

A conceptual framework linking pollen limitation and seed dispersal effectiveness

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April 11, 2023

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Statement of authorship: LCL and MHK conceived the framework, LCL wrote the first draft of the manuscript, and both contributed substantially to revisions.

Data accessibility statement: No quantitative data was used in the manuscript.

Type of article: Perspective Paper

Abstract: 177 words

Main text: 7492 words

Number of references: 159

Additional elements: 3 figures and 1 table.

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Abstract

Seed production and dispersal are crucial ecological processes impacting plant demography, species distributions, and community assembly. Plant-animal interactions commonly mediate both seed production and seed dispersal, but current research often examines pollination and seed dispersal separately, which hinders our understanding of how pollination services affect downstream dispersal services. To fill this gap, we propose a conceptual framework exploring how pollen limitation can impact the effectiveness of seed dispersal for endozoochorous and myrmecochorous plant species. We summarize the quantitative and qualitative effects of pollen limitation on plant reproduction and use Optimal Foraging Theory to predict its impact on the foraging behavior of seed dispersers. In doing so, we offer a new framework that poses numerous hypotheses and empirical tests to investigate downstream effects of pollen limitation on seed dispersal effectiveness and, consequently, post-dispersal ecological processes occurring at different levels of biological organization. Finally, considering the importance of pollination and seed dispersal outcomes to plant eco-evolutionary dynamics, we discussed the implications of our framework for future studies exploring the demographic and evolutionary impacts of pollen limitation for animal-dispersed plants.

Keywords: elaiosome, frugivory, mutualistic interactions, pollination biology, populational dynamic, optimal foraging theory, seed disperser behavior

1. Introduction

Pollination is crucial for sexual reproduction in flowering plants. Over 80% of Angiosperms (including 75% of crop species), rely on animal vectors for pollen transport between or within flowers (Herrera and Pellmyr 2002, Ollerton et al. 2011). When pollen deposition is inadequate to fertilize all available ovules, plants face pollen limitation (PL) (Ashman *et al.* 2004a). Such pollen inadequacy can be driven by various mechanisms, such as the low frequency of effective pollinator visits and/or low quantity or quality of conspecific pollen deposited in the stigmas (Ashman *et al.* 2004; Knight *et al.* 2005). Regardless of the mechanism, meta-analyses compiling the effect sizes of PL on fruit and/or seed production have shown that pollen-limited plants can produce, on average, 75% less fruits and/or seeds than pollen-supplemented flowers (not pollen-limited) (Knight *et al.* 2005). This negative effect of PL is observed in most Angiosperm species investigated so far (see García-Camacho & Totland 2009; Wolowski *et al.* 2014; Burns *et al.* 2019). In the near future, the negative effects of human activities on pollinators worldwide are expected to progressively increase PL (González-Varo *et al.* 2013; Neuschulz *et al.* 2016), raising concerns about the impacts of PL on the reproductive success and population dynamics of plant species in pristine and human-disturbed habitats (e.g. Knight 2004; Ward & Johnson 2005; Freitas *et al.* 2020; Soltani *et al.* 2021).

Despite PL being a pivotal subject in plant reproductive biology, one important consequence of PL has received little to no attention: its effect on seed dispersal effectiveness, especially for plant species dispersed by animals. The seeds of many Angiosperms, including 25-80% of temperate and 50-90% of tropical species flora, are animal-dispersed (Jordano & Schupp 2000). For those plants, variation in seed recruitment and the spatial distribution of plants is dictated by the outcome of disperser-plant interactions (Jordano 1995; Galetti *et al.* 2013; Snell *et al.* 2019). Because the magnitude of PL experienced by a population directly impacts the quantity and quality of dispersal units (i.e. unit of propagation of a plant species and, in our case, the entity located and removed by the disperser animals) produced by a plant, PL could have cascading effects on the dynamics of plant-disperser interactions, patterns of post-dispersal seed success, and ultimately, on the spatial distribution of plants.

A search on the Web of Science database reveals that this link between PL and seed dispersal has been dismissed, at least in part, due to the non-integrative nature of studies evaluating the outcomes of pollination and seed dispersal to plants. In February 2023, we found 3,765 and 20,219 studies focusing on PL *or* plant seed dispersal, respectively (Boolean operators: “pollen limitation” OR “plant seed dispersal”). However, only 328 studies (8.7% of total PL studies and 1.1% of total dispersal studies) focused on any connection between these two ecological processes (Boolean operators: “pollen limitation” AND “plant seed dispersal”). This suggests that most studies quantifying PL and/or evaluating its effects on plant reproductive success neglect natural processes following seed formation. Similarly, studies describing the dynamic of seed dispersal by animals have focused on a spatial snapshot of a particular dispersal system, mostly neglecting the pre-dispersal processes

driving the availability of dispersal units, such as PL. Considering that pollination and seed dispersal are two of the most threatened processes regulating plant demography and regeneration (Neuschulz *et al.* 2016), we propose an integrative approach that allow us to evaluate the interplay between these processes, improving our ability to predict and manage plant populations in different ecological scenarios.

