

Direct costs of forest reproduction, bee-cycling and the efficiency of pollination modes

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Abstract. The bee guild represents direct primary costs of angiosperm reproduction. Tropical flower visitors take an amount comparable to herbivores, exceeding 3% of net primary production energy. Therefore herbivory and aboveground net primary production have been underestimated. Comparing pollinators to other herbivores, harvest in mature forest by tropical bees is greater than leafcutter ants, game animals, frugivores, vertebrate folivores, insect defoliators excluding ants, flower-feeding birds and bats, but not soil organisms. The ratio of total aboveground net primary production to investment in pollen, nectar and resin used by pollinators suggests wind pollination is several times more efficient in temperate forests than is animal pollination in neotropical moist forest. Animal pollination may be favoured by habitat mosaics and an unpredictable or sparse dispersion of conspecifics — consequences of fluctuating abiotic and biotic environments. Natural selection evidently favours diminished direct reproductive costs in forests, for example by wind pollination, regardless of latitude and disturbance regime. An example is "wind pollination by proxy" of dominant trees in seasonal southeast Asian forests. They flower only occasionally and their pollen is dispersed by tiny winged insects that are primarily carried by the wind — rather than the nectar-hungry bees, bats, birds and moths used by most tropical flora. Increasing evapotranspiration is associated with greater net primary production; I show its correlation with species richness of social tropical bees across the isthmus of Panama, which may indicate increasing forest reproductive effort devoted to flowering, and its monopolization by unspecialized flower visitors in wetter and less seasonal lowland forests.

Keywords. Bees; pollinators; forest reproduction; primary production.

1. Introduction

Bees benefit from plant reproductive efforts by using pollen, nectar, resin and oils from flowers, and also by utilizing extra-floral resin, nectar and sap that constitute plant defenses against herbivores. Until now such materials were not considered in calculations of forest primary productivity (Heithaus 1974; Southwick 1984; Roubik 1989) nor were there estimates of total energy utilization by animals that feed primarily at flowers (figure 1). By analysing diverse information for some tropical and temperate forests, I hope to improve our understanding of production ecology, the impact of various consumer guilds, and the evolution of plant reproductive biology. Furthermore, in order to explore plant-pollinator communities and their responses to fluctuations or unpredictability in the abundance of mutualists in pace and time, I present a standardized index for the "direct costs of reproduction". This is but one component of lifetime investment in reproduction made by a plant, which also must include fruit and seeds, but it is fully revealed in the diversity and abundance of pollinator populations

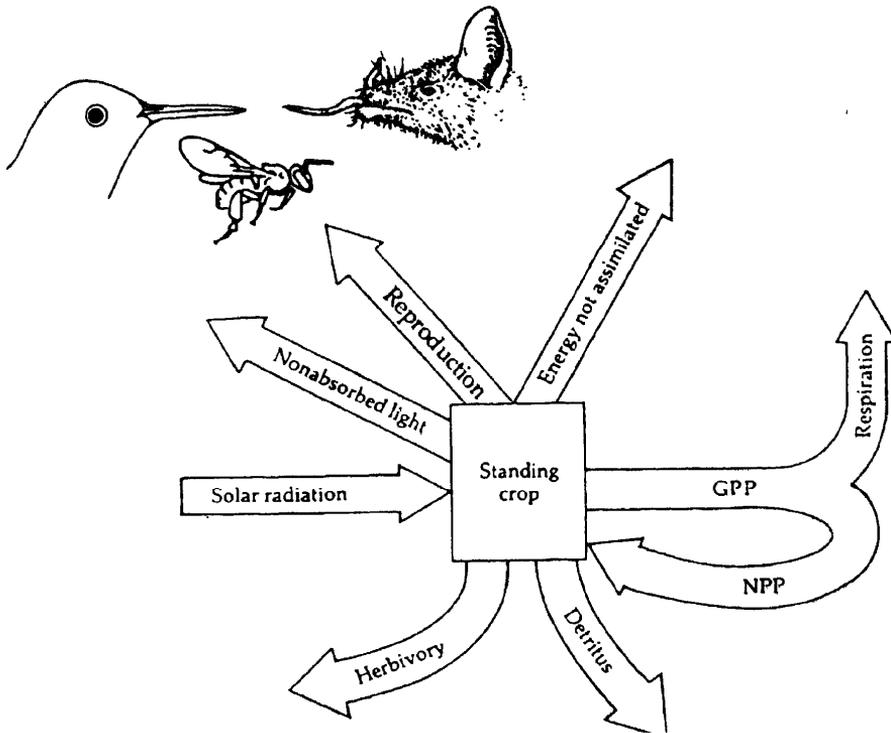


Figure 1. Routes of energy cycling in a forest (after Barbour *et al* 1987), with expenditure in direct costs of reproduction added here.

