

CAVEATS TO QUANTIFYING ECOSYSTEM SERVICES: FRUIT ABORTION BLURS BENEFITS FROM CROP POLLINATION

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Abstract. The recent trend to place monetary values on ecosystem services has led to studies on the economic importance of pollinators for agricultural crops. Several recent studies indicate regional, long-term pollinator declines, and economic consequences have been derived from declining pollination efficiencies. However, use of pollinator services as economic incentives for conservation must consider environmental factors such as drought, pests, and diseases, which can also limit yields. Moreover, “flower excess” is a well-known reproductive strategy of plants as insurance against unpredictable, external factors that limit reproduction. With three case studies on the importance of pollination levels for amounts of harvested fruits of three tropical crops (passion fruit in Brazil, coffee in Ecuador, and cacao in Indonesia) we illustrate how reproductive strategies and environmental stress can obscure initial benefits from improved pollination. By interpreting these results with findings from evolutionary sciences, agronomy, and studies on wild-plant populations, we argue that studies on economic benefits from pollinators should include the total of ecosystem processes that (1) lead to successful pollination and (2) mobilize nutrients and improve plant quality to the extent that crop yields indeed benefit from enhanced pollinator services. Conservation incentives that use quantifications of nature’s services to human welfare will benefit from approaches at the ecosystem level that take into account the broad spectrum of biological processes that limit or deliver the service.

Key words: *bet-hedging; carrying capacity; ecosystem services; flower surplus; fruit maturation; ovule fertilization; pollen production; pollinator decline.*

INTRODUCTION

Human-induced modifications to the environment continue to reduce biodiversity on a global scale (Vitousek et al. 1996), prompting concern over the potential loss of important ecosystem services, on which human health and welfare depend (Foley et al. 2005, Kremen and Ostfeld 2005). This concern has led to the estimation of monetary values for ecosystem services (Costanza et al. 1997, Schroter et al. 2005), which provide an economic justification for species conservation (Kearns et al. 1998, Balmford et al. 2002, Kremen et al. 2002, Steffan-Dewenter et al. 2005).

Pollination by insects comprises an important ecosystem service, as reproduction and yields of many

flowering wild (Larson and Barrett 2000) and crop plants (Klein et al. 2007) benefit from faunal pollinating vectors. This service to human agriculture has been shown to be negatively related to anthropogenic habitat changes, such as land use intensification and habitat isolation (Steffan-Dewenter and Tscharntke 1999, Klein et al. 2003b, Quesada et al. 2003, Kremen et al. 2004, Ricketts 2004, Chacoff and Aizen 2006, Greenleaf and Kremen 2006), and the possible economic consequences of these losses have been derived (Ricketts et al. 2004, Morandin and Winston 2006, Olschewski et al. 2006, Priess et al. 2007). Long-term declines in pollinator populations and related threats to plant reproduction have led to concerns of a widespread loss of pollination services in which pollen-limited plants will suffer reduced yields from declining pollen supply (Fig. 1A; Kremen et al. 2002, Steffan-Dewenter et al. 2005, Biesmeijer et al. 2006).

A review of evolutionary approaches to the common phenomenon of high flower-to-fruit ratios in hermaphroditic plants revealed adaptive flowering strategies aimed at optimizing the female (fruit production) vs. male (pollen production) contribution to the plant’s fitness (Ehrlen 1991). Moreover, apparent flower surpluses may serve as insurance for hermaphroditic plants against fluctuations in pollinator and nutrient availability (i.e., “bet-hedging”; Bond 1995, Brown and McNeil

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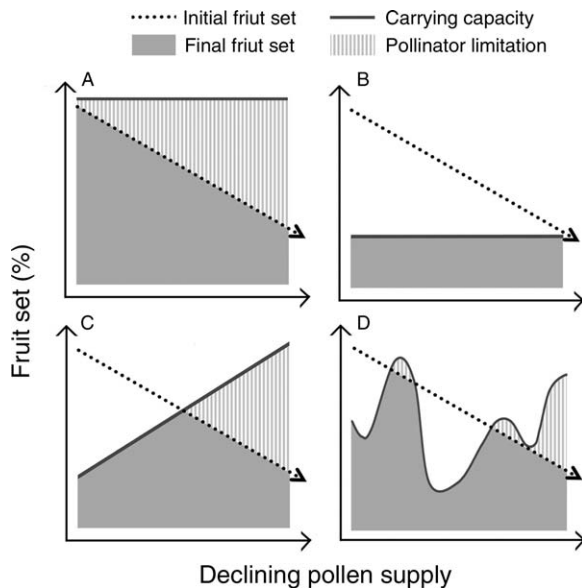


