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Abstract Food-deceptive orchid species have traditionally been considered pollination specialized to bees or butterflies. However, it is unclear to which concept of specialization this assumption is related; if to that of phenotypic specialization or of functional specialization. The main aim of this work was to verify if pollinators of five widespread food-deceptive orchid species (*Anacamptis morio* (L.) R.M. Bateman, Pridgeon & M.W. Chase, *Anacamptis pyramidalis* (L.) Rich., *Himantoglossum adriaticum* H. Baumann, *Orchis purpurea* Huds. and *Orchis simia* Lam.) predicted from the phenotypic point of view matched with the observed ones. We addressed the question by defining target orchid phenotypic specialization on the basis of their floral traits, and we compared the expected guilds of pollinators with the observed ones. Target orchid pollinators were collected by conducting a meta-analysis of the available literature and adding unpublished field observations, carried out in temperate dry grasslands in NE Italy. Pollinator species were subsequently grouped into guilds and differences in the guild spectra among orchid species grouped according to their phenotype were tested. In contradiction to expectations derived from the phenotypic point of view, food-deceptive orchid species were found to be highly functionally generalized for pollinators, and no differences in the pollinator guild spectra could be revealed among orchid groups. Our results may lead to reconsider food-deceptive orchid pollination ecology by reevaluating the traditional equation orchid-pollination specialization.

Keywords Dry grasslands · Food-deceptive orchids · Functional specialization · Pollination · Specialization trade-offs

Introduction

Specialization in plants may arise as an adaptive response to a particular environmental state defined by a narrow combination of environmental parameters, such as abiotic factors (e.g., soil moisture or climate parameters; Pierce et al. 2017), structural community features (e.g., above-ground cover density and vertical structure), or interspecific interactions (Sburlino et al. 2008; Buffa and Villani 2012; Vamosi et al. 2014). Specialization is considered as the ultimate response of plant species to the environment, with ‘advanced’ plants being more specialized than ‘primitive’ plants, because more effective in the provision of needed resources under different as well as original environmental conditions (Ollerton 1999; Gómez and Zamora 2006). However, at least in pollination interactions, several authors proved that the ultimate response may be also an increased degree of generalization (Armbruster et al. 2000; Tripp and Manson 2008). In fact, being a specialized species often claims cost: specialized species are under greater extinction risk than generalist species, especially when they totally depend on a restricted combination of environmental resources (Gumbert et al. 1999; Dante et al. 2013).

The linkage between specialization and rarity has been proven also for orchids, with almost half of the extinct orchid species being temperate terrestrial perennials (IUCN 1999). In terrestrial orchids, specialization has been mostly found to pertain processes related to seeds germination and biotic pollination (Selosse et al. 2002; Otero et al. 2004; Anderson et al. 2005). Orchid seeds may have very specific ecological requirements to overcome dormancy and initiate the growth of the embryo (Baskin and Baskin 2014). In many terrestrial orchids, seed germination and growth is subordinate to

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mycorrhizal associations (Warcup 1973; Rasmussen 2002), which can extend to adulthood, when mature plants remain colonized by mycorrhizal fungi (Batty et al. 2002; Rasmussen and Whigham 2002). Moreover, the establishment of some terrestrial orchid species is affected by the structure of the surrounding vegetation, which would constrain both seed germination and seedling establishment (Slaviero et al. 2016).

Orchid specialization becomes even more outstanding when examining pollination processes. In fact, orchids are widely believed to have the highest degree of pollinator specialization when compared with other families of flowering plants (Tremblay 1992; Ibisch et al. 1996). In plant-pollinator interactions, specialization of plant species for pollinators can be defined according to three different approaches. First, by counting the number of interacting pollinator species, thus defining specialized plants as those that attract a particular subset of the available animal species. This rigorous partner selection has been defined as ecological specialization, to distinguish it from phenotypic specialization (Ollerton et al. 2007). Phenotypic specialization (second definition) assigns plant species degree of specialization a priori according to a particular set of morphological traits (e.g., length of the corolla tube) by following the pollination syndrome approach (Fægri and van der Pijl 1979). Accordingly, one of the major features of flowering plants is that particular suites of floral characters can be associated with a specific functional group of animal pollinators which, however, may or may not be confirmed by observations (Stebbins 1970; Fægri and van der Pijl 1979; Pellmyr 2002; Fantinato et al. 2016a). Phenotypic specialization is often associated with functional specialization (third definition), that occurs when a plant species is observed to be visited exclusively by species of functionally similar pollinators (namely, pollinator guilds), for example butterflies (Fenster et al. 2004).