Here, we present a new conceptual framework about the mechanisms through which PL can directly and/or indirectly affect the outcome of seed dispersal by animals (Fig. 1). We incorporate the quantitative and qualitative effects of PL on plant reproduction (pre-dispersal processes) into the Seed Dispersal Effectiveness approach (SDE) – the most common approach used to evaluate the outcome of seed dispersal for plant species. According to the SDE, the outcome (or effectiveness) of seed dispersal for a given plant is determined by the product of the number of seeds dispersed by all dispersers in the community (quantitative component) and the probability that dispersed seeds survive to adulthood (qualitative component) (Schupp *et al.* 2010). While providing a valuable guide for SDE quantification, this approach still neglects the role of the pre-dispersal processes, such as PL. To bridge this gap, we first describe the direct effects of PL on quantitative and qualitative traits of dispersal units produced by animal-dispersed plants. Several of these effects can interfere with the value of a plant population as a foraging patch to dispersers, as well as the value of dispersal units as a food resource to dispersers (Donahue *et al.* 2003; Valenta & Nevo 2020). Then, we use Optimal Foraging Theory (OFT) (MacArthur & Pianka 1966) to predict how the effects of PL on dispersal units can affect disperser foraging behavior and, consequently, quantitative and qualitative components of SDE. Finally, we discuss the consequences of this indirect link between two key ecological processes for the ecological and evolutionary dynamic of animal-dispersed plants. To bolster our framework, we use two of the most common types of seed dispersal observed in nature as models: endozoochory (i.e. seed dispersal by frugivores that ingest the fruits while visiting the mother plants - Soltani *et al.* 2018) and myrmecochory (i.e. seed dispersal by ants that transport the diaspores to their nest – observed in more than 23,000 Angiosperm species - Lengyel *et al.* 2010). Using these dispersal strategies, we propose scenarios in which PL should affect specific outcomes for dispersal, hoping to spur novel research directions on the subject.

2. Effects of pollen limitation on dispersal unit and seed traits

PL can quantitatively and qualitatively affect the reproductive success of plants dispersed by animals (Ashman *et al.* 2004a; Knight *et al.* 2005). In fact, most of the physiological mechanisms underlying these effects, especially the qualitative ones, are relatively unknown, and little information that exists has not yet been synthesized. For this reason, we summarize some of the main effects of PL on dispersal unit traits, focusing on the traits that could be related to seed dispersal.

2.1. Pollen limitation impacts on the dispersal unit traits

Quantitative effects of PL on seed set are by far the most common effects of PL reported in literature (Knight *et al.* 2005). Reviews on the effect of PL on plant reproductive success are rife with examples in which the number of fruits per plant and/or seeds per fruit were negatively affected by the inadequacy of pollen receipt (See Burd 1994, Ashman *et al.* 2004, Knight *et al.* 2005, Wolowski *et al.* 2014, Camacho & Totland 2018, Burns *et al.* 2019 and references therein). This negative effect can be expected for both endozoochorous and myrmecochorous plant species since fruit and seed development depend on the success of ovule fertilization regardless of the dispersal system.

In addition to its quantitative effects, PL can also strongly influence traits of the dispersal units mediating attraction of dispersers. These effects have been relatively neglected in pollination studies. However, physiological studies, mainly focused on crop plant species, indicate that such effects are likely driven by patterns of hormone secretion during fruit development. Most hormones regulating the differentiation of ovaries into fruits are secreted by seeds -especially auxin and gibberellin (Osga & Reineck 2003, Pattinson *et al.* 2014, Balanguera-Lopez *et al.* 2020). Auxin secreted by seeds also boosts ethylene production, another plant hormone directly driving fruit ripening and, consequently, seed development (Balanguera-Lopez *et al.* 2020). By negatively affecting the number of seeds per fruit, PL can directly interfere with the volume of hormones secreted and, consequently, with patterns of fruit development.

For endozoochoric plants producing fleshy fruits, the decline in the number of seeds per fruit has been associated with changes in fruit shape, a trait that can determine the chances of fruit removal by dispersers (Valenta & Nevo 2020 - but see section 3.1). Several studies focusing on endozoochorous crop plant species such as apples (Brookfield *et al.* 1996; Bucchini & Di Vaio 2005), kiwi (Lai *et al.* 1990), cherimoya (Gonzalez *et al.* 2006), and grapes (Boselli *et al.* 1995) have shown that the variability of fruit shapes is higher when seed number per fruit is low. For apples and cherimoya, specifically, the formation of misshapen fruits was associated with a low frequency of pollinator visitation (Brookfield *et al.* 1996, Matsumoto *et al.* 2012) and/or low pollen load (Gonzalez *et al.* 2006), two of the main mechanisms leading to PL for plants (Ashman *et al.* 2004a). Therefore, dispersal units from pollen-limited flowers are more likely to be more variable in shape than the ones from not pollen-limited flowers.

Reduced seed number in fleshy endozoochorous fruits has also been associated with changes in the chemical composition of the fleshy pulp, fruit size, and the time of maturation (Pattison *et al.* 2014). Regarding pulp composition, the hormones secreted by the seeds increase the activity and strength of fruits as a sink organ within the plant (Balaguera-López *et al.* 2020). The more seeds per fruit, the greater the secretion of such hormones and likely the higher the resource allocation from other plant parts to fruits (Olivieri *et al.* 1994; Knight *et al.* 2006 and references therein). Therefore, by receiving relatively fewer resources, fruits from pollen-limited flowers should be smaller and/or less nutritionally valuable than those from non-pollen-limited flowers (but see Petit 2011). Like the studies investigating the relationship between seed number and fruit shape, studies investigating the relationship between seed number, fruit size, and pulp composition have mainly used crop plant species as models. In *Vitis vinifera* (Vitaceae), for instance, there is a strong positive relationship among seed number, acidity, and solid soluble content of the fruit's pulp (Boselli *et al.* 1995). A similar relationship was observed for apple lineages in which fruit size and weight, calcium concentration, and pulp firmness was positively related to seed number per fruit (Keulemans *et al.* 1996, Bucchini & Vaio 2005). In addition to its effects on fruit composition, PL can interfere with the timing of fruit maturation since fruits bearing more seeds tend to mature faster (Gorchov 1985, Patterson 1990). Therefore, by reducing the number of seeds per fruit, PL can indirectly affect not only the quality of the pulp consumed by the frugivores but also the temporal patterns of fruit availability to the endozoochorous dispersers.

