

# 8

## Plant-Animal Interactions — Update 2014

K. Greg Murray & Judith L. Bronstein

### Plant-pollinator Interactions

The suites of morphological, phenological, and behavioral characteristics of plants and pollinators that comprise “pollination syndromes” remain useful for predicting the players in pollination mutualisms. For example, red tubular flowers are likely to be visited by hummingbirds, and short-tongued bees are more likely to visit flowers with a more open morphology that doesn’t restrict their access to nectar and pollen. However, the frequent finding that floral visitors aren’t restricted just to those usually associated with a particular syndrome has increasingly led to criticism of the utility of the syndrome idea itself (e.g., Ollerton 2009, but see Rosas-Guerrero 2014), as has the realization that many animals feed at flowers usually associated with different types of pollinators. {Muchhala, 2003, Exploring the boundary between pollination syndromes: bats and hummingbirds as pollinators of *Burmeistera cyclostigmata* and *B-tenuiflora* (Campanulaceae)} work with *Burmeistera tenuiflora* and *B. cyclostigmata* at Monteverde demonstrates some of the ambiguity of

pollination syndromes. He found that both birds and bats visited flowers of both plant species, but that only bats effectively pollinated both. Hummingbirds effectively pollinated *B. tenuiflora*, but because the reproductive parts of *B. cyclostigmata* extend further from the nectaries, birds can access nectar without contacting the anthers and stigma. This work nicely demonstrates the need for caution in assuming too much about the identity of pollinators merely on the basis of floral morphology and timing of nectar secretion. Muchhala suggests that these species of *Burmeistera* demonstrate generalization for pollination by both bats and hummingbirds.

Work at Monteverde since 2000 has added detailed information on the basic reproductive biology of local plants as well. {Cascante-Marin, 2005, Reproductive biology of the epiphytic bromeliad *Werauhia gladioliflora* in a premontane tropical forest}, for example, studied the flowering phenology and breeding system of the bat-pollinated bromeliad *Werauhia* (formerly *Vriesia*) *gladiolifolia*, and {Bush, 2009, Early autonomous selfing in the

hummingbird-pollinated epiphyte *Pitcairnia brittoniana* (Bromeliaceae)} elucidated the breeding system of the hummingbird-pollinated bromeliad *Pitcairnia brittoniana*. Both species were capable of self-pollination, and both fruit- and seed set were equivalent in plants limited to self-pollination as in those available to pollinators. Self-pollination is common among epiphytes, which may suffer unpredictable visitation due to their isolation and limited floral displays {Bush, 1995, Breeding systems of epiphytes in a tropical montane wet forest}, but Bush and Guilbeau found that pollen loads deposited by hummingbirds were also sufficient to ensure nearly full seed set in *P. brittoniana*. As they noted for *P. brittoniana*, it seems likely that many epiphytes cross-pollinate when pollinators are available, but self-pollinate when they are scarce.

Another contribution from Monteverde is Judy Stone's work with colleagues on pollination ecology and breeding system evolution in *Witheringia solanacea*. Self-compatibility has evolved independently many times, but the conditions that favor it remain somewhat controversial because theory predicts that they must outweigh the costs of self-fertilization (primarily lowered fitness via the production of offspring with two copies of deleterious alleles). Most investigations of the evolution of self-compatibility rely on comparisons of different but closely related species, but {Stone, 2006, Variation in the self-incompatibility response within and among populations of the tropical shrub *Witheringia solanacea* (Solanaceae)} found populations of *W. solanacea* with both self-incompatible (SI) and self-compatible (SC) genotypes at Monteverde and Varablanca. SI genotypes of *W. solanacea* suffered nearly complete embryonic lethality when experimentally self-pollinated ({Stone, 2010, Embryonic inbreeding depression varies among populations and by mating system in *Witheringia solanacea* (Solanaceae)}, but SC genotypes did not, and Stone et al. concluded that deleterious alleles had already been largely purged from the SC genotypes. Such purging is most likely to occur when plants are severely pollen-limited, and *W. solanacea* populations near the MCFP did indeed have lower pollinator (bee) visitation

