A framework for comparing pollinator performance: effectiveness and efficiency

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ABSTRACT

Measuring pollinator performance has become increasingly important with emerging needs for risk assessment in conservation and sustainable agriculture that require multi-year and multi-site comparisons across studies. However, comparing pollinator performance across studies is difficult because of the diversity of concepts and disparate methods in use. Our review of the literature shows many unresolved ambiguities. Two different assessment concepts predominate: the first estimates stigmatic pollen deposition and the underlying pollinator behaviour parameters, while the second estimates the pollinator's contribution to plant reproductive success, for example in terms of seed set. Both concepts include a number of parameters combined in diverse ways and named under a diversity of synonyms and homonyms. However, these concepts are overlapping because pollen deposition success is the most frequently used proxy for assessing the pollinator's contribution to plant reproductive success. We analyse the diverse concepts and methods in the context of a new proposed conceptual framework with a modular approach based on pollen deposition, visit frequency, and contribution to seed set relative to the plant's maximum female reproductive potential. A system of equations is proposed to optimize the balance between idealised theoretical concepts and practical operational methods. Our framework permits comparisons over a range of floral phenotypes, and spatial and temporal scales, because scaling up is based on the same fundamental unit of analysis, the single visit.

Key words: pollen deposition, pollen quality, pollinator performance, pollinator effectiveness, pollination efficiency, seed set, visit frequency.

CONTENTS

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I. INTRODUCTION

Comparing the success or performance of different flower visitors in achieving pollination and consequent seed set has been a perennial problem in pollination biology. A number of alternative terms for pollinator performance have been used such as effectiveness, efficiency, efficacy, importance *etc*. We include all of these in the general term "pollinator performance" to avoid semantic issues arising from the diverse and confusing proliferation of terms used in the literature. In spite of over 30 years of assessing pollinator performance, no commonly accepted conceptual framework or consensus on definitions or methodology has been adopted. This problem is a barrier to making multi-site, multi-year comparisons across different investigations, particularly those needed for international long-term assessments of the status and trends of pollinators.

Comparing pollinator performance is integral to several fields of investigation. Ecologists are interested in ranking pollinators of a given plant species and relating their performance to flower morphology, habitat type, temporal or spatial patterns of plant distribution (individuals or populations), and changes in the environment (Potts, Dafni & Ne'eman, 2001). In addition, plant breeders and agronomists are interested in the effectiveness of pollination methods, i.e. which methods result in the highest seed or fruit set of a crop (e.g. mechanical or wind pollination compared to different types of pollinators) (e.g. Morison *et al.,* 2000). Conservation biologists are concerned with pollinator diversity and the effects of pollinator extinction on the reproduction of rare plants and their populations (Biesmeijer *et al.,* 2006; Bond, 1994; Kearns, Inouye & Waser, 1998). Evolutionary biologists are interested in whether floral or other plant traits are adaptations to a specific pollinator species, type or assemblage (Fenster *et al.,* 2004; Johnson & Steiner, 2000; Waser *et al.,* 1996).

Floral characteristics are considered to have evolved mainly in response to a suite of traits of the pollinator with the best 'performance' and contribution to plant reproductive success (Stebbins, 1970; Grant, 1971; Wilson & Thomson, 1991; Olsen, 1997). Pollinators may have shaped the evolution of floral characteristics (Campbell, 1989; Wilson, 1995; Wilson & Thomson, 1996; Schemske & Bradshaw, 1999) and of plant lineages (Stebbins, 1970; Crepet, 1983; Grimaldi, 1991). In his 'most effective pollinator principle', Stebbins (1970, p. 318) described the underlying processes in the adaptation of flowers to their pollinators and stated, "the characteristics of flowers will be moulded by those pollinators that visit it most frequently and effectively". This definition clearly highlights the two key components of pollinator actions that shape pollinator performance: the 'frequency' and 'effectiveness' of flower visits. While 'frequency' is usually simply defined as the number of visits per flower per unit time, the 'effectiveness' component, often also called 'efficiency', is open to various, and sometimes contrasting, interpretations. These two components of pollinator activity are independent: less frequent pollinators may deposit more pollen and elicit more seeds (Mayfield, Waser & Price, 2001). In a refinement of Stebbin's (1970) 'most effective pollinator principle', Aigner (2001, 2004, 2006) used optimality modeling to

calculate fitness trade-offs of plant-pollinator interactions. Aigner (2001, 2004, 2006) argued that a plant should evolve greater specialization to a particular pollinator when the marginal fitness gain exceeds the marginal fitness loss from becoming less adapted to all other pollinators. Aigner (2004) demonstrated that phenotypic specialization for hummingbirds in *Dudleya greenei* (Crassulaceae) might evolve without trading-off the effectiveness of bumblebees.

We argue that such lack of standardisation has limited the ability to compare the performance of different pollinators. Considerable ambiguity arises from the diversity of synonyms and homonyms as demonstrated in Table 1. In addition, frequent partial overlap among these concepts has prevented meaningful comparisons across pollination studies. These issues arise from the many different methods that have been used to estimate pollinator performance, which in turn depend upon the particular criteria prioritized in each conceptual approach. Conceptual approaches are often influenced by logistical constraints on investigations in terms of what can be measured with the available resources and what opportunities are provided by the study organisms at the sites. Compounding these issues are the general problems that usually arise from the need to select different spatial and temporal scales and levels of analyses to suit the objectives of the study. A reconciliation of concepts, definitions, and methods that incorporates scale issues would permit fruitful comparisons across studies.

This review analyses the concepts, terms and methods in use and provides an integrated conceptual framework and methodology that can be used to compare pollinator performance across studies. Based on a comprehensive review of the literature and focusing on 70 representative studies from 1975 to 2007 we analyse the issues described above by categorising the various conceptual approaches according to the types of parameters that have been combined. We then clarify definitions for 'effectiveness' and 'efficiency' and the use of the terms 'actual' and 'potential' for pollinator performance measures. Finally, we present a modular approach based on fundamental units defined at the single visit level that can be scaled up temporally and spatially so that subsequent equations can be tailored to different purposes.

II. PREVIOUS CONCEPTS AND METHODS

(1) Background and problems

At present, the terms 'pollination efficiency' or 'pollinator efficiency' have more than 30 different definitions (Table 1), which demonstrates the level of ambiguity in the use of such terms. This ambiguity led Inouye *et al.* (1994) to exclude the terms 'effectiveness' and 'efficiency' from their lexicon, proposing more specific terms for future use. Although they formulated a consistent terminology of all aspects of the pollination processes, 'efficiency' and 'effectiveness' are still widely used and discussion of how to evaluate pollinator performance has continued in the literature. Consequently, there is still a need to establish a standardized conceptual framework to clarify our understanding and communication of 'what we are measuring and what it means'. This standardisation is essential to facilitate comparisons of pollinator performance in terms of both evolutionary and ecological contexts as well as agronomic and conservation applications.

A few examples illustrate the issues for the most widely used terms. For instance, Ivey, Martinez & Wyatt (2003) defined 'pollinator effectiveness' as any characteristic of a pollinator or a pollinator's behaviour that contributes to its ability to affect plant fitness, including components of both pollen quality and quantity. Under this wide umbrella they consider various factors such as visitation frequency, the duration of a single visit, pollen transfer ability, number of visits per plant (affecting the degree of geitonogamy and breeding systems) and constancy (affecting proper pollen transfer). By contrast, Sihag (1997), defined: "the term pollination efficiency (PE), which would better estimate the effectiveness of a pollinator species, as the average number of flowers actually pollinated by a forager per unit time specific to a species as a whole. PE is the result of three parameters viz. (a) foraging mode (b) foraging rate and (c) population abundance of a pollinator species on a plant species". On the other hand, Keys, Buchmann & Smith (1995) defined 'pollination efficiency' as "the relative ability of an insect to pollinate flowers effectively as measured by seed/fruit production per some unit of measure". Fishbein & Venable (1996) noted that 'pollination effectiveness' can be partitioned into components, including visitation rate, pollen removal, and pollen deposition. Mayfield *et al.* (2001) defined 'pollination effectiveness' as the amount of pollen transferred to a virgin flower after a single visit, and the resulting seed set. Javorek, Mackenzie & Vander Kloet (2002) measured 'pollination effectiveness' in terms of floral visitation rate, percentage of flowers pollinated, and pollen deposition. In addition, terms other than effectiveness and efficiency have been used, particularly efficacy, importance or intensity, but much less frequently. In summary, the diversity in conceptual approaches for selecting and combining parameters to construct indices and the inconsistent use of terms (both synonyms and homonyms) underpins the problems in comparing pollinator performance across studies.

(2) Conceptual overview and analysis

Our analysis of the literature supports the conclusion by Gross (2005) that there are two main types of assessment concepts for comparing pollinator performance: (1) 'pollination success' (contribution to stigmatic pollen deposition) and (2) the consequent 'female reproductive success' (contribution to seed set) of the pollinated plants. However, our conceptual framework shows that in many studies pollen deposition is used as a proxy for seed set (see Fig. 1). In addition, both approaches can be further analysed from the perspective of both male or female fitness of the plant. However, for most questions about

Table 1. Overview of the various terms used to describe pollinator performance and the variables used to quantify them classified into direct and indirect methods as in Fig. 1.