The effects of PL on myrmecochorous fruits should differ from those of endozoochorous fruits because myrmecochorous fruits are not fleshy. Myrmecochorous plants instead produce dehiscent dry fruits that shelter a few to several diaspores comprised of a seed plus elaiosome, a lipidic ant-attractive appendage attached to the seed that serves as a food reward to ants (Beattie 1985). Worldwide, myrmecochorous fruits release these diaspores in two ways (Lengyel *et al.* 2010). The first and most common is ballistic ejection of diaspores from explosively dehiscent fruits (Rico-Gray & Oliveira 2007). Alternatively, ripe fruits can dehisce (sometimes while still connected to the parental plant), dropping mature diaspores beneath the maternal plant (Gorb & Gorb 2003). Regardless of the strategy, disperser ants interact only with diaspores scattered over the soil surface and are therefore, not directly attracted to fruits. Thus, any potential PL effect on the traits of myrmecochorous fruits should play a minor role in the attraction of disperser ants. For this reason, we focus on the potential effects of PL on myrmecochorous diaspore traits (seed + elaiosome).

Compared to endozoochorous fruits, there is limited data on the physiological mechanism regulating myrmecochorous diaspore development and the influence of PL on it. This is especially true if we focus on elaiosome development. Structures classified as elaiosomes can develop from different tissues across taxa (i.e. parts of fruits, seeds, and less frequently flowers) (Mayer *et al.* 2005), meaning that physiological mechanisms governing their development should also be markedly variable across species. Regardless of its structural origin, however, elaiosome development still depends on ovule fertilization and patterns of plant resource allocation to fruits (Ciccarelli *et al.* 2005). Therefore, the development of myrmecochorous diaspores should be driven by the same general mechanisms regulating fruit and seed development in other species. It is thus likely that pollen-limited myrmecochorous fruits that produce fewer seeds should secrete less fruit-regulating hormones and receive fewer resources from the maternal plant. In this case, myrmecochorous diaspores from pollen-limited flowers should be smaller and bear a smaller and/or less nutritious elaiosome than the ones produced by not pollen-limited flowers. These are important traits determining diaspores attractiveness to

ants—diaspores bearing larger elaiosomes, with higher lipidic content are more likely to be removed by ants (Mark & Olesen 1996; Fischer *et al.* 2008; Clark & King 2012). These generalizations about the PL effect on myrmecochorous diaspores traits, however, are still largely hypothetical due to the lack of empirical data and remain to be evaluated.

Pollen limitation effects on seed traits

Attributes of seed vigor, like the likelihood of seed germination and establishment, are important for determining a seed's success post-dispersal, regardless the dispersal mode (Baskin & Baskin 2014). Although not directly related to disperser's responses to dispersal units, seed vigor may interact with disperser's responses to dispersal unit traits (see 3.2) and consequently drive the qualitative SDE component of animal-dispersed plant species. For this reason, the effects of PL on this seed vigor will be included in our framework.

Theoretical models predict that PL should reduce the number of seeds produced while increasing seed mass – a parameter directly correlated to seed vigor (Petit 2011; Huang *et al.* 2017; Huang & Burd 2019a, a; Lalonde & Roitberg 2022). According to such models, by reducing the number of fertilized ovules, PL modifies the trade-off between seed number and seed size, increasing resources allocated to each seed (Ida *et al.* 2015). Considering that seed mass is one of the main traits determining the chances of seed survival and establishment (seed vigor, from now on) (Saatkamp *et al.* 2014), these models suggest that the negative quantitative effect of PL on plant reproductive success may be compensated, at least partially, by its positive effect on the chances of seed post-dispersal survival. However, empirical studies evaluating the relationship between seed number and size have reported positive (e.g. Johnston 1991), negative (Navarro 1998; Hegland & Totland 2007; Baskin & Baskin 2018), or even neutral effects (e.g. Niesenbaum 1993; Hegland & Totland 2007, 2008; Runquist & Moeller 2013; Chen & Zhao 2017). These studies have also shown that PL can affect seed vigor even when it does not affect the seed number/size trade-off (Winsor *et al.* 2000, Kalla & Ashman 2002, Colling 2004, Russo *et al.* 2006). For instance, in *Ranunculus acris* (Ranunculaceae), a facultative bird-dispersed species, PL did not affect the number of seeds produced per fruit but reduced seed mass by 18% (Hegland & Totland 2007), a result likely driven by a decline in the quality of pollen fertilizing the ovules. Together, theoretical and empirical evidence indicate that PL effects on seed vigor can vary from negative to positive, depending on the plant species and/or conditions under which plants are grown (Baskin & Baskin 2014, 2018).

Indirect effects of pollen limitation on dispersers behavior and seed dispersal effectiveness (SDE)

Seed dispersal is a product of the foraging behavior and movement of animals consuming fruits or diaspores (Russo *et al.* 2006). For this reason, its outcome can be directly or indirectly influenced by any factor interfering with disperser foraging and movement decisions. Based on the quantitative and qualitative effects of PL on plant reproduction described above, PL has the strong potential to modify the relative value of fruit resources to dispersers and the spatial and temporal configuration of these fruit resources to dispersers (i.e. resource landscape), consequently affecting the patterns of dispersers feeding, movement, and seed transportation within the habitat (Abrahms *et al.* 2021). Therefore, the PL indirect effect on the dispersers foraging behavior should be the main mechanism driving PL effects on SDE of animal-dispersed plant species.

The Optimal Foraging Theory (OFT - MacArthur & Pianka 1966) is a valuable theoretical framework that allow us to predict the fine-scale behavioral decisions of disperser species in response to the quantitative and qualitative effect of PL on plant reproductive success. According to OFT, seed dispersers make foraging decisions to maximize their energy intake and fitness, moving between food sources accordingly (Schoener 1971; Abrahms *et al.* 2021). Dispersers are thus expected to strategically maximize acquired energy relative to the energetic costs of searching, handling, and consuming food resources, consuming non-optimal food items with decreasing probability (MacArthur & Pianka 1966, Sobral *et al.* 2010, Sebastian-Gonzalez *et al.* 2016). Therefore, whenever modifying the relative value of plants and/or dispersal units to dispersers, PL can predictably modify the dispersers foraging decisions (Westcott *et al.* 2005; Russo *et al.* 2006), and consequently the SDE of animal-dispersed plants. Some of these PL-SDE effects are predictable and supported by empirical

evidence, allowing us to propose directional hypotheses about the influences of PL on different components of SDE. However, in some cases, the direction and strength of PL's effects on disperser's behavior still rely on empirical evidence of PL's effects on the qualitative traits of plant dispersal units. In these cases, we proposed non-directional hypotheses and explored alternative scenarios as a way of fueling new research on the underlying mechanisms driving the effects of PL on SDE. Both directional and non-directional hypotheses are summarized in Table 01.