The majority of orchid species rely on biotic pollen vectors to reproduce (Nilsson et al. 1992), often by establishing highly ecological specialized interactions. It is supposed that the 60% of orchids are pollinated by only one or few pollinator species (Tremblay 1992). However, much uncertainty remains over, because in many cases the pollinator has never been observed. Orchids pollination is even more controversial because about the 30% (Ackerman 1986) employ among the most complex deception systems known in angiosperms to secure pollination without offering rewards (Tremblay et al. 2005; Jersáková et al. 2006). Visitors are deceived by various means; most commonly the deception is based on sexual advertisements or on a general resemblance to rewarding producing plants (Tremblay et al. 2005). Sexual deception occurs in 18 orchid genera (Jersáková et al. 2006), in which flowers resemble the females of the pollinating species and are pollinated by the males during attempts at mating (pseudocopulation; e.g., Schiestl et al. 2003).

However, in non-rewarding orchids, food-deception is reported as the most common pollination mechanism (reported in 38 genera; Jersáková et al. 2006). Food-deceptive orchids exploit pollinators' innate food-foraging behavior (Nilsson 1980; Dafni 1983) by mimicking typical rewarding flower traits, such as inflorescence shape, flower colour, nectar guides, spurs and pollen-like papillae (Gumbert and Kunze 2001; Galizia et al. 2005). Originally, Darwin (1885), reinforced by Müller's (1873) and Delpino's (1868–1875) observations, asserted that “bees (...) should persevere in visiting flower after flower of the above named Orchids, (...) in the hope of obtaining nectar which is never present”. Hence, from Darwin's time onwards, food-deceptive orchid species have been generically considered to be visited by a narrow functional group of pollinators (e.g., Inda et al. 2012; Schiestl 2012). Literature data report that, contrarily to sexual-deceptive orchids, food-deceptive orchids are ecologically generalized because they are visited by a relatively diverse group of pollinators (Cozzolino et al. 2005), but that all pollinators belong to the guild of bees (or rarely of butterflies; Cozzolino and Widmer 2005). However, it is not clear to which concept of specialization this assumption is related; if to that of phenotypic specialization or of functional specialization.

In the light of these considerations, our goal was to assess the degree of functional specialization for pollinators of five food-deceptive orchid species native to temperate dry calcareous grasslands (i.e., *Anacamptis morio* (L.) R.M. Bateman, Pridgeon and M.W. Chase, *Anacamptis pyramidalis* (L.) Rich., *Himantoglossum adriaticum* H. Baumann, *Orchis purpurea* Huds. and *Orchis simia* Lam.). Especially, we answered the following questions: (1) does the expected guild of pollinators predict the observed one? (2) are target orchid species functionally specialized for pollinators? We addressed the problem by defining target orchids phenotypic specialization on the basis of their floral traits (sensu Fægri and van der Pijl 1979), and we compared the expected guilds of pollinators with the observed ones.

Materials and methods

Literature search

We carried out an extensive literature search in the ISI Web of Knowledge database using as keyword combinations the scientific name of target orchids followed by ‘pollination’ or ‘pollinators’ in the topic field. We also included insect species reported in Claessens and Kleylen (2011) and not included in the studies found via the ISI Web of Knowledge. We retained only insects identified at species level and referred to as carrying pollinia on their body, and we sorted synonyms.