Type	Term used	What it measures/estimates	Source
		Direct measure of pollen deposition success (as pollen deposition on stigma)	
A1	Pollination intensity	The number of pollen grains deposited on a virgin stigma after a single visit by a specific pollinator	Primack & Silander (1975); Rodet et al. (1998); Falque et al. (1996); Mitchell (1997)
	Pollination efficiency		Waser & Price (1990); Ashman & Stanton (1991); Pettersson (1991); Willmott & Burquez (1996); Cane & Schiffhauer (2001); Hiei & Suzuki (2001, Bloch et al. (2006
	Pollination efficacy		Cane & Schiffhauer (2003)
	Per visit effectiveness		Mayfield et al. (2001)
	Pollinator effectiveness		Dieringer (1992); Osorio-Beristain et al. (1997)
	Stigma pollen load per visit		Kearns & Inouye (1993); Inouye et al. (1994)
	Pollination effectiveness		Motten et al. (1981); Suzuki et al. (2002)
A2	Pollination efficiency	Cumulative pollen deposition on stigma during the flower's lifespan	Arroyo & Dafni (1995); Tandon et al. (2001)
	Pollination intensity		Vaissière (1991); Mitchell (1997); Falque et al. (1996)
	Pollination level		Morandin et al. (2001)
		Estimating pollen deposition success with pollinator behaviour parameters	
B1	Pollination effectiveness	Number of pollen grains removed from anthers per single visit	Suzuki et al. (2002)
B1, B2	Pollination efficiency	Percentage of flower visits with stigma touch in a given foraging bout	Dafni et al. (1987)
B2	Pollinator efficiency	Visit frequency in a given flower	Calzoni & Speranza (1998)
		Time it takes for a flower visitor to visit a given number (10 or 50) of flowers	Richards (1987)
		Combining pollen deposition success with pollinator behaviour parameters	
A1, B1	Pollination efficiency	Fraction of the pollen load of the vector that was deposited on the stigma in a single visit	Kearns & Inouye (1993); Lau & Galloway (2004)
A, B1	Vector pollinating efficiency	The relative pollen load contributed by a specific pollinator	Inouye et al. (1994)
A, B1	Absolute pollination efficiency	Probability of the removed pollen reaching the target stigma	Galen & Stanton (1989)
A1, B2	Index of pollen transfer effectiveness	Mean flower number visited per time unit, multiplied by mean number of pollen grains deposited on the stigma in a single visit	Herrera (1990)
A, B2	Pollinator importance	Proportion of visited flowers that receive pollen	Bloch et al. (2006)
A, B2	Pollinator effectiveness		Herrera (1987)
(A), B2	Pollinator importance	The product of a species' pollination effectiveness and its relative abundance, where relative abundance is calculated as the number of visits made by the species divided by the total number of insect visits observed during the period of study	Olsen (1997)
		Combining pollen deposition success with plant parameters	
A, D1, D3	Pollination efficiency	Proportion of the conspecific pollen load on stigma in relation to number of ovules	Richards (1996)
	Stigmatic fertilisation success		Kearns & Inouye (1993)

Table 1. (*cont.*)

Type	Term used	What it measures/estimates	Source
	Pollination intensity		Beatie (1976)
	Pollen deposition efficiency		Gómez & Zamora (1999)
A1, D1	Pollination effectiveness	The number of pollen grains of the right morphotype deposited in a single visit on reproductive parts of the flower	Muchhala (2003)
A1, D1, D2	Pollinator effectiveness	Proportion of deposited pollen in single visits that develops pollen tubes reaching the ovules	Motten (1986)
A2, D1	Pollination efficiency / Germination number	Presence or absence of germinated pollen grains	Guo et al. (1990) / Inyoue et al. (1994)
A2, D1	Pollination efficiency	Average number of conspecific pollen grains on the stigma during the activity period of a given pollinator population	Vaïssière 1991
A, D3	Pollination efficiency	Fraction of the produced pollen that reaches the stigma	Richards (1986)
A2, D3	Pollination efficiency	Number of pollen grains deposited per stigma in relation to the total pollen production of the flower	Cruden et al. (1990)
	Total source efficiency		Inouye et al. (1994)
	Combining pollen deposition success with pollinator behaviour parameters and plant parameters		
A, B1, D1	Pollinator efficiency	Proportion of removed pollen that actually fertilises an ovule	LeBuhn & Holsinger (1998)
A1, B2, D1	Pollination intensity	Number of functional (compatible) pollen grains per one visit 'converted' into chances of siring seeds, multiplied by visitation rate	Galen & Newport (1987)
A, B1, B2, D1	Pollination efficiency	The pollination efficiency was assessed in four ways: (i) pollen deposition (stained pollen grains with a pollen tube were counted), (ii) pollen removal, (iii) visit frequency, (iv) response to nectar production pattern	Canto-Aguilar & Parra-Tabla (2000)
A1, B2, D2	Index of pollination effectiveness	Stigmatic pollen load related to a given pollinator while stigma is receptive	Potts et al. (2001)
	Combining pollinator behaviour parameters with plant parameters		
B1, D1	Pollinator efficiency;	Amount of pollen a given visitor carries and proportion which is conspecific	Schlindwein & Wittman (1995)
B1, D1	Pollination relative efficiency	Amount and the identity of pollen grains on the visitor's body	Ashman & Stanton (1991)
B1, B2, D2	Pollinator efficacy	Relative potential of a flower visitor species as successful pollen vector for a given population of plants	Sugden (1986)
B1, B2, D1, (D2 *via* pollen germination)	Pollinator efficiency	Yield of germinated pollen grains at end of anthesis in relation to maximum possible transferred pollen grain number during flower anthesis (= mean pollen load on the vector multiplied by number of flower visits a female flower receives during anthesis)	Nepi & Pacini
	Direct measure of plant female reproductive success (seed set, fruit set)		
C	Pollination effectiveness	Fruit set as a result of intermorph pollinations with stuffed hummingbirds	Ornelas et al. (2004)

Table 1. *(cont.)*

Type	Term used	What it measures/estimates	Source
C1	Pollination effectiveness	Seed set per flower as a result of individual visits of different pollinators (in an enclosure)	Waser & Price (1983)
C1	Pollination effectiveness	Percentage of receptive florets in an inflorescence setting seed following one visit by a given species	Olsen (1997)
C1	Pollinator effectiveness Pollination effectiveness Pollination efficiency Seed set per visit	Seed yield as a result of single visits to a virgin flower	Motten *et al.* (1981) Vaissière *et al.* (1996); Mayfield *et al.* (2001) Suzuki & Akazome (2000); Kandori (2002) Inouye *et al.* (1994)
C1	Pollination efficiency Seed set per visit	Seed yield per single visit per flower head of a sunflower	Parker (1981) Inouye *et al.* (1994)
C1	Pollen transfer efficiency	Per cent fruit set as a result of one visit	Klein *et al.* (2003) Sampson & Cane (2000)
C1	Pollination efficiency Pollination efficiency Fruit set per visit	Fruit set per visit	Schemske & Horvitz (1984) Inouye *et al.* (1994)
C2	Female pollination efficiency	Seed set per flower	Andersson (1996)
C2	Pollination efficiency	Fruit production per unit time of pollinator activity in the inflorescence	Keys *et al.* (1995)
C2	Pollination efficiency	Percentage of fruit set attributed to a specific activity period of different pollinators	Dafni *et al.* (1987)
C2	Pollination efficiency Pollinating efficiency	Seed and fruit yield as a result of the pollinator activity	Guo *et al.* (1990); Cauich *et al.* (2004) Vicens & Bosch (2000)
		Combining plant female reproductive success with pollinator behaviour parameters	
C, (B2)	Pollination efficiency	Number of pollinator visits needed for 100% seed production	Spears (1983); Titze (2000)
C2, (B1)	Pollination effectiveness	The relative contribution to seed set of pollinators active at different times of the day (measured as seed production and pollen movement distance)	Young (2002)
C, B	Pollination efficiency	Fruit production per unit distance the vector travels in the inflorescence	Keys *et al.* (1995)
C, B2	Pollination efficiency	Correlation between the forager visitation frequency and seed set. (Seed set plotted against visit frequency per flower for each pollinator for an individual plant)	Waser & Price (1990)
C, B, B2	Pollinator effectiveness	The relative pollinator effectiveness was assessed in three ways: (i) observation of visitor behaviour, (ii) effect of visitors on seed production in experiments, (iii) correlation between seed and fruit set and flower visitation	Montalvo & Ackerman (1986)
		Combining pollen deposition success with plant female reproductive success	
C, (A)	Pollination effectiveness	Percentage of fruits resulting from pollinated flowers	Gudin & Arene (1991)

Table 1. *(cont.)*

Type	Term used	What it measures/estimates	Source
C, A	Fertilisation efficiency	Relative contribution of a given pollinator to seed set in relation to the pollen deposited by a given pollinator	Vaissière (1991)
C1, A	Stigmatic seed set success	Proportion of deposited pollen that produces seeds	Kearns & Inouye (1993)
		Combining plant female reproductive success with plant parameters	
C1, C2, D5	Pollination efficiency	Seed production ratio between spontaneous and open pollination. Relative proportions of spontaneous self-pollination and apomixis to the final seed production compared with free pollination under natural open conditions	Spears (1983)
C, D3	Pollination efficiency	Percentage of ovules that developed into seeds in an inflorescence	Tamura & Kudo (2000)
C, D3	Pollination effectiveness	Percentage of flowers that develop into fruit	Mesquida & Renard (1981); Donovan & Read (1991); Meisles & Chiasson (1997); Motten *et al.* (1981)
	Pollination efficiency		Schneider *et al.* (2002); Van Praagh & Hauschildt (1991)
	Fruit set per 100 flowers		Inouye *et al.* (1994)
		Plant parameters	
D3	Pollination efficiency	Reciprocal of pollen-ovule ratio	Richards (1996)

pollinator performance logistical constraints have resulted in studies primarily focused on the female perspective (pollen deposition on receptive stigma, fertilized ovules, seeds produced per plant). In the field, it is much easier to follow the fate of all ovules of a given plant and to compare the absolute (total number of seeds) or relative (number of seeds in relation to the number of ovules) success among plants than to follow the fate of pollen grains. Nevertheless, a significant research trend for assessing male fitness has been to include pollen removal and pollen loss or wastage in pollinator performance measures as found in pollen presentation theory (PPT) (Harder & Wilson, 1994; LeBuhn & Holsinger, 1998; Thomson *et al.*, 2000; Thomson, 2006). This measure enables evaluation of 'pollen transfer efficiency' (Thomson, 2006) into four different categories based on high or low pollen deposit in relation to high or low pollen removal (Thomson *et al.*, 2000). Good pollinators may become parasites in the presence of better pollinators if they are wasting pollen that the better pollinator could have been depositing. This focus on the fate of the pollen that has been picked up has been used to predict pollen presentation schedules and address consequences for male fitness. These types of indices and the male fitness component are not considered herein because they are proxies of male success with a particular focus on male function. At this point measuring male success involves complex and expensive laboratory techniques, not suitable for large-scale comparative pollination field studies. In this review we are primarily interested in the contribution of different pollinator species to plant reproductive success (e.g. in terms of seed set, that is a combination of male and female success) and not separately in male and female function.

Our conceptual scheme (Fig. 1) to analyse the different approaches to measuring pollinator performance is divided into two main assessment concepts: (1) pollination success (how much pollen has been deposited?) and (2) plant reproductive success (has a sufficient amount and quality of pollen grains been deposited to reach full seed set?). We propose the use of a fundamental unit of analysis at the level of a single visit to one flower that can then be combined with other measures to scale up to higher order levels such as temporal replicates (i.e. per unit time) or spatial replicates (i.e. per sample observation units such as a patch of flowers: Sih & Baltus, 1987; Fumero-Cabán & Meléndez-Ackerman, 2007). From this basis other modifications to produce higher order estimates can be developed although they often cost more time in the field. We emphasise the difference between direct and indirect measures as highlighted in our scheme to indicate the large gap between theoretical (ideal) concepts and operational (practical) estimates to address these concepts.

