonoid	–	Galetti (2002)
Glochidion sumatranum	Tannin; Terpenoids	–	Galetti (2002)
Margaritaria nobilis	Total alkaloids	–	Cattze et al. (2008)
	Fiber; Protein; Lipids; Others (glucose, fructose, phenol, tannins, etc.)	–	Cattze et al. (2008)
Harpullia arborea	Saponin	–	Galetti (2002)

hypothesis has been supported by some evidence, support remains controversial due to experimental conditions. In addition, relatively little research has been done on the ecological functions of the visual, olfactory, gustatory, and tactile signals displayed by mimetic seeds, as well as their independent or coupled effects.

In this mini-review, we use information of reported and potential mimetic-seed species throughout the world to discuss key characteristics of mimetic seeds. We focus on three questions: 1) How did the current geographical distribution of mimetic-seed species form? 2) Why do mimetic seeds usually have high conspicuousness but provide little nutritive reward for frugivorous birds? 3) What is the ecological and evolutionary significance of key characteristics of mimetic seeds and their secondary metabolites? Further, we propose approaches to study the evolutionary ecology of mimetic-seed dispersal.

2. The global distribution of mimetic-seed species

Preliminarily analysis of the global distribution of mimetic-seed species was done in R (R Core Team, 2023). We first downloaded raw occurrence data of mimetic-seed species from GBIF database using package "*rgbif*" (Chamberlain et al., 2024), then cleaned the data using package "*CoordinateCleaner*" (Zizka et al., 2019) to remove outliers (e.g., occurrence data located at sea). After that, we uploaded the cleaned data on the interface of the package "*wallace*" (Kass et al., 2023) to thin data (the "Thinning Distance" was set as

