

ADVANCES IN POLLINATION ECOLOGY FROM TROPICAL PLANTATION CROPS

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Abstract. Although ecologists traditionally focus on natural ecosystems, there is growing awareness that mixed landscapes of managed and unmanaged systems provide a research environment for understanding basic ecological relationships on a large scale. Here, we show how tropical agroforestry systems can be used to develop ideas about the mechanisms that influence species diversity and subsequent biotic interactions at different spatial scales. Our focus is on tropical plantation crops, mainly coffee and cacao, and their pollinators, which are of basic ecological interest as partners in an important mutualistic interaction. We review how insect-mediated pollination services depend on local agroforest and natural habitats in surrounding landscapes. Further, we evaluate the functional significance of pollinator diversity and the explanatory value of species traits, and we provide an intercontinental comparison of pollinator assemblages. We found that optimal pollination success might be best understood as a consequence of niche complementarities among pollinators in landscapes harboring various species. We further show that small cavity-nesting bees and small generalist beetles were especially affected by isolation from forest and that larger-bodied insects in the same landscapes were not similarly affected. We suggest that mixed tropical landscapes with agroforestry systems have great potential for future research on the interactions between plants and pollinators.

Key words: agroforestry; biodiversity–ecosystem function (BDEF); functional diversity; landscape ecology; niche complementarity.

INTRODUCTION

Ecologists have traditionally focused on natural ecosystems, although 75% of terrestrial ecosystems are now under human use (Pimentel et al. 1992), and this level of impact is growing (Bawa et al. 2004). Therefore, the functioning of terrestrial ecosystems cannot be understood without examining the strong and often dominant influence of human activities (Vitousek et al. 1997, Steffan-Dewenter et al. 2007). Accordingly, ecologists are turning to examine the important roles that tropical agroecosystems play in conserving terrestrial biodiversity (Bawa et al. 2004). Furthermore, such tropical landscapes provide a research environment for understanding basic ecological relationships on a large scale.

Crop pollination is an important ecosystem service for human welfare (Klein et al. 2007, Kremen et al. 2007). In tropical agroforests, two insect-pollinated plantation crops, coffee and cacao, represent different breeding systems (from mainly self-compatible to strictly self-

incompatible) allowing us to compare responses of different plant functional types to shifts in pollinator richness and community composition. Further, both crops are grown under a broad spectrum of agroecosystems ranging from structurally diverse agroforests, shaded and unshaded monocultures (Perfecto et al. 1996, Moguel and Toledo 1999, Schroth et al. 2004). In these agroecosystems, the diversity of organisms is manipulated at local scales by management decisions and at a landscape scale by long-term habitat conversion. These landscapes provide unparalleled opportunities to conduct large-scale studies of landscape and habitat effects with comparable habitat conditions, and a range of distances to natural forest habitats. Further, the crops provide researchers dominant focal plant species with resource availability that varies much less than in natural systems, allowing spatial comparisons that would otherwise be logistically difficult. Here, we illustrate how research in agroforestry has contributed to a deeper understanding of factors influencing pollinator diversity and plant–pollinator interactions. We start by reviewing current knowledge of the pollination systems of two major tropical agroforestry crops: coffee and cacao. We then use two independent data sets to analyze the spatial scales of response, followed by a new analysis of the functional role of

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pollinator diversity and the trait-dependent response of different pollinator guilds. We provide an intercontinental pollinator community structure. In the course of this discussion, we address the following questions: (1) At what spatial scales do different pollinator groups respond to landscape modification? (2) How do shifts in pollinator diversity influence pollination and what are the mechanisms to explain diversity–function effects? (3) Are results from one continent transferable to other continents?

COFFEE AND CACAO POLLINATION SYSTEMS

The genus *Coffea* (Rubiaceae) is native to tropical and subtropical Africa. Two coffee species are important crops in many tropical countries: Highland coffee, *Coffea arabica* L., native to the mountains of Ethiopia, and lowland coffee, *C. canephora* Pierre ex Froehner, syn. *Coffea robusta*, originally from the lowlands of central Africa. Highland coffee is grown throughout Latin America, Central and East Africa, India, and Southeast Asia. *C. arabica* is tetraploid and self-compatible (Free 1993). Autonomous self pollination occurs when pollen is shed from stamens on to the stigma. The relative benefits of cross pollination vs. self pollination have only recently been examined, with bagging experiments showing that autonomous self pollination leads to 45% initial fruit set, manual self pollination to 60%, and cross pollination (mix of self-pollen and allo-pollen) to 75% (Klein et al. 2003c). Fruit weight is approximately 25% greater when pollinators have access to flowers (Manrique and Thiemann 2002, Roubik 2002, Ricketts et al. 2004). Because flowering is induced by heavy rain, coffee blooms synchronously for short periods annually. The primary pollinators are social bees (Roubik 2002, Ricketts 2004, Veddeler et al. 2006, Bos et al. 2007; Appendix C: Table C1), and less abundant solitary bees (Klein et al. 2003a).