rates and appear to be more pollen-limited than those at lower elevations (e.g., San Luis) or those further south in Costa Rica (i.e., Las Cruces and Las Alturas; {Stone, 2008, Pollinator abundance and pollen limitation of a solanaceous shrub at premontane and lower montane sites}). However, when {Stone, 2014, Transmission advantage favors selfing allele in experimental populations of self-incompatible *Witheringia solanacea* (Solanaceae)} created experimental gardens with both genotypes and allowed them to be pollinated naturally, SC and SI plants had roughly equivalent fruit- and seed set but less than 10% of SC seeds resulted from self-fertilization. They concluded that embryonic inbreeding depression was still substantial in SC plants, but suggested that these genotypes will continue to spread because the transmission advantage of selfing through male function effectively outweighs even severe inbreeding depression.

### **Plant-Frugivore Interactions**

Much of the work on plant-frugivore interactions in Monteverde since the book's publication has focused on the post-dispersal fates of seeds. To a large degree this emphasis mirrors that in the field of plant-frugivore interactions in general. It is motivated by the understanding that the evolutionary consequences of seed dispersal for plants (including coevolution with frugivores) are mediated by the effects of dispersal on seed fate and plant demography. Some of Wenny's work on dispersal of large-seeded species also deals explicitly with dispersal *per se*, however. Wenny (1999) showed that seeds of *Beilschmiedia pendula*, one of the largest seeds dispersed by birds at Monteverde, are rarely deposited more than 10 m beyond the crowns of fruiting trees, but that seeds dispersed even short distances from the parent suffer less predation (from rodents and beetle larvae) than those deposited directly beneath the crown. His work demonstrates that dispersal is indeed beneficial for *B. pendula*, and that the effect occurs on quite a small spatial scale. In contrast, seeds of *Ocotea endresiana* suffered nearly complete removal by predators regardless of dispersal distance from the parent tree {Wenny, 2000, Seed dispersal of a high quality fruit by

specialized frugivores: High quality dispersal?). Most birds moved seeds less than 25 m, but male Three-wattled Bellbirds (*Procnias tricarunculata*) often deposited them beneath courtship display perches, many of which overhang treefall gaps. Wenny's experiments failed to show any difference in gap vs. understory seed removal rates, but seedlings in gaps grew more rapidly and suffered less mortality from pathogenic fungi than did those in understory. Thus, male Bellbirds provide a good example of directed dispersal (*sensu* Howe and Smallwood 1982), and may be disproportionately important for recruitment of *O. endresiana*. Determining the strength of the effect relative to that of other dispersers will require more detailed study, however.

Another example of directed dispersal at Monteverde is provided by {Sheldon, 2013, Spatial and Temporal Variation of Seed Rain in the Canopy and on the Ground of a Tropical Cloud Forest} study, which compared the "seed rain" deposited on the forest floor with that deposited in the forest canopy in part of the MCFP. Their study employed seed traps, with those in the canopy estimating seeds that are deposited and that accumulate in epiphyte mats and the soil associated with them. Despite broad overlap, the species composition of the seed rain was statistically distinct in each habitat: epiphyte seeds dominated in the canopy, while those of large trees were most common on the forest floor, suggesting that dispersers do move epiphyte seeds to especially appropriate establishment sites more often than would be expected by chance. Seeds dispersed by birds (rather than by mammals or wind) dominated in both habitats and over all seasons, highlighting the importance of animal dispersers – especially birds – in maintaining the ecological integrity of the Monteverde forest.

{Wenny, 1999, Two-stage dispersal of *Guarea glabra* and *G. kunthiana* (Meliaceae) in Monteverde, Costa Rica} studied the effects of primary (by birds and non-flying mammals) and secondary (by scatter hoarding rodents, e.g., agoutis) dispersal on survival and germination in two species of *Guarea*. Seeds were moved up to 65 m beyond parent tree crowns by primary dispersers, but median distances were within 15 m for both *G. glabra* and *G. kunthiana*.