Indirect effects of pollen limitation on the quantitative component of Seed Dispersal Effectiveness (SDE)

The number of dispersal units (i.e. fruits for endozoochory; diaspores for myrmecochory), dispersal unit size, and dispersal unit shape are the more intuitive plant attributes that can indirectly affect the SDE quantitative component of pollen-limited plants (Fig.1, Table 1). These attributes are not only the main ones affected by PL but also the primary traits influencing the disperser's foraging decisions within and between habitats (Jordano 1987; Westcott *et al.* 2005; Côrtes & Uriarte 2013). As such, they are the best traits to set the initial pathways for future studies investigating indirect links between PL and seed dispersal.

Within a given habitat, fruiting plants represent favorable foraging patches to the dispersers, with dispersers moving non-randomly among these plants (Westcott *et al.* 2005; Côrtes & Uriarte 2013). Plants producing more dispersal units can be considered high-quality foraging patches since the relatively higher abundance of food resources to dispersers might maximize their energy intake while reducing search costs (Russo *et al.* 2006). Following OFT, it is expected then that dispersers not only visit high-quality fruiting plants more frequently but also leave these less frequently than the poor-quality ones (Donahue *et al.* 2003; Abrahms *et al.* 2021; King & Marshall 2022). Therefore, by reducing the number of dispersal units produced by the plants, PL can indirectly compromise the frequency of disperser visits, the time of disperser residence at plants, and, consequently, the number of seeds removed from the parental plant (Fig.1 and Table 1).

The positive relationship between the number of dispersal units produced by plants and their attractiveness to dispersers is reported in several empirical and theoretical studies evaluating the foraging decisions of frugivores within and between populations of endozoochorous plant species. For instance, frugivorous birds (e.g. Jordano 1995, Russo 2003, Christianini & Oliveira 2009, Palacio *et al.* 2015, Guerra *et al.* 2017) and mammals (e.g. Guitian & Munilla 2010, Lambert *et al.* 2006, Nakagawa *et al.* 2007) track fruit abundance on individual plants leading to a positive relationship between fruit set, visitation frequency, and fruit removal rates. Additionally, some studies have shown that frugivore's visitation rate and duration are positively associated with the number of seeds removed per frugivore's visit in most of the endozoochorous plants (e.g. Howe & De Steven 1979; Jordano 1987; Jordano & Schupp 2000). Thus, the negative PL effect on the plant fruit set can indirectly compromise the seed dispersal rate, and consequently the quantitative component of SDE of endozoochorous plants (Table 1).

Although ant dispersers do not directly interact with the myrmecochorous fruits, variation in fruit set can also drive patterns of ant interaction with the diaspores. Some studies have shown that ant dispersers are more likely to interact with diaspores produced by non-ballistic myrmecochorous plants with larger fruit sets, since the diaspores tend to accumulate around these plants and become more attractive to the disperser ants (Gorb & Gorb 2000; Boulay *et al.* 2007). Even in myrmecochorous taxa with primary ballistic dispersal, the diaspores are ejected over short distances from the parent plant (commonly less than one meter) (Culver & Beattie 1978; Leal *et al.* 2007; Beaumont *et al.* 2009). Thus, diaspore density should be higher near parent plants with higher reproductive output, regardless of their primary dispersal mechanism. In this scenario, PL can indirectly affect ant disperser decisions, which may prefer to forage away from pollen limited myrmecochorous plants or patches within their foraging area. If so, pollen-limited myrmecochorous individuals should contribute disproportionately less to the seed dispersal to other microsites than not pollen-limited ones (SDE quantitative component) (Table 01).

In addition to the variation in the number of dispersal units, the effects of PL on dispersal unit traits can modify their relative value to dispersers and, consequently, the quantitative component of SDE for the plants (Fig.01). For endozoochorous plants, as described above, fruits bearing fewer seeds tend to be smaller,

commonly offering less nutritious rewards to dispersers (Johnson *et al.* 1985; Herrera 1987). In this case, OFT predicts that the preferential consumption of the larger fruits with higher nutritional content (i.e., those from not pollen-limited plants) maximizes the frugivore's energetic gain per fruit removed (May *et al.* 2019; Ghosh *et al.* 2020). Indeed, there is a large body of empirical studies showing that fruit size is one of the main traits driving the patterns of frugivores interactions with endozoochoric fruits (Wheelwright 1993; Woodward *et al.* 2005; Martínez *et al.* 2008). Additionally, dispersers can differ in their nutritional requirements which can mediate their preferences for fruits available in the community (Albrecht *et al.* 2018; Valenta & Nevo 2020). Therefore, if PL negatively affects fruit size and/or nutritional value to frugivores, it may indirectly interfere with the frugivore visitation rate, and consequently, the number of seeds removed from pollen-limited endozoochoric plants (Fig.1; Table 1).

For myrmecochorous plants, diaspore traits are the main factors determining ant foraging preferences. In general, disperser ants interact preferentially with larger diaspores, diaspores with a higher elaiosome-to-seed ratio, and those bearing elaiosomes with higher lipidic content (Gómez *et al.* 2005; Boulay *et al.* 2006; Leal *et al.* 2014b, a; Miller *et al.* 2020). Like in endozoochory, this preference is predicted by OFT because the higher the elaiosome-to-seed ratio, and/or the elaiosome lipidic content, the higher the net energetic intake for ants per diaspore removed (Bono & Heithaus 2002; Byk & Del-Claro 2011). Therefore, PL can indirectly modify the patterns of myrmecochorous diaspores removal whenever negatively affecting elaiosome size and/or lipidic content. The magnitude of the effect of PL on ant foraging preferences will depend though on the quantification of the PL impacts on myrmecochorous diaspores traits, which remains to be addressed in future studies (see 2.2; Table 1).