Site selection and data collection

The field study took place in the Euganean Hills (NE Italy), a group of about 100 individual hills (15,096 ha) isolated in the Po plain, characterized by conic shapes of different elevations (peaks altitude ranges from 13 to 601 m a.s.l.). The hills are of submarine volcanic origin, emerged during two phases occurred between 45 million and 35 million years ago. This led volcanic and calcareous formations to co-exist nearby each other. The site shows a warm-rainy climate (Kaltenrieder et al. 2010). The mean annual temperature is of 13.0 °C with the peak of the mean high temperature in July and the low in January. The average annual rainfall is of 720 mm peaking in April and September, intermingled by two minimum in July and December. Study sites (Table 1) were represented by small- to medium-sized *Bromus erectus*-dominated dry grasslands, extending from 0.27 to 6.95 ha (ranging from 68 to 284 m a.s.l.; Fantinato et al. 2016b). Dry grasslands were chosen because, among natural and semi-natural habitats, they host important orchid populations when low-intensity agricultural regimes are maintained (Pierce and Belotti 2011; Slaviero et al. 2016; Biella et al. 2017). In Europe, dry grassland communities also achieved a legal status as they are listed as endangered habitat in Annex I of the Habitats Directive 92/43 (EEC 1992). Furthermore the habitat is considered a priority type if it is an important orchid site (EEC 2013).

Target orchids are listed in the Annex I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) of Washington (1973; www.cites.org), and in the national and regional red list

of vascular plants (Rossi et al. 2013; Buffa et al. 2016). According to the regional red list of vascular plants (Buffa et al. 2016), *A. morio*, *A. pyramidalis*, *O. purpurea* and *O. simia* were classified as Least Concern (IUCN 2013), while *H. adriaticum* as Near Threatened (IUCN 2013). Even though at regional level, target orchid species were assessed under the threshold of extinction, they are increasingly threatened by the decline of their habitat, which has been listed as Vulnerable in the European Red List of Habitat (Janssen et al. 2016).

Overall, 20 (4 m²) plots were selected through a preferential sampling design (on target orchids populations). *A. morio* occurred in 13 plots with an average number of 33.53 ± 27.00 (mean \pm SD) individuals, *A. pyramidalis* in 6 plots with 2.40 ± 1.51 individuals, *H. adriaticum* in 3 plots with 4.33 ± 5.77 individuals, *O. purpurea* in 3 plots with 4.00 ± 0.00 individuals and *O. simia* in 6 plots with 7.83 ± 6.64 individuals. The number of plots was proportional to the target orchids frequency in the study site and in many cases different orchid species co-occurred in the same plot.

For each target orchid species we collected floral traits (Table 2) on five flowers per species. We measured the length and the width of the spur and ascertained the presence of nectar at its bottom by using microcapillary tubes (Kearns and Inouye 1993). Additionally, we recorded floral symmetry and the presence of nectar guides on the labellum in the field, while brightness and colour based on the BioFlor database (Klotz et al. 2002). Floral traits were chosen on the basis of their acknowledged relevance for the identification of pollination syndromes (Fægri and van der Pijl 1979; Willmer 2011).

Target orchids flowering length (Table 2) and pollinators were recorded every 15 days, during the entire flowering season in 2016 (1st April to 15th June), under warm and sunny weather conditions.

Interactions between target orchids and visiting insects were monitored in each plot during 15 min (from 10 a.m. to 1 p.m.) and repeated for 5 surveys to cover the entire flowering season. Orchid visitors were identified to species, and presence and position of pollinia on insects' body after each visit was ascertained (Table 2). Both

Table 1 Localities, coordinates (Decimal degrees) and altitude (m a.s.l.) of the sampled grasslands

Locality	Latitude N	Longitude E	Altitude (m a.s.l.)
Mt Mottolone	45.287431	11.705459	273
Val di Spin	45.280217	11.704192	202
Sassonegro	45.265562	11.699706	104
Mt Cecilia	45.255150	11.699845	112

Table 2 Floral traits collected for the five target orchid species

	<i>A. morio</i>	<i>A. pyramidalis</i>	<i>H. adriaticum</i>	<i>O. purpurea</i>	<i>O. simia</i>
Brightness	Low	High	Low	Low	Low
Colour	Purple	Red	White	Purple	White
Floral symmetry	Bilateral	Bilateral	Bilateral	Bilateral	Bilateral
Flowering length (surveys nr)	2	3	2	2	1
Mean spur length \pm SD (mm)	0.80 ± 0.10	1.34 ± 0.11	0.39 ± 0.02	0.61 ± 0.16	0.42 ± 0.07
Mean spur width \pm SD (mm)	0.17 ± 0.05	0.10 ± 0.00	0.20 ± 0.00	0.20 ± 0.00	0.20 ± 0.00
Nectar guides	Present	Absent	Present	Present	Present
Nectar presence	Absent	Absent	Absent	Absent	Absent
Pollen deposition	Head and tongue	Head and tongue	Head and tongue	Head and tongue	Head and tongue