Lowland coffee is grown primarily in West and Central Africa, throughout Southeast Asia and in Brazil. *C. canephora* is diploid and predominately self-incompatible. Cross pollination is mediated by insects and less efficiently by wind (Willmer and Stone 1989, Free 1993, Klein et al. 2003c). Like *C. arabica*, flowering is synchronous and induced by rain, but scattered flowering can occur over several months. The pollinator community is similar to that of highland coffee. During mass-flowering, social bees (honey and stingless bees) are the most abundant flower visitors, but when only single coffee plants are flowering, solitary bees are dominant and social bees are often absent (Willmer and Stone 1989).

Cacao, *Theobroma cacao* L. (Sterculiaceae) is native to Central and South America. It is grown as a crop throughout the humid tropics, with the most important cacao-exporting countries being Ivory Coast, Ghana, and Indonesia (Young 1994, International Cocoa Organization 2005). Cacao is generally self-incompatible, although a few self-compatible varieties exist

(Falque et al. 1996). All varieties are strictly dependent on insect pollination, because the anthers with their sticky pollen are each enclosed by a folded petal. Flowers are cauliflorous and are present year-round, although peaks may occur in early wet seasons (Bos et al. 2007). The primary pollinators are biting midges of the family Ceratopogonidae, especially those of the genus *Forcipomyia* (Free 1993, Young 1994). Cacao pollinators depend on moist habitats and long dry seasons can decimate pollinator populations (Young 1982, Ruf 1995). Other small insects like phorid flies, gall midges of the family Cecidomyiidae, microlepidoptera, thrips, and stingless or solitary bees also visit flowers, but there is no clear evidence that they act as pollinators (Entwistle 1972, Young 1994; Appendix C: Table C1).

POLLINATION RESPONSES TO HABITAT AND LANDSCAPE SCALE FOR TROPICAL PLANTATION CROPS

Local and landscape management lead to shifts in pollinator assemblages (reviewed in Klein et al. [2007] and Kremen et al. [2007]). Pollination studies of local management and landscape effects on tropical plantation crops have examined *C. arabica* in Panama (Roubik 2002), Indonesia (Klein et al. 2003a), Costa Rica (Ricketts 2004, Ricketts et al. 2004), and Brazil (DeMarco and Coehlo 2004) and *C. canephora* in Indonesia (Klein et al. 2003b). Complex agroforestry systems, in terms of plant diversity, were found to support higher bee diversity and bee visits to coffee flowers compared to monocultures or simple shaded systems (Klein et al. 2003a, b, DeMarco and Coehlo 2004, Veddeler et al. 2006). Similarly, such landscape effects on pollination have been examined for three tropical plantation crops in Australia: macadamia (*Macadamia integrifolia*; Heard and Exley 1994, Blanche et al. 2006) atemoya (*Annona squamosa* L. *A. cherimola* Mill.; Blanche and Cunningham 2005), and longan (*Dimocarpus longan*; Blanche et al. 2006), and for grapefruit (*Citrus paradisi*) in Argentina (Chacoff and Aizen 2006). These studies all found fewer insect visits to flowers in locations more isolated from non-crop vegetation, but the pattern of change depended upon the suite of insect visitors, which varies by crop and location. For longan (Blanche et al. 2006) and macadamia (Heard and Exley 1994) in Australia, *C. arabica* in Costa Rica (Ricketts 2004), and grapefruit in Argentina (Chacoff and Aizen 2006), native social stingless bees declined in abundance with increasing distance from native forest more rapidly than did *Apis mellifera*. Although some solitary species declined with distance from forest in coffee (Klein et al. 2003c) and grapefruit (Chacoff and Aizen 2006), many solitary species responded more to local phenomena, in particular light intensity and plant diversity (Klein et al. 2003b). Solitary bees (e.g., *Heriades* and *Paracella* in the Megachilidae, *Nomia* in the Halictidae, and *Ceratina* in the Anthophoridae) often have small flight ranges and depend on

local nesting sites (e.g., open soil, dead wood) and particular floral resources (Wcislo and Cane 1996, Kremen et al. 2002, Klein et al. 2003b). Therefore solitary bees are often especially affected by local agroforestry management practices like pruning of shade trees and weeding (Klein et al. 2003b).