2. Primary direct costs of reproduction in plants

Pollen and spore production totals 10^5 – 10^6 kJ ha⁻¹ y⁻¹ (6 to 80 kg) in European pine forests where wind-pollination predominates (Faegri and Iversen 1975). This is a straightforward computation involving energy values (table 1). For neotropical forests, where animal pollination is the rule (Bawa 1990), my calculations here for seasonal moist forest in Panama suggest that bees recycle 10^6 – 10^7 kJ ha⁻¹ y⁻¹, thereby sustaining an important part in the trophic network. The rationale and steps required to reach this conclusion are substantiated in the following section.

When animal pollination is considered, the problem of finding the 'direct cost of reproduction' becomes one of determining how much pollen, nectar and other resources are sequestered by animals, and whether this differs significantly from total production in the plant community. Studies of "pollen rain" in neotropical forests imply that pollen is lost from the system—serving neither to sustain pollinators nor fertilize flowers (Palacios-Chavez 1985; Bush 1991). A census of flowers and their potential resources thus might provide the most accurate figures for aboveground net primary production (ANPP) at the community level. However, I see several problems to this approach. First, without aerial survey techniques, access to the forest canopy and an accurate count of flowers would be next to impossible. Second, nectar from individual flowers is resorbed by the plant if not

Table 1. Energetic values of plant products used for computing primary production of the forest and energy use by bees.

Resource	Energetic value (kJ/g)	Reference
Nectar*	6.6	Southwick and Pimentel 1981, Simpson and Neff 1983
Pollen	25.0	Colin and Jones 1980
Wood	17.5	Golley 1969
Leaves	15.6	Golley 1969
Forest litter	17.0	Golley 1969
Fruit	17.9	Golley 1969
Resin**	33.5	Buchmann and Roubik (unpublished)
Adult bees	22.2	Wightman and Rogers 1978
Bee provisions	38.1	Wightman and Rogers 1978, Roubik 1989
Floral oil	40.2	Simpson and Neff 1983

*40% sucrose.

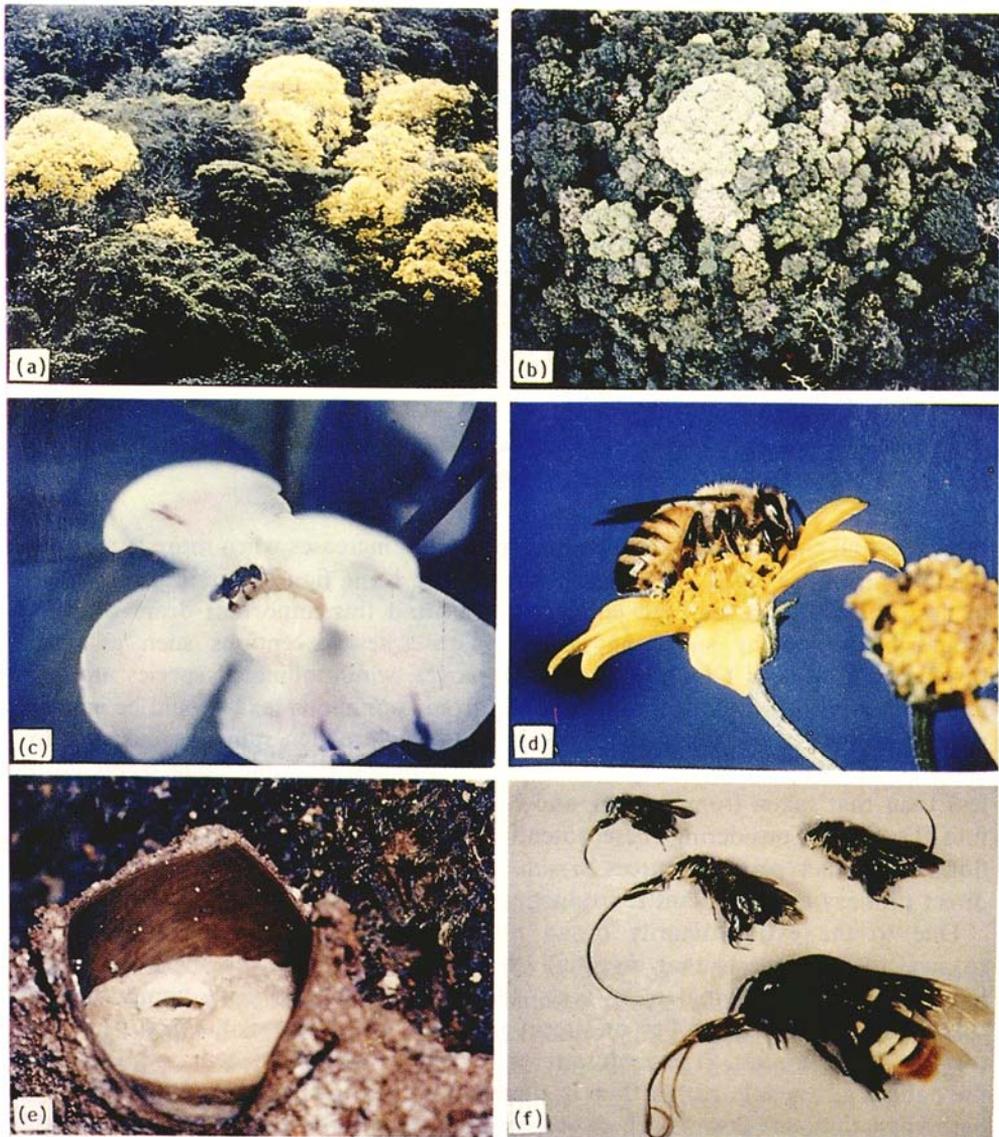
**Bomb calorimetry results for *Calophyllum* (Guttiferae) resin and the combined resin collected by the stingless bee *Scaptotrigona barrocoloradensis*.