Brightness and colour were derived from the BioFlor database (Klotz et al. 2002); while all the other traits were recorded in the field. *A. morio*, *Anacamptis morio*; *A. pyramidalis*, *Anacamptis pyramidalis*; *H. adriaticum*, *Himantoglossum adriaticum*; *O. purpurea*, *Orchis purpurea*; *O. simia*, *Orchis simia*

pollinators found in literature and those recorded in the field were grouped following the classical pollination syndrome (Fægri and van der Pijl 1979) into five guilds: bees, beetles, butterflies, flies and moths. Furthermore, the pollinator guild of bees, which is traditionally considered as a single guild by the pollination syndrome theory, has been split into three guilds according to bee tongue length, following Fenster et al. (2004) and Scopce et al. (2007). Especially, we identified long tongue bees (>8 mm), medium tongue bees (>6 and <8 mm) and short tongue bees (<6 mm; Goulson et al. 2005; Willmer 2011). The grouping of pollinators into guilds allowed us to highlight interactions from a functional perspective rather than taxonomical (e.g., Fang and Huang 2012; Fontaine et al. 2006).

Data analysis

Overall pattern of floral trait variation and its relation to species' identity were investigated using principal component analysis (PCA; Legendre and Legendre 1998). Since floral symmetry (bilateral), nectar volume (absent) and pollen deposition (head and tongue) were constant for all the target orchid species, we excluded them from

the PCA. For each group of orchid species resulting from the PCA we inferred expected guilds of pollinators according to Willmer (2011).

Furthermore, we tested if observed guilds of pollinators differed significantly among orchid species grouped according to their phenotype by using one-way PERMANOVA with 9999 randomization (Past software; Hammer et al. 2001). Analysis were performed by taking into account pollinators reported in the literature along with insects observed in the field. In both cases, only flower visitors recorded as carrying pollinia on their body were considered. This, according to literature on orchid pollination ecology (e.g., Cozzolino et al. 2005; Jersáková et al. 2016; Braunschmid et al. 2017) allowed us to count them as potential pollinators, and to distinguish them from simple floral visitors ineffective in carrying pollinia.

Results

The ordination of floral traits variation and their relation to target orchid species displayed two clear gradients (Fig. 1; Table 3). The first PCA axis explained the 76.30% of total floral trait variation and discriminated

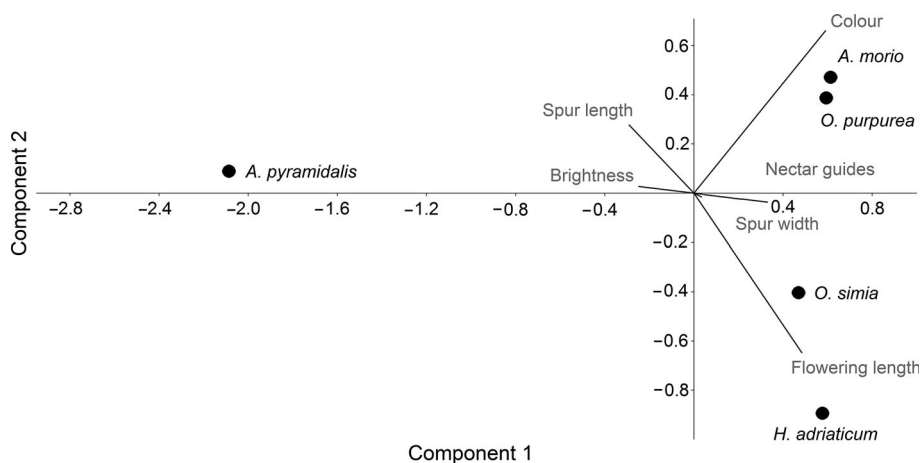


Fig. 1 First two axes of the principal component analysis of target orchid species based on floral traits. For abbreviations of orchid genus name, see Table 2 in the caption