The links between dispersal unit size, nutrient content, and attractiveness to dispersers are often linear and well explored in the literature, allowing us to propose testable predictions about the indirect effect of PL on the quantitative SDE component (Table 01). However, the consequences of PL's impact on other dispersal units' traits to the SDE quantitative component are more difficult to infer. For instance, endozoochoric fruits from pollen-limited flowers should differ in shape and color from non-limited ones. Both fruit color and shape influence fruit attractiveness to frugivores (Valido *et al.* 2011; Duan *et al.* 2015). Therefore, PL's effect on these traits should also affect the patterns of frugivore's interaction with fruits. However, dispersers' responses to these traits are expected to be more variable and context-dependent than their response to propagule size and nutrient content. While net energy income is a universal currency determining the success of foraging strategies across all disperser clades, disperser's responses to fruit shape and color will depend on the cognitive and learning ability of dispersers in associating these traits with fruit quality (Nevo *et al.* 2018). Commonly, endozoochoric plants are visited by a diverse set of frugivore species such as lizards (Valido & Olesen 2019), birds (Howe 1987), bats (Charles-Dominique & Cockle 2001), rodents (Godo *et al.* 2022), and other mammals (Matias *et al.* 2010), that largely vary in their learning and cognitive abilities. Therefore, PL may affect the quantitative SDE component if it results in the formation of misshapen and/or miscolored fruits, but this effect should largely depend on the type of seed dispersers available and their cognitive abilities (Healy & Jones 2002; Duan *et al.* 2015) (Table 01).

Finally, PL's effects on color and shape are expected to have little or no influence on the quantitative component of SDE for myrmecochorous plant species. Ants use chemical cues to locate food resources within their foraging area, including myrmecochorous diaspores and, so far, we lack evidence that they can respond to the visual cues of the diaspores (Sheridan *et al.* 1996; Reifenrath *et al.* 2012). For this reason, PL is more likely to shape ant responses to myrmecochorous diaspores if it affects diaspores chemical signals or concentrations, which has never been evaluated.

Indirect effects of pollen limitation on the qualitative component of Seed Dispersal Effectiveness (SDE)

Pollen limitation can affect the qualitative component of SDE by influencing: (i) the probability of pre-dispersal predation, (ii) the frequency of long-distance dispersal events, and (iii) the probability of seed survival and (iv) post-dispersal seed germination (Fig. 1; Table 1). PL can indirectly affect the probability of dispersal units' damage by natural enemies in two opposing directions. For some plant species, producing many fruits is a strategy that satiate seed predators, ensuring that some seeds escape pre-dispersal predation

and be dispersed to potentially favorable microsites (Jordano 1987; Bonal *et al.* 2007; Francisco *et al.* 2008). For those plants, PL can indirectly reduce predator's satiation when reducing fruit or seed number and, consequently, reduce the number of seeds escaping predation. For plants in which fruit or seed set is not associated with the satiation of predators, PL may increase the chance of seeds escaping predation by reducing plant attractiveness to predators. Like seed dispersers, pre-dispersal seed predators should preferentially forage in dense resource patches to maximize energy intake (Donahue *et al.* 2003; King & Marshall 2022). Accordingly, plants that do not experience PL could become more attractive to pre-disperser seed predators (e.g. Trivedi *et al.* 2004; Borchert & DeFalco 2016; Bruno *et al.* 2021). In this case, PL could indirectly benefit the plants by reducing fruit density and, consequently, the chances of the dispersal unit's predation before removal by an effective disperser. It is even plausible that the negative effect of PL for dispersal due to a reduction in plant attractiveness to dispersers may be offset by a reduction in the chance of seed pre-dispersal predation. Such compensation has been observed in species producing fruits rich in secondary metabolites which simultaneously reduces attractiveness to both dispersers and predators (see Nelson & Whitehead 2021 and references therein).

Future studies should consider that the effect of PL on pre-dispersal predation will depend on 1) the magnitude of the pre-dispersal predation effect on SDE of plants occurring in different habitats and 2) on the relative effect of the number of dispersal units on the attractiveness of plants to dispersers and predators. PL effects should be stronger in plant taxa for which the impact of pre-dispersal predation on reproductive success is strong. Similarly, PL may have a neutral or even positive effect on pre-dispersal predation when its negative impact on plant attraction to seed predators is equal or higher than its influence on the attractiveness of effective dispersers. Therefore, the direction and magnitude of PL's indirect effects on the patterns of pre-dispersal predation are likely variable across plant species and habitats and remain to be tested (Table 1).

By compromising seed production, PL can indirectly affect the frequency of long-distance seed removal. Most seeds dispersed by animals are transported over relatively short distances from the source, while only a small subset are moved over long distances (Nathan *et al.* 2008; Schurr *et al.* 2018; Rogers *et al.* 2019). Long-distance removals disproportionally influence the SDE qualitative component (Schupp *et al.* 2010) since the seeds dispersed farther from parental plants escape the zone of density-dependent mortality near the parental plant, increasing the chances of survival and establishment (Howe & Smallwood 1982; Howe & Miriti 2000). Despite their significance, long-distance dispersal events are rare, and their probability is directly related to the number of seeds removed by dispersers – something easily observed in studies reporting dispersal kernel plots. These plots depict a probability-density function characterizing the dispersal distance of seeds from a common source, assuming an equal probability of dispersal in all directions (Nathan *et al.* 2012; Rogers *et al.* 2019). Studies evaluating the relationship between seed production and the frequency of long-distance dispersal events showed that increases in seed production lift the entire dispersal kernel, resulting in more long-distance dispersal events (Schurr *et al.* 2018; Schupp *et al.* 2019). These results suggest that PL can indirectly compromise the frequency of long-distance removals whenever reducing seed production.