removed, and the total amount secreted sometimes increases when more is removed (Bentley and Elias 1983). Third, as shown in table 1 and figure 2, resin used by bees in nest construction has high energy content, and this important drain on NPP would be missed by surveying flowers, with a few exceptions such as resin-producing flowers of *Clusia* (figure 2). Moreover, wind-pollinated species are very uncommon in tropical forests — pollen rain from zoophilous taxa should be *minimal* relative to that harvested at the flowers. Thus, while pollen rain does account for some of the NPP not used by flower-visiting animals, its total value seems much less than that taken from flowers, and nectar that is not consumed is taken back into the plant. Considering these potential shortcomings of attempting to measure floral and other plant resources *in situ*, an indirect approach for calculating the direct primary costs of plant reproduction seems desirable.

Due to the extraordinarily broad representation of highly eusocial bees in tropical forests, insects that essentially behave like plants in having a fixed nest location, usually in living trees, there exists a means for indirectly computing the total amount of nectar, pollen and resin removed from forest plants in the lowland tropics. The computation procedure relies upon absolute abundance (*i.e.* numbers in the habitat as a whole, rather than in some temporally-defined subset thereof) of the herbivores that visit flowers. These consumers include birds, bats, marsupials, moths and butterflies, flies, beetles, wasps and other insects, but primarily they are the bees. Absolute abundance of this group can be estimated by using the highly eusocial bees as "marked" individuals in a direct mark-recapture survey (see Dowdeswell *et al* 1940; Southwood 1971) of the bee population. No statistical variance or confidence intervals can be assigned to the population estimate, but this refinement might be devised later, in addition to better survey techniques for highly eusocial bees and the other animals that visit flowers.

3. Estimates of bee populations

Absolute population sizes of forest bees were estimated from field census studies in



Guanacaste, Costa Rica and in central Panama. All my calculations rest upon estimated abundance of perennially active stingless bee colonies (Meliponinae), which include 5–25% of the 200–250 bee species commonly encountered in neotropical forests (Roubik 1989; Ayala 1990). When combined with an intensive, year-round census of relative abundances of all types of bees at flowers, known meliponine foragers per hectare provide baseline data, which I then use to derive absolute numbers of non-meliponine bees in the same habitat. In Guanacaste 54% of bees sampled at flowers during a year were meliponines (Heithaus 1979). There are at least 16 resident meliponine species (D H Janzen and D W Roubik, unpublished,



Figure 2. Direct costs of forest reproduction and corresponding consumers. (a, b) Views of the forest: canopy in lowland moist forest (central Panama) and flowering by one tree species. (c) *Trigona* (Meliponinae) collecting resin from the flower of *Clusia* (Guttiferae). (d) *Apis mellifera scutellata* collecting pollen and nectar from a composite flower. (e) Egg of an *Epicharis ruscica* (Anthophoridae) on its pollen provisions in the cell. (f) Nectar feeding structures of euglossine bees with their extremely long proboscides partly extended. (g) Resin nest entrance of *Trigona* (*Heterotrigona*) *fimbriata*. (h) Resin nest entrance of *Trigona* (*Heterotrigona*) *apicalis*. (i) Mature larva of *Epicharis ruscica*, showing pollen remaining in the cell after feeding has terminated.

see also Appendix 1), but nest densities have been estimated only for 5 of them; they range from 10–40 km⁻² (Hubbell and Johnson 1977; Roubik 1983, 1989; Johnson and Hubbell 1984). Hubbell and Johnson (1977) encountered 67 nests of 9 species in their survey of 36.7 ha in Costa Rican dry forest, and the 5 species for which their data were comprehensive provided an estimate of 4.4 nests ha⁻¹. Another study (Appendix 1 and Roubik 1983) in wet lowland forest in Panama produced 30 nests of 14 species in 5 ha, yielding an estimated density of 6.0 nests ha⁻¹. Finally, Johnson and Hubbell (1984) sampled nests of forest on Barro Colorado Island, Panama—moist forest intermediate in rainfall and in stingless bee species richness between dry forest and wet forest locations in the lowland forest of the Isthmian region (Appendix 1)—and they derived similar figures of nest density of the same species or those closely related to bees studied in Guanacaste. Let us assume that about four colonies of stingless bees, regardless of size or species, occur within the dry tropical forest. The average colony contains 6000 adult bees (SD = 2000), only one-third of which are foragers (*op. cit.* Roubik 1979; Sakagami 1982). Yearlong sampling in this habitat produced 8 stingless bees for every 15 bees collected (Heithaus 1979). Considering there are about 2,000 foragers in each of the four nests within a hectare, the yearly abundance of foraging bees was therefore $15/8$ (8000) = 15,000 ha⁻¹.