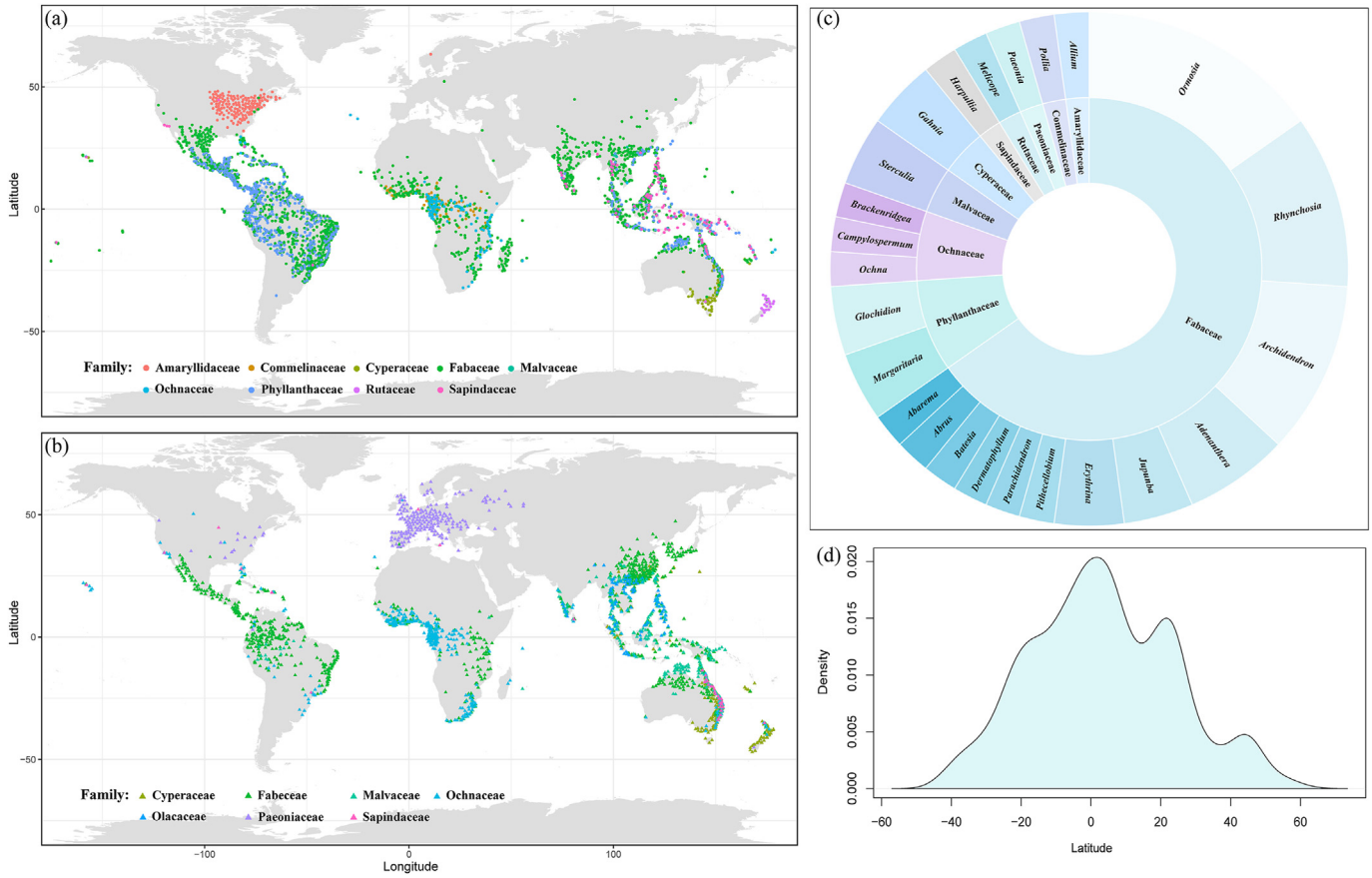

Fig. 1. Global richness of mimetic-seed species in Angiosperm. (a) Occurrence of reported mimetic-seed species throughout the world (Due to the presence of unidentified species, such as *Paeonia* spp., the distribution is underestimated). (b) Occurrence of potential mimetic-seed species throughout the world. (c) Relative richness of mimetic-seed species in different plant families (only reported species are included in this diagram, and families and genera are colored to ease their differentiation). (d) Density of mimetic-seed species at different latitudes.

100 km, *ca.* 1° latitude apart) and thus presented data more clearly without changing the distribution pattern of mimetic-seed species. We visualized the thinned data using package "*maps*" (Becker et al., 2023) and "*ggplot2*" (Wickham, 2016).

We found that mimetic-seed species occur in both tropical and temperate regions, but mainly in the tropics (*ca.* 74%, Fig. 1a; Appendix A). Species density peaks near the equator and decreases with increasing latitude north and south (Fig. 1c), nearly consistent with global patterns of bird richness (Gaston, 2000). Previous studies have demonstrated the ubiquitous interspecific and intraspecific competition among fruiting species for bird dispersers in the tropics (Howe and Estabrook, 1977; Manasse and Howe, 1983; Poulin et al., 1999). Fedorov (1966) has reckoned that in the absence of interference in the tropics, competition mainly occurs between species sharing similar ecological niches. He also believed that the origin of phylogenetic species may be caused by a few mutations that subsequently directly or indirectly alter the morphogenesis of different species. We thus hypothesize that one possible explanation for the occurrence of mimetic-seed species is gene mutation in phylogenetically related non-mimetic-seed species under the selection by bird dispersers in the tropics.

Mimetic-seed species density was found to be high along coastal areas and on small islands (Fig. 1a). One reason for such a distribution could be seed dispersal by ocean current, as has been documented in *Abrus precatorius* (Murray, 1986) and *Ormosia monosperma* (Torke et al., 2022). However, birds may also provide trans-oceanic seed dispersal (Nogales et al., 2012).