To demonstrate how PL can influence the frequency of long-distance removals, we built dispersal kernel plot predicting the probability-density function of seed dispersal from pollen-limited and non-pollen limited plants (Fig. 2). We simulated two datasets: one representing the distribution of 1000 seeds, representing the seed set of plants that do not experience PL (Fig. 2A), and another set representing the distribution of 250 seeds (Fig. 2B), representing the mean effect size of PL on the number of dispersal units produced by plants estimated by Knight *et al.* (2005) (75% decline in seed set). As expected, the dispersal kernel plot from an adequately pollinated plant, exhibited a longer tail than the one from the pollen-limited plant (Fig. 3), indicating that long-distance removal events are indeed more likely for plant not experiencing PL. For the pollen-limited plant, the maximum removal distance was 37.22% lower than the not pollen-limited ones. This indicates that PL's effect on crop size can indirectly negatively affect not only the frequency of long-distance dispersal events but also the maximum dispersal distance. This effect of PL on the frequency of long-distance dispersal is expected for both endozoochorous and myrmecochorous plants, because long-distance removals are rare, regardless of dispersal mode.

In addition to its numeric effect, PL may also impact the frequency of long-distance dispersal events through its effects on dispersal unit traits mediating interactions with high-quality dispersers. Within a community, seed transportation is performed by several disperser species that disperse the seeds over different distances (Jordano & Schupp 2000). For both endozoochorous and myrmecochorous systems, the range of seed dispersal distance and the frequency of long-distance events performed by a given disperser can be predicted by physiological, behavioral, and morphological traits of the disperser species (Stanton 2003; Dehling *et al.* 2014). Frugivores or ants species foraging over larger areas, for instance, are more likely to transport seeds over long distances and are therefore considered high-quality dispersers (Giladi 2006; Jordano *et al.* 2007; Schurr *et al.* 2018; Anjos *et al.* 2020; Godinez-Alvarez *et al.* 2020). Additionally, variation in the disperser traits can also affect their responses to dispersal units' traits, since low and high-quality dispersers can differ in their foraging preferences (e.g. Russo 2003; Leal *et al.* 2014b; Palacio *et al.* 2020). Therefore, by influencing the dispersal units' traits, PL can indirectly affect the assemblage of dispersers interacting with the dispersal units and, consequently, the quality of seed dispersal received by pollen-limited plants.

In the case of myrmecochory, omnivorous small-bodied ant species, foraging in groups and exhibiting recruitment behavior tend to consume the elaiosomes where the diaspores are found, rarely removing the seeds over long distances (Gunther & Lanza 1989; Ness *et al.* 2004; Gove *et al.* 2007; Leal *et al.* 2014a). Therefore, these species are considered low-quality dispersers (Giladi 2006; Ben-Zvriet *et al.* 2021). Conversely, large-bodied carnivorous ant species are considered high-quality dispersers, responsible for most of the long-distance removal events of myrmecochorous diaspores (Giladi 2006; Gove *et al.* 2007). Interestingly, high, and low-quality ant dispersers respond differently to diaspore traits. While high-quality disperser ants interact preferentially with larger diaspores and lipid-rich elaiosomes, low-quality ants exhibit weak or no response to intra- and interspecific variation in elaiosome size and composition (Skidmore & Heithaus 1988; Boulay *et al.* 2006, 2007; Gammanset *et al.* 2006; Leal *et al.* 2014b, a). Therefore, PL can compromise the SDE qualitative component of myrmecochorous plant species whenever influencing the diaspores traits mediating attractiveness to high-quality dispersers (Fig. 01).

Similar to myrmecochory, frugivore body size tends to correlate positively with home range area (Jetz *et al.* 2004) and fruit consumption per visit (Jordano & Schupp 2000). Then, long-distance dispersal events for endozoochorous plants rely on a small subset of large-bodied dispersers (Howe & Smallwood 1982; Jordano *et al.* 2007; Spiegel & Nathan 2007; Schurr *et al.* 2018; Naniwadekaret *et al.* 2019). Generally, high-quality large-bodied dispersers prefer large fruits (Wheelwright 1985; Burns 2013; Sebastian-Gonzalez *et al.* 2017). Therefore, by interfering with fruit and/or seed size, PL can reduce the chances of seed dispersal by large-bodied high-quality dispersers, and consequently the quality of seed dispersal service received by the pollen-limited plants (Table 1).

Following dispersal, seed germination and seedling establishment depend on seed vigor – a seed physiological property determining its potential for germination, emergence, and development (*sensu* Rajjou *et al.* 2012). Differently from the other mechanisms explored in this section, PL's effect on seed vigor should play no role in disperser's foraging decisions. However, this effect can directly influence the chances of post-dispersal seed survival, germination, and establishment and, consequently the qualitative SDE component of animal-dispersed plants (Fig. 2). Seed vigor is ultimately determined by embryo traits and the amount and quality of resources allocated to the seed's nutrient reserves (e.g. endosperms). It is expected that larger seeds, with larger embryos and/or more nutritional reserves, are more vigorous than the smaller ones (TeKrony & Egli 1991; Ambika *et al.* 2014; Saatkamp *et al.* 2019; Reed *et al.* 2022). For this reason, any processes decreasing seed size, as in the case of PL (Ashman *et al.* 2004a; Huang & Burd 2019), can directly compromise seed vigor and, consequently, the outcome of all post-dispersal processes driving the SDE qualitative component.