Table 3 Principal component analysis of target orchid species based on floral traits

	Axis 1	Axis 2	Axis 3	Axis 4
Variation explained (%)	76.30	20.88	2.66	1.44
Trait	Loadings			
Brightness	-0.37	0.04	0.37	-0.45
Colour	0.62	0.69	0.27	-0.22
Flowering length	0.49	-0.66	0.56	0.00
Nectar guides	0.37	-0.04	-0.38	0.46
Spur length	-0.28	0.27	0.56	0.71
Spur width	0.03	-0.01	-0.05	-0.15

orchid species according to the flower colour, and the flowering length. The second PCA axis, explaining the 20.88% of trait variation, separated orchid species mainly according to the colour and the spur length. Therefore, according to the phenotypic point of view, target orchid species could be assigned to three distinct groups, which reflected three different pollination syndromes. *H. adriaticum* and *O. simia*, being characterized by a bilateral symmetry, a relative short spur, and light colours coupled with the presence of marked nectar guides were assigned to the syndrome of short tongue bees. Likewise, *A. morio* and *O. purpurea* showed a bilateral symmetry and the presence of nectar guides, however a longer spur made them better described by the syndrome of medium tongue bees. Lastly, *A. pyramidalis* having long-spurred pink flowers resembled the traditional butterfly syndrome.

The meta-analysis allowed us to identify 19 publications from all over Europe (ESM 1). Out of these publications, 6 were about *A. morio*, 11 about *A. pyramidalis*, 3 about *H. adriaticum*, 2 about *O. purpurea* and 3 about *O. simia*. In total, 81 pollinator species were reported in literature: 25 for *A. morio*, 50 for *A. pyramidalis*, 8 for *H. adriaticum*, 2 for *O. purpurea*, and 4 for *O. simia*.

Field survey allowed the observation and identification of 6 pollinia-carrying visitor species for *A. morio* (Table 4), 6 for *A. pyramidalis* (Table 4), 4 for *H. adriaticum* (Table 5), 2 for *O. purpurea* (Table 5) and 2 for *O. simia* (Table 5).

Overall, in contradiction to expectations derived from the phenotypic point of view, we showed that target orchid species interacted with a wide spectrum of guilds of pollinators (Fig. 2). *A. morio* and *A. pyramidalis* were the most generalist, because observed to interact with 6 guilds of pollinators; *H. adriaticum* and *O. simia* with 4 guilds of pollinators; while *O. purpurea* with 3 pollinator guilds. Furthermore, guilds of pollinators were widely shared by orchid species groups; in fact, no significant differences in the proportion of the observed pollinator guilds were revealed by PERMANOVA ($F = 7.99$; $P > 0.05$).

Discussion

We found *A. morio*, *A. pyramidalis*, *H. adriaticum*, *O. purpurea*, and *O. simia* to be more functionally generalized for pollinators than expected from the phenotypic point of view. According to Ollerton et al. (2009), primary pollinators can be predicted by the floral pheno-

Table 4 Identity of pollinators caught on *Anacamptis morio* and *Anacamptis pyramidalis* inflorescences

	<i>Anacamptis morio</i>	<i>Anacamptis pyramidalis</i>
Beetles	* <i>Tropinota hirta</i> (Poda, 1761)	* <i>Tropinota squalida</i> (Scopoli, 1783)
Moths	* <i>Macroglossum stellatarum</i> (L., 1758)	* <i>Zygaena carniolica</i> (Scopoli, 1763) * <i>Zygaena trifolii</i> (Esper, 1783) * <i>Epysirphus balteatus</i> (De Geer, 1776)
Flies		
Short tongue bees	* <i>Dasypoda hirtipes</i> (F., 1793)	
Medium tongue bees	* <i>Bombus pascuorum</i> (Scopoli, 1763)	* <i>Apis mellifera</i> (L., 1758)
Long tongue bees	* <i>Anthophora retusa</i> (L., 1758) * <i>Bombus hortorum</i> (L., 1761)	* <i>Bombus hortorum</i> (L., 1761)
Other visitors	<i>Bombylius major</i> (L., 1758)	<i>Melanargia galathea</i> (L., 1758) <i>Pieris brassicae</i> (L., 1758) <i>Scolia flavifrons</i> (F., 1775) <i>Vanessa cardui</i> (L., 1758)