FIG. 1. Four scenarios for possible effects of declining pollen supply (for example, as a result of habitat destruction or agricultural intensification) on initial and final fruit set with a fruit carrying capacity of the crop that (A) is always higher than initial fruit set (i.e., pollinator limitation increases with decreasing pollination), (B) is always lower than initial fruit set (e.g., as a result from species-specific adaptive flowering strategies), (C) increases along the intensification gradient (e.g., because of intensifying fertilization regimes), and (D) is not related to the intensification gradient (e.g., plant-specific in highly heterogeneous, low-intensity, tropical landscapes).

2006). Agronomic approaches to crop yields and studies on wild plant populations compared benefits from pollinator services with the effects of environmental factors. Environmental factors that limit fruit maturation are from the plant's perspective unpredictable and include stressors such as drought (Windus and Snow 1993), nutrient deficiencies (Pías and Guitián 2006), herbivory (Windus and Snow 1993, Knight 2004), or within-plant competition for assimilates (Valle et al. 1990, Brown and McNeil 2006). Thus, whether or not effects of pollination declines are reflected in agricultural crop productivity may depend on species-specific flowering strategies (Fig. 1B) and on context-dependent carrying capacities of plants (Fig. 1C, D), which may differ greatly in time, space, and between plant parts (Ghazoul 2005, Knight et al. 2005). True limitation of fruit production by pollen supply is most likely for self-incompatible, animal-pollinated fruit crops that are pollinator specific and grown with optimal nutrient availability and absence of fruit- or seed-attacking pests (e.g., fertilization and pesticide use in agricultural systems; Fig. 1A; Ghazoul 2005).

Recent studies that use premature measures of yield, such as pollen deposition (Kremen et al. 2002, Quesada et al. 2003, Ricketts 2004, Larsen et al. 2005) or fruit set before harvest (Klein et al. 2003a, b, c, Morandin and Winston 2005), in assessing the importance of pollinator

declines for agricultural productivity do not acknowledge possible persistence of adaptive flowering strategies that may also explain flower excess in cultivated crops and the effects that spatial and temporal fluctuations in the environment may have on fruit maturation. If premature loss of pollinated flowers (fruit abortion) would not occur or comprise a constant proportion of set fruits, analysis of premature measures would be adequate for comparing pollination efficiency and inferring pollen limitation (Fig. 1A). Conversely, if plants are limited by other factors that are not related to declines in pollination, premature measurements might lead to overestimation of the actual importance of pollination limitation (Fig. 1B–D). Increasing pollination can in such instances be superfluous, as it may result in fruit set that exceeds the energetic budget of the mother plant, disrupting its metabolism and causing decreasing seed quality (Stanton et al. 1987) or even elevated rates of fruit abortion (Stephenson 1981, Sutherland 1987, Ehrlén 1991, Brown and McNeil 2006).

With case studies on the pollination of passion fruit in Brazil, coffee in Ecuador, and cacao in Indonesia, we investigate the importance of pollinator services to fruit set at two points in time: as soon as successful pollination was visible (“initial fruit set,” a premature measure) and at the time of harvest (“final fruit set”). We evaluate the effect of fruit losses between “initial” and “final fruit set” on the benefit of increased pollination to fruit set, which is important for quantifying the economic role of pollinators.

CASE STUDIES: MATERIALS AND METHODS

We defined initial fruit set as the proportion of flowers that was successfully pollinated (quantified as soon as successful pollination was visible) and final fruit set as the proportion of flowers that eventually resulted in mature, harvested fruits. Fruit abortion was quantified as the proportion of fruits that was lost between initial and final fruit set.

In the following, we outline the locations and methods for each crop studied. Responsibility for fieldwork was as follows: passion fruit, A. K. Bogdanski; coffee, Dorthé Veddele; and cacao, M. M. Bos. The studied crops are hermaphroditic (both male and female parts per flower) and, except for highland coffee, self-incompatible.