The PL effects on seed vigor are expected to happen on both endozoochorous and myrmecochorous plants since they should occur upstream of dispersal activity. However, in endozoochorous plants, the impact of PL on the probability of seed germination and establishment after dispersal will be likely driving by an interaction between PL effects on seed vigor and the efficiency of seed cleaning by dispersers. For instance, the pulp of endozoochorous fruits, especially drupes and berries, often contains germination inhibitors preventing

seed germination while the fruit is still connected to the maternal plant (Robertson *et al.* 2006). Pulp attached to seeds after dispersal can also preclude germination by affecting the microenvironment for seed germination (Meyer & Witmer 1998; Samuels & Levey 2005). Therefore, post-dispersal germination of seeds from endozoochorous species will also depend on the efficiency of dispersers in separating seeds from pulp (see Traveset & Verdu 2002 and references therein). This efficiency is determined by interactions among fruit chemistry, morphology, and disperser identity (Traveset *et al.* 2007 and references therein). Because PL can directly influence fruit chemistry and morphology and, PL could indirectly affect the patterns of fruit handling and seed cleaning by dispersers. Thus, by affecting fruit traits, PL can indirectly affect the efficiency of pulp removal which can determine the capacity of post-dispersal seed germination (Table 1).

Challenges and future directions

4.1. The context-dependent nature of PL and its effects on SDE

The processes mediating direct and indirect effects included in our framework - plant physiological responses to PL, the magnitude of PL effects on plant reproduction, behavioral responses of dispersers to plant and fruit traits, and SDE outcomes - are likely to be highly variable across space and time (Ashman *et al.* 2004b; Knight *et al.* 2006; Burns *et al.* 2019; Schupp *et al.* 2019; van Leeuwen *et al.* 2022). Such variability results from external factors that jointly impact the magnitude of PL effect on plant reproductive success and the plant and seed disperser responses to these effects. For the sake of brevity, we will not explore all the extrinsic factors that can modulate PL-SDE effects. Instead, we described the main ones in Fig. 3 to detail our rationale about the context-dependent nature of our framework. For instance, the magnitude of PL can be influenced by factors such as the density of plants within (e.g. Fausto *et al.* 2001), the composition and structure of pollination assemblage (e.g. Gomez *et al.* 2010), the environmental and biotic conditions (e.g. plant and pollinator competition and predation pressure -Benoit & Kalisz 2020 and references therein), and the pollinator's physiological condition (Woodard & Jha 2017) (Fig. 3). All these factors will likely modulate the magnitude of any PL indirect effect on the SDE of animal-dispersal plants. In addition, the effects of PL on plant reproduction and responses of seed dispersers to it will likely be influenced by factors regulating patterns of plant resource allocation and the strategies of disperser's foraging and movement, respectively. Some of these potential factors are the plant's and dispersers' physiological condition (e.g. Navarro 1998; Moore *et al.* 2022), competition and predation pressure of the plant and dispersers (e.g. Houle *et al.* 2010; Burgos *et al.* 2022), the abundance of alternative feeding resources to dispersers (e.g. Correa & Winemiller 2014) (Fig. 3). Therefore, direct and indirect effects of PL on SDE should vary predictably according to the factors regulating the ecological processes presented in our framework.

Surely, this variability will provide challenges to future studies evaluating part or the entire PL-SDE framework. For instance, because of its context-dependent nature, individual study cases may not provide robust evidence about the overall PL-SDE effects occurring in different habitats and/or involving different species. This generalization will only be possible in the long-term, after accumulating empirical evidence about the mechanisms proposed here. To reach this goal, future studies must acknowledge the context-dependent nature of their empirical evidence, directly evaluating the mechanisms underlying PL-SDE effects across different geographical and temporal scales whenever possible. Because most of the mechanisms underlying our PL-SDE framework still rely on future evidence, it would be speculative to propose directional hypotheses about how these extrinsic factors can moderate the magnitude of the PL-SDE effects. For instance, although the disperser's physiological state can influence how dispersers will interact with the fruiting plants (Warne *et al.* 2019), the magnitude and direction of such interference will depend on the magnitude and direction of PL on fruit quantity and quality. For this reason, we understand that the set of innovative hypotheses proposed here (Table 01) are the starting point for investigation into PL-SDE connections. Among those, we strongly suggest that researchers focus immediate effort on understanding PL's direct effects on plant reproductive physiology and dispersal unit traits - the most neglected PL effect explored in the literature. We suggest that because all the effects described here will likely depend on the magnitude of PL effects on plant reproductive success (Ashman *et al.* 2004b; Knight *et al.* 2005; Huang & Burd 2019). For instance, future studies should experimentally manipulate the magnitude of PL in focal populations, measure quantitative and qualitative

effects of PL on fruits, and then ideally, relate these to disperser feeding strategies, and ultimately dispersal within and/or across different reproductive seasons. Alternatively, identifying populations that experience a range of PL severity could be an observational approach to examining our framework. Studies focused on the downstream effects of PL on dispersal will also benefit from a predictive approach based on OFT— a theory that has largely benefited our comprehension of the ecology and evolution of animal foraging strategies, including seed dispersers (Pyke 2019).

4.2 Population, community, and evolutionary consequences of the PL-SDE link

Pollination and seed dispersal outcomes have long been recognized as ecological processes regulating plant demography, geographical distribution, and population growth (see Baer & Maron 2018; Snell *et al.* 2019; Dawson-Glass & Hargreaves 2022). Our framework adds a new layer of complexity to this scenario, showing that pollination and seed dispersal outcomes are not independent processes in animal-dispersed plants. This non-independence modifies our perspectives about the pathways through which pollination can influence plant population dynamics. It highlights the (i) pollination’s role as a moderator of population processes of animal-dispersed plants is not only dependent on the pollination outcome itself, but also on its consequences for ecological processes occurring after fruit maturation, and (ii) the role of PL on population dynamics of animal-dispersed plant species can be more pervasive than previously expected, influencing a number of post-dispersal processes and their consequences to other levels of biological organization (e.g. assemblage composition and community structure).