The relationship between pollinator abundance and species richness with distance to forest is influenced by pollinator size and nesting requirements. We reanalyzed data from Klein et al. (2003a) to test the tenet that cavity-nesting bees are more affected than ground-nesting bees on forested habitats. Moreover, we investigated the influence of body size on the relation between forest distance and diversity. We found that species richness ($F_{1,22} = 41.43$, $r = -0.81$, $P < 0.0001$) and abundance ($F_{1,22} = 52.44$, $r = -0.84$, $P < 0.001$) of cavity-nesting bees significantly declined with increasing forest distance, whereas species richness ($F_{1,22} = 2.98$, $r = -0.35$, $P = 0.099$) and abundance ($F_{1,22} = 0.18$, $r = -0.09$, $P = 0.679$) of ground-nesting bees (see Plate 1) were not related to forest distance, but to light availability on the ground (species richness: $F_{1,22} = 16.94$, $r = 0.65$, $P < 0.001$; abundance: $F_{1,22} = 24.70$, $r = 0.73$, $P < 0.001$; no relationship with light availability for the cavity-nesting bees could be found). Using four size-group classes (method described in Appendix A), we found that very small cavity-nesting bees (e.g., stingless bees were most abundant within 600 m of the forest margin, data not shown) and large bees (e.g., giant honey bee *Apis dorsata*; see Plate 1) decreased significantly in abundance with forest distance (*A. dorsata* was more abundant in sites close to forest, but was also found in sites > 1 km from the forest margin; data not shown) and that small bees (e.g., some honey bees, leaf-cutting bees) declined, but not significantly. Only the abundance of the very large bees (carpenter and large leaf-cutting bees) was not significantly related to forest distance (Fig. 1A). Very large bees even tended to be more abundant in sites far from forest (Fig. 1A, B), showing that response to isolation from forest can be linked to body size. The pattern considering species richness in each size-class groups was similar, but the steepness of the relationship differed slightly (Fig. 1B).

The midges that pollinate cacao and the nitidulid beetles that pollinate atemoya breed in rotting fruits and similar substrates in the litter layer, and are expected to have smaller flight ranges than bees. For example, the most important cacao pollinators, ceratopognid flies can only fly up to 6 m, although their foraging range can be enlarged up to 35 m by wind (Decazy et al. 1981). Hence, in plantations where farmers remove leaf litter, pollinator populations are expected to depend on adjacent habitats with suitable breeding substrate. The dispersal range and behavior of the atemoya pollinators remains largely unknown, although it has been shown that their diversity and abundance benefit from proximity to rain forest (Blanche and Cunningham 2005), possibly because farmers generally remove old fruits and other

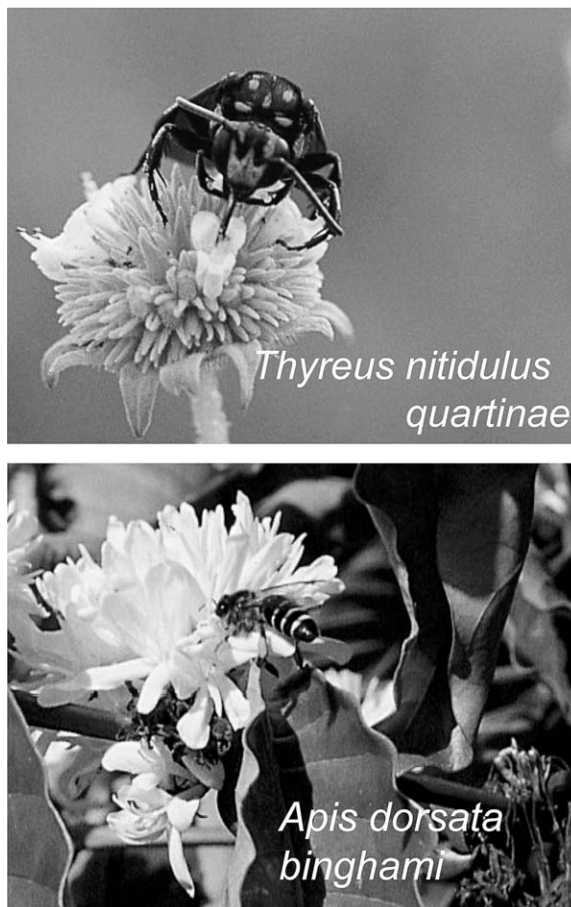


PLATE 1. (Top) the neon cuckoo bee, *Thyreus nitidulus quartinae*, a solitary species, forages in the understory flowers of Indonesian coffee agroforests, where it nests in the ground. Although it does not carry much pollen, this species can influence pollination success because: (1) it is a kleptoparasite, damaging the brood of other bee species (*Amegilla* sp.) that carry large amounts of coffee pollen and effectively pollinate coffee flowers; and (2) it interacts with other coffee-foraging bees in ways that may change pollination behavior and success. This species was mainly observed foraging on coffee flowers when honey bee activity at the same forage source was very low. (Bottom) The giant honey bee, *Apis dorsata binghami*, shown foraging on lowland coffee, *Coffea canephora*, is one of the three honey bee species and four stingless bee species (all eusocial) that are the main pollinating species for coffee in Sulawesi, Indonesia. Photo credits: A. M. Klein.

waste from plantations and thus, as for cacao, unwittingly diminish pollinator habitat within their plantations. These examples suggest that particularly small, generalist pollinating insects can be also influenced by the landscape matrix.