Although secondary dispersers increased median distances only slightly, they did have a profound effect on seed fate by burying seeds 1-3 cm deep in the soil. Buried seeds were far more likely to survive than those that remained on the soil surface, which were killed mostly by rodents and insects (*G. glabra*) or by Collared Peccaries (*G. kunthiana*). Wenny's work on seed fate at Monteverde also included comparisons among ten additional species with different seed sizes, and although highly variable within size categories, seed survival tended to be higher for the largest seeds. Because these seeds continued to suffer rodent attack after germination, however, the relationship between seed size and seedling recruitment was complex. {Wenny, 2005, Post-dispersal seed fate of some cloud forest tree species in Costa Rica} estimated that five species of small rodents were responsible for about 70% of seed predation. Insect infestation was also common in some species, but mostly occurred before dispersal. Secondary movement of seeds (by rodents) for short distances was common, but only *Guarea* was commonly cached and often buried; most seed movement thus resulted in predation.

Given the importance of mammalian seed predators as mediators of plant population dynamics, how forest fragmentation and distributional changes driven by climate change will affect mammal populations is of great importance in montane habitats like those in Monteverde {Gibson, 2013, Near-Complete Extinction of Native Small Mammal Fauna 25 Years After Forest Fragmentation; Meserve, 2011, Global climate change and small mammal populations in north-central Chile; Sheldon, 2011, Climate change and community disassembly: impacts of warming on tropical and temperate montane community structure}. {Chinchilla, 2009, Seed predation by mammals in forest fragments in Monteverde, Costa Rica} compared mammalian seed predator populations and seed removal rates in a large tract of continuous forest (including the MCFR) and in two nearby forest fragments of 350 and 20 ha. As expected, the fragments were missing some of the larger species of seed predators (e.g., peccaries and pacas), but experienced seed removal rates that were only marginally lower than those in intact forest. Chinchilla attributed

much of the compensatory predation in the fragments to the higher abundance of the specialist seed predator *Heteromys desmarestianus* there, compared to intact forest, where it was uncommon.

Murray and Garcia-C. (2002) reported on a long-term study of the roles played by seed dispersal and seed survival in facilitating coexistence of a large guild of pioneer plant species that depend upon a limited resource: space in recently formed treefall gaps. They found that the top 10 cm of Monteverde soils contains 3000 to 6500 viable but dormant pioneer seeds per square meter - seeds that germinate rapidly in response to gap formation. And because species richness is high even on very small spatial scales (ca. 20-25 species per 625 cm<sup>2</sup> sample), both intra- and interspecific competition for space in recent treefall gaps is intense. Murray and Garcia-C's work showed that spatial heterogeneity of the soil "seed bank" was extremely high, however, so that competitively inferior pioneer species were likely sometimes to germinate in gaps without any superior competitors nearby. This phenomenon, termed "recruitment limitation," can facilitate coexistence by reducing the intensity of competition on ecologically relevant spatial scales. Part of the spatial patchiness in the seed bank resulted from patchiness in the seed rain, but site-to-site differences in density and species composition were also magnified by survival probabilities in the soil that varied by species.

Despite the fact that the life histories of most pioneers include a soil seed bank, Murray and Garcia-C. found a wide range in the ability of seeds to survive for long periods in the soil. Some, like *Phytolacca rivinoides*, *Bocconia frutescens*, and *Guettarda poasana*, maintain soil seed banks with densities several orders of magnitude higher than the annual seed rain, suggesting that seeds survive in Monteverde's soil for tens to hundreds of years. In contrast, other species of pioneers, like *Cecropia polyphlebia* and *Urera elata*, maintain soil seed banks with only a year's worth of seed rain, suggesting high mortality rates. Only *Hampea appendiculata* and *Piper umbellatum* among the 23 species studied in detail did not maintain a seed bank at all. Results of replicated field