The Guanacaste data are useful for extrapolation of bee abundance in another community where forest primary productivity and herbivores have been studied, but no year-long bee survey at flowers has been performed. I estimated bee biomass for Barro Colorado Island (BCI) by comparing its bee fauna to that of Guanacaste. The calculations were made in two steps: first by determining stingless bee colony density, then by changing the expected biomass of all other bees according to the ratio of BCI to Guanacaste stingless bee nests. Plant biomass and productivity increase from drier to wetter tropical forests (Murphy and Lugo 1986); dry forest ANPP is typically as low as half or less that of wet forest. Stingless bee nest density and species suggest the trend in productivity is also applicable to direct reproductive effort (Appendix 1), although it seems less likely to produce a general trend for forest bee species richness. There are, on average, six stingless bee colonies ha⁻¹ in the wetter lowland forests of Panama, an increase of 50% compared to the four found in the Guanacaste dry forest (Hubbell and Johnson 1977; Roubik 1983, 1989). Remarkably similar estimates came from surveys of standing trees in 16 ha (Johnson and Hubbell 1984) and felled trees within 5 ha (Roubik 1983), provided that the nest densities given for the former are applied to all of the resident species. Forests in the Isthmian region ranging from drier Pacific lowlands to Caribbean wet forests contain from 20 to 42 stingless bee species, respectively (Appendix 1). Further, the stingless bees were 68% of all diurnal bees caught in light traps during seven years on BCI (Wolda and Roubik 1986) but traps attracted only one-fourth or less of other resident bee species. The number of stingless bee colonies may reflect a trend in the entire bee guild. It seems likely, however, that stingless bees on the whole are more abundant at BCI and moist or wet forests because of their greater share of bee species richness. If stingless bees are 54% the total foragers on BCI as in Guanacaste — a reasonable assumption since almost all stingless bee species of Guanacaste also occur in central Panama—the biomass of other bees on BCI might be close to 120% ($0.54/0.68 \times 150\%$) that of Guanacaste. Thus total foraging bees on BCI should number about 20,000 ha⁻¹, and total adult bees, including stingless bees that do not forage, 44,000 ha⁻¹.

4. Estimates of ANPP and herbivore impact

Detailed studies of primary production in tropical moist forest of BCI (figure 3), suggest ANPP is $2.3 \cdot 10^8 \text{ kJ ha}^{-1} \text{ y}^{-1}$ (11.5 dry tons of leaf production, fruit and forest litter combined with 4.5 tons of wood growth $\text{ha}^{-1} \text{ y}^{-1}$; Leigh and Windsor 1982; E G Leigh Jr, personal communication). These authors demonstrated a 10% consumption of this amount by folivores and frugivores as diverse as mammals, insects and birds. However, the stipulated folivore impact is conservative, due to extrapolation from leaf damage only and a lack of data on the leaves completely removed. Annual energy use by bees, examined below, was approximately 40% that of all other insects combined in the analysis of Leigh and Windsor (1982), and equal to consumption by vertebrate folivores or by frugivores (figure 3).

How much energy and material is invested to produce the adult bees in a tropical forest community, and how many times yearly does the population renew itself? (My computations give energy values for an entire year and as such could also be expressed as Watts, where $1 \text{ W} = 86.5 \text{ kJ d}^{-1}$; but here I prefer SI units of energy and discuss kJ y^{-1} , where 1 joule = 4.18 calories.) According to studies on and near BCI, about 75% of immature bees (non-Meliponinae) die before becoming adults and thus, eight cells must be provisioned by each female if she replaces herself and her mate (Roubik 1989, 1990a). Stingless bees may have negligible brood mortality; their continuous brood-rearing activity results in eight annual brood cycles (Roubik 1982, table 2). Forager to brood ratios for stingless bees are about 10.5:1 (Roubik 1979; 1983, Roubik and Peralta 1983). Other bees often produce 2-3 broods y^{-1} , suggesting the average number of 2.5 used here (Roubik 1989, see table 2). Similarly, the energy contained in the provisions given to a larval bee during its development may equal two to three times the energy value of the adult bee (Wightman and Rogers 1978; Danforth 1990); a conversion factor of 2.5 was used for this estimate. Major components of the bee community's energy consumption are thus:

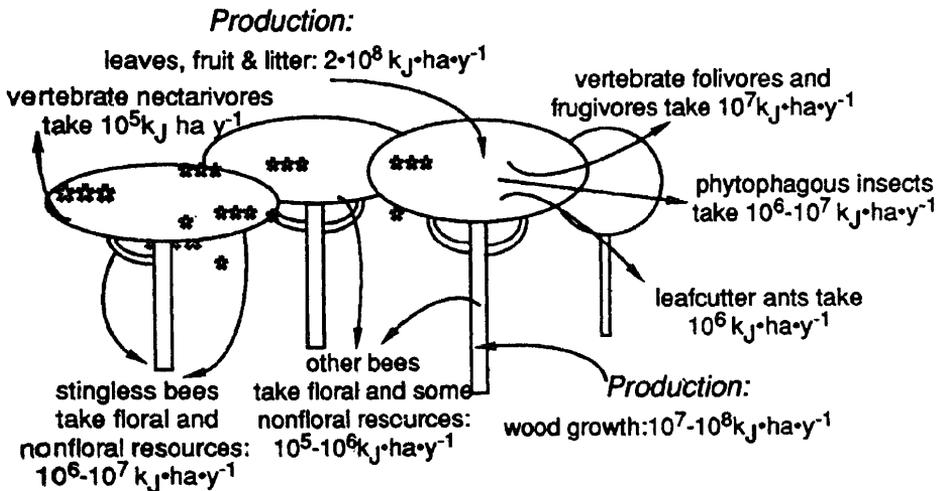


Figure 3. Forest net primary production in energy units (joules) and energy consumption by herbivores, folivores, nectarivores and bees on Barro Colorado Island, Panama. Energy values computed from table 1 and biomass estimates given by Leigh and Windsor (1982). Note that one dry ton of vegetation is the energetic equivalent of $1.5 \cdot 10^7 \text{ kJ}$.

Table 2. Energy cycled through a bee community and the variables used to compute total yearly energy consumption of bees within one hectare of forest on Barro Colorado Island, Panama. The grand total is $7.4 \cdot 10^6 \text{ kJ ha}^{-1} \text{ y}^{-1}$, where annual ANPP is approximately $2.3 \cdot 10^8 \text{ kJ ha}^{-1} \text{ y}^{-1}$ (see text).

Bee group	Parameters	Yearly energy value (product)
Stingless bees	8 broods y^{-1} ; $3.6 \cdot 10^4$ adults ha^{-1} ; 3.5 immatures adult^{-1} ; P^{**} ; W^*	$3.8 \cdot 10^5 \text{ kJ}$
Other bees	2.5 broods y^{-1} ; $8.3 \cdot 10^3$ adults ha^{-1} ; 4.0 immatures adult^{-1} ; P^{**} ; W^*	$4.5 \cdot 10^4 \text{ kJ}$
Stingless bees	0.016 g nectar use day^{-1} ; $3.6 \cdot 10^4$ adults ha^{-1} ; S^{***} ; 365 d	$1.4 \cdot 10^6 \text{ kJ}$
Other bees	0.032 g nectar use day^{-1} ; $8.3 \cdot 10^3$ adults ha^{-1} ; S^{***} ; 365 d	$0.6 \cdot 10^6 \text{ kJ}$
Stingless bees	$1.4 \cdot 10^6$ resin loads $\text{colony}^{-1} \text{ y}^{-1}$; 6 colonies ha^{-1} ; 16 mg ; $R\#$	$4.6 \cdot 10^6 \text{ kJ}$
Stingless bees	2 l stored honey $\text{colony}^{-1} \text{ y}^{-1}$; 6 colonies ha^{-1} ; $1.7 \cdot 10^4 \text{ kJ l honey}^{-1}$	$2.0 \cdot 10^5 \text{ kJ}$
Stingless bees	1 l stored pollen $\text{colony}^{-1} \text{ y}^{-1}$; 6 colonies ha^{-1} ; $2.6 \cdot 10^4 \text{ kJ l pollen}^{-1}$	$1.6 \cdot 10^5 \text{ kJ}$

* W , Average weights of stingless bees (0.016 g live weight) other bees (0.032 g live weight), determined from measurement of several species then estimated for all species in a survey in Costa Rica (Heithaus 1979). ** P , Energy content of brood provisions (38.1 kJ g^{-1}), bomb calorimetric estimates published for seven species of stingless bees, *Megachile* and *Xylocopa* (Roubik 1989). Other variables were measured directly or computed from energetic values (table 1) | S^{***} , energy g^{-1} nectar containing 40% sugar. $R\#$, resin energy (34 kJ g^{-1}); colonies gathered an average of two resin loads forager $^{-1} \text{ d}^{-1}$

(i) Average standing biomass of bees on BCI, which requires a total investment of 10^5 - 10^6 kJ ha⁻¹ y⁻¹ in larval provisions (figure 3, table 2).