We reexamined this relationship between abundance of atemoya pollinators and distance from forest for beetles classified in two size classes (Appendix A; Blanche and Cunningham 2005; Fig. 2). There was a strong and significant relationship between abundance of small beetles in flowers and forest distance, but not between abundance of large beetles and forest distance

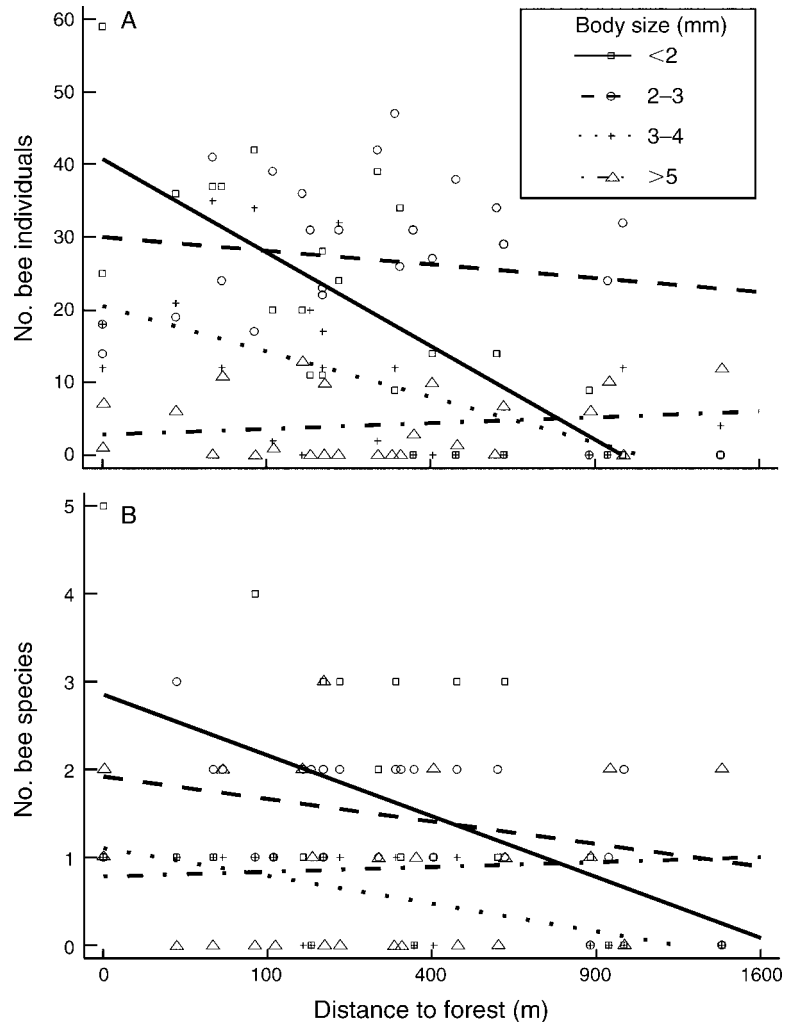


FIG. 1. (A) Relationship between the number of bee individuals observed on coffee (*Coffea arabica*) flowers in 24 agroforestry systems and distance to forest in Indonesia for the four body size classes: very small (>2 mm), $y = 40.81 - 1.29\sqrt{x}$, $F_{1,22} = 31.11$, $r = -0.77$, $P < 0.0001$; small (2–3 mm), $y = 29.95 - 0.19\sqrt{x}$, $F_{1,22} = 0.54$, $r = -0.16$, $P < 0.4686$; medium (3–5 mm), $y = 20.54 - 0.63\sqrt{x}$, $F_{1,22} = 8.73$, $r = -0.54$, $P < 0.0073$; and large (>5 mm) $y = 2.75 + 0.08\sqrt{x}$, $F_{1,22} = 0.65$, $r = 0.17$, $P = 0.4301$. Comparison of regression line slopes, $F_{1,22} = 8.32$, $P = 0.0001$. (B) Relationship between the number of bee species and distance to forest for the four body size classes (as in A): very small, $y = 2.85 - 0.07\sqrt{x}$, $F_{1,22} = 5.35$, $r = -0.44$, $P < 0.0305$; small, $y = 29.94 - 0.19\sqrt{x}$, $F_{1,22} = 0.54$, $r = -0.16$, $P < 0.4686$; medium, $y = 20.54 - 0.63\sqrt{x}$, $F_{1,22} = 8.73$, $r = -0.53$, $P < 0.0073$; large, $y = 0.78 + 0.01\sqrt{x}$, $F_{1,22} = 0.07$, $r = 0.06$, $P = 0.7894$. For the comparison of regression line slopes, $F_{1,22} = 2.35$, $P = 0.0776$. The square-root transformed distance values were recalculated into the measured values.