Pollination and fruit set of passion fruit

We carried out the study on passion fruit (yellow passion fruit, *Passiflora edulis* Sims. forma *flavicarpa* O. Deg., Passifloraceae) in Juazeiro, Bahia State, northeast Brazil (9°24'38" S, 40°30'26" W, 286 m above sea level). This region is characterized by a deficit of nesting habitats for solitary bees from the genus *Xylocopa*, the natural pollinators attending the large and conspicuous flowers (A. K. Bogdanski, unpublished data). Cultivated honey bees (*Apis mellifera*) were also observed attending flowers, but were not observed depositing pollen on

flower stigmas (A. K. Bogdanski, *unpublished data*). Therefore, farmers in this region often pollinate the large flowers by hand. All studied passion fruit fields were fertilized by the farmers.

In each of 16 sites we used 30 flowers for each of three different pollination treatments: natural pollination, manual cross-pollination (with pollen from different plants to avoid effects of self-incompatibility), and exclusion of pollination by animals, making a total of $16 \times 30 \times 3 = 1440$ flowers. With the latter two treatments, flowers were enclosed in mesh gauze bags to avoid additional pollination by insects before and after the treatments. For the manual cross-pollination treatment, pollen was transferred by hand, similar to the method used by the plantation workers. The experiments began in March 2005 and ended eight weeks later with the harvest of the fruits.

Pollination and fruit set of coffee

We carried out pollination experiments on the self-compatible highland coffee (*Coffea arabica* L., Rubiaceae) from October 2003 to August 2004 in the cantons Jipijapa (1°19'60" S, 80°34'60" W, 259 m above sea level), Pajan (1°34'00" S, 80°25'00" W, 142 m above sea level), and Noboa (1°24'00" S, 80°23'00" W, 260 m above sea level), Manabi province, coastal Ecuador. Coffee is the second most traded commodity (after oil) in the world, and its production affects the livelihood and income of millions of farmers throughout the tropics (Perfecto and Armbrecht 2003; International Coffee Organization, *available online*).⁵ In the study area, highland coffee ("Caturra" variety) was cultivated in traditional agroforestry systems under a canopy of various shade trees. No fertilizers or other chemical inputs were used. In the region, coffee flowered during one or two days, once per year in the dry season. After flowering, fertilized ovules remained dormant until the rainy season (generally one to three months later) when fruit development began synchronously.

In each of 22 agroforestry systems, we selected three inflorescences on four trees, making a total of $22 \times 3 \times 4 = 264$ inflorescences (3311 flowers), and investigated the importance of three pollination types (methodology described in Klein et al. [2003a]): self-pollination by enclosing flowers in bags of fine nylon mesh gauze (10 μ m) to exclude pollination by insects and wind; wind pollination by enclosing flowers in bags of cotton mesh (0.8–1.0 mm), which allowed self-pollination and pollen transfer by wind (not by insects); and natural pollination of flowers by leaving inflorescences open for free access by pollinators (self- and wind pollination included). Bags were placed around inflorescences before flowering. The short, synchronous flowering periods made it logistically unfeasible to include manual pollination treatments. We applied sticky glue to the branches to

prevent ants from disturbing the experiment. Mesh bags were removed when flowers withered and began to fall off. Inflorescences subjected to the experiment were marked and numbered with tape. Numbers of flowers were counted before the buds opened. Initial fruit set was recorded in March 2004 (approximately five weeks after initiation of fruit development, as in Klein et al. [2003a]), and final harvest was recorded when the fruits were harvested in August 2004.

Pollination and fruit set of cacao

We carried out pollination experiments on cacao trees (*Theobroma cacao* L., Sterculiaceae) within agroforestry systems around the village of Toro, on the western border of the Lore Lindu National Park, Central Sulawesi, Indonesia (1°30'24" S, 120°2'11" E, 800–900 m above sea level). The Island of Sulawesi is among the world's most productive cacao-growing regions (ICCO 2005), and Central Sulawesi particularly recently underwent a drastic increase in cacao production (Potter 2001). Despite its economic importance, little is known about the pollination biology of cacao. The generalist pollination system mainly involves pollination of the small, cauliflorous flowers by small midges of the family Ceratopogonidae (Entwistle 1972), which depend on dense shade and high humidity (Young 1982). In the agroforestry systems selected for the experiment, no chemical inputs such as fertilizers or herbicides were used, which was typical for the region.