3. Interaction between mimetic seeds and their bird dispersers

Mimetic-seed dispersal has been reported in several studies (Table 2). During seed dispersal interactions, birds can select fruit traits using their outstanding visual capability, as well as relatively poorer tactile, gustatory, and olfactory capabilities (Ridley, 1930; van der Pijl, 1982; Willson and Whelan, 1990; Corlett, 2011; Renoult et al., 2013). Birds also learn to associate pre-ingestive sensory cues with post-ingestive feedback to acquire foraging experience (Schaefer et al., 2008; Corlett, 2011). Notably, seed traits can interact with the digestive processes of bird dispersers, and subsequently influence seed fate (Kleyheeg et al., 2018). Thus, we hypothesize that the characteristics of mimetic seeds interact with the sensory capabilities and the digestive strategies of the different bird dispersers.

Mimetic seeds have been shown to attract birds using conspicuous visual cues. Many birds have cone visual pigments that are ultraviolet-wavelength sensitive (UVS) and long-wavelength sensitive (LWS) (Hart, 2001). Thus, birds can quickly detect conspicuous fruits with high reflectance at long wavelength and/or ultraviolet wavelengths, such as red fleshy fruits and berries with

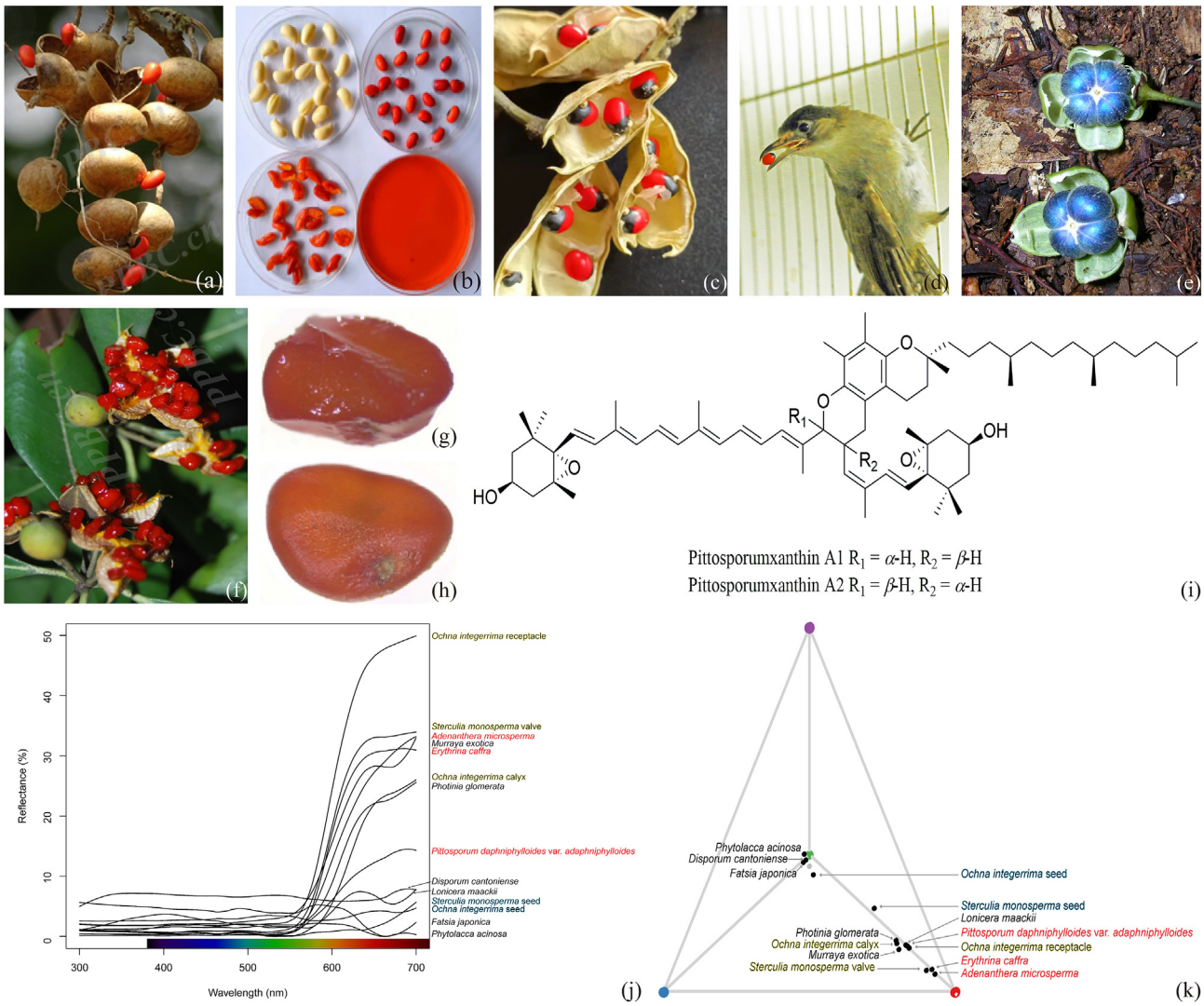

Fig. 2. Conspicuous mimetic seeds of several plant species. (a) Mimetic seeds of *Erythrina caffra*. (b) Crude extract of pigment from seed coat of *E. caffra*. (c) and (d) Mimetic seeds of *Abrus precatorius* and their potential seed disperser, *Pycnonotus xanthorrhous*. (e) Mimetic seeds of *Margaritaria nobilis*. (f) Potential mimetic seeds of *Pittosporum tobira*. (g) Seeds collected from mother plant of *P. tobira*. (h) Seeds collected from faeces of *P. xanthorrhous*, suggesting that these seeds cannot be destroyed after gut passage by *P. xanthorrhou*. (i) The special C_{69} carotenoids contributing to red seed color of *P. tobira* (Fujiwara and Maoka, 2001). (j and k) Spectral reflection curves and color loci (in UVS-bird color vision) of different mimetic seeds and red or black fleshy fruits, indicating the color similarity between mimetic seeds and fleshy fruits (red letters = red mimetic seeds; blue letters = black mimetic seeds; yellow letters = red part of fleshy fruits; black letters = fleshy fruits).