(Fig. 2). This relationship is parallel to the patterns seen in the analysis of coffee bees (Fig. 1A, B) and may similarly be influenced by a relationship between body size and dispersal power, although over a greater distance gradient. The biogeographic origin of the beetles may have an effect as well. Although most of the small species are native, large species tend to be exotic and cosmopolitan (Blanche and Cunningham 2005). They may be better adapted to human modified landscapes, possibly traveling in fruits and other material that humans transport around the landscape.

Studies of cacao pollinators have focused entirely on the local availability of breeding substrates, at the

expense of landscape level studies. Young (1982) successfully enhanced local breeding opportunities for pollinators in cacao plantations by providing decaying segments of banana stem, showing a significant increase in pollinator density and fruit set on trees within the breeding substrate treatment. Cacao pollinators may suffer when organic waste is removed from plantations (Young 1982, citing Dessart 1961), and so the possibility remains that as for atemoya plantations, pollinators in “cleaned” plantations might be dispersed by wind from neighboring forest; this would lead to a proximity effect on a landscape scale. The behavior and foraging ranges of pollinating beetles and midges deserve more study to

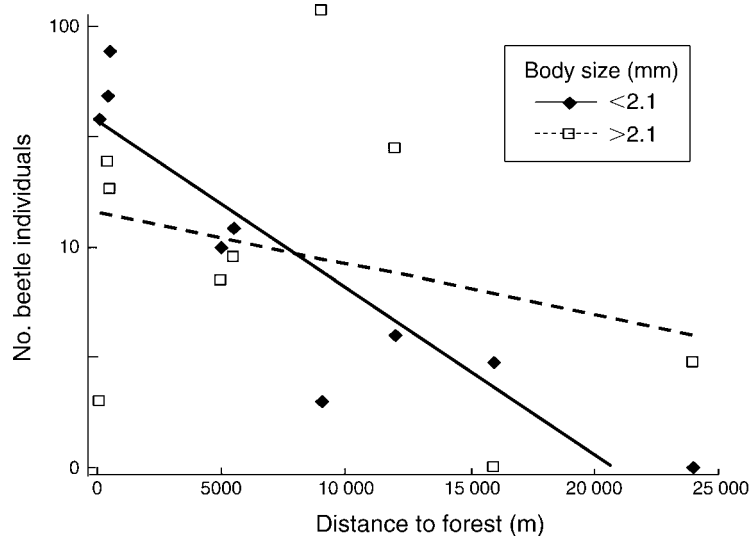


FIG. 2. Relationship between the number of beetle individuals observed on atemoya (*Annona squamosa* L. \times *A. cherimola* Mill.) flowers in nine plantations and distance to forest in tropical Australia for two size classes: small (<2.1 mm), $\log(y + 1) = 1.55 - 0.07x$, $F_{1,13} = 33.27$, $r = -0.90$, $P < 0.001$; large (>2.1 mm), $\log(y + 1) = 1.16 - 0.02x$, $F_{1,13} = 0.64$, $r = -0.29$, $P = 0.449$. For the comparison of regression line slopes, $F_{1,13} = 6.37$, $P = 0.0244$.

see how they are dispersing and to evaluate the scale dependence of forest proximity.

Most plantation crops are open to a range of pollinators, and therefore are pollinated by at least a few species even when relatively isolated from natural habitats in a highly agricultural environment. For plants that attract a range of pollinators, the community of visitors at any one point in time and space is the net effect of taxon-specific responses to habitat characteristics at different scales. However, tropical crop species with a narrow range of specialized pollinators, such as Brazil nut (*Bertholletia excelsa*) and oil palm (*Elaeis guineensis*), are likely to suffer more extreme pollinator shortage when grown in highly modified landscapes (Klein et al. 2007). Ricketts (2004) found that the pollination deficit in *C. arabica* was greatest in locations with low visitor diversity and that a decline between years in the dominant visitor to *C. arabica* was compensated by other flower-visiting bees, but only in locations near forest vegetation.