In the first assessment concept (pollination success as measured by stigmatic pollen deposition), the performance of the pollinator ends with the deposition of pollen on the stigma, so the direct measurable indicator of pollinator performance is the number of pollen grains deposited per (receptive) stigma (A in Fig. 1). In practice, pollinator performance measured as pollen deposition has frequently been modified by or substituted with other parameters such
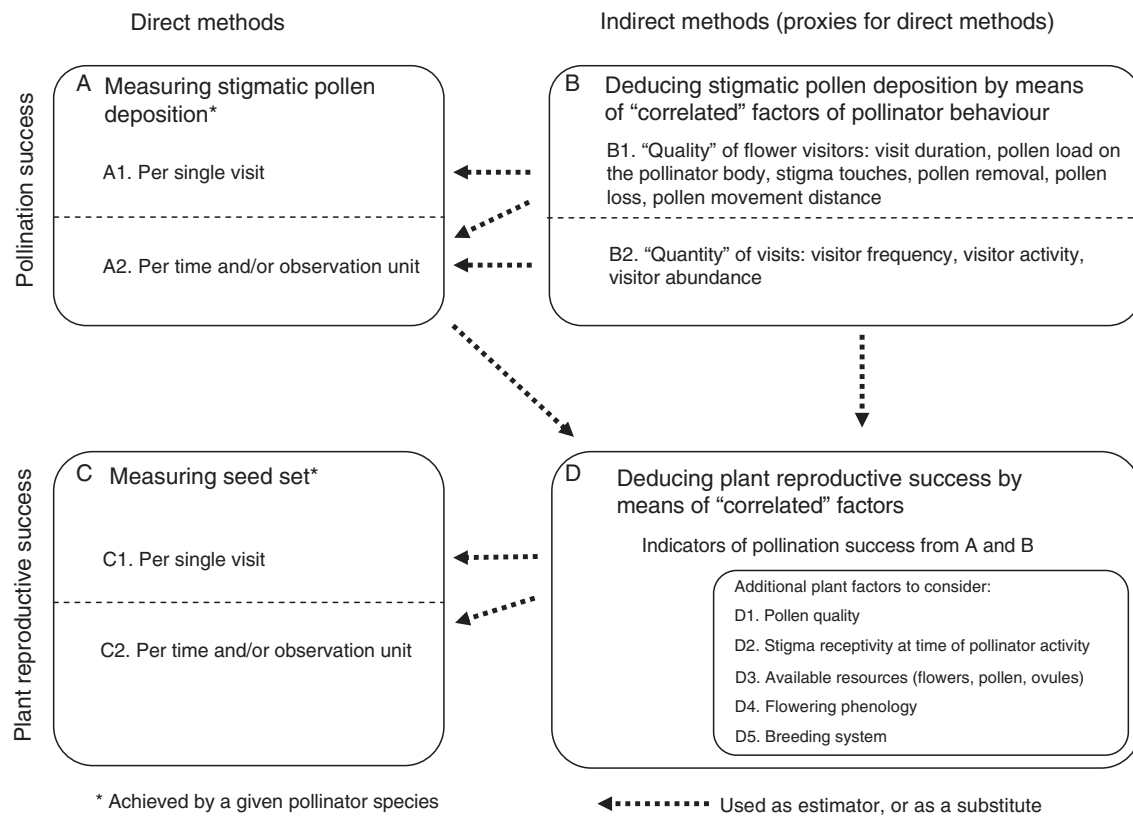
Direct methods   Indirect methods (proxies for direct methods)

Fig. 1. Overview of the direct and indirect methods used to measure pollen deposition success (pollen deposition) and plant female reproductive success (seed set) of a given pollinator, pollinator group, or the total pollinator assemblage.

as pollinator behaviour in the flower (duration of visit) or by pollinator visit frequency or abundance (B in Fig. 1).

In the second assessment concept (female reproductive success, usually measured in terms of seed set), characteristics of the plant are also included and a number of stages of the pollination process leading to seed set are incorporated. For this concept, many parameters have been used often in combination with pollination success in order to assess the contribution that a pollinator makes to female reproductive success. The essential question is: how much of the pollen deposited on the stigma has the potential to fertilise ovules and sire seeds (C in Fig. 1). The direct link between a given pollinator and the production of a seed is often not accessible for estimation, so other types of variables parameters are commonly substituted to estimate female reproductive success, including measures pertaining to pollen deposition success (A and B in Fig. 1) and variables pertaining to plant characters (D in Fig. 1).

Based on our comprehensive literature review, we categorised 11 different ways that such variables have been combined or substituted based on three main types of measures: pollen deposition, plant characters and pollinator behaviour characters. These diverse methods generally aimed to measure either pollen deposition success or female reproductive success but this cannot be discerned from the terms used for them. Some indices are narrow special purpose estimates

while others are highly generalised. It is beyond the scope of this review to evaluate all of the types of combinations; instead. we review here the most important variables that promise to be the most biologically meaningful and practical.

(a) Pollinator behaviour and visit frequency

A pollinator's behaviour in the flower and its frequency of visits have often been used as proxies for either pollen deposition success or female reproductive success. Stebbins (1970) highlighted visit frequency as an integral component of pollinator performance. We use this parameter to scale up from a single visit in a single flower temporally or spatially to derive a rate of pollen deposition (see A in Fig. 1). The term 'pollinator importance' has frequently been used for the product of two parameters: (i) the probability of a visit (e.g. measured as visit frequency or relative abundance, following Armbruster (1988), and (ii) the pollinator performance per visit or unit time (e.g. average number of seeds produced, per cent fruit set, or pollen grains deposited by a pollinator during a single visit to a plant; in for example, Waser & Price, 1983; Schemske & Horvitz, 1984; Inouye *et al.*, 1994; Olsen, 1997). In a review of 17 plant species, Sahli & Conner (2006) showed that, for most species, pollinator importance was determined primarily by differences in visitation rates rather than by differences in performance per visit. However, due to the limited number of species included in their analysis, Sahli &

Conner (2006) could not address whether performance per visit is more important for species with specialized pollen removal/deposition mechanisms, although the two species of *Asclepias* that were included in the study support this idea. Vazquez. Morris & Jordano (2005) indicated at the importance of visitation frequency as a proxy for pollination success using a meta-analysis.

It is important to understand that visitation rate has two components: (i) each individual pollinator's visit activity per unit time, and (ii) the number of visitors per flower per unit time or per patch of flowers. This has significant consequences for analysing pollen deposition patterns in plant populations. For example, 10 flower visitors making one visit per plant per unit time compared to a single flower visitor making 10 visits per plant in a sequence may result in the delivery of different pollen quantity or quality. The reproductive output could be quite different particularly when self-incompatible plants are concerned.

One of the problems in monitoring visitation frequencies is the assumption of a random visitation pattern i.e. all flowers have equal probabilities of being visited. Preferential visits to particular flowers due to differential reward availability are well-documented (Andersson, 1988). Thus, in cases where significant deviation from a random visitation pattern is suspected, e.g. bees visiting male-stage flowers for pollen collection more often than female-stage flowers, flower visitation preferences could be an issue. Using frequency distributions of pollinator visits per flower instead of average visit frequencies would underpin more realistic models. Preferential visits of flower visitors to certain flowering stages or sexes may be due to (i) specific food resources that are available only at a certain time or from a certain sex (e.g. pollen), (ii) differential nectar production by flowers at different ages or sexual stages (e.g. higher production in male phase). Furthermore, there may be an unbalanced ratio of male to female (stage) flowers (Harder & Wilson, 1998; Thomson, 2001). In practice this would be difficult to observe or measure, and more field studies are needed to identify the underlying distribution patterns of visits that best represent the real situation in natural plant populations and crop species.

(b) Pollen deposition on the stigma

The number of pollen grains deposited on the stigma per single visit (A1 in Fig. 1), or per unit time (A2 in Fig. 1) regardless of their chances to germinate and sire seeds, has often been used as a measure of pollinator performance. It is sometimes not feasible to measure directly stigmatic pollen deposition per single visit. There are some plants (e.g. some Brassicaceae and Asteraceae) which already have a full self pollen load on the non-receptive stigma at anthesis, and therefore it is not possible to determine how many pollen grains are being deposited by a single pollinator visit. In such cases a number of estimators are substituted, for example, visit frequency, visit duration, stigma contact and pollen load on the pollinator's body (B in Fig. 1). Scaling up beyond the single-visit level to estimate pollen deposition per unit time requires the inclusion of pollinator visitation rates as a parameter.

Pollen deposition success is used in combination with other parameters to (i) measure the potential (context independent) performance of a given pollinator species, regardless of other factors (e.g. comparison to other pollinator species) that influence the final plant reproductive success, or (ii) infer the actual (context dependent) performance of a given pollinator. Estimates of the potential pollinator performance play a particular role in conservation and agriculture in analysing the ability of a given pollinator species (or group of species) to be sufficient to produce full seed set for a given plant or crop. For measuring the actual pollinator performance, which is more important for evolutionary questions, factors like time of pollen deposition (during the day or season) need to be considered. Or in other words: flower visitor species A may only become the best performer in the absence of flower visitor species B because B deposits the pollen earlier and pollen competition for ovules plays a role.

(c) Plant reproductive success

To represent female reproductive success, seed and fruit set have been measured as a result of single sequential or unrestricted visits of several pollinators and all these have been used in assessing the performance of pollinators (see C in Table 1). In some studies reproductive output has been related to plant input such as ovule or flower production, pollinator input such as pollen deposition, or to pollinator behaviour such as visit frequency (see Fig. 1 and Table 1).

Analysis of literature indicates that most indices do not include female reproductive success outcomes that are directly measured, namely, 'how many pollen grains deposited on the stigma develop into seeds'. There may be several reasons for this. First, Cane & Schiffhauer (2003) pointed out that a drawback of using seed set as a measure of pollinator performance is that post-pollination processes can reduce actual relative to potential fruit or seed set. Despite adequate pollination, a developing fruit may abort if limited maternal resources are usurped by neighbouring fruits (e.g. Stephenson, 1981; Corbet, 1998), leading to under-estimation of pollinator performance. Second, a potential source of error in measuring pollinator performance in terms of seed set from single visits derives from the assumption that single visits relate to a monotonic, incremental increase in seed set for successive visits of the same pollinator to the same flower, which is rarely true (Motten *et al.*, 1981; Olsen, 1997). Third, using single visits for measuring pollinator performance may not work in species with numerous ovules per flower because flowers may require a minimum threshold number of pollen grains to be deposited before any fruit can develop and any seeds are produced (see Vaughton & Ramsey, 2000; Cane & Schiffhauer, 2003). Because such factors may influence measures of seed set from a given pollinator and these measures are often impractical, several indirect methods have been substituted to estimate pollinator performance based on female reproductive success (see Fig. 1). Of wide use are measures of pollinator activity

and abundance such as visitation frequency and visit duration (B in Fig. 1) as well as pollen deposition per flower and per unit time (A1 and A2 in Fig. 1) which are also used as proxies for pollen deposition success. The results of some studies indicate that pollinator activity can be directly related to seed production or fruit set with or without data on pollen deposition on the stigma. For example an increase in visitation frequency of a pollinator may increase the chances of pollen delivery (Motten *et al.*, 1981; Schemske & Horvitz, 1984), the number of pollen grains deposited (Bertin, 1982; Herrera, 1987), and consequent plant female reproductive success (Schemske & Horvitz, 1984). However, female reproductive success is not always correlated with pollen deposition success, nor is it always correlated with other variables such as the abundance of flower visitors or their visit frequency (Crome & Irvine, 1986; Sahli & Conner, 2006).

