



“Bee-Flower-People Relationships, Field Biologists, and Conservation in Northwest Urban Costa Rica and Beyond.”

G. W. FRANKIE¹, R. E. COVILLE², J. C. PAWELE³, C. C. JADALLAH¹, S. B. VINSON⁴ & L. E. S. MARTINEZ⁵

¹University of California, Berkeley, CA, 94720

²Professional Entomologist/Photographer, El Cerrito, CA, 94804

³Professional Landscape Designer and Bee Taxonomist, Richmond, CA, 94805

⁴Texas A&M University, College Station, TX, 77843

⁵Private Naturalist/Bee Ecologist, Bagaces, Guanacaste, Costa Rica

Abstract

The forests of Costa Rica are rich in a wide variety of pollinator types and a very diverse flora that supports them. Our research group from the University of California, Berkeley and Texas A & M University, College Station has been researching the ecology of one pollinator group, the bees, in the northwest Guanacaste dry forest region since 1969. Much natural forest existed in this area when we first began the work. But, many land use changes have occurred over the years to present day to the point that it is difficult to find tracts of undisturbed forest suitable for field research, especially those not affected by wildfires, which are now common.

Further, urban areas in the region continue to grow with increasing numbers of people populating the region. In this paper we provide an overview of our past bee-flower work for a historical perspective, and then weave in people that have now become an obvious ecological component of current bee-flower relationships. We also explore new questions that have become relevant through time, especially those related to researchers and potential conservation opportunities to share their stories with audiences that may extend their knowledge for practical use. Finally, we propose that researchers plan to devote some of their precious time establishing relationships with people in conserving what is left of bee-flower relationships in urban environments in Guanacaste and beyond in the country. Avenues for extending this knowledge are explored in this paper.

Key words: Native bees, bee-flower relationships, tropical ornamentals, bees and people, research outreach, outreach evaluation, environmental education, bees and children, pollination ecology

Introduction

Numerous scientific papers have been published on bee pollinators and pollination in Central America, and especially in Costa Rica over the past several decades. Most of these studies have been published in English language journals and books (see numerous references in Janzen 1967, 1971; Frankie *et al.* 1976, 1983, 2013; Bawa 1974, 2004; Gentry 1974; Heithaus 1974, 1979a, 1979b; and Frankie and Haber 1983). Very little of this information has been made available in Spanish for local residents in a form suitable for this audience. Further, most scientific studies concern wild tropical areas, which are removed, by design, from immediate urban influences and impacts. However, natural areas are continuing to be impacted by human activities, even remote ones (Terbough 1999). Urban areas are greatly expanding, and these trends are expected to continue (Adler and Tanner 2013; Forman 2014). There are other trends at work here as well, and one of these is an increasing awareness that urban areas have interesting organisms that humans can enjoy with the proper introduction and exposure (Grissell 2001, 2010; Tallamay, 2007; Owen 2010; Frankie *et al.* 2014).

Recent work on bee pollinators and pollination, although limited, has been done in urban areas around the world, including tropical areas (Cane 2005; Zanette *et al.* 2005; Nates-Parra *et al.* 2006; Viana *et al.* 2006;

Nemesio and Silveira 2007; Hernandez *et al.* 2009; Frankie *et al.* 2013). In this paper, we present an overview of our ongoing bee-flower pollination work in two urban areas of NW Costa Rica and in selected cities of the Central Valley of the country (Fig. 1). We focus on ecological and morphological diversity of species visiting urban ornamental native and nonnative plant species.



FIGURE 1. Map of Costa Rica with relevant points of interest, Bagaces is midway between Cañas and Liberia.

We also ask whether we as field biologists should continue filling pages of English-language publications with interesting insect pollinators, especially bees, and pollination stories, with the hope that the information will be picked up by someone, some day, and extended in an appropriate form to local urban audiences. Alternatively, should field biologists recognize an additional role for themselves in joining the “extenders” to urban and other audiences with the goal of raising awareness that could be translated into conserving pollinators and their habitat, both natural and constructed. There already exists an infrastructure of government, public, private, and nonprofit institutions providing extension in countries like the United States. The agricultural experiment stations of land grant institutions in each state are examples of well-organized infrastructure designed to do outreach and environmental education. Researchers may be able to fill in some of the gaps in tropical countries where this extension infrastructure is lacking. There are numerous strategies that department chairs, deans, and provosts should consider to support faculty outreach as doing so can help further institutional missions of public service (O’Meara, 2003).