Pollination deficits may be related to the functional diversity of pollinators which, in turn, is related to local environment and the proximity of forest. Based on data of Klein et al. (2003a, b; see Appendix A for methods), functional group richness of flower visitors decreased with increasing forest distance for bees visiting *C. arabica* ($F_{1,22} = 8.72$, $r = -0.53$, $P = 0.007$) and *C. canephora* ($F_{1,13} = 5.14$, $r = -0.53$, $P = 0.041$) in Indonesia. Functional group richness was affected by local habitat characteristics in that it increased with increasing light availability on the ground (*C. arabica*, $F_{1,22} = 10.45$, $r = 0.57$, $P = 0.004$; *C. canephora*, $F_{1,13} = 23.66$, $r = 0.80$, $P < 0.001$) and with plant diversity (*C.*

arabica, $F_{1,22} = 11.05$, $r = 0.58$, $P = 0.003$; but not for *C. canephora*, $F_{1,13} = 0.80$, $r = 0.24$, $P = 0.388$).

In summary, pollination studies in tropical agricultural landscapes reveal a number of important ecological phenomena. Pollinators are unevenly distributed across the landscape, and pollinating taxa respond differently to landscape and habitat elements. Variation and quality of flower and nesting resources over time could be examined further to understand potential interspecific competition for these resources. Comparison across crops will allow generalization of pollinator responses to land-use changes at habitat and landscape scales.

FUNCTIONAL RESPONSES TO POLLINATOR DIVERSITY

Pollination depends on visitor abundance, visitor diversity, or both (Vazquez et al. 2005). Although abundance of a single species have been reported to affect coffee yields in South America (Roubik 2002), pollinator diversity in Indonesia is probably more important to pollination than abundance (Klein et al. 2003a).

Most BDEF (biodiversity–ecosystem function) studies focus on functional diversity, rather than species richness, assuming that the number of functional groups is more likely to have ecosystem effects than the number of species with redundant traits (Naeem and Wright 2003, Wright et al. 2006). Three mechanisms could explain a positive relationship between diversity and ecosystem functioning: (1) sampling effect, in which high species richness increases the likelihood of having efficient species in the community (Tilman et al. 1997, Ives et al. 2005), e.g., a greater chance of having a pollinator species that perfectly fits the flower morphology leading to more reliable pollination; (2) niche

TABLE 1. Results of general linear models (GLM) using Type I sums of squares, testing effects of functional group richness (entered first), species richness (entered second), and abundance (entered third, followed by interaction terms among the three variables) on pollination success of *Coffea arabica* and *C. canephora*.

Model and predictor variable	df	SS	F	P
<i>Coffea arabica</i>				
Pollinator functional richness	1	2390.3	21.8	0.0002
Error	22	1861.8		
Overall model	1	2390.3	16.8	0.0005
<i>Coffea canephora</i>				
Pollinator functional richness	1	894.6	6.1	0.0381
Error	13	222.6		
Overall model	1	894.6	7.8	0.0150

Notes: The overall models present the results of multiple regressions. Only significant variables are shown; nonsignificant variables were removed from the model by backward stepwise elimination. GLM results when changing the order of entering variables are given in Appendix B.

complementarity, in which high species richness increases functional effectiveness by increasing the efficiency of resource use in space and time (Fargione and Tilman 2005, Cardinale et al. 2006, Fontaine et al. 2006), e.g., all receptive flowers over an extended blooming period receive optimal pollination service; (3) functional facilitation, in which a species has a positive effect on the functional capability of other species (Cardinale et al. 2002), e.g., one species disturbs another during foraging leading to higher frequencies of cross pollination.

To date, only one experimental study has shown a positive effect of the number of pollinator functional traits on plant reproduction (Fontaine et al. 2006). In this study, cages were used to manipulate pollinator functional richness using two functional pollinator groups. Pollinators may behave differently under such artificial conditions and it is therefore important to manipulate pollinator diversity under more natural conditions and to use multiple morphological and behavioral characteristics to measure functional diversity.

We tested whether pollinator functional diversity contributes more to the quantity of initial fruit set of highland and lowland coffee than either pure abundance or total species richness of pollinator assemblages. Because quantitative data on cacao pollination in response to pollinator richness are not available, we base our analyses on coffee data collected by Klein et al. (2003a, b; see Appendix A). Using a priori classification we established nine functional pollinator groups differing in body size, sociality, and floral resource use (see Table 1). In a comparison of the effects of functional group richness, species richness, and abundance on pollination, functional group richness explained most variance for self-compatible *C. arabica* and for self-incompatible *C. canephora* (Table 1). Species richness was highly correlated with functional group richness (*C. arabica*, $F_{1,22} = 41.62$, $r = 0.81$, $P < 0.001$; *C. canephora*, $F_{1,13} = 9.67$, $r =$

0.65 , $P = 0.008$) and with abundance (*C. arabica*, $F_{1,22} = 8.98$, $r = 0.54$, $P = 0.007$; *C. canephora*, $F_{1,13} = 11.63$, $r = 0.69$, $P = 0.005$) and abundance with functional group richness (*C. arabica*, $F_{1,22} = 6.39$, $r = 0.47$, $P = 0.019$; *C. canephora*, $F_{1,13} = 5.13$, $r = 0.53$, $P = 0.041$). Therefore, we changed the order of variables entered into the models and showed that functional richness persistently explained most variance in pollination of *C. arabica* and *C. canephora* (Appendix B: Table B1).