(d) Other variables

(*i*) *Stigma receptivity.*   The main roles of the stigma are pollen-capture ability which depends mainly on its physical characteristics and stigma selectivity which depends on physiological and developmental processes such as supply of germination substrate, receptivity and pollen recognition (Lord & Russell, 2002). Stigma receptivity is an important factor when measuring flower visitor activity, because only visits to receptive stigmas can be regarded as successful visits. Stigma receptivity (D2 in Fig. 1) has been used mostly in combination with pollen deposition but also with other factors.

(*ii*) *Pollen quality.*   Different aspects of 'pollen quality' (D1 in Fig. 1) have been used in combination with several factors. From the plant's viewpoint pollen quality is related to a number of factors: conspecific pollen grains in a pollen load (Rathcke, 1983; Wilcock & Neiland, 2002), pollen viability (Dafni & Firmage, 2000), pollen compatibility (De Jong *et al.*, 1992; Ramsey & Vaughton, 2000), the genetic identity and number of conspecific pollen donors represented in the pollen load (Bertin, 1986; Price & Waser, 1979), pollen allelopathy (Morison *et al.*, 2000), or pollen clogging (Ashman, Galloway & Stanton, 1993). Pollen quality is influenced by a single pollinator's behaviour because it affects the composition of the pollen load brought to the stigma. However, the quality of a stigmatic pollen load can be assessed only in relation to the specific features of a given plant. The number of pollen donors contributing to the stigmatic pollen load may also influence the quality of the offspring (Bertin, 1986). Pollinator foraging behaviour clearly influences pollen quality *via* improper pollen transfer (*sensu* Rathcke, 1983) as well as geitonogamous pollination (in self-incompatible species). Long flight distance may improve the quality of the deposited pollen on the stigma by increasing the probability of cross pollination (Herrera, 1987), but outcrossing depression may also occur.

(*iii*) *Pollen numbers, ovule numbers and seed numbers.*   A number of studies combine pollinator behaviour parameters with plant parameters such as number of pollen grains and ovules produced (D3 in Fig. 1). This combination follows an economics approach to judge pollinator performance in relation to the used (or wasted) resources. Finally, some studies use plant parameters alone as an indicator of pollinator performance. In an evolutionary context the pollen/ovule ratio (P/O) can be interpreted as an indicator that reflects the effectiveness of pollination (Cruden, 1977), and the reciprocal term O/P has been called 'pollination efficiency' (Richards, 1996). The minimum number of pollen grains that have the ability to fertilize ovules (pollen quality) and are required to be deposited on the stigma for maximal seed production is an important factor affecting pollination efficiency but has hardly been investigated. Cruden (2002) estimated that 4–6 pollen grains are required per ovule in general. However, Hoffman (2006) found that on average 1.6 pollen grains per ovule were sufficient for maximal seed production (3.4 seeds) under natural condition in *Micromeria fruticosa* (Lamiaceae). Although data are lacking, this value is expected to vary among species or even populations. Therefore, in the absence of available knowledge, we have to assume that the minimal number of good pollen grains needed for maximal seed production per flower equals the maximal number of seeds produced under natural conditions. The exact solution of this problem is to analyse the dose-response relationships between the number of pollen grains in stigmatic loads and the consequent seed set (Bosch & Waser, 2001; Cane & Schiffhauer, 2003; Hoffmann, 2006). However, constructing such a pollen saturation curve is labour intensive. Therefore, a practical approach would be to ignore correction for the threshold number of pollen grains needed for seed set per ovule but it could be incorporated as needed if it was feasible.

III. A MODULAR APPROACH

We suggest a modular approach to measuring pollinator performance based on our proposed conceptual scheme (Fig. 1) and analysis of the most meaningful and practical parameters from the literature outlined above. We follow the two main assessment concepts for comparing pollinator performance. The two most critical questions are: (1) what is the contribution by a flower-visiting species to the pollen deposited on a given plant species, and (2) what is the contribution to the plant's female reproductive success (in terms of seed set)?

We deliberately avoid using the terms pollination efficiency and pollinator effectiveness to avoid further confusion. As can be seen from Table 1, each term has many variations. However, an important component of our modular approach is to use the terms effectiveness and efficiency to signify different aspects of performance. Although these terms are sometimes used interchangeably in ordinary English and this is reflected in Table 1, we propose a more precise definition. We define 'effectiveness' here in the narrow sense as the potential to bring about an effect that is the capability of, or success in, achieving a given goal. On the other hand,

'efficiency' is here defined as an effect in relation to the resources spent or the input or output of a system. Because the essence of effectiveness is the achievement of the goal as such and is not related to the resources spent or available, then we can define 'pollen deposition effectiveness' as the pollinator's contribution to pollen deposition alone. This does not take into account any variables involved in the plant's female reproductive success such as pollen quality, plant input in pollen or ovule production, or any consequent seed set.

By contrast, because our definition of efficiency includes a consideration of how well the goal is achieved given the available resources, we need to assess how much a given pollinator contributes to female reproductive success. To do this we need to consider seed set, which depends on plant variables such as the quality of the pollen and the availability of ovules to receive the pollen. Thus, to judge whether a pollinator is a 'good' pollinator in terms of seed set we need to relate the pollinator's contribution to the available maximal seed set of the flower under the given resource constraints of the plant. We therefore define 'pollen deposition efficiency' as the pollinator's contribution, by deposition of conspecific, compatible and viable pollen grains on the receptive target stigma in relation to the maximal possible female reproductive success (i.e. maximum seed set with no pollen limitation). Thus, pollen deposition efficiency refers to a measure that reflects whether a pollinator deposits enough pollen to achieve full seed set per flower. Pollen deposition efficiency ranges from 0 to 1, that is, from no contribution to full maximum contribution to seed set.

These definitions of effectiveness and efficiency mean that not every floral visitor that is effective ('good' in terms of pollen deposition) is also efficient ('good' in terms of seed production), but any visitor that is efficient has also to be effective. We can extend these connotations to look at indices for other parts of the pollination process. Hence the term 'pollen transfer efficiency' is an appropriate derived index because it relates to the efficiency of the transfer process in terms of the pollen removed that gets wasted; this term is well defined and consistently used in PPT (see above).

The modular approach that we are proposing is built upon a key basic unit, the number of pollen grains deposited on the stigma at the single visit level. The next level is based on temporal and spatial scaling up by incorporating visit frequency (visits per flower per hour) when observing a flowering patch. Both pollen deposition effectiveness and pollen deposition efficiency can be scaled up to the per hour level. From this second level, it is possible to develop higher order indices by adding more parameters or summarising to higher temporal or spatial scales (e.g. day or seasonal levels or whole pollinator assemblage). Higher order derived indices can be reduced back to their basic units permitting comparisons across different temporal and spatial scales to facilitate comparisons between different investigations.

IV. EQUATIONS FOR THE MODULES

(1) Pollen deposition effectiveness

(a) *Single visit scale*

The single visit of a pollinator to a flower is the fundamental unit of analysis for the entire pollination process in our modular approach. Pollen deposition effectiveness D_v at the single-visit level is equal to the number of pollen grains delivered d by a given pollinator to the stigma of a given flower in a single visit (Equation 1). Inouye *et al.* (1994) called this the "stigmatic pollen load". In practice the researcher waits in front of a virgin flower with a receptive stigma (or a patch of virgin flowers) until a pollinator visits and then counts the pollen deposited from this visit.

$$D_v = d. \tag{1}$$

(b) *Per time scale*

Scaling up from the single-visit level is important because pollen deposition can be improved if the flower receives more visits over time and the rate of successive deposition episodes is a critical part of the pollination process. A pollinator species with low deposition per single visit can increase its overall deposition by making more frequent visits (activity of individuals) or by having many individuals visiting the same flower (abundance of individuals). We define pollen deposition effectiveness at the per hour level (D_t, Equation 2) as the pollen deposition effecriveness per single visit multiplied by visit frequency f.

$$D_t = D_v \, f \, r. \tag{2}$$

Here, r is the proportion of flowers in the observed patch of flowers that actually have receptive stigmata. Visits to unreceptive flowers or flowers in their male stage do not contribute to seed set. Ideally, this measure would be the proportion of the pollinator visits to flowers with receptive stigmata out of the total number of flowers visited by the given pollinator. Measuring the actual visits would reveal if visits to flowers in male or female stages diverge from a random pattern. For practical reasons and under the assumption of a random visitation pattern to all flowers, the proportion of visits to receptive flowers can be inferred from the percentage of flowers with receptive stigmata in the patch during flower visitor observations. We have also to consider that when flowers are chemically marked with scent by their visitors (Eltz, 2006; Saleh & Chittka, 2006, and references therein) the visits may not be at random but may depend on the half-life of the chemical marking.

Another issue in estimating the per-hour pollen deposition level is the variability of visitation frquency during the day for different pollinators. Pollen deposition effectiveness can be calculated for each period separately, and the daily effectiveness then calculated as a weighted average of the specific visitation rates during the day. Variable visitation

rates over longer periods such as seasonal activity of pollinators is discussed in Section V.1.

(2) Pollen deposition efficiency

Pollen deposition efficiency (P) is a measure of how much the pollinator is able to contribute to maximal seed set per flower *via* pollen deposition. In other words, P indicates whether the deposited pollen on the stigma is sufficient to produce full seed set. This is related to the quality of the pollen and to the maximal female reproductive potential of the flower under no pollen limitation but considering resource constraints. Because of the practical difficulties in assessing pollinator performance, by measuring seed set after single visits (see D in Fig. 1), we have elected to use the number of pollen grains deposited on the stigma (A in Fig. 1) as a proxy for the potential seed set that a given pollinator can contribute to a given plant.