(ii) Nesting biology of bees, which entails input of plant material. Bees make nests from leaves, seeds, wood, plant lipids and resins, but quantitative data are available only on resin harvest by stingless bees. Foragers of 10 nests of *Trigona*, *Cephalotrigona*, and *Melipona* were monitored throughout the day 42 times, in wet and dry seasons on BCI (D W Roubik, N M Holbrook and G Parra, unpublished). These colonies gathered resin loads averaging 2 forager⁻¹ day⁻¹, thus 24,000 loads ha⁻¹ d⁻¹ were collected, weighing 192 g if two full (two-legged) resin loads equal the weight of a forager. Theoretical maximum foraging loads are equal to the weight of a bee and often apply to single nectar loads (Roubik 1989); my estimate for total daily resin loads was the bee's live weight. From preliminary investigations (S L Buchmann and D W Roubik, unpublished) we know that resins have an energy value of approximately 34 kJ g⁻¹ (table 1); meliponine average weights are roughly 16 mg (figure 2). Therefore, annual resin harvest by stingless bees is approximately 4-5 10⁶ kJ ha⁻¹ y⁻¹.

(iii) Forager flights consume considerable energy but flight ranges of stingless bees and many others are too poorly known to estimate energy use as a function of distance traveled by bees (in contrast to Southwick and Pimentel 1981, for *Apis mellifera*). Another general energy budget estimate (for homeotherms) suggests that three times basal metabolism at rest (BMR) is utilized during the daily activity cycle (Hume 1982); this approximates the estimate derived here for heterotherm (occasionally self-warming) bees. One temperate bumblebee species, studied in a flight room, used the equivalent of its body weight in nectar each day (Bertsch 1984). Preliminary studies with euglossine bees in Panama showed that they will fill their crops with nectar five times daily (Kato *et al* 1992), effectively equalling body weight. Nectars gathered by bees average 40% sugar by weight, or 47.069 g 100 ml⁻¹ = 7.75kJ ml⁻¹ (Kearns and Inouye 1993). Because 1 g sugar equals 16.5kJ energy, and adult bee biomass on BCI is approximately 0.53 kg ha⁻¹ dry weight (0.86 kg live weight, see Bertsch 1984), my estimate of the annual energy needs of adult bees is 2.0 10⁶ kJ ha⁻¹ y⁻¹, or about 5,600 kJ d⁻¹ (table 2).

(iv) Honey and pollen in nests of stingless bees adds to the energy value of their colonies. This energy is stored and therefore absent in calculations of daily energy consumption by adults. This is in marked contrast to bumble bees, which store relatively little honey [the preceding estimates of Bertsch (1984) for foragers were based upon male bees, and thus involved their energy needs alone] Honey averaged 735 g per stingless bee nest in Panama, which I found equal to 516 g sucrose or 8,500kJ; 0.251 pollen was stored by an average colony (Roubik 1983). The six nests of stingless bees ha⁻¹ forest contain about 10⁵ kJ of stored food which, replenished few times each year, contributes 10⁵—10⁶ kJ to ANPP captured by bees. Adding all components (figure 2, table 2), the local bee assemblage uses 7.4 10⁶kJ ha⁻¹ y⁻¹, an average of 2 10⁴ kJ each day.

From the preceding, it is evident that summed maintenance and reproductive costs of the bee community, given in nectar consumption by adults and materials chiefly pollen and nectar, and some floral oils) are approximately equal to half the energy value of harvested nesting materials-or resin.

If bees were the only consumers of the plant products, then ANPP would be at east 3% greater than present estimates for BCI (figure 3, table 2). However, bats,

birds and many insects also feed on tropical nectar and sap (Fleming *et al* 1972; Wolf *et al* 1976; Faegri and van der Pijl 1979; Howell 1983; Terborgh *et al* 1990; Leigh and Handley 1991). My calculations (table 3) suggest that the vertebrate nectarivores require 1–10% the energy used by bees, slightly increasing the figure for corrected ANPP.

Few estimates are available for bat populations or their pollen and nectar consumption. Bats feed at flowers in the dry season and the metabolic rate of *Glossophaga*, the chief nectarivore on Barro Colorado Island, is known (Fleming *et al* 1972; Howell 1983). If this bat forages 3 h nightly and was as abundant as a considerably more common species of frugivorous bat (2–3 ha⁻¹ or 4000 resident animals on BCI, Leigh and Handley 1991) it would consume 10³–10⁴ kJ ha⁻¹ y⁻¹. This is a liberal estimate, perhaps adequate to cover the still unknown realm of floral product consumption by tropical bats in general. Avian nectarivore absolute biomass (Terborgh *et al* 1990) and the energy needs of neotropical hummingbirds (Wolf *et al* 1976) suggest bracketing nectar consumption at 10³–10⁴ kJ ha⁻¹ y⁻¹ (figure 2). Although the range of parameters indicated in figure 2 and table 3 allow other estimates, my figures should be low because they do not include: (i) pollen and nectar not removed from flowers by any animal, (ii) standing crops of resin and wax incorporated in nests of bees, and (iii) colony and brood mortality of stingless bees

Table 3. Consumer guilds and their annual energy consumption. Aboveground net primary production (ANPP) for BCI is approximately 2.3 10⁸ kJ ha⁻¹ y⁻¹, see text; estimates for other habitats considered here are given in Fittkau and Klinge (1973); 2.0 10⁸ kJ ha⁻¹ y⁻¹ for the Amazon — and DeAngelis *et al* (1981) for beech forest: 1.2 10⁸ kJ ha⁻¹ y⁻¹.