The above results provide insight into the applicability of the three hypotheses for the benefits of functional diversity outlined above. Most importantly, the benefits from pollinator diversity might be best understood as a consequence of niche complementarity, indicating a low level of redundancy in the system. A diversity of morphological and social traits contributes more to optimal pollination levels than simple species richness. Small or long-tongued bees are probably more successful cross-pollinators in coffee, as they can easily reach the stamen and stigma to transfer pollen from flower to flower. Large bees, with their greater weight, might be more likely to dislodge pollen inside flowers when landing or moving around. Sociality is often important in that social bees can communicate the presence of resources to their colony and recruit in large number to mass-flowering plants like coffee. Social bees tend to focus foraging on a single full-blooming plant (Klein et al. 2003a) and therefore, are most effective in transferring pollen between flowers of the same individual, making them better pollinators for selfing, and less effective for outcrossing. The two coffee species are self compatible to different degrees (around 55% in *C. arabica*, 10% in *C. canephora* [Klein et al. 2003c]), so this pattern would have different consequences for each species. Social bees also prefer to visit plants on the first day of flowering, whereas by the third day solitary bees, butterflies, syrphid flies, and beetles often were the only visitors (A. M. Klein, *personal observations*).

Functional facilitation might play a role in coffee pollination in Indonesia in that some solitary bee species from the family Anthophoridae and Megachilidae were observed to change behavior when honey bees were abundant, moving more often between plants and foraging more on flowers closer to the ground. In this way the presence of one guild might facilitate the efficiency of the other (A. M. Klein, *personal observation*). A similar phenomenon has recently been demonstrated in hybrid sunflowers in California, where higher pollen transfer between hybrid male and female plants was observed when solitary and honey bees interacted on flowers, leading to greater seed numbers (Greenleaf and Kremen 2006). Social bees are known to prefer mass-flowering plants, whereas solitary bees were more species-rich and abundant on plants with fewer flowers (Table 2; Willmer and Stone 1989). Reduced visitation of mass flowering plants by solitary bees might be explained by competitive superiority of social compared to solitary species. In contrast, worker bees might be less

likely to communicate the presence of a plant with few flowers, leading to less recruitment. As a consequence, coffee plants blooming before or after the mass-flowering time of coffee experience different services than plants flowering during the peak.

In summary, species diversity increases the number of functional types in the community, and diversity of functional traits correlates with increased pollination success. It has been argued that the predictive power of a priori functional group classification is often not better than random (Wright et al. 2006). We suggest that a priori functional group classification provides a simple test of the hypothesis that there is a function–diversity relationship. Failure to reject the hypothesis provides support to pursue a more mechanistic exploration of the phenomenon, which can be pursued using post hoc functional group classifications. For example spatiotemporal complementarity (e.g., pollinator's use of horizontal vs. vertical flowers and the preferred time of day) along with pollination efficiency (pollen grains they transfer to stigma) and pollination effectiveness (single pollinator visits of bagged flowers only opening for a specific pollinator) could be examined to identify a set of functional groups. Such research requires that one manipulates pollinator diversity at a landscape-scale and in cage experiments to disentangle the effects of species richness, functional richness and abundance (Fontaine et al. 2006). For cacao, Falque et al. (1995) showed that successful pollination (seed per fruit) was highest after pollen deposition that was about 10 times higher than after a single visit by a pollinating midge. The current imbalance in knowledge of coffee and cacao pollination makes it difficult to compare the sensitivity to reductions in pollination services between these two crops. The cacao research demonstrates the importance of pollinator abundance to ensure multiple visits per flower, but more research on cacao pollination is needed to evaluate the role of functional diversity for optimal pollination.