waxy bloom (Burkhardt, 1982; Schaefer et al., 2006). Moreover, smooth and waxy testa of mimetic seeds of several species, such as *Erythrina caffra* (Fig. 2a) and *Abrus precatorius* (Fig. 2c), likely amplify the conspicuousness of seeds to bird dispersers by reflecting ultraviolet light. In addition, fruits with contrasting colors are also conspicuous to avian vision (Schmidt et al., 2004; Melo et al., 2011). Studies have shown that red fruits have higher chromatic contrast, whereas black fruits have higher achromatic contrast against the same background (Schaefer et al., 2006). These red-black bicolor fruits have also been shown to enhance fruit removal rates (Willson and Melampy, 1983). Our analysis indicates that most mimetic seeds are red and/or black (Table 1 and Fig. 2), which is consistent with the idea that mimetic seeds can further increase conspicuousness by maximizing color contrast against the same background.

Mimetic seeds may deceive birds into seed dispersal through food resource mimicry. The main colors of bird-dispersed fleshy fruits are red and black (Willson and Whelan, 1990; Schaefer and Schaefer, 2007), indicating a potential convergence among fleshy-fruited species. Birds have been shown to associate fruit colors with nutritive reward (Schaefer et al., 2008). Some birds, however, may be subject to "receiver bias" (Schiestl, 2017) and may be disproportionately drawn to conspicuous red or black colors during their foraging process. For example, naive birds of some species tend to prefer red and/or black fruit (Schmidt and Schaefer, 2004; Duan et al., 2014). Burns (2005) found that, compared with orange fruits, the red fruits of *Rubus spectabilis* attracted more birds by mimicking the sympatric red fruits of *R. parviflorus*, implying that the red signal could be vital for the occurrence of mimicry between the mimic and their sympatric model. Another distinct group of mimetic seeds (e.g., seeds of *Margaritaria nobilis*, *Pollia condensata* and *Rhynchosia mannii*) display bluish colors (van der Pijl, 1982; Cazetta et al., 2008; Vignolini et al., 2012, Fig. 2e). Interestingly, such bizarre bluish colors are assumed to mimic the appearance of insect prey to deceive insectivorous birds or to attract birds for nest decoration or mating (van der Pijl, 1982; Vignolini et al., 2012).