In addition to influencing our perspectives about the role of pollination on plant population dynamics, our framework also brings novel and concerning implications for flowering plant populations in human-disturbed habitats. In pristine communities, the long-term consequences of PL-SDE effects on population dynamics will likely depend on their consistency over time and space. In these non-disturbed habitats, PL impacts on plant population dynamic via SDE can be counterbalanced by the influx of transported seeds from other populations that are not pollen-limited (Kendrick *et al.* 2017), or in the case of iteroparous plant species, by seeds produced in subsequent reproductive seasons when PL is less severe (Schermer *et al.* 2019; but see Tye *et al.* 2020). However, plant species in human-modified landscapes experience a relatively constant or even progressively higher PL over time (Eckert *et al.* 2010; Sapire *et al.* 2015) often due to the negative effects of anthropogenic disturbances on the richness and abundance of pollinator assemblages (Keith *et al.* 2023). In disturbed habitats, the strong and relatively constant PL could reduce the relative abundance of pollen-limited species, progressively shifting communities towards those dominated by species less prone to PL (e.g. self-compatible species; Knight (Knight *et al.* 2005; Cisternas-Fuentes *et al.* 2023). Anthropogenic disturbances also modify seed disperser assemblage, eroding seed dispersal services provided to endozoochorous and myrmecochorous plants in disturbed habitats (Leal *et al.* 2014a; Valiente-Banuet *et al.* 2015). Therefore, the concomitant decline in both pollinators and seed dispersers could synergistically compromise plant population growth and regeneration of plants through the links between PL and SDE in disturbed habitats, which represent about 97% of terrestrial ecosystems (Plumptre *et al.* 2021).

Finally, demographic impacts of PL on plant populations that are mediated through dispersal have the potential to drive eco-evolutionary feedbacks impacting floral traits involved in pollinator attraction and plant mating systems (Fig.3). For instance, strong PL in a given generation could negatively impact plant densities in the following generation due to an overall reduction in the height of the seed dispersal kernel (Fig. 3). A low density of reproductive plants can reduce pollinator attraction and further exacerbate PL in the following generation (Kunin 1993; Wailes & Agren 2004; Weber & Kolb 2013; Koski 2023). Increasingly PL should result in stronger pollinator-mediated selection which frequently favors individuals with larger or showier floral displays (Trunschke *et al.* 2017), and/or those with a higher capacity for self-fertilization in species with mixed mating systems (Pannell *et al.* 2015). Finally, if the seeds of plants favored by fecundity selection are also more effectively dispersed, their offspring have a higher chance of long-distance dispersal. Thus, the spatial distribution of genotypes with favorable floral traits could be wider than those with unfavorable traits following severe pollinator limitation.

4.3. PL-SDE framework and its caveats as an opportunity for multidisciplinary collaboration

Historically, different types of ecological interactions have been studied in isolation from one another, mostly neglecting that individual fitness emerges from the interplay of these interactions across the individual's lifespan. To overcome this, it is fundamental to improve the bonds among different research areas. Our framework (Fig.1) and the testable hypotheses associated with it (Table 1) exemplify innovative ideas arising from multidisciplinary collaborations. To propose our framework connecting two processes for the fitness of animal-dispersed plants, we incorporated evidence from different research areas such as pollination and dispersal ecology, agronomy, plant physiology, and behavioral ecology. During our literature search, the isolation between disciplines was made clear (e.g. agronomy from pollination and dispersal ecology). Although our framework provides a guideline for future studies focusing on PL-SDE connections, future investigations will be challenged by the need for new multi-disciplinary collaborations. For instance, ecological studies on PL would benefit from collaboration with plant physiologists and biochemists to move beyond the common quantification of PL's effects on fruit and/or seed set. Similarly, studies focused on SDE would benefit from inclusion of pollination biologists and behavioral ecologist to unravel the mechanisms indirectly driving the PL effect on different SDE components. Without incorporating theoretical and empirical tools from different but related areas, the knowledge gaps brought to the surface by our study will persist and prevent the proposition of innovative questions that can change our perspectives on the forces driving the outcome of plant-animal interactions. Therefore, beyond connecting the knowledge from different disciplines, our PL-SDE framework provides a valuable opportunity to reduce the isolation of related disciplines and enhance our understanding of the role of ecological interactions in regulating plant population and community dynamics.

Acknowledgments

We would like to thank Amanda Vieira, Paulo Enrique Peixoto, and Alexandre Palaoro for their valuable suggestions in the first draft of this manuscript. L.C. Leal thanks Sao Paulo Research Foundation (International Research scholarship – 2022/02501-6), the Clemson International Services and the Department of Ecology and Evolutionary Ecology from the Federal University of Sao Paulo – specially Cinthia A. Brasileiro and Jose Eduardo de Carvalho – for all the help along her sabbatical at Clemson University.

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Figure captions

Figure 1: By affecting the number and the traits of dispersal units produced by plant species dispersed by animals, pollen limitation can indirectly interfere with the foraging decisions of disperser animals and, consequently, with their behavior when exploring fruiting plants (yellow boxes). These disperser behaviors are directly related to the outcome of some of the main factors determining the quantitative (orange boxes) and qualitative components (green boxes) of Seed Dispersal effectiveness for animal-dispersed plants. In this scheme, seed vigor is the only plant trait that can directly affect the qualitative component of SDE, without interfering with the disperser behavior. Despite it, this trait was included in the scheme for the sake of clarity of our rationale.

Figure 2: Hypothetical dispersal kernel plots representing the effect of pollen limitation on crop size and its consequences for the distance of seeds dispersed by animals. Since it is a theoretical model, it represents the expected seed dispersal pattern regardless the metric unit used to measure seed dispersal distance in study cases. According to Knight et al. (2005), pollen-limited plants produced 75% fewer fruits than not pollen-limited ones. For this reason, we created two data sets simulating this mean effect on plant seed set – 1000 seeds for pollen-limited plants (A) and 250 for not pollen-limited ones (B). Then, we modeled the expected distribution of these seeds over a distance gradient following a probability-density function.

Figure 3 : General flowchart representing a simplified version of our PL-SDE framework, its context-dependent nature, and its implications to populational eco-evolutionary processes. In the dashed boxes, we pointed out the main extrinsic effects that can drive the outcome of PL-SDE effects and its consequences to animal-dispersed plants. We also highlight the existence of ecological and evolutionary consequences of PL-SDE links to plant demography and plant floral traits, respectively.