INTERCONTINENTAL COMPARISON

Coffee and cacao agroforestry systems are located in a number of biogeographically distinct tropical rainforest regions around the world. This offers the opportunity to study differences and consider the generality of patterns across regions (Corlett and Primack 2006). Coffee was introduced to South America and Southeast Asia during the 17th century (Anthony et al. 2002). Africanized honey bees were brought to Brazil during the 1950s and established large colonies throughout South America (Sanford 2006). Therefore, coffee agroforestry systems can be used to study plant–pollinator interactions in (1) regions with coffee in its native range and native pollinators (Africa), (2) regions where coffee is introduced, but pollinators are native to the region (some regions in Southeast Asia), and (3) regions where coffee is introduced and nonnative pollinators dominate the bee assemblages (some regions in South America).

TABLE 2. Flower-visiting bee species (and their abundance) on *Coffea canephora* plants.

Plant and bee type	No. species	No. individuals
Single-blooming coffee plants		
Social bees	1	1
Solitary bees	20	178
Mass-blooming coffee plants		
Social bees	7	190
Solitary bees	12	89

Notes: Ten single-blooming plant individuals and 10 mass-blooming plant individuals, all approximately of 1.5 m tall, were observed each for 15 minutes from early December to the middle of January in 1999. Plants were observed in different coffee agroforestry systems in Sulawesi, Indonesia (for detailed information on methods, see Klein et al. [2002]).

Cacao can be also studied in its native and nonnative ranges, but little is known about the role of non-native species in pollination. To date, the taxonomy of the most important cacao pollinators (ceratopogonid midges) is obscure and mainly studied in the South American species (J. A. Winder, *personal communication*). In contrast, coffee-pollinating assemblages are not described in the native range. Hence, we can only compare current coffee pollinators between two major biogeographic regions (South America, Southeast Asia). A simple listing of flower visitors and pollinators from these two tropical continents shows that there is no species overlap (Appendix C, Table 2). *C. arabica* in South America is predominately pollinated by the nonnative Africanized honey bee, *Apis mellifera scutellata* Lepeletier (hybrid between European and African honey bees), whereas the native Eastern honey bee, *Apis cerana* Fabricius, and the Giant honey bee, *A. dorsata* Fabricius, dominate in Indonesia, Southeast Asia (Klein et al. 2003a). In locations where honey bees are rare, native stingless bees are abundant in South America (Ricketts et al. 2004, Philpott et al. 2006, Veddeler et al. 2006), and visitation by many different solitary bee species can be high in Indonesia, Southeast Asia (Klein et al. 2003a). Although pollination effectiveness varies between bee taxa (Klein et al. 2003a, b), bee assemblages of both regions seem to adequately pollinate coffee (e.g., Roubik 2002, Klein et al. 2003a, b) because coffee has a highly generalized pollination system (Appendix C, Table 2). Nevertheless, coffee pollination in sites dominated strongly by a single species can be disadvantaged. For example honey bee abundance can be low in some years and other more attractive mass-foraging resources can attract them away. Consequently, in years with low honey bee abundance, crops might not receive adequate pollination (see Ricketts 2004).

In summary, coffee pollinator assemblages differ among the continents, and the differences include shifts in functional groups, therefore caution should be applied before transferring results between regions and continents. There is a great, yet unexploited potential, to

compare coffee and cacao pollination in agroforestry settings in their native and nonnative ranges to study biogeography of plant-pollinator interactions and assess generality of the relationship between different pollinator assemblages and their functional role.

CONCLUSIONS

We show that pollination studies in tropical agroforestry reveal important insights into a number of ecological phenomena. Optimal pollination success might result from niche complementarities among flower-visiting species, and facilitation among visitors and the importance of a diversity of functional traits in the community can be important for pollination success in landscapes harboring various pollinators in space and time. Different pollinating taxa responded to different landscape and habitat elements, e.g., small cavity-nesting bees and generalist beetles required natural forest habitats near their foraging areas, whereas insects with large body size explored a larger spatial scale and where therefore less sensitive to isolation from forest.

Tropical agroforestry has many elements of naturally forest, but organized in a way that allows simplified analysis of landscape elements that facilitates hypothesis testing. Coffee and other plantation crops have received different levels of research attention, but comparing results for coffee, cacao, and atemoya show the importance of understanding patterns and processes in agroforestry systems. Continents differ greatly in their pollinator assemblages and the diversity of taxonomic groups, so results can not be freely transferred, but cross-experiments among continents allow contrasts of ecological processes in the native and nonnative ranges of subject species permitting more powerful generalizations.

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APPENDIX A

Methodology of flower-visiting insect observations, pollination experiments, and functional group classification (*Ecological Archives* E089-054-A1).

APPENDIX B

Results of general linear models using Type I sums of squares, testing the effects of functional group richness, species richness, and abundance on the pollination success of *Coffea arabica* and *Coffea canephora* (*Ecological Archives* E089-054-A2).

APPENDIX C

Flower-visiting and pollinating insect groups and species of coffee and cacao in South America and Southeast Asia (*Ecological Archives* E089-054-A3).