* Indicate that pollinia were observed on the insect body

Table 5 Identity of pollinators caught on *Himantoglossum adriaticum*, *Orchis purpurea* and *Orchis simia* inflorescences

	<i>Himantoglossum adriaticum</i>	<i>Orchis purpurea</i>	<i>Orchis simia</i>
Beetles	* <i>Tropinota squalida</i> (Scopoli, 1783)	* <i>Tropinota hirta</i> (Poda, 1761)	* <i>Tropinota hirta</i> (Poda, 1761)
Butterflies		* <i>Iphiclides podalirius</i> (L., 1758)	
Short tongue bees	* <i>Anthidium manicatum</i> (L., 1758)		
Medium tongue bees	* <i>Apis mellifera</i> (L., 1758)		* <i>Apis mellifera</i> (L., 1758)
Long tongue bees	* <i>Colletes daviesanus</i> (Smith, 1846)		
Other visitors	<i>Eristalis arbustorum</i> (L., 1758) <i>Scolia hirta</i> (Schrank, 1781)	<i>Bombus terrestris</i> (L., 1758)	<i>Bombylius major</i> (L., 1758) <i>Lasioglossum marginatum</i> (B., 1832) <i>Vanessa cardui</i> (L., 1758)

Asterisks indicate that pollinia were observed on the insect body

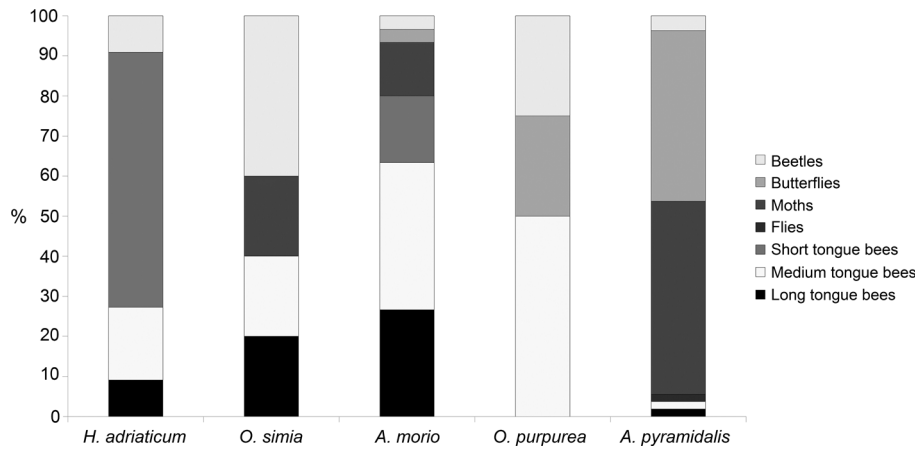


Fig. 2 Relative abundance of pollinator guilds for the five orchid species. For abbreviations of orchid genus name, see Table 2 in the caption

type only for one-third of plant species. It is widely acknowledged that adaptive phenotypic responses of floral traits might arise through selection by the most effective guild of pollinators (Fantinato et al. 2016a; Stebbins 1970), implying that floral characteristics should reflect adaptation to the pollinator that transfers the most pollen (Mayfield 2001; Souza et al. 2017). However, specific floral traits for the most common guild of visitors, or the one most effective in transferring pollen, may not preclude visits by less efficient floral visitors (i.e., secondary pollinators; Stebbins 1970), which in many cases have been proven to contribute to pollination (Rosas-Guerrero et al. 2014). Thus, floral adaptations might be triggered also by secondary pollinators (Aigner 2001, 2006), as well as by antagonistic floral visitors (e.g. Strauss and Armbruster 1997; Strauss and Irwin 2004), or by mixtures of different guilds of pollinators (e.g. Hurlbert et al. 1996; Waser 1998), which can ultimately contribute to generate mismatch between predicted and observed guilds of pollinators. Furthermore, deceptive orchid species often show a remarkable degree of variation in floral traits (e.g., colour; Nilsson 1980; Petterson and Nilsson 1993; Johnson 1994), which might contribute to attract a broader than expected range of pollinator guilds, which often respond to different floral signals. This in turn may ensure pollination events to occur even in the case of fluctuations in pollinator abundance and diversity, thus guaranteeing the reproductive success of at least some individuals within a population.