Guild and location	Biomass and/or energy use (kJ ha ⁻¹ y ⁻¹)	ANPP (%)	References
Soil organisms			
Central Amazon	165 kg ha ⁻¹ 2.0 10 ⁷	10.0	Fittkau and Klinge 1973
Beech Forest	150–250 kg ha ⁻¹ 1.6 10 ⁷	13.0	Edwards <i>et al</i> 1970
Leafcutter ants			
Central Amazon	0.6 10 ⁶	0.3	Fowler <i>et al</i> 1990, Vasconcelos 1987
Barro Colorado Island (BCI)	4.2 10 ⁶	2.0	Leigh and Windsor 1982
Nectarivores			
Bats; Central America, Panama (BCI)	10 ³ – 10 ⁴	0.002	Fleming <i>et al</i> 1972, Howell 1983, Leigh and Handley 1991
Hummingbirds, Western Amazon	10 ³ – 10 ⁴	0.003	Wolf <i>et al</i> 1976, Terborgh <i>et al</i> 1990
Bees, Panama (BCI)	7.4 10 ⁶	3.2	Present paper
Vertebrate folivores, Barro Colorado Island	4.2 10 ⁶	2.0	Leigh and Windsor 1982
Frugivores, Barro Colorado Island	4.2 10 ⁶	2.0	Leigh and Windsor 1982
Game animals (ungulates, primates, rodents, edentates)*			
Neotropics	1.9 kg ha ⁻¹ (sust. harvest) 3.0 10 ⁵	0.02	Robinson and Redford 1991

*Energy values for activity were extrapolated from BMR (Hume 1982, see text), and for game animals it was assumed that 40 kilojoules were required to produce 1 g protein (Robinson and Redford 1991).

consumed by diverse predators (see Roubik 1989). European *Apis mellifera* in a temperate forest (Seeley 1985) is present in densities of one colony km⁻² and large colonies consume 10⁶kJ y⁻¹ (Southwick and Pimentel 1981), equivalent to 10⁴kJ ha y⁻¹. I conclude that the bee guild in neotropical forest uses hundreds of times more energy than is taken by natural honey bee colonies in temperate forest.

The total harvest of food and material per hectare of a neotropical moist forest by all organisms using nectar, pollen and resin is thus between five and ten million kilojoules per hectare each year, an amount nearly half of the energy available for human consumption from a tropical hectare's annual rice or corn crop (Norman *et al* 1984). Other consumer guilds listed in absolute abundance and biomass within some tropical forests are evaluated in table 3. By comparison, bees constitute one of the largest consumer guilds in terrestrial communities. Carbon contained in plant products utilized by bees, and in the bees themselves, comprise slightly more than 50% dry weight. In addition, bee standing biomass of about 2 kg dry weight ha⁻¹, recycled several times a year, adds to the estimated sum of carbon removed from the atmosphere by forests (Brown and Lugo 1984; Kauppi *et al* 1992).

5. Values of pollination

As stated by Givnish (1980), Waller (1988), and others, wind pollination is not necessarily inefficient compared to animal pollination. It is a derived trait in many angiosperms, also present in many monocots, and not 'primitive' for the vascular plants in general (Midgley and Bond 1991; Eriksson and Bremer 1992). My analysis of energetics provides a further reason for accepting the efficiency hypothesis, at least at the community level. Temperate and tropical forest NPP tends to display levels predicted by evapotranspiration, although variable due to soil fertility and rainfall regimes (DeAngelis *et al* 1981; Leith 1972; Barbour *et al* 1987). That animal-pollinated plants usually produce nectar does not warrant the conclusion that such pollination efforts must be more costly, because pollen and floral resin are other costs that must be taken into account (table 1). Reproduction is relatively more costly, in terms of direct expenditure for nectar, floral displays, pollen and also for resins (floral and extrafloral), in a tropical moist forest than in conifer forests such as fir or pine. Alaskan spruce forests at 62° N latitude produce a total of 10⁸ kJ ha y⁻¹ ANPP (DeAngelis *et al* 1981) and have a maximum pollen and spore production near 1% this amount (Faegri and Iversen 1975). A semi-mature forest such as that on BCI in Panama makes 2.3 10⁸ kJ ANPP available to consumers each year. Flower-visitors and pollinators utilize close to 10⁷ kJ, or more than 3.2% of ANPP.

Interesting comparisons could be made of lifetime direct reproductive expenditure of tropical and temperate trees, and also in seed, fruit and resin production, emphasizing the fact that many tropical trees display variable flowering intensity or do not flower every year (Appanah 1993). Equally informative would be comparisons of pollen production by tropical conifers, such as *Agathis* or *Araucaria*, with those in the temperate zone, or to compare tropical angiosperms with wind-pollinated temperate angiosperms such as *Acer* or *Fagus*.

The most pronounced semi-annual flowering occurs among mass-flowering and mast-fruited trees of seasonal, lowland southeast Asia. Such variability seems to have had a profound impact on the structure of bee communities, making them the

Appendix 1. Stingless bee communities in different 'Isthmian' lowland tropical forests*.