Thus, mimetic seeds may deceive birds by mimicking the appearance of their food or other resources, probably with sympatrically occurring fleshy fruits being mimicked at high frequency.

We examined color similarity between mimetic seeds and fleshy fruits by measuring reflectance data of several mimetic seeds and fleshy fruits. We then constructed a tetrahedron color space for UVS-birds using the R package "*pavo*", in which color was presented as a point (Goldsmith, 1990; Maia et al., 2019). We found that UVS-birds may not be able to distinguish several mimetic seeds from fleshy fruits (Fig. 2j and k). We thus assume that the red and/or black colors of mimetic seeds are an adaptation to the color vision of bird dispersers. Galetti (2002), however, has argued that the color of mimetic seeds is an exaptation rather than adaptation to present-day bird dispersers, noting the color of mimetic seeds may result from phylogenetic constraints. These two conjectures require further research.

Deceptive mimetic-seed dispersal is affected by three main factors: the foraging experience and learning ability of different birds, environmental heterogeneity, and the density of mimetic-seed species. Mimetic seeds can sporadically deceive birds to dispersal, especially those naïve individuals lacking foraging experience, as in seed dispersal of *Ormosia arborea* and *Rhynchosia melanocarpa* (Galetti, 2002; Pizo et al., 2020). It is assumed that as birds increase their foraging experience, the efficiency of mimetic-seed dispersal will decrease. Mimetic-seed species seem to adopt different fruiting tactics in heterogenous and homogenous environments. For example, in more homogenous forests in south-east Brazil, *Ormosia arborea* produce dehiscent pods with mimetic seeds for long time, thus, benefitting from remaining relatively rare in the community all year, producing an even dispersal pattern (Galetti, 2002). In a heterogenous environment, *Rhynchosia melanocarpa* is thought to benefit more from the "willingness" of birds to eat fruits and potential migratory bird dispersers by producing mimetic seeds relatively abundant early in the fruiting season (Pizo et al., 2020). In addition, environmental heterogeneity can disrupt foraging memory and lower the foraging efficiency of birds (Hirvonen et al., 1999), which may increase mimetic-seed dispersal by birds. The density of mimetic-seed species is generally low (Peres and van Roosmalen, 1996; Foster and Delay, 1998; Pizo et al., 2020). If it increases in the environment, this will inevitably influence the fitness of bird dispersers, because they have fewer eatable food sources. As a response, some birds will seek food in other places, which, will decrease the dispersal frequency of mimetic seeds in turn.

