
Pollination System Stability in Tropical America

Two large-scale terrestrial experiments are now occurring in the Neotropical landscape: human exploitation of wildlands and colonization by honeybees from Africa. These events likely surpass past disturbances and have strong consequences for plants, their pollinators, and a several-fold larger group of organisms dependent on them. If we are to apply the functional and conceptual intricacies of pollination ecology, then pollinator dynamics, pollination success, and the response of each to habitat change must be known. I outline principal findings and challenges in these three areas.

African honeybees were the first exotic bees to invade Neotropical wildlands, where they interact directly with roughly one-fourth of the flora and many flower visitors (Roubik 1978, 1989, 1996a, 1996b, 2000a; Roubik & Wolda 2000). European honeybees were never feral in tropical America. As I will indicate, the effects of the recent arrival of African *Apis mellifera* on pollination systems are measurable but varied. Although the effects of competition with native bees often are detectable, a large impact on their populations is not.

Habitat alteration and the African honeybee invasion during the course of on-going pollination research has provided both general and occasionally unexpected insights (Kevan 1999). In Costa Rica, for instance, Frankie et al. (cited in Kevan 1999) used a focal tree species to show marked change in native bees present at the beginning and end of a 23-year interval. During this period the African honeybee arrived, but habitat loss and fire appeared more decisive in determining native bee abundance. Begin-

ning at the time of African honeybee arrival, I used focal flower patch methods over 17 years to monitor pollinator visitation in French Guiana. At a site with some disturbance from urban expansion, the proportion of honeybee visits to flowers increased gradually to almost 100% over this time. Among comparative forest plots, visits per flower, plus seed and fruit set, diminished in proportion to dominance of honeybees (Roubik 1996b).

Other examples of honeybee interactions with native or cultivated plants have been neutral or beneficial. In Argentina, Aizen and Feinsinger (1994) compared pollen deposition on stigmas by African honeybees and native bees. The flowers visited by honeybees tended to show no decline in pollen deposition with increasing fragmentation, even though some native bees were lost in this process. Seed production bore little relation to visitor identity. In contrast, the coffee-producing highlands of Panama now have a pollinator that augments yield by 56%, also the feral African honeybee (Roubik 2000c).

The generalist African bees are so successful in part because they are preadapted as colonists to find food and nesting sites or to emigrate when they do not. Often, they exploit flowers pollinated by nocturnal animals such as bats and moths or wind-pollinated crops such as corn without pollinating them (Roubik 1989). But a generalist demanding a constant or large supply of resources cannot necessarily invade all ecological systems, no matter how successful its competitive mechanisms. For example, I have found no African honeybees in a nature preserve in the Napo region of Ecuador, one of the most diverse lowland forests in the Neo-

tropics. Elsewhere in the Amazon basin, African honeybees are common. Why the Napo forest has resisted invasion of the bees may lie in its flowering phenology, natural enemies, or abundance of bee competitors. More highly social bees occur there, 63 species, than at any other site. The foregoing observations expose the fallacy of regarding invading African bees as ecological juggernauts, or of seeing all diverse communities as equally vulnerable.

Taking a longer view of disturbance regimes, the native bees and wasps exploited for honey at the time of the Inca empire are the same species as those used for honey today (Cobo 1653; T. Platt & D. R., unpublished observation). Evidently, neither colonization by honeybees nor habitat disturbance has caused loss of native species since the 1500s. More important, in French Guiana and Panama continuous studies performed in relatively intact forests for two decades showed no declines in abundance of native bees (Roubik 1996b, 2000b; Roubik & Wolda 2000). Therefore, temporary ecological replacement of one visitor by another appears to occur commonly, whereas regional extinction and geographical decline seem much rarer. Scant data on pollinator abundance or pollination success in many regions of tropical America prevent conclusive generalizations.

Genetic conservation in plants, borne on the wings of pollinators and the activities of seed dispersers, provides a similar range of results. Gene flow via pollinators often expands in scale following disturbances that turn forests into mosaics as pollinators search for resources among more isolated patches (Janzen 1974;

Roubik 1993, 2000*b*; Aldrich & Hamrick 1998; White and Boshier 2000). Many pollinators are shared by many plants, and flexibility or opportunism are common (Renner 1997; Roubik 2000*a*). Large bees, birds, moths, or bats have foraging radii of 8–25 km, providing access to 200–2000 km² of foraging territory (Roubik 1989; Gribel et al. 1999). Landscapes may stay connected for plants in certain “pollination compartments” (Corbet, this issue), but eventually the system falls apart when gene flow is inevitably cut off.

Understanding natural variation in pollination mutualism is a critical area of investigation (Thompson 1999). Highly diverse systems may be able to sustain new interactions, including the pollination of exotic plant species (Roubik 1995), while at the same time conserving the pollinating interactions of native species. We have no theory to foresee the advantages or disadvantages of adding species to natural-agricultural systems. Potentially, enriching natural biological communities with crops or pollinators, instead of attempting to manage artificial landscapes of domesticated organisms, could be a better way to ensure both habitat stability and agricultural production.

A serious threat to conserving pollination systems is the paucity of verifiable scientific data on pollinator abundance or effect. Pollination systems need to be studied on their own terms, some of which involve scarce nesting sites, enormous foraging ranges, periodic flowering peaks, and opportunism. Special methods of analysis (e.g., continuous time series) and scrupulous, taxonomically cor-

rect attention to net reproductive success, floral choice, seed germination, and migratory routes are prescribed. Study areas ideally should include entire ranges (Robinson et al. 1995). Although such studies seem within our grasp, too few are being conducted.

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