In three agroforests we selected four trees (total of 12 trees) and divided the main stems into three zones: one where all flowers were left for natural pollination, one where each emerging flower was manually cross-pollinated and around one zone we constructed a net of mesh gauze to exclude insects from pollinating each emerging flower. The positions of the three zones on the main stems were randomized per tree. Manual cross-pollination was carried out by rubbing anthers from flowers of three different, non-neighbor trees against the flower stigma using a pair of tweezers. Treatments were carried out on the 1758 flowers that emerged during the 50 days starting 17 October 2004, and the number of flowers did not differ significantly between treatments. The resulting fruits were harvested between 18 and 22 weeks after pollination.

Statistical analyses

The effects of the different pollination treatments were tested in general linear models (GLMs) with treatment as a fixed factor. Using type I sequential sums of squares, site (random factor) entered the model first, followed by trees (random factor) nested within sites (coffee and cacao only), then by pollination treatment. Thus, trees or shrubs within sites were not treated as independent from one another. All models were carried out in Statistica 7.0 (Statsoft, Tulsa, Oklahoma, USA). The response variables, initial fruit set and final harvest, were calculated as proportion of

⁵ <http://www.ico.org>

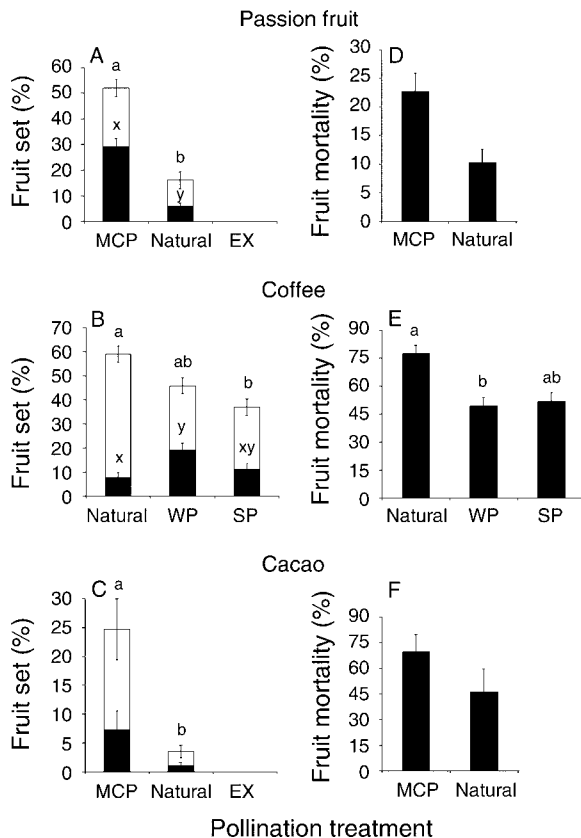


FIG. 2. Fruit set (percentage of flowers developing fruits) just after the pollination treatments (white) and at the time of harvest (black) and fruit mortality (percentage of fruits) of (A, D) passion fruit in Brazil, (B, E) coffee in Ecuador, and (C, F) cacao in Indonesia. Treatment abbreviations are: Natural, natural pollination; MCP, manual cross-pollination; EX, pollinator exclusion; WP, wind pollination; SP, self-pollination. Data are means with error bars showing \pm SE. Lowercase letters above bars indicate significant differences based on Tukey's hsd post hoc tests.

flowers, and abortion was calculated as the proportion of fruits that were lost. Therefore, the response variables were arcsine square-root transformed before analyses to meet the assumptions of normality and homogeneity of variances. Arithmetic means are given \pm SE.

RESULTS

Passion fruit (Passiflora edulis)

The proportion of flowers that set fruit on passion fruit (initial fruit set) was significantly higher after manual cross-pollination than after natural pollination (Fig. 2A, Table 1). Exclusion of insects from flowers completely prevented fruit set, which indicates that pollination of this cultivar required a vector for pollen transfer. Because the exclusion treatments did not lead to fruit set, this treatment was excluded from the GLMs that were used to analyze fruit abortion. On average $17\% \pm 2\%$ ($n = 16$ sites) of all fruits were aborted, which did not differ significantly between the pollination

treatments (Fig. 2D, Table 2). The proportion of flowers that eventually resulted in mature fruits (final fruit set) was significantly higher after manual cross-pollination (Fig. 2A, Table 1). Interaction effects between sites and treatments on the response variables were not tested because the 30 flowers per site were selected randomly.