The effectiveness of a pollinator guild in carrying pollen can greatly influence plant species reproductive success, with most effective pollinators carrying more pollen than less effective ones (Barrios et al. 2016). In most orchid species (including target orchids) pollen is gathered in two compact and coherent masses, the so-called pollinia; thus the effectiveness of an orchid pollinator in carrying pollen depends just on the chance of making contact with them. Pollinia are attached to a sticky plate called ‘viscidium’, which enable them to

adhere to the pollinator body, thus to be entirely removed from the flower. Our results showed insect species belonging to guilds of pollinators unexpected from the phenotypic point of view (e.g., beetles, flies, moths) to actually carry pollinia, thus potentially contributing to target orchid species pollination. In fact, one of the limitations of our study is that our approach allowed us to evaluate only the male fitness component of orchid reproductive success (i.e., pollinia removal), and we cannot conclude that all recorded flower visitors carrying pollinia will proceed to deposit them onto receptive orchid stigmas like effective pollinators. However, previous studies have shown a positive correlation between pollinia removal and the overall effectiveness of pollination (Nilsson et al. 1992, O’Connell and Johnston 1998).

To our knowledge our findings are consistent with those of only one other study (Scopece et al. 2007). In fact, according to the majority of the literature, *A. pyramidalis* should be functionally specialized to butterflies, while *A. morio*, *H. adriaticum*, *O. purpurea*, and *O. simia* to bees (although we should consider at least three different sub-guilds of bees). In the light of our results we hypothesize this assumption to derive mostly from the concept of phenotypic specialization rather than of functional specialization. For example, in the attempt to explore pollen dispersal patterns of *A. pyramidalis*, Lind et al. (2007) focused a priori on butterflies, assuming them as the major guild of pollinators of *A. pyramidalis* on the basis of its floral phenotype. According to the same principle, Cozzolino et al. (2005) chose to investigate the extent to which deceptive orchid species share pollinators by catching just bees and large dipterans. Similarly, other studies (e.g., Johnson et al. 2003; Schiestl 2005; Biró et al. 2015) focused on a single or on narrow groups of pollinators, always composed of medium or long tongue bees. Furthermore, inferences regarding orchid pollinators have been widely advanced because direct observation of orchid pollination events are notoriously difficult to record, especially in orchids

with a deceptive pollination system, since pollination rates are typically low (Neiland and Wilcock 1995).

From an ecological perspective a high degree of generalization for pollinators may enhance the chances of pollination, especially when pollinators are non evenly distributed in space and time. According to Purvis et al. (2000) species that tend to have a high risk of extinction generally show a high dependence on other components of the ecosystem. In the case of interspecific interactions the risk of extinction may be even more pronounced because interactions can involve just two or few more species, thus being highly specialized. Furthermore, the degree of specialization has been highlighted as both cause and consequence of species rarity, acting as a constrain to species frequency and distribution (Dixon 2010; Swarts et al. 2010). As far as pollination is concerned, the presumed high degree of specialization has been often highlighted as cause of orchids rarity (Swarts and Dixon 2009). Food-deceptive orchids have been shown to be highly ecologically specialized (Warcup 1973; Rasmussen 2002; Slaviero et al. 2016). Their ecological specialization pertain to different stages of their life cycle, exposing them to an overall high risk of extinction. A high degree of functional generalization for pollinators may therefore counterbalance their broad ecological specialization, indicating specialization trade-offs during different stages in their life cycle. Costs and benefits of being specialized may lead to modulate the degree of specialization, making specialization advantageous during some stages, while detrimental during others.

Our results may lead to reconsider food-deceptive orchid pollination ecology; the equation orchid-pollination specialization should be reevaluated, and findings may be much more unpredictable than expected.

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