(a) Pollen quality

In contrast to pollen deposition effectiveness, which concerns only the number of deposited pollen grains, pollen deposition efficiency requires an evaluation of pollen quality. We define 'pollen quality' (q), as the number of pollen grains deposited that are able to fertilize ovules and sire seeds. The quality of pollen is determined by three independent factors: pollen must be conspecific (k), viable (m) and compatible (n). To determine this value it is necessary to determine how much of the deposited pollen (d) meets all three conditions at the same time. Mathematically this is equivalent to the subset of deposited pollen grains that represent the intersection of all three conditions ($q = |k \cap m \cap n|$). While pollen conspecificity and viability can be determined easily by microscopic techniques and enzymatic tests (Dafni, Pacini & Nepi, 2005), determining pollen compatibility is a complicated task that depends on the breeding system, degree of self compatibility and the previous activity of the pollen vector. Partitioning the total pollen load for a given pollen vector into foreign outcrossing and local geitonogamous or autogamous pollen is important mainly for self-incompatible multi-flowered species (Sage, Husband & Routley, 2005). So far, no fast and simple method exists to determine the proportion of compatible pollen grains in a deposited pollen load. Time-consuming investigations of the breeding system, prior pollinator behaviour, and pollen deposition patterns are necessary to estimate the proportion of compatible pollen deposited. Using genetic markers will enable direct measurements of the proportion of outcrossing *versus* selfing pollen (Sage *et al.*, 2005). In self-compatible plants compatible pollen (n) can be assumed to equal 1, but in cases of self-incompatible plants with a high proportion of pollinator-mediated geitonogamy pollen compatibility can not be ignored (De Jong, Waser & Klinkhamer, 1993; Snow *et al.*, 1996; Sage *et al.*, 2005).

(b) Pollen surplus

The second step in estimating the pollinator's contribution to seed set is to relate the amount of deposited pollen to how much is needed for maximum seed set under given environmental conditions and no pollen limitations. While pollen limitation is a well known concept in pollination biology (Burd, 1994) (i.e. the reception of less pollen than required to produce full seed set), the concept of pollen surplus (i.e. the reception of more pollen than required to produce full seed set) has received less attention. However, for the assessment of pollen deposition efficiency this concept is important as there seems to be no advantage to the plant if a pollinator deposits surplus pollen compared to one that deposits just the required amount for a maximal number of seeds (unless a threshold level of excess pollen is needed or additional pollen has an effect on seed quality via pollen competition). The number of quality pollen grains (q) should not exceed the number needed, thus it must be capped at the maximum potential seed set per flower by subtracting out the surplus pollen delivered. This gives the capped value for quality pollen (c).

To calculate capped quality pollen (c), we first need to estimate the maximal seed set capacity of a flower under field conditions with no pollen limitation. The maximum potential seed set (s) is estimated by artificially supplementing pollen on flowers that are exposed to natural pollination given current resource constraints. If the amount of quality pollen in a single visit (q) is larger than the maximum potential seed set (s) then q is capped at the upper limit of s to give c. If, on the other hand the amount of quality pollen in a single visit is less that the upper limit of s, then c is equal to the value of q.

It is essential to calculate the final value of c in the correct sequence. Capping to the limit of s should not be performed on the overall average of quality pollen (q) for a given pollinator. The truncation must be performed separately for every value of quality pollen (q) at the single visit level before averaging over all replicates. This sets s as the upper limit for each single visit to a flower so that no extremely high value of quality pollen will skew the results of the average capped quality pollen (c). When maximum potential seed production data are not available, average number of ovules per flower can be used as an estimate to derive pollen deposition efficiency. However, since it is common that due to resource limitations or other constraints not all ovules develop into seeds, such calculation of pollen deposition efficiency overestimates the female reproductive potential of the plant leading to an underestimation of pollen deposition efficiency. Nevertheless, the relationship of the deposited pollen to the potential seed set is addressed.

(c) Deriving pollen deposition efficiency

(*i*) *Single visit scale.*   Once the two preceding steps are completed, pollen deposition efficiency can be calculated. Pollen deposition efficiency (P_v, Equation 3) is the capped quality pollen (c) divided by the maximum seed set potential

for the flower (*s*). Because the value for capped quality pollen can never exceed the maximum number of potential seed set, this ratio will range from 0 to 1.

$$P_v = c/s. \tag{3}$$

(*ii*) *Per time scale.* The pollen deposition efficiency per hour (P_t, Equation 4) is calculated by a method similar to the pollinator deposition effectiveness per hour (Equation 2) using visit frequency (*f*) and the proportion of flowers with receptive stigma (*r*). In addition, capping for pollen surplus should also be applied in a similar manner for pollen deposition efficiency per hour setting the upper limit of P_t at 1.

$$P_t = P_v f r. \tag{4}$$

V. USING THE MODULAR APPROACH

(1) Plant-pollinator overlap: duration and timing

One of the issues in making generalisations concerning pollinator performance is the conversion from event-related (single visits, Equations 1, 3) or time related (per hour, Equations 2, 4) measurements of pollinator activity to longer periods such as the lifetime of the flower. It is well known that different pollinator species may have different duration (length) and timing (start and end) of activity during the day. For example, a certain bee species may be active only during the early morning while another may be active over the whole day (Herrera, 1990; Hoffmann, 2006). If observation units are randomly (or evenly) distributed over the entire lifetime of the flower at the appropriate resolution for capturing these differences then the results of the time-related indices at the per hour level (Equations 2 and 4) can reflect the different overlap times.

Observations of pollinator activity should be carefully designed and evenly distributed during the activity period of the pollinator for the entire lifetime of a flower to ensure that the differential floral overlap durations are captured for different pollinators. In addition, special attention should be given to the chronological time of flower visitor activity. If a pollinator starts early in the morning, it may have already deposited sufficient pollen for producing full seed set. Then all subsequent flower visitors will not contribute to the actual seed set, even if they are good pollinators with a potential for inducing high seed set in the given plant species, e.g. in the absence of other pollinators (Herrera, 1990; Thomson *et al.*, 2000).

If a practical sampling regime cannot capture the differences in overlap then a detailed analysis is required for accurate pollinator performance comparisons. A measure of the duration and timing of the overlap between stigma receptivity of the flower and the pollinator's activity can be devised and incorporated into the equations as another level of analysis as shown below. There is clear potential

for this type of modification of the basic equations to be scaled up to other levels such as the inflorescence, plant or population, or over longer durations such as the entire season, *etc*. Developing such higher order indices will be valuable for comparing pollinators' performance at the level of seed yield for the flowering season of plant populations. The following equations are calculated at the single-flower level over the lifetime of the flower.

(a) Pollen deposition effectiveness over flower lifetime

In order to calculate the stigmatic pollen deposition over the lifetime of the flower, we must take into account pollen deposition rate and floral lifespan. In other words, we need to know the duration of stigma receptivity in relation to the timing and duration of pollinator activity. The number of hours in which pollinator visits overlap with stigma receptivity (*l*) gives the duration of pollinator activity that can be compared to other pollinators. For example in some cases, pollinator activity does not overlap with the entire duration of stigma receptivity, e.g. the stigma receptivity lasts for three days (72 h) but the bees are active only during daytime (36 h). Because high pollen deposition effectiveness per time (D_t) of a pollinator assemblage enhances pollination and consequently shortens floral longevity and stigma receptivity, by introducing the term *l*, pollen deposition effectiveness of a given pollinator species over flower lifetime (D_l) depends on the performance of other pollinator species because this will reduce flower lifetime (stigma receptivity). In contrast to Equation 2 that is context independent, Equation 5 reflects the actual (context-dependent) pollen deposition effectiveness.

$$D_l = D_t l. \tag{5}$$

(b) Pollen deposition efficiency over flower lifetime

Pollen deposition efficiency over flower lifetime (P_l) describes, in a quantitative way, the contribution of any given pollinator to the deposition of sufficient pollen (in terms of quantity and quality) to produce maximal seed set. P_l is calculated by multiplying P_t (per hour) by the number of overlapping hours of stigma receptivity and pollinator activity *l* (Equation 6). Because the index has an upper limit of 1, then capping pollen surplus should be applied to this result as well. This is achieved in a similar way as for the per hour scale (P_t, Equation 4).

$$P_l = P_t l. \tag{6}$$

(2) Entire pollinator assemblages

(a) Pollen deposition effectiveness of pollinator assemblages

By summing pollen deposition effectiveness indices (D_t or D_l) over all major pollinating species that visit the flowers of a given plant species we obtain the corresponding effectiveness of the whole pollinator assemblage per hour

($\sum D_t$, Equation 7), or for flower lifetime scale ($\sum D_l$, Equation 8). These indices, summing over all pollinator species (from $i = 1$ to $i = n$) in the assemblage, allow comparisons of whole pollinator assemblages of a given plant species among sites, habitats and estimations of seasonal as well as yearly variations.

$$\sum D_t = \sum_1^i D_t,$$ (7)

$$\sum D_l = \sum_1^i D_l.$$ (8)

(b) Pollen deposition efficiency of pollinator assemblages

Similarly, the $\sum P_t$ and the $\sum P_l$ indices (Equations 9 and 10) express the pollen deposition efficiency of the whole pollinator assemblage of a given plant species at a given time period or for flower lifetime receptivity.

$$\sum P_t = \sum_1^i P_t,$$ (9)

$$\sum P_l = \sum_1^i P_l.$$ (10)

The greater the number of pollinator species studied the more accurately will the index estimate the overall efficiency of the pollinator assemblage. The results for the pollination deposition efficiency of the total pollinator assemblage can be compared with the autonomous selfing efficiency (see Equation 11) and the open pollination efficiency (see Equation 12).