Coffee (Coffea arabica)

The proportion of coffee flowers that was successfully pollinated (initial fruit set) was highest after natural pollination and lowest among flowers that were self-pollinated (Fig. 2B, Table 1), but differed significantly between sites. The proportion of aborted fruits was high ($60\% \pm 3\%$; $n = 66$ plants) and significantly affected by the pollination treatment, with highest proportions aborted after natural pollination (Fig. 2E, Table 2). The proportion of flowers that resulted in mature fruits was highest after wind pollination and lowest after natural pollination (Fig. 2B, Table 1).

Cacao (Theobroma cacao)

The proportion of cacao flowers that was successfully pollinated (initial fruit set) was highest after manual cross-pollination (Fig. 2C, Table 1) and exclusion of flying insects did not result in any pollinated flower. Because the exclusion treatments did not lead to fruit set, this treatment was excluded from the GLMs that were used to analyze fruit abortion. Overall, abortion of fruits was high ($58\% \pm 9\%$, $n = 12$ trees) and did not significantly differ between the pollination treatments (Fig. 2F). Abortion rates differed significantly between trees (Table 2), and manual cross-pollination resulted in higher proportions of aborted fruits, although that difference was only marginally significant (Table 2). Overall, abortion rates offset the increase in initial fruit set, such that the proportion of flowers that eventually resulted in mature fruits (final fruit set) did not differ significantly between open and manually pollinated flowers (Fig. 2C, Table 1). The interaction effect between pollination treatment and site was highly significant on initial fruit set and on the proportion of flowers that resulted in mature fruits. In one site, the effect of the pollination treatment on initial fruit set was significantly lower than in the two other sites. The interaction effect between site and treatment on the proportion of flowers that resulted in mature fruits was significant.

DISCUSSION

In each crop, abortion of set fruits was highest after the highest levels of pollination and thus decreased the initial benefits from increased pollination (although this was only statistically significant for coffee and cacao). In passion fruit, abortion rates were high overall ($17\% \pm 2\%$), but did not differ between pollination treatments such that fruit set at the time of harvest still reflected the benefits from enhanced pollination. In coffee, fruit abortion reversed the benefit of the treatments to initial

TABLE 1. Results of general linear models of fruit set and harvest (as a percentage of flowers) in response to site and treatment for passion fruit in Brazil, coffee in Ecuador, and cacao in Indonesia.

Factors, by variables	Effect	SS	df	MS	<i>F</i>	<i>P</i>
Passion fruit						
Initial fruit set						
Site	random	0.30	15	0.02	1.49	0.17
Treatment	fixed	4.34	2	2.17	162.84	0.00
Error		0.40	30	0.01		
Final fruit set						
Site	random	0.19	15	0.01	1.15	0.36
Treatment	fixed	2.32	2	1.16	105.47	0.00
Error		0.33	30	0.01		
Coffee						
Initial fruit set						
Site	random	10.78	21	0.51	3.15	0.00
Tree(site)	random	9.69	66	0.15	1.93	0.00
Treatment	fixed	3.18	2	1.59	17.30	0.00
Treatment × site	random	3.86	42	0.09	1.21	0.21
Error		10.01	132	0.08		
Final fruit set						
Site	random	4.21	21	0.20	1.83	0.07
Tree(site)	random	5.81	66	0.09	1.08	0.36
Treatment	fixed	1.54	2	0.77	7.43	0.00
Treatment × site	random	4.34	42	0.10	1.26	0.16
Error		10.81	132	0.08		
Cacao						
Initial fruit set						
Site	random	0.13	2	0.07	0.98	0.45
Tree(site)	random	0.11	9	0.01	1.04	0.45
Treatment	fixed	1.30	2	0.65	9.79	0.03
Treatment × site	random	0.27	4	0.07	5.58	0.00
Error		0.21	18	0.01		
Final fruit set						
Site	random	0.15	2	0.08	1.36	0.36
Tree(site)	random	0.06	9	0.01	0.68	0.72
Treatment	fixed	0.19	2	0.09	1.60	0.31
Treatment × site	random	0.24	4	0.06	6.60	0.00
Error		0.16	18	0.01		

Notes: Models were of type I variance decomposition, and variables are given in the order of model entry. Before analyses, data were arcsine square-root transformed.

fruit set, such that final fruit set was highest after wind pollination, perhaps due to less dry and harsh microclimatic conditions in the bagged treatments. For cacao the high abortion rates overshadowed the initial benefit of intensive pollination to fruit set, such that final fruit set was not significantly higher after manual cross-pollination compared with natural pollination.