Mimetic seeds often remain intact through the digestive system of bird dispersers because of their smooth and hard exterior. The smoothness of mimetic seeds may enhance the ingestion rate by avian species, thereby leading to a delayed ingestive response. This delay could potentially hinder the development of foraging experience in birds, ultimately promoting the dispersal of mimetic seeds. Yet there is a possible trade-off: smooth mimetic seeds that benefit from rapid dispersal suffer from short dispersal distances. For example, mimetic seeds of *Erythrina caffra* are too smooth for birds to take easily, causing many seeds to fall into the seed shadow of the mother plant (G. Chen, personal observation). According to the "hard-seed for grit" hypothesis, the hardness of mimetic seeds serves as a crucial factor in facilitating the mutualism between mimetic seeds and bird dispersers. This is attributed to its ability to enhance digestion by birds and mitigate seed damage resulting from avian digestion. Furthermore, seed hardness has the potential to increase seed survival rates following consumption by grazing animals, reduce predation by rodents, prevent deterioration during the rainy season prior to dispersal, regulate germination timing, and contribute to the establishment of a resilient soil seed bank (Taylor, 2005; Brancalion et al., 2010; Paulsen et al., 2013). However, the foraging habits (for example, frugivory, herbivory or insectivory) and the foraging maneuvers (for example, perch-plucks, sally-plucks or hover-plucks) employed by birds will directly affect their digestive capabilities, and therefore influence the seed fate of any mimetic seeds eaten. Terrestrial granivorous birds have more powerful digestive guts and are able to abrade the hard coats of mimetic seeds, thus benefiting the germination of excreted seeds (Peres and van Roosmalen, 1996; Foster and Delay, 1998). Compared to terrestrial birds, arboreal bird dispersers can carry mimetic seeds farther from the mother plant, particularly during periods of fruit scarcity (Foster and Delay, 1998). However, the impact of such variation on seed fate in mimetic-seed dispersal remains unclear, as digestive capability varies among bird species (Gionfriddo and Best, 1996; Rehm et al., 2019).

4. The potential function of key secondary metabolites in mimetic seeds

Mimetic-seed species have allocated energy to certain secondary metabolites to form key functional characteristics, including conspicuous color, hard seed coat, certain toxic secondary metabolites, and perhaps a smooth waxy layer. The spatiotemporal variation of those characteristics may primarily be based on the evolution of certain key secondary metabolites. Red or black pigments may result from the presence of anthocyanins, carotenoids, or perhaps alkaloids (Lancaster et al., 1997; Schaefer et al., 2008; Roy et al., 2022), and the bluish structural colors of several mimetic seeds largely originate from the helical cellulose (Vignolini et al., 2012, 2016). Hardness may depend on the presence of phenolic compounds (Mohamed-Yasseen et al., 1994). The evolution of the waxy layer may have occurred together with that of the metabolism of long-chain fatty acids (Place and Stiles, 1992; Kunst and Samuels, 2009). Mimetic seed toxicity may result from certain toxic secondary metabolites, especially alkaloids.

Although relatively rare, alkaloids are found in mimetic seeds of several species, such as *Abrus precatorius*. Some alkaloids may be detrimental to rodents, birds and perhaps also to humans (Table 3). For example, quinolizidine alkaloids in the seeds of *Ormosia arborea* can inhibit seed predation by agoutis (Guimarães et al., 2003). Notably, Foster and Delay (1998) proposed that seed predators may be deterred by the aposematic red seed color of *Ormosia* species, since it might signal the presence of toxic alkaloids. Although this hypothesis has been refuted in subsequent research (Galetti, 2002), it is reasonable, as the presence of functional alkaloids in different plant tissues (roots, flowers, etc.) are associated with the bright red signal (He et al., 2017; Roy et al., 2022). If it is true, there would exist a possible trade-off behind the bright red signal of mimetic seeds, attracting birds on the one hand, but causing them damage on the other. Several toxic alkaloids, however, may not be harmful to birds (Cipollini and Levey, 1997).

The specific secondary metabolites contributing to those key characteristics in mimetic seeds, however, remain largely unknown due to a lack of research or limited analytical techniques. Our field observation showed that *Pittosporum tobira*, a potential mimetic-seed species, deceived birds into dispersal by its bright reddish seed color. The seeds of *P. tobira* have been reported to contain novel pittosporumxanthins A1 and A2, suggesting the red seed color is attributed to highly stable C_{69} carotenoids (Fujiwara and Maoka, 2001). Intriguingly, during our behavioral experiments, the reddish seed color of *P. tobira* remained nearly unchanged even after passing through the guts of the frugivorous bird *Pycnonotus xanthorrhous*, further indicating that it could be a deceptive signal (Fig. 2f, g, h and i). The reddish seeds of *E. caffra* also deceives birds

into dispersal. However, the main pigment of its reddish signal remains as yet unidentified, probably due to its low detection limit and unique characteristics (Fig. 2b). Evaluating the evolution of key secondary metabolites in mimetic seeds is thus challenging but meaningful.