(3) Autonomous selfing efficiency

In some plants, autonomous self-pollination may make a significant contribution to pollen deposition and subsequent seed set in the absence or presence of pollinator activity. Plants with a high rate of autonomous self-pollination are not dependent on pollinator services for seed set, however they may suffer from inbreeding depression (Charlesworth & Charlesworth, 1987; Byers & Waller, 1999). Although measuring seed set as a result of autonomous self-pollination under pollinator exclosure represents the potential of a flower for autonomous selfing and not the actual value under a natural pollination regime, it is the only available field method. In self-compatible species, with a high degree of autonomous self-pollination, the autonomous selfing efficiency (A) can be calculated as the proportion of the number of seeds produced under pollinator exclosure (a, Equation 11) out of the maximal potential seed production under no pollen limitation achieved by artificial supplementary cross pollination of open naturally pollinated

flowers (s).

$$A = a/s.$$ (11)

(4) Open pollination efficiency

Open pollination efficiency (O) is the proportion of seed set in naturally open-pollinated flowers (o, Equation 12) out of the maximal seed production (s), achieved by artificial supplementary cross pollination of open naturally pollinated flowers. This index can serve as an alternative to estimating the performance of the whole pollinator assemblage. However, this equation does not allow distinguishing between the performances of different pollinator species or outcrossed from selfed progeny.

$$O = o/s.$$ (12)

VI. FUTURE RESEARCH

Our modular approach needs to be tested using sensitivity analyses to determine which variables are in fact the best predictors. Partitioning of the total pollen load into the outcrossing pollen and autogamous or geitonogamous pollen is important mainly for self-incompatible multi-flowered species (Morris et al., 1994; Sage et al., 2005; Di Pasquale, & Jacobi, 1998) and the development of such a method is a future challenge. Furthermore, our model does not address the issue of competition for ovules within pollen loads. Differences in the genetic composition and/or variability of the pollen loads may result in differences in their pollen tube growth rate and consequent ability to sire seeds as well as in offspring fitness (Janzen, 1977; Lee, 1984). Moreover, pollinating species that deposit more pollen grains per visit, even where the average pollen deposition is the same in the long term, may have an advantage because there is evidence that plants selectively mature fruits from flowers in which there has been more pollen competition (Niesenbaum & Casper, 1994; Niesenbaum, 1999).

VII. CONCLUSIONS

(1) Comparing the success or performance of different flower visitors in achieving pollination and consequent seed set is integral to several fields of investigation but has been a perennial problem in pollination biology. We argue that the lack of standardisation has limited the ability to compare the performance of different pollinators. Here we analyse the concepts, terms and methods in use and provide an integrated conceptual framework and methodology that can be used to compare pollinator performance across studies.

(2) Our conceptual scheme is divided into two main assessment components: pollination success and plant reproductive success. We define pollen deposition

effectiveness as the pollinator's contribution to pollen deposition alone. This does not take into account any variables involved in the plant's female reproductive success. We define pollen deposition efficiency as the pollinator's contribution, by deposition of conspecific, compatible and viable pollen grains on the receptive target stigma in relation to the maximal possible female reproductive success.

(3) Our modular approach is based upon a key basic unit, the number of pollen grains deposited on the stigma at the single-visit level. The next level is based on temporal and spatial scaling up by incorporating visit frequency when observing a flowering patch. Both pollen deposition effectiveness and pollen deposition efficiency can be scaled up to flower lifetime. From this level, it is possible to develop higher order indices e.g. seasonal or whole pollinator assemblage levels.

(4) Using our standardized methodology enables the categorization of flower visitors by their relative role as pollinators and contribution to plant female success. It also allows us to estimate the effectiveness and efficiency of the whole pollinator assemblage of a given flowering species and to compare it with other species. Future challenges include development of field techniques that will allow application of our equations to self-incompatible species and plants with small flowers or with special structures.

VIII. ACKNOWLEDGEMENTS

IX. REFERENCES

AIGNER, P. A. (2001). Optimality modeling and fitness trade-offs: when should plants become pollinator specialists? *Oikos* **95**, 177.

AIGNER, P. A. (2004). Floral specialization without trade-offs: optimal corolla flare in contrasting pollination environments. *Ecology* **85**, 2560–69.

AIGNER, P. A. (2006). The evolution of specialized floral phenotypes in a fine-grained pollination environment. In *Plant Pollinator Interactions from Specialization to Generalization* (eds. N. M. Waser, J. Ollerton), pp. 23–46. University of Chicago Press, Chicago.

ANDERSSON, S. (1988). Size dependent pollination efficiency in *Anchusa officinalis* (Boraginaceae): causes and consequences. *Oecologia* **76**, 125–30.

ANDERSSON, S. (1996). Floral variation in *Saxifraga granulata* - phenotypic selection, quantitative genetics and predicted response to selection. *Heredity* **77**, 217–23.

ARMBRUSTER, W. S. (1988). Multilevel comparative analysis of the morphology, function, and evolution of *Dalechampia* blossoms. *Ecology* **69**, 1746–761.

ARROYO, J. & DAFNI, A. (1995). Variation in habitat, season, flower traits, and pollinators in dimorphic *Narcissus tazetta* L. (Amaryllidaceae) in Israel. *New Phytologist* **129**, 135–45.

ASHMAN, T.-L., GALLOWAY, F. & STANTON, M. L. (1993). Apparent vs. effective mating in an experimental population of *Raphanus sativus*. *Oecologia* **96**, 102–07.

ASHMAN, T.-L. & STANTON, M. L. (1991). Seasonal variation in pollination dynamics of sexually dimorphic *Sidalcea oregana* spp. *spicata* (Malvaceae). *Ecology* **72**, 993–1003.

BEATIE, A. J. (1976). Plant dispersion, pollination and gene flow in *Viola*. *Oecologia* **25**, 291–300.

BERTIN, R. I. (1982). Floral biology, hummingbird pollination and fruit production of trumpet creeper (*Campsis radicans*, Bignoniaceae). *American Journal of Botany* **69**, 122–34.

BERTIN, R. I. (1986). Consequences of mixed pollinations in *Campsis radicans*. *Oecologia* **70**, 1–5.

BIESMEIJER, J. C., ROBERTS, S. P. M., REEMER, M., OHLEMÜLLER, R., EDWARDS, M., PEETERS, T., SCHAFFERS, A. P., POTTS, S. G., KLEUKERS, R., THOMAS, C. D., SETTELE, J. & KUNIN, W. E. (2006). Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science* **313**, 351–54.

BLOCH, D., WERDENBERG, N. & ERHARDT, A. (2006). Pollination crisis in the butterfly-pollinated wild carnation *Dianthus carthusianorum*? *New Phytologist* **169**, 699–706.

BOND, W. J. (1994). Do mutualisms matter? Assessing the impact of pollinators disperser disruption on plant extinction. *Philosophical Transactions of the Royal Society of London Series B* **344**, 83–90.

BOSCH, M. & WASER, N. M. (2001). Experimental manipulation of plant density and its effect on pollination and reproduction of two confamilial montane herbs. *Oecologia* **126**, 76–83.

BURD, M. (1994). Bateman's principle and plant reproduction: the role of pollen limitation in fruit and seed set. *Botanical Reviews* **60**, 83–139.

BYERS, D. L. & WALLER, D. M. (1999). Do plant populations purge their genetic load? Effects of population size and mating history on inbreeding depression. *Annual Review of Ecology and Systematics* **30**, 479–513.

CALZONI, G. L. & SPERANZA, A. (1998). Insect controlled pollination in Japanese plum (*Prunus salicinia* Lindl.). *Scientia Horticulturae* **72**, 227–37.

CAMPBELL, D. R. (1989). Measurements of selection in a hermaphroditic plant: variation in male and female pollination success. *Evolution* **43**, 318–34.

CANE, J. H. & SCHIFFHAUER, D. (2001). Pollinator genetics and pollination: do honey bee colonies selected for pollen-hoarding field better pollinators of cranberry *Vaccinium macrocarpon*? *Ecological Entomology* **26**, 117–23.

CANE, J. H. & SCHIFFHAUER, D. (2003). Dose-response relationships between pollination and fruiting refine pollinator comparisons for cranberry (*Vaccinium macrocarpon* [Ericaceae]). *American Journal of Botany* **90**, 1425–32.

CANTO-AGUILAR, M. A. & PARRA-TABLA, V. (2000). Importance of conserving alternative pollinators: assessing the pollination efficiency of the squash bee, *Peponapis limitaris* in *Cucurbita moschata* (Cucurbitaceae). *Journal of Insect Conservation* **4**, 203–10.

CAUICH, O., QUEZADA-EUAN, J. J., MACIAS-MACIAS, J. O., REYES-OREGEL, V., MEDINA-PERALTA, S. & PARRA-TABLA, V. (2004). Behavior and pollination efficiency of *Nannotrigona perilampoides* (Hymenoptera: Meliponini) on greenhouse tomatoes (*Lycopersicon esculentum*) in subtropical Mexico. *Journal of Economic Entomology* **97**, 475–81.

CHARLESWORTH, D. & CHARLESWORTH, B. (1987). Inbreeding depression and its evolutionary consequences. *Annual Review of Ecology and Systematics* **18**, 237–68.

CORBET, S. A. (1998). Fruit and seed production in relation to pollination and resources in bluebell, *Hyacinthoides non-scripta*. *Oecologia* **114**, 349–60.

CREPET, W. L. (1983). The role of insect pollination in the evolution of angiosperms. In *Pollination Biology* (ed. L Real), pp. 31–48. Academic Press, New York.

CROME, F. & IRVINE, A. (1986). 'Two bob each way': the pollination and breeding system of the Australian rainforest tree *Syzigium cormiflorum* (Myrtaceae). *Biotropica* **18**, 115–25.

CRUDEN, R. W. (1977). Pollen-ovule ratios: a conservative indicator of breeding systems in flowering plants. *Evolution* **31**, 32–46.

CRUDEN, R. W., BAKER, K. K., CULLINAN T. E., DISBROW, K. A., DOUGLAS, K. L., WEIER, J. A. & WILLMOTT, S. R. (1990). The mating system and pollination biology of three species of *Verbena* (Verbenaceae). *Journal of the Iowa Acadamy of Science* **97**, 178–83.

CRUDEN, R. W. (2002). Pollen grains: why so many? *Plant Systematics and Evolution* **222**, 143–65.

DAFNI, A., EISIKOWITCH, D. & IVRI, Y. (1987). Nectar flow and pollinator's efficiency in two co-occurring species of *Capparis* (Capparaceae) in Israel. *Plant Systematics and Evolution* **157**, 181–86.

DAFNI, A. & FIRMAGE, D. (2000). Pollen viability and longevity: practical, ecological and evolutionary implications. *Plant Systematics and Evolution* **222**, 113–32.

DAFNI, A., PACINI, E. & NEPI, M. (2005). Pollen and stigma biology. In *Practical Pollination Biology* (eds. A. Dafni, P. G. Kevan, B. C. Husband), pp. 83–142. Enviroquest, Cambridge (Ontario, Canada).

DE JONG, T. J., WASER, N. M., & KLINKHAMER, P. G. L. (1993). geitonogamy: the neglected side of selfing. *Trends in Ecology and Evolution* **8**, 321–325.

DE JONG, T. J., WASER, N. M., PRICE, M. V. & RING, R. M. (1992). Plant size, geitonogamy and seed set in *Ipomopsis aggregata*. *Oecologia* **89**, 310–15.

DIERINGER, G. (1992). Pollinator effectiveness and seed set in populations of *Agalinis strictifolia* (Scrophulariaceae). *American Journal of Botany* **79**, 1018–23.