Of the three studied crops, highland coffee was the only self-compatible crop, although initial fruit set increased when insects had access to the flowers. Traditionally, productivity of this crop was thought to be independent of faunal pollinating vectors (Reddy et al. 1988, Free 1993), and Philpott et al. (2006) found no effect of flying pollinators on fruit set or fruit mass of coffee in Mexico, except in the presence of positive interactions with ants, which were excluded in our study. Other recent studies from Indonesia and Central America showed the value of insect pollination for coffee pollination, fruit set, and harvest (Manrique and

Thimann 2002, Klein et al. 2003*a, b, c*, De Marco and Coelho 2004, Ricketts 2004, Ricketts et al. 2004). Roubik (2002) observed up to 50% harvest increases from highland coffee concomitant with an increase in abundance of naturalized honey bees on plantations in Panama and suggested a link between global pollinator declines and global declines in coffee harvests. The contrasts with our results on final fruit set suggest strong regional differences in the benefits of pollinators to coffee production, possibly due to low local nutrient availability, or climatic differences and differences between cultivars.

The large differences in initial fruit set we recorded between sites and trees emphasize the importance of studying coffee's pollinator limitation at different spatial scales (Veddeler et al. 2006). Our results underline the importance for future research on the exact processes that affect the relationships between environmental

TABLE 2. Results of general linear models of fruit abortion (as a percentage of fruits) in response to site and treatment.

Factors, by variables	Effect	SS	df	MS	F	P
Passion fruit						
Site	random	1.85	15	0.12	1.08	0.45
Treatment	fixed	0.01	1	0.01	0.13	0.72
Error		1.72	15	0.11		
Coffee						
Site	random	17.36	21	0.83	2.96	0.00
Tree(site)	random	17.60	66	0.27	1.29	0.11
Treatment	fixed	6.95	2	3.48	15.86	0.00
Treatment × site	random	9.21	42	0.22	1.06	0.39
Error		27.22	132	0.21		
Cacao						
Site	random	0.82	2	0.41	1.17	0.37
Tree(site)	random	3.66	9	0.41	4.17	0.02
Treatment	fixed	0.56	1	0.56	14.57	0.06
Treatment × site	random	0.08	2	0.04	0.40	0.68
Error		0.88	9	0.10		

Notes: Models were of type I variance decomposition, and variables are given in the order of model entry. Before analyses, data were arcsine square-root transformed.

factors, pollination intensity, ovule fertilization, and coffee berry maturation at multiple spatial scales.

Most cultivars of cacao are self-incompatible (Entwistle 1972, Falque et al. 1995, Klein et al. 2007), and the cacao trees used in this study required pollinating vectors, made clear by the differences between pollination treatments. Cacao flowers have been observed to be attended by various small insects (reviewed by Entwistle 1972), and natural initial fruit set generally ranges from <5% to 40% (Young 1982; S. G. Sporn, *unpublished data*). The observed increase in initial cacao fruit set after intensive manual cross-pollination compared with open pollination is in accordance with previous studies (Valle et al. 1990, Falque et al. 1995), and such apparent excesses of flowers are often used to infer pollinator limitation (reviewed by Knight et al. 2005). However, effects of pollen supplementation were site-dependent on initial and final fruit set. These results emphasize the importance of site-specific factors in addition to pollinator availability. Such factors that impede cacao's productivity can include locally distinct management practices such as cropping density and shade-tree stands and a wide range of aspects that mediate soil quality and pest pressures (Entwistle 1972, Young 1982, Bos et al. 2007). To increase our understanding of the site dependence of cacao's pollinator limitation, future studies should increase the number of sites to account for differences in site-specific factors.

The results of our cacao study are supported by theory that explains high flower-to-fruit ratios in plants as a bet-hedging strategy in times of poor pollination or low resource availability (Sutherland 1987, Brown and McNeil 2006). Additionally, because cacao fruits contain up to 400 times more energy than flowers (Valle et al. 1990), flower surpluses are predicted to be a strategy

of plants for maintaining high male fitness in terms of pollen production (Ehrlen 1991).