experiments were consistent with the comparisons between seed bank and annual seed rain densities outlined above: seeds of the same species with high seed bank : annual seed rain ratios also survived well in the field since 1993 (Murray and Garcia-C 2002). {Veldman, 2007, Chemical defense and the persistence of pioneer plant seeds in the soil of a tropical cloud forest} investigated the chemical basis for the patterns of mortality among six of the pioneer species in Murray and Garcia-C's (2002) study (*P. rivinoides*, *C. polyphlebia*, *G. poasana*, *U. elata*, *B. frutescens*, and *Witheringia meiantha*), and found that seed extracts from species that survive for long periods in the soil were indeed more toxic to arthropods and fungi in the laboratory. The responsible chemicals in *B. frutescens* were identified as three related alkaloids, all of which were much more concentrated in seeds than in leaf tissue. *P. rivinoides* and *G. poasana* contain chemicals toxic to fungi as well, but they remain as yet unidentified (Veldman et al. 2007, K. G. Murray, *unpublished data*). Chemical defense of pioneer plant seeds is thus clearly important, and much work remains to be done.

{Nadkarni, 2009, Canopy Seed Banks as Time Capsules of Biodiversity in Pasture-Remnant Tree Canopies} found that the soils and epiphyte mats that accumulate in tree canopies also accumulate seed banks, just as do soils on the forest floor. Moreover, they surveyed such seed banks in the canopies of remnant pasture trees to determine whether such seed banks might augment other effects that render remnant trees effective "regeneration foci." They found that these seed banks contained dense and diverse assemblages of seeds, including many woody species characteristic of primary forest, and concluded that pasture canopy seed banks could function as "time capsules" of forest biodiversity that could speed forest regeneration recovery on pastures. Nadkarni and Haber also compared the seed banks in remnant tree canopies with those in primary forest tree canopies and in soils from the forest floor. Seed densities and species richness in forest floor soils, but those from pasture and primary forest tree canopies did not differ from one another

Earlier work on plant-frugivore interactions at Monteverde demonstrated that some of the

most important fruit-eating birds migrated altitudinally, and suggested that these movements were driven by seasonal patterns in fruit availability at different elevations. Since the publication of Nadkarni and Wheelwright (2000), these patterns have been further investigated by Chaves-Campos et al. (2003), Chaves-Campos (2004), Powell and Bjork (2004), and Papes et al. (2012). {Powell, 2004, Habitat linkages and the conservation of tropical Biodiversity as indicated by seasonal migrations of three-wattled bellbirds} elucidated the migratory patterns of Three-wattled Bellbirds in detail using radiotelemetry, and found that birds breeding on the Atlantic slope of the Cordillera de Tilaran crossed over to highly fragmented forest on the Pacific slope just 5-15 km away after the breeding season. In September and October, they migrate to the lowlands of northeastern Costa Rica and southeastern Nicaragua, and in November and December they migrate to southwestern Costa Rica, where they remain until returning in March to the Atlantic slope near Monteverde to breed. Powell and Bjork suggested that the birds are following the availability of their primary food sources (fruits in the family Lauraceae) as the fruiting seasons of species in different parts of the bellbird's range wax and wane, rather than following an invariant migratory route. Whatever the reason, the four areas used over the annual cycle were separated by as much as 280 km, and much of the land in three of the four areas (lowlands of northeastern and southwestern Costa Rica, and middle elevations on the Pacific slope of Costa Rica near Monteverde) is highly fragmented and poorly protected. Powell and Bjork concluded that the bellbird population (and hence the forests in which they perform important seed dispersal services) are thus vulnerable, despite adequate protection of the forests used during the breeding season. In part as a result of their work, the Costa Rican government and several private-sector organizations are cooperating to create the Bellbird Biological Corridor, which will protect a migratory corridor on the Pacific slope by promoting habitat restoration and protection, largely on privately held lands.

Similarly, {Chaves-Campos, 2003, Altitudinal movements and conservation of bare-necked Umbrellabird *Cephalopterus glabricollis*

of the Tilaran Mountains', Costa Rica} studied the occurrence of Bare-necked Umbrella birds at different elevations in the Monteverde-Arenal-San Ramon region of the Cordillera de Tilaran, and found that their movements over an elevation range from 400-1400 m correlated to seasonal patterns in fruit availability. And as with Bellbirds, elevations used for breeding were fairly well-protected, while those used outside the breeding season were not. Like {Powell, 2004, Habitat linkages and the conservation of tropical Biodiversity as indicated by seasonal migrations of three-wattled bellbirds}, Chaves-Campos concluded that the inadequacy of protected lands used during the non-breeding season constituted a significant threat to the species in the region.