DI PASQUALE, C. & JACOBI, C. M. (1998). Dynamics of pollination: A model of insect-mediated pollen transfer in self-incompatible plants. *Ecological Modelling* **109**, 25–34.

DONOVAN, B. J. & READ, P. E. C. (1991). Efficiency of honey bees as pollinators of kiwifruit. *Acta Horticulturae* **288**, 220–24.

ELTZ, T. (2006). Tracing pollinator footprint on natural flowers. *Journal of Chemical Ecology* **32**, 907–915.

FALQUE, M., LESDALONS, C. & ESKES, A. B. (1996). Comparison of two cacao (*Theobroma cacao* L.) clones for the effect of pollination intensity on fruit set and seed content. *Sexual Plant Reproduction* **9**, 221–27.

FENSTER, C. B., ARMBRUSTER, W. S., WILSON, P., DUDASH, M. R. & THOMSON, J. D. (2004). Pollination syndromes and floral specialization. *Annual Reviews of Ecology, Evolution and Systematics* **35**, 375–403.

FISHBEIN, M. & VENABLE, D. L. (1996). Diversity and temporal change in the effective pollinators of *Asclepias tuberosa*. *Ecology* **77**, 1961–73.

FUMERO-CABÁN, J. J. & MELÉNDEZ-ACKERMAN, E. J. (2007). Relative pollination efficiency of floral visitors of *Pitcairnia angustifolia* (Boraginaceae). *American Journal of Botany* **94**, 419–44.

GALEN, C. & NEWPORT, M. E. A. (1987). Bumble bee behavior and selection on flower size in the sky pilot, *Polemonium viscosum*. *Oecologia* **74**, 20–23.

GALEN, C. & STANTON, M. L. (1989). Bumble bee pollination and floral morphology: factors influencing pollen dispersal in the alpine sky pilot, *Polemonium viscosum* (Polemoniaceae). *American Journal of Botany* **76**, 419–26.

GÓMEZ, J. M. & ZAMORA, R. (1999). Generalization in the interaction between *Hormathophylla spinosa* (Cruciferae) and its pollinators. *Ecology* **80**, 796–805.

GRANT, V. (1971). *Plant Speciation*. Columbia University Press, New York.

GRIMALDI, D. (1991). The co-radiations of pollinating insects and angiosperms in the Cretaceous. *Annals of the Missouri Botanical Garden* **86**, 373–406.

GROSS, C. L. (2005). Pollination efficiency and pollinator effectiveness. In *Practical Pollination Biology* (eds. A. Dafni, P. G. Kevan, B. C. Husband), pp. 354–63. Enviroquest, Cambridge (Ontario, Canada).

GUDIN, S. & ARENE, L. (1991). Influence of the pH of the stigmatic exudates on male–female interaction in *Rosa hybrida* L. *Sexual Plant Reproduction* **4**, 110–12.

GUO, Y-H., SPERRY, R., COOK, C. D. K. & COX, P. A. (1990). The pollination ecology of *Zannichellia palustris* L. (Zannichelliaceae). *Aquatic Botany* **38**, 341–56.

HARDER, L. D. & WILSON, W. G. (1994). Floral evolution and male reproductive success: Optimal dispensing schedules for pollen dispersal by animal-pollinated plants. *Evolutionary Ecology* **8**, 542–59.

HARDER, L. D. & WILSON, W. G. (1998). Theoretical consequences of heterogeneous transport conditions for pollen dispersal by animals. *Ecology* **79**, 2789–807.

HERRERA, C. M. (1987). Components of pollinator 'quality': comparative analysis of a diverse insect assemblage. *Oikos* **50**, 79–90.

HERRERA, C. M. (1990). Daily patterns of pollinator activity, differential pollinating effectiveness, and floral resource availability, in a summer-flowering Mediterranean shrub. *Oikos* **58**, 277–88.

HIEI, K. & SUZUKI, K. (2001). Visitation frequency of *Melampyrum roseum* var. *japonicum* (Scrophulariaceae) by three bumblebee species and its relation to pollination efficiency. *Canadian Journal of Botany* **79**, 1167–74.

HOFFMANN, I. (2006). *Seasonal changes in the pollination system of Micromereia fruticosa L. (Lamiaceae) and its efficiency in two populations on Mt. Carmel*. M.Sc. thesis. Univ. Haifa, Israel.

INOUYE, D. W., GILL, D. E., DUDASH, M. R. & FENSTER, C. B. (1994). A model and lexicon for pollen fate. *American Journal of Botany* **81**, 1517–30.

IVEY, C. T., MARTINEZ, P. & WYATT, R. (2003). Variation in pollinator effectiveness in swamp milkweed, *Asclepias incarnata* (Apocynaceae). *American Journal of Botany* **90**, 214–25.

JANZEN, D. H. (1977). A note on optimal mate selection by plants. *American Naturalist* **111**, 365–71.

JAVOREK, S. K., MACKENZIE, K. E. & VANDER KLOET, S. P. (2002). Comparative pollination effectiveness among bees (Hymenoptera: Apoidea) on lowbush blueberry (Ericaceae: *Vaccinium angustifolium*). *Annals of the Entomological Society of America* **95**, 345–51.

JOHNSON, S. D. & STEINER, K. E. (2000). Generalization versus specialization in plant pollinator systems. *Trends in Ecology and Evolution* **15**, 140–44.

KANDORI, I. (2002). Diverse visitors with various pollinator importance and temporal change in the important pollinators of *Geranium thunbergii* (Geraniaceae). *Ecological Research* **17**, 283–94.

KEARNS, C. A. & INOUYE, D. W. (1993). *Techniques for Pollination Biologists*. Boulder: University Press of Colorado.

KEARNS, C. A., INOUYE, D. W. & WASER, N. M. (1998). Endangered mutualism: conservation of plant-pollinator interactions. *Annual Review of Ecology and Systematics* **29**, 83–112.

KEYS, R. N., BUCHMANN, S. L. & SMITH, S. E. (1995). Pollination effectiveness and pollination efficiency of insects foraging *Prosopis velutina* in south-eastern Arizona. *Journal Applied Ecology* **32**, 519–27.

KLEIN, A. M., STEFFAN-DEWENTER, I. & TSCHARNTKE, T. (2003). Pollination of *Coffea canephora* in relation to local and regional agroforestry management. *Journal Applied Ecology* **40**, 837–45.

LAU, J. A. & GALLOWAY, L. F. (2004). Effects of low-efficiency pollinators on plant fitness and floral trait evolution in *Campanula americana* (Campanulaceae). *Oecologia* **141**, 562–76.

LEBUHN, G. & HOLSINGER, K. (1998). A sensitivity analysis of pollen-dispensing schedules. *Evolutionary Ecology* **12**, 111–21.

LEE, T. D. (1984). Patterns of fruit maturation: a gametophyte competition hypothesis. *American Naturalist* **123**, 427–32.

LORD, E. M. & RUSSELL, S. D. (2002). The mechanisms of pollination and fertilization in plants. *Annual Review of Cell and Developmental Biology* **18**, 81–105.

MAYFIELD, M., WASER, N. M. & PRICE, M. (2001). Exploring the 'Most effective pollinator principle' with complex flowers: bumblebees and *Ipomopsis aggregata*. *Annals of Botany* **88**, 591–96.

MEISLES, S. & CHIASSON, H. (1997). Effectiveness of *Bombus impatiens* Cr. as pollinators of greenhouse sweet peppers (*Capsicum annuum* L.). *Acta Horticulturae* **437**, 425–29.

MESQUIDA, J. & RENARD, M. (1981). Pollination of male-fertile and male-sterile lines of winter oilseed rape (*Brassica napus* L. var. *oleifera* Metzger) by honeybees (*Apis mellifera* L.): Incidences on plant phenology and yield (in French). *Apidologie* **12**, 345–62.

MITCHELL, R. J. (1997). Effects on pollination intensity on *Lesquerella fendleri* seed set: variation among plants. *Oecologia* **109**, 382–88.

MONTALVO, A. M. & ACKERMAN, J. D. (1986). Relative pollinator effectiveness and evolution of floral traits in *Spathiphyllum friedrichsthalii* (Araceae). *American Journal of Botany* **73**, 1665–76.

MORANDIN, L. A., LAVERTY, T. M. & KEVAN, P. G. (2001). Bumble bee (Hymenoptera: Apidae) activity and pollination levels in commercial tomato greenhouses. *Journal of Economic Entomology* **94**, 462–67.

MORISON, N., VAISSIERE, B. E., MARTIN, F., PECAUT, P. & CAMBON, G. (2000). Pollination of globe artichoke (*Cynara scolymus* L.) by honey bees (*Apis mellifera* L.) to produce hybrid seed under enclosure. *Apidologie* **31**, 115–28.

MORRIS, W. F., PRICE, M. V., WASER, N. M., THOMSON, J. D., THOMSON, B. & STRATTON, D. A. (1994). Systematic increase in pollen carryover and its consequences for geitonogamy in plant populations. *Oikos* **71**, 431–40.

MOTTEN, A. F. (1986). Pollination ecology of the spring wildflower community of a temperate deciduous forest. *Ecological Monographs* **56**, 21–42.

MOTTEN, A. F., CAMPBELL, D. R., ALEXANDER, D. E. & MILLER, H. L. (1981). Pollination effectiveness of specialist and generalist visitors to a North Carolina population of *Claytonia virginica*. *Ecology* **62**, 1278–87.

MUCHHALA, N. (2003). Exploring the boundary between pollination syndromes: bats and hummingbirds as pollinators of *Burmeistera cyclostigmata* and *B. tenuiflora* (Campanulaceae). *Oecologia* **134**, 373–80.

NEPI, M. & PACINI, E. (1993). Pollination, pollen viability and pistil receptivity in *Cucurbita pepo*. *Annals of Botany* **72**, 527–36.

NIESENBAUM, R. A. (1999). The effects of pollen load size and donor diversity on pollen performance, selective abortion, and progeny vigor in *Mirabilis jalapa* (Nyctaginaceae). *American Journal of Botany* **86**, 261–68.

NIESENBAUM, R. A. & CASPER, B. B. (1994). Pollen tube numbers and selective fruit maturation in *Lindera benzoin*. *American Naturalist* **144**, 184–91.

OLSEN, K. M. (1997). Pollination effectiveness and pollinator importance in a population of *Heterotheca subaxillaris* (Asteraceae). *Oecologia* **109**, 114–21.

ORNELAS, J. F., JIMÉNEZ, L., GONZÁLES, C. & HERNÁNDEZ, A. (2004). Reproductive ecology of distylous *Palicourea padifolia* (Rubiaceae) in a tropical montane cloud forest. I Hummingbirds' effectiveness as pollen vectors. *American Journal of Botany* **91**, 1052–60.