In our study, passion fruit was the only crop that showed true pollen limitation of productivity. Both initial and final fruit set increased after manual cross-pollination compared to natural pollination, and pollination required insect pollinators. Although rates of fruit abortion did not differ significantly between treatments, abortion was high and reduced overall yields. Passion fruit also meets all the criteria proposed by Ghazoul (2005) for sensitivity to pollinator declines: it is a fruit crop, self-incompatible, animal pollinated, pollinator- rather than resource-limited (due to fertilizer inputs), and it is pollinator-specific (carpenter bees of the genus *Xylocopa*). In contrast, coffee can also be wind pollinated and cacao is less pollinator-specific. Moreover, the studied coffee and cacao agroforests lacked external inputs such as fertilizers, which might have reduced the carrying capacity in the systems and increased the chance that factors other than pollination were limiting final fruit set (see Fig. 1B). Thus, pollination limitation for coffee and cacao might be more important in intensified systems with high nutrient inputs.

Our results call for further comparative studies to assess how representative our case studies are. Temporal turnover in tropical pollinator communities is known to be high and sensitive to anthropogenic habitat changes (Tylianakis et al. 2005). Because we investigated the extent to which initial fruit set can indicate levels of final harvests, our studies had a limited time span. Thus, we did not assess the importance of temporal changes for pollinator limitation, which are of particular importance when interpreting agricultural yields from perennial plant species such as our study crops. Furthermore, by studying the effect of enhanced pollination at the per



PLATE 1. Harvest in a cacao plantation in Central Sulawesi, Indonesia. Particularly in such traditional agroecosystems, fruit abortion can blur the benefits from enhanced pollinator services. Photo credit: M. M. Bos.

tree level for coffee and cacao and at the site level for passion fruit, our experimental setup could not detect effects of within-plant relocation of nutrients. This is a limitation of most pollen supplementation experiments (reviewed by Knight et al. 2005) and can be accounted for by conducting studies at multiple scales combined with fertilization experiments.

Implications and perspectives

Pollination is a crucial stage in the reproduction of most flowering plants, and pollen vectors are essential for maintaining genetic transfer (Kearns et al. 1998). However, in each of the three studied tropical cash crops the premature measure of “initial fruit set” would have lead to overestimates of pollination benefits to agricultural yields (measured as “final fruit set” in our studies). Under non-intensive, heterogeneous agricultural management, premature measures overestimate yields (Fig. 1B) or complicate the interpretation of patterns (Fig. 1D). Similarly, pollination limitation along a gradient of agricultural intensification may be confounded by reduced nutrient limitation and pest pressures (due to application of fertilizers and pesticides) and by increases in crop densities to an extent beyond the capacity of local pollinator populations. Hence, pollination may be a particularly limiting factor for yields in intensively managed land (Fig. 1C).

Moreover, plant reproductive strategies may have evolved to cope with fluctuating pollination levels by producing more flowers than the plant could possibly generate mature fruits. Flower surpluses may serve as bet-hedging strategies to assure maximum reproductive

output with environmental factors that fluctuate in time and space, and declines in pollination services may not have immediate effects on fruit production (Fig. 1B). The rates of fruit abortion we observed following increased pollination suggest the persistence of such strategies in our study crops, particularly under low management intensity that characterizes traditional tropical agroecosystems (see Plate 1).

Measurements of initial fruit set would only provide a proportional estimate of pollinator benefits for passion fruit, but could result in wrong estimates of pollinator benefits for coffee and cacao. Thus, the dependence of ovule fertilization on pollinators is not sufficient in all cases to infer that pollination services limit agricultural yields. Therefore, we urge caution in the use of economic justifications for biodiversity conservation derived from incomplete (premature) measures of ecosystem services and recommend more careful use of terminology relating to pollen limitation. Future studies addressing the effects of habitat destruction and agricultural intensification on agricultural productivity should aim to include other important services that mediate nutritional and herbivore pressures (e.g., Bardgett et al. 1998, Arnold et al. 2003, Poveda et al. 2003, Bos et al. 2007) and even future economic benefits through insurance effects (Yachi and Loreau 1999, Kremen et al. 2002). The chain of ecosystem services that facilitates fruit maturation is only as strong as its weakest link.

Quantifications of ecosystem services to agricultural yields will benefit from a holistic approach, considering the wide variety of ecosystem services and their synergies. In order to strengthen our case in the

conservation of biodiversity we need to understand the services that mobilize nutrients and improve plant quality to the extent that crop yields can optimally benefit from pollinator services.

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