Species and taxonomic data	Distribution			No. nests ha ⁻¹ in census**	
	Pacific	Mid Atlantic	Atlantic	CR dry	PAN mois PAN wet
<i>Melipona compressipes triplariidis</i> Cockerell, 1925 (= <i>M. interrupta triplariidis</i>)	x	x	x		
<i>Melipona eburnea panamica</i> Cockerell, 1919 (new combination = <i>M. fasciata</i>)		x	x	0-12	0-40
<i>Melipona fuliginosa</i> Lepeletier, 1836 (= <i>M. flavipennis</i>)		x	x		
<i>Melipona micheneri</i> Schwarz, 1951 (= <i>M. marginata micheneri</i> , new status)		x	x	0-12	0-20
<i>Melipona favosa orbigny</i> Guerin, 1844 (= <i>M. favosa phenax</i>)	x				
<i>Trigona nigerrima</i> Cresson, 1878	x	x	x		0-20
<i>Trigona amalthaea sibestriana</i> Vachal, 1908		x	x	0-14	0-20
<i>Trigona cornina</i> Cockerell, 1913		x	x	0-20	
<i>Trigona fuscipennis</i> Friese, 1908	x	x	x		
<i>Trigona fulviventris</i> Guerin, 1835	x	x	x		
<i>Trigona muzoensis</i> Schwarz, 1948 (= <i>T. pallida</i> , <i>T. pollens</i>)	x	x	x		
<i>Trigona cilipes</i> Fabricius, 1804	x	x	x		
<i>Trigona ferricauda</i> Cockerell, 1917		x	x		
<i>Trigona necrophaga</i> Camargo and Roubik, 1991		x	x		
<i>Trigona (Frieseomelitta) nigra paupera</i> (Provancher, 1888)	x	x	x		
<i>Trigona (Tetragonisca) angustula</i> Illiger, 1806 (= <i>T. jaty</i>)	x	x	x	0-30	
<i>Trigona (Tetragonisca) buchwaldi</i> Friese, 1900		x	x		
<i>Trigona (Tetragona) dorsalis ziegleri</i> Friese, 1900 (= <i>T. dorsalis dorsalis</i>)	x	x	x	0-24	0-40
<i>Trigona (Tetragona) perangulata</i> Cockerell, 1917		x	x		
<i>Trigona (Geotrigona) leucogastira chiriquiensis</i> Schwarz, 1951	x				
<i>Cephalotrigona capitata zexmeniae</i> Cockerell, 1912	x	x	x	0-14	0-20
<i>Scaptotrigona barrocoloradensis</i> Schwarz, 1951		x	x	0-25	
<i>Scaptotrigona pectoralis</i> Dalla Torre, 1896	x	x	x		
<i>Scaptotrigona luteipennis</i> Friese, 1902 (= <i>S. pachysoma</i>)	x	x	x	0-24	
<i>Paratrigona lophocoryphe</i> Moure, 1963 (= <i>P. opaca</i>)	?	x	x		
<i>Paratrigona ornaticeps</i> Schwarz, 1935		x	x		
<i>Paratrigona (Aparatrigona) isopterophila</i> Schwarz, 1934		x	x		0-40

least species-rich of any ancient tropical forest ecosystems (Roubik 1990b, 1991). The irregularity in flowering might be self-sustaining, given that specialist pollinators are very uncommon and hundreds of plant species use the same pool of generalist pollinators. If flowering occurred each year in the mass-flowering habitats, which appear to require the ENSO phenomenon (El Niño-Southern Oscillation) as a stimulus to flower (Ashton *et al* 1988) the direct costs of reproduction might be prohibitive. Unless a large number of individuals of a given species flower, there may be inadequate pollinator movement between plants and little temporal specialization by pollinators. Selection could thus favour delayed, highly synchronized flowering of trees, notwithstanding the advantages of mast-fruiting in predator satiation (Appanah 1985, 1993; Ashton *et al* 1988).

The shift from animal to wind pollination has actually occurred in some of the dominant southeast Asian trees, many of them dipterocarps whose floral corollas are eaten by thrips, tiny winged insects scarcely capable of powered flight, much less of directed pollen placement between well-separated individual tree canopies. They can move between trees, but their strato-orientation appears to consist simply of flying upwards to the canopy, after which they are dispersed until close enough to a recognizable inflorescence to steer towards it. These insects are nonetheless the only confirmed means of reproduction by these trees, and are best viewed as agents of wind pollination, rather than energy-demanding pollinators in the usual sense of nectarivores and pollenophagous animals. Their efficiency is permitted by the abundance and synchrony in the appearance of flowers, although many details of potentially specialized pollinating thrips remain to be investigated. Natural selection has all but eliminated animal pollination in some of the dipterocarps of the drier southeast Asian forests. Perhaps with simplification in forest structure, plant reproduction is promptly reduced to less costly, more efficient pollination systems that do not rely on intelligent pollen dispersers.

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