5. Future directions

Evolutionary games usually consist of different players, payoffs, and strategies, accompanied by the variation of continuous traits of different players (Riechert and Hammerstein, 1983; McGill and Brown, 2007). We consider mimetic-seed dispersal an evolutionary game between mimetic-seed species, fleshy-fruited species, and their bird dispersers. The respective fitness of each player is the payoff of the game, and each player evolves optimal strategies to gain fitness. We assume that mimetic-seed species have adopted an "energy-reallocation strategy" (i.e., mimetic-seed species allocate energy to produce key secondary metabolites rather than to form nutritive seed tissues which could benefit birds), while fleshy-fruited species have adopted a "reward strategy" (i.e., providing a nutritive reward to birds) to attract birds for seed dispersal. In the "energy-reallocation strategy", if allocating energy in key secondary metabolites can suppress the cost of producing nutritive reward, it would be more profitable for plant fitness. It is expected that a portion of sympatric species currently with fleshy fruits may eventually evolve an "energy-reallocation strategy". However, if the true metabolizable energy (TME) provided by mimetic seeds for birds is lower than that provided by fleshy fruits, the fitness of birds would decrease. Once the frequency of mimetic-seed species increases in the environment, this will inevitably influence the fitness of bird dispersers. Consequently, some birds may seek food resources with higher TME value elsewhere, subsequently reducing the fitness of both mimetic seeds and fleshy fruits. Untangling this dynamic game can therefore shed light on the ecological and evolutionary processes occurring in mimetic-seed dispersal.

There are few issues of concern. The global richness of mimetic-seed species has likely been underestimated (Appendix A). In addition, little is known about the evolution of several key characteristics or the evolution of secondary metabolites related to them. In this mini-review, we have discussed four hypotheses that attempt to explain mimetic-seed dispersal. Our preliminary work supports the parasitism (deception) hypothesis, however, further research should continue to test the remaining hypotheses.

Here, we propose five approaches to study mimetic-seed dispersal in the future. 1) Seed dispersal mode (i.e., by ocean current or birds) should be classified for mimetic-seed species (including potential mimetic-seed species) growing along coastal areas and sympatric fleshy-fruited species. 2) We should also integrate occurrence data of mimetic-seed species with global climate data, allowing predictions on distribution pattern of global mimetic seeds in the future. 3) The key characteristics of mimetic-seed species, phylogenetically-related species, and sympatric fleshy-fruited species should be evaluated. Specifically, future research should evaluate dispersal mode, seed color, seed hardness and seed nutriment of these plant species. This evaluation of characteristics should include estimations of divergence times and reconstructions of ancestor characters and ancestor range. 4) Future studies should identify the structures of specific secondary metabolites related to key characteristics of mimetic seeds. One potentially rewarding approach would be to use multi-omics to analyze their spatiotemporal variation. 5) We also recommend using "game theory" to decode interactions between mimetic-seed species, fleshy-fruited species, and their bird dispersers, especially calculating the true metabolizable energy value of mimetic seeds and their sympatric fleshy fruits for bird dispersers.

CRediT authorship contribution statement

Min-Fei Jin: Investigation, Data curation, Formal analysis, Writing original draft, Writing – review & editing, Visualization. **Xiang-Hai Cai:** Methodology, Resources, Validation. **Gao Chen:** Conceptualization, Writing – review & editing, Supervision, Funding acquisition.

Declaration of competing interest

No potential conflict of interest was reported by the authors.

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Appendix A. Supplementary data

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