{Chaves-Campos, 2004, Elevational movements of large frugivorous birds and temporal variation in abundance of fruits along an elevational gradient} studied changes in the abundances of large fruit-eating birds between 400 and 1400 meters elevation in the Cordillera de Tilaran in relation to the availability of fruits, and found mixed evidence that the migratory movements of these birds are driven in large part by fruit availability. Although small sample sizes and high variation among replicates made statistical comparisons difficult, Chaves-Campos suggested that migratory movements of these birds were driven by fruit availability in the non-breeding season, but not during the breeding season.

Most recently, {Papeş, 2012, - Vegetation dynamics and avian seasonal migration: clues from remotely sensed vegetation indices and ecological niche modelling} investigated the possibility of explaining bellbird movements on the basis of remote sensing data that could serve as a proxy for forest canopy characteristics. They generated ecological niche models based on several remotely sensed vegetation indices that reflect seasonal changes in canopy structure and productivity, but these did not explain seasonal bellbird movements in the Monteverde region reliably. Rather, these models suggested that much of the Atlantic slope is suitable for breeding, but that factors other than vegetation seasonality, e.g., lower rates of nest predation at middle elevations, may attract bellbirds to middle elevations for breeding.

Animal-mediated seed dispersal and cattle pasture regeneration

Since Groom's (2000) study of woody plant regeneration in abandoned pastures, much of the work on seed dispersal at Monteverde has concerned the role that such dispersal by animals plays in pasture regeneration. Cattle production now occupies over 27% of rural land area in Latin America (Murgueitio, 2011, Native trees and shrubs for the productive rehabilitation of tropical cattle ranching lands), yet the ultimate fate of most pasture lands is abandonment or conversion to some other use, often via regeneration to forest. Much of the work on pasture regeneration concerns the physical and biological barriers that limit the rate and constrain the trajectory of regeneration (e.g., Holl, 2000, Tropical Montane Forest Restoration in Costa Rica: Overcoming Barriers to Dispersal and Establishment), and since limited seed availability is one of the more obvious factors, many have concentrated on the roles that seed dispersing animals play in transporting seeds from surrounding forest into pastures.

{Murray, 2008, The roles of disperser behavior and physical habitat structure in regeneration of post-agricultural fields} reported on a long-term study of regeneration in two pastures near the MCFP, and found that nearly all early colonization by woody plants with animal-dispersed seeds was beneath the crowns of bordering trees and "forest remnant" trees that were left standing in the pasture when it was created. In contrast, wind-dispersed species colonized areas without overhanging vegetation just as frequently as areas beneath remnant trees. Concentration of early colonists beneath remnant trees or planted "tree islands" has been found in many other studies as well (e.g., Sandor, 2014, Remnant Trees Affect Species Composition but Not Structure of Tropical Second-Growth Forest} and references cited therein; {Zahawi, 2006, Tropical forest restoration: Tree islands as recruitment foci in degraded lands of Honduras} – a pattern that results in part from the attraction of forest birds to habitats with greater structural complexity and in part to the tendency of birds to defecate and regurgitate seeds while perched rather than in flight. The attraction of birds to isolated

pasture trees at Monteverde was demonstrated directly by {Sheldon, 2013, The use of pasture trees by birds in a tropical montane landscape in Monteverde, Costa Rica}, who documented over 900 visits by 52 species in 20 different families to just one common pasture tree species (*Sapium glandulosum*). They also found that the size of the tree, its degree of isolation from other trees, and the size of its epiphyte load increased bird visitation. Surprisingly, Murray et al. (2008) found that wind-dispersed remnant trees were just as effective as recruitment foci for animal-dispersed colonists as were trees that themselves produced fleshy fruits sought by animals, presumably because seed dispersers are also attracted to the elevated perch sites, cover, and perhaps insect food resources that such trees provide.