OSORIO-BERISTAIN, M., DOMINGUEZ, C. A., EGUIARTE, L. E. & BENREY, B. (1997). Pollination efficiency of native and invading africanized bees in the tropical dry forest annual plant, *Kallstroemia grandiflora* Torr ex Gray. *Apidologie* **28**, 11–16.

PARKER, F. D. (1981). How efficient are bees in pollinating sunflowers? *Journal of the Kansas Entomological Society* **54**, 61–67.

PETTERSSON, M. W. (1991). Pollination by a guild of fluctuating moth populations: option for unspecialization in *Silene vulgaris*. *Journal of Ecology* **79**, 591–604.

POTTS, S. G., DAFNI, A. & NE'EMAN G. (2001). Pollination of a core flowering shrub species in Mediterranean phrygana: variations in pollinator diversity, abundance and effectiveness in response to fire. *Oikos* **92**, 71–80.

PRICE, M. V. & WASER, N. M. (1979). Pollen dispersal and optimal outcrossing in *Delphinium nelsonii*. *Nature* **277**, 294–97.

PRIMACK, R. B. & SILANDER, J. A. (1975). Measuring the relative importance of different pollinators to plants. *Nature* **255**, 143–44.

RAMSEY, M. & VAUGHTON, G. (2000). Pollen quality limits seed set in *Burchardia umbellata* (Colchicaceae). *American Journal of Botany* **87**, 845–52.

RATHCKE, B. (1983). Competition and facilitation among plants for pollination. In *Pollination Biology*, (ed. L. Real), pp. 305–29. Academic Press, New York.

RICHARDS, A. J. (1986). *Plant Breeding Systems*. Allen and Unwin, London.

RICHARDS, K. W. (1987). Diversity, density, efficiency, and effectiveness of pollinators of cicer milkvetch, *Astragalus cicer* L. *Canadian Journal of Zoology* **65**, 2168–68.

RICHARDS, K. W. (1996). Comparative efficacy of bee species for pollination of legume seed crops. In *The Conservation of Bees (Linnean Society Symposium Series)* (eds. A. Matheson, C. O'Toole, I. Williams, S. L. Buchmann, P. Westrich), pp. 81–104. Academic Press, London.

RODET, G., VAISSIÈRE, B. E., BRÉVAULT, T. & GROSSA, J-P. T. (1998). Status of self-pollen in bee pollination efficiency of white clover (*Trifolium repens* L.). *Oecologia* **114**, 93–99.

SAGE, T. L., HUSBAND, B. C. & ROUTLEY, M. T. (2005). Plant breeding systems and pollen dispersal: intrinsic attributes of the breeding system. In *Practical Pollination*

Biology (eds. A. Dafni, P. G. Kevan, B. C. Husband), pp. 23–49. Enviroquest, Cambridge (Ontario, Canada).

SAHLI, H. F. & CONNER, J. K. (2006). Characterizing ecological generalization in plant-pollination systems. *Oecologia* **148**, 365–72.

SALEH, A. & CHITTKA, L. (2006). The importance of experience in interpretation of conspecific chemical signals. *Behavioral Ecology and Sociobiology* **61**, 215–220.

SAMPSON, B. J. & CANE, J. H. (2000). Pollination efficiencies of three bee (Hymenoptera: Apoidea) species visiting rabbiteye blueberry. *Journal of Economic Entomology* **93**, 1726–31.

SCHEMSKE, D. W. & BRADSHAW, H. D. Jr. (1999). Pollinator preference and the evolution of floral traits in monkeyflowers (*Mimulus*). *Proceedings of the National Academy of Sciences U.S.A.* **96**, 11910–15.

SCHEMSKE, D. W. & HORVITZ, C. C. (1984). Variation among floral visitors in pollination ability: a precondition for mutualism specialization. *Science* **225**, 519–21.

SCHLINDWEIN, C. & WITTMAN, D. (1995). Specialized solitary bees as effective pollinators of South Brazilian species of *Notocactus* and *Gymnocalycium* (Cactaceae). *Bradleya* **13**, 25–34.

SCHNEIDER, D., STERN, R. A., EISIKOWITCH, D. & GOLDWAY, M. (2002). The relationship between floral structure and honeybee pollination efficiency in 'Jonathan' and 'Topred' apple cultivars. *Journal of Horticultural Science & Biotechnology* **77**, 48–51.

SIH, A. & BALTUS, M. S. (1987). patch size, pollinator behavior and pollinator limitation in catnip. *Ecology* **68**, 1679–95.

SIHAG, R. C. (1997). Determining the efficiency of pollinators. In *Pollination Biology: Basic and Applied Principles* (ed. R. C. Sihag), pp. 171–86. Scientific Publishers, Hisar Rajendra.

SNOW, A. A., SPIRA, T. P., SIMPSON, R. & KLIPS, R. A. (1996). The ecology of geitonogamous pollination. In *Floral Biology: Studies on Floral Evolution in Animal-Pollinated Plants* (eds. D. G. Lloyd, S. C. H. Barrett), pp. 191–216. Chapman & Hall, New York.

SPEARS, E. (1983). A direct measure of pollinator effectiveness. *Oecologia* **57**, 196–99.

STEBBINS, G. L. (1970). Adaptive radiation of reproductive characteristics in angiosperms, I: Pollination mechanisms. *Annual Review of Ecology and Systematics* **1**, 307–26.

STEPHENSON, A. G. (1981). Flower and fruit abortion: proximate causes and ultimate functions. *Annual Review of Ecology and Systematics* **12**, 253–79.

SUGDEN, E. (1986). Anthecology and pollinator efficacy of *Styrax officinale* subsp. *redivivum* (Styracaceae). *American Journal of Botany* **73**, 919–30.

SUZUKI, K. & AKAZOME, Y. (2000). Flexibility of pollinator-flower relationship in *Isodon umbrosus* and *I. effuses* (Lamiaceae) and its relation to fruit-set and seed-set. *Journal of Plant Research* **113**, 149–55.

SUZUKI, K., DOHZONO, I., HIEI, K. & FUKUDA, Y. (2002). Pollination effectiveness of the three bumblebee species on flowers of *Hosta sieboldiana* (Liliaceae) and its relation to floral structure and pollinator size. *Plant Species Biology* **17**, 139–46.

TAMURA, S. & KUDO, G. (2000). Wind pollination and insect pollination of two temperate willow species, *Salix miyabeana* and *Salix sachalinensis*. *Plant Ecology* **147**, 185–92.

TANDON, R., MANOHARA, T. N., NIJALINGAPPA, B. H. M. & SHIVANNA, K. R. (2001). Pollination and pollen–pistil interaction in oil palm, *Elaeis guineensis*. *Annals of Botany* **87**, 831–38.

THOMSON, J. D. (2001). How do visitation patterns vary among pollinators in relation to floral display and floral design in a generalist pollination system. *Oecologia* **126**, 386–94.

THOMSON, J. D. (2006). Tactics for male reproductive success in plants: contrasting insights of sex allocation theory and pollen presentation theory. *Integrative and Comparative Biology* **46**, 390–97.

THOMSON, J. D., WILSON, P., VALENZUELA, M. & MALZONE, M. (2000). Pollen presentation and pollination syndromes, with special reference to *Penstemon*. *Plant Species Biology* **15**, 11–29.

TITZE, A. (2000). The efficiency of insect pollination of the neophyte *Impatiens glandulifera* (Balsaminaceae). *Nordic Journal of Botany* **20**, 33–42.

VAISSIÈRE, B. E. (1991). *Honey bees, Apis mellifera L. (Hymenoptera: Apidae), as pollinators of upland cotton, Gossypium hirsutum L. (Malvaceae), for hybrid seed production*. PhD thesis. Texas A&M Univ., College Station.

VAISSIÈRE, B. E., RODET, G., COUSIN, M., BOTELLA, L. & TORRE GROSSA, J-P. (1996). Pollination effectiveness of honey bees (Hymenoptera: Apidae) in a kiwifruit orchard. *Journal of Economic Entomology* **89**, 453–61.

VAN PRAAGH, G. P. & HAUSCHILDT, H. (1991). Evaluation of shoot-bending, pruning and pollination for increasing fruit-set and yield on young 'Cox' trees. *Acta Horticulturae* **288**, 244–48.

VAZQUEZ, D. P., MORRIS, W. F. & JORDANO, P. (2005). Interaction frequency as a surrogate for the total effect of animal mutualists on plants. *Ecology Letters* **8**, 1088–94.

VAUGHTON, G. & RAMSEY, M. (2000). Pollinators and seed production. In *Seed Development and Germination* (eds. J. Kigel, G. Galili), pp. 475–90. New Marcel Dekker, York, Basel, Hong Kong.

VICENS, N. & BOSCH, J. (2000). Pollination efficacy of *Osmia cornuta* and *Apis mellifera* (Hymenoptera: Megachilidae, Apidae) on 'Red Delicious' Apple. *Environmental Entomology* **29**, 235–40.

WASER, N. M., CHITTKA, L., NEAL, M. V., WILLIAMS, M. & OLLERTON J. (1996). Generalization in pollination systems, and why it matters. *Ecology* **77**, 1043–60.

WASER, N. M. & PRICE, M. V. (1983). Pollinator behavior and natural selection for flower colour in *Delphinium nelsonii*. *Nature* **302**, 422–24.

WASER, N. M. & PRICE, M. V. (1990). Pollination efficiency and effectiveness of bumble bees and hummingbirds visiting *Delphinium nelsonii*. *Collectanea Botanica* **19**, 9–20.

WILCOCK, C. C. & NEILAND, M. R. M. (2002). Pollination failure in plants: why it happens and when it matters. *Trends in Plant Science* **7**, 270–77.

WILLMOTT, A. P. & BURQUEZ, A. (1996). The pollination of *Merremia palmeri* (Convolvulaceae): Can hawkmoths be trusted? *American Journal of Botany* **83**, 1050–56.

WILSON, P. (1995). Selection for pollination success and the mechanical fit of *Impatiens* flowers around bumblebee bodies. *Biological Journal of the Linnean Society* **55**, 355–83.

WILSON, P. & THOMSON, J. D. (1991). Heterogeneity among floral visitors leads to discordance between removal and deposition of pollen. *Ecology* **72**, 1503–07.

WILSON, P. & THOMSON J. D. (1996). How do flowers diverge? In *Floral Biology* (eds. D. G. Lloyd, S. C. H. Barrett), pp. 88–111. Chapman & Hall, New York

YOUNG, H. J. (2002). Diurnal and nocturnal pollination of *Silene alba* (Caryophyllaceae). *American Journal of Botany* **89**, 433–40.