Murray and colleagues also tracked the progress of regeneration to determine how the spatial and compositional patterns of regrowth that were initiated by seed dispersers changed over time. As has been found elsewhere (e.g., Schlawn, 2008, 'Nucleating' succession in recovering neotropical wet forests: The legacy of remnant trees}, the concentration of pasture colonists beneath remnant trees formed "recruitment foci" or "nucleation sites" for forest plant species. Subsequent censuses of the same and similar plots 14 and 30 years post-abandonment showed that the initial strong effect of remnant trees on the density and species richness of regeneration became weaker over time – by 30 years post-abandonment, both density and species richness of pasture colonists was just as high in parts of the original pasture that had lacked overhanging tree crowns as in areas beneath remnant trees. The reason, of course, was that as the pasture colonists grew and formed expanding islands of regenerating forest centered on the original remnant trees, the colonists themselves served as perch sites for animals carrying seeds and the land area without overhanging tree crowns decreased to zero.

The work of {Harvey, 2000, COLONIZATION OF AGRICULTURAL WINDBREAKS BY FOREST TREES: EFFECTS OF CONNECTIVITY AND REMNANT TREES; Harvey, 2000, WINDBREAKS ENHANCE SEED DISPERSAL INTO AGRICULTURAL

LANDSCAPES IN MONTEVERDE, COSTA RICA} in planted windbreaks between active pastures in the Monteverde region also demonstrates the importance of animal seed dispersers in forest regeneration in agricultural landscapes. As was the case for remnant trees, the seed rain of woody species beneath windbreaks was orders of magnitude more dense and far more diverse than in pasture just 5 meters away (Harvey 2000a). Bird-dispersed species predominated, but pastures received almost as many bat-dispersed seeds as windbreaks, perhaps because bats defecate in flight as well as when perched. Harvey (2000b) also studied colonization of windbreaks and adjacent pastures by surveying seedlings of forest plants recruited into them, and in many ways her findings parallel those of Harvey (2000a): forest plants readily recruited into windbreaks, especially those forest plants dispersed by birds. Moreover, both density and diversity of colonists was significantly higher in windbreaks connected to adjacent forest patches than in those not so connected.

Neither Harvey (2000a,b), Murray et al. (2008), nor Sheldon and Nadkarni (2013b) found any correlation between seed input, recruit density or bird visitation with distance to the nearest forest edge, perhaps because the pastures typical of the region are relatively small – rarely more than a few hundreds of meters across. Neither did {Aide, 1996, Forest recovery in abandoned cattle pastures along an elevational gradient in northeastern Puerto Rico}) in Puerto Rico, where pastures are also relatively small. In regions like Amazonia, however, where pastures can be kilometers across, distance effects may be common. {DaSilva, 1996, Plant succession, landscape management, and the ecology of frugivorous birds in abandoned Amazonian pastures}), for example, found that even tanagers that frequent the forest/pasture boundary rarely travel more than 150 meters into pasture.

Nadkarni and Haber (2009) elucidated another way in which remnant pasture trees may act as effective regeneration foci and thereby facilitate forest regeneration on abandoned pastures: via the seed banks that accumulate in soils and epiphyte mats in the canopies of remnant pasture trees. They found dense and

diverse assemblages of seeds, including many woody species characteristic of primary forest and concluded that pasture canopy seed banks could function as “time capsules” of forest biodiversity that could speed forest regeneration on abandoned pastures.

Clearly, both remnant trees and windbreaks facilitate forest regeneration in agricultural landscapes at Monteverde and elsewhere, largely because of the interaction of their physical structure with the behavior of dispersers – especially birds. These patterns highlight both the importance of maintaining healthy disperser populations as well as managing landscape features such as pasture size and composition, so as to maintain the interactions that facilitate forest regeneration.

### **Fig biology**

Figs remain a subject of fascination to biologists, especially those who work in the tropics. Our understanding of figs' complex interactions with other species has been reviewed most recently by Herre et al. 2008, but new information continues to accumulate at a rapid pace. Yet, in spite of growing worldwide interest in figs, no publications have appeared over the past fifteen years describing research carried out at Monteverde. *Ficus pertusa*, which has attracted the great majority of attention in Monteverde, has been studied a little more elsewhere in Costa Rica as well as in Mexico and Brazil, mostly in the context of its flowering phenology and seed dispersal. *Ficus yoponensis* remains a species of great interest to researchers at Barro Colorado, Panama, where it is consumed heavily by bats that act as highly effective seed dispersers (Heer et al. 2010). *Ficus tuerckheimii*, *F. crassiuscula*, and *F. velutina* remain little-studied from the pollination and seed dispersal perspective.

It is particularly unfortunate that *F. tuerckheimii* has not attracted more attention, because it offers one of the clearest exceptions to a major piece of conventional wisdom about figs: that every one of the >750 fig species has a unique pollinator. As Ramirez (1970) first showed and several unpublished undergraduate course projects in Monteverde have followed up on, *F. tuerckheimii* has two pollinators (not “no” as the original text of this chapter erroneously

states), often cohabiting a single fig inflorescence. They are easily distinguished by color: *Pegoscapus carlosi* is black and *P. mariae* yellow. New molecular data that allow fig wasps that appear identical to the human eye to be discriminated have made it clear that *F. tuerckheimii* may not be that unusual in hosting multiple pollinators (Marussich and Machado 2007). Conversely, certain pairs of fig species are now known to share a single pollinator (Moe et al. 2011). Overturning a related assumption - that figs and fig wasps must usually speciate together, given that there are hundreds of mostly one-to-one interactions - reconstruction of evolutionary relationships using molecular data reveals a much messier picture (Machado et al. 2005, Lopez-Vaamonde et al. 2009). However, how speciation occurs and how associations between particular pairs of fig and pollinator species arise remain unresolved (Cook et al. 2010).

The most surprising change in our ecological understanding of the fig pollination mutualism is that developing fig wasps do not, as was believed for over a century, consume fig seeds. Rather, before laying an egg, a female fig wasp deposits a secretion that transforms an ovule into a gall; her offspring feeds upon sterile tissue (Jousselin and Kjellberg 2001, Martinson et al. 2013). This leads to the obvious question of why these wasps transfer pollen at all, given that their offspring don't eat seeds! There is some evidence that in seedless figs, wasp larvae develop very poorly (Jousselin et al. 2003). Thus, regardless of their diet, active pollination by the mother does appear to increase the success of her offspring. Even though fig wasp larvae don't consume seeds, each one still develops within an ovule that would otherwise produce a seed. It remains unresolved why fig wasps don't lay eggs in every ovule, which would appear to benefit fig wasps in the short run but which could lead to the demise of fig reproduction and the extinction of both partners in the long run. New ideas for how this uneasy relationship can persist over evolutionary time

appear regularly (e.g., Herre et al. 2008, Jandér et al. 2012).

Work has accelerated in recent years documenting seed dispersal and the dominant role fig fruits play in the diets of tropical vertebrates. A comprehensive review of fig consumers worldwide is now available (Shanahan et al. 2001), as is a detailed investigation of how fig fruit characteristics have evolved in suites or "syndromes" (Lomascolo et al. 2010). Intriguing geographical differences within individual fig species continue to appear and still remain to be explored. For example, new work finds *F. pertusa* seeds to be abundant in bat droppings in Brazil (Teixiera et al. 2009), suggesting a primary role for bats as seed dispersers there. This is consistent with observations from Panama, but distinctly different from Monteverde, where bats reject the red-ripe fruits.

Ecologists increasingly identify figs as keystone resources for fruit consumers. The health of fig populations worldwide is, however, threatened by habitat loss, habitat fragmentation, and selective harvest for wood (e.g., Felton et al. 2013). Furthermore, invasive frugivores deplete fruits essential to the well-being of native vertebrates, while at the same time failing to disperse fig seeds in a germinable condition (Staddon et al. 2010). There is a pressing need to treat figs as key targets for tropical conservation. They may also hold promising roles for forest restoration.

These and earlier studies at Monteverde highlight both the complexity of the interactions among mutualists and their role in the maintenance of whole ecological communities. As important, they demonstrate how important it is to base conservation planning on sound knowledge about the natural history of the organisms involved. Going forward, we hope that biologists will continue to be drawn to Monteverde both for the opportunity to understand the natural world better and to satisfy their own need to preserve a particularly worthy corner of it.