The long-term consideration is that environmental education programs can aid in the creation of a more environmentally aware and sensitive populace. There is evidence that children’s participation in these experiences may result in development of proenvironmental attitudes that persist through time (Bogner 2010; Farmer *et al.* 2010). Influencing children to both understand and care about the natural world may affect their later environmental behavior at multiple scales, from the level of individual actions (e.g. planting a bee garden) to that of civic participation (e.g. deciding on green candidates interested in protecting the environment). Environmental stewardship can take many forms, and it is through community networks that environmentally sensitive citizens can start a ripple effect. One study in the Costa Rican town of Quebrada Ganado demonstrated how children who learned about the natural history and conservation of the Scarlet Macaw in their schools transferred information to their parents, while both groups (children and their parents) transferred information to their neighbors (Vaughan *et al.* 2003). Researchers who engage in extension have the potential to tap into these networks and influence an entire community’s environmental attitudes, potentially spurring conservation action.

Why bees?

Bees are considered the most important pollinators in tropical and temperate environments (Frankie and Thorp 2003). In Costa Rica, we estimate that ~60% of the flowering plant species are pollinated by bees. Other animal pollinators include nocturnal flowers visited by bats and moths (Haber and Frankie 1983), diurnal flies, hummingbirds, wasps, and very few beetle systems. These animal-plant relationships reflect a characteristic coevolutionary history for each system type. David Roubik also estimates that about 60% of the flowering plants in tropical Latin America are pollinated by native bee species (Roubik 1989 and pers. comm.).

It is estimated that there are ~8,500 flowering plant species in Costa Rica (Michael Grayum, MO Botanic Garden, pers. com., 2013). At least 60% of these are pollinated by native bee species. Without bees and other animal pollinators, most of these plants would not be able to reproduce (however, some are selfers or have other reproductive mechanisms in addition to animal services). Clearly, Costa Rica joins other plant rich areas of the world, such as South Africa and California, with its amazingly diverse flora.

Native bee species are also known to be good pollinators of agricultural crop flowers such as watermelons, other melon types, chayote, squash (several types), beans, and tomatoes. Information on this ecosystem service is limited, but bees are active on crop flowers unless pesticide sprays are used, and these amounts can be considerable in some situations (see Galt 2014).

Study Area of Guanacaste and Vicinity

Much of the Northwest Guanacaste region of Costa Rica was forested when we first started our plant phenology and pollination research there in 1968 (Holdridge *et al.* 1971; Frankie *et al.* 1974) (Fig 2). Since that year, we have progressively recorded and observed many land use changes throughout all of Guanacaste. The prominent ones include forest clearing for agricultural use; irrigation of many areas from the main water project at nearby Lago Arenal; increased fire episodes during the dry season and especially exacerbated with the spread of introduced jaragua grass *Hyparrhenia rufa* from Africa (locally known as “gasolina” because of its high combustion and adaption to fire events); and revegetation of burnt and fallowed areas with new combinations of mostly pioneer plant species, giving a false impression that diverse and original plant species have returned. Return to original composition of native plants takes several years, with no major disturbances along the way.



FIGURE 2. Forested Guanacaste region in ~1970. Yellow flowering tree is *Tabebuia ochracea*.

Almost all urban areas of Guanacaste are experiencing human population growth; some faster than others. Liberia, the capital of Guanacaste, is one of the fastest growing cities. In 1970, the population was about

20,000; today, it is ~50,000 and growing. Bagaces was about 2,500 in 1970; today it is ~5,000 (Frankie *et al.* 2013). Other cities in the region such as Cañas and Santa Cruz are also experiencing human population increases.

Recent Bee Pollinator Work in Urban Guanacaste: An Overview

A survey research study conducted from 2004-2013 in urban Bagaces and Liberia revealed that 102 plant species were visited by native bee species for their floral resources (Frankie *et al.* 2013). These plants represented 41 families and 81 genera. Of the 102 species, 62 were native to Costa Rica; 40 were nonnatives. Twenty of the 62 were considered weedy. Common families included Fabaceae and Bignoniaceae.

Each plant species had a relatively predictable group of bees visiting its flowers, which is characteristic of plants of the greater dry forest of Northwest Costa Rica (Frankie *et al.* 2013). The same predictable pattern occurs in urban California where we have conducted similar surveys and bee frequency counts and find that ornamental plant species there attract certain bee species and rarely others (Frankie *et al.* 2005, 2009, 2014). A total of 125 bee species were collected during the 10-year survey in Costa Rica. There are 700+ bee species recorded from the country (Griswold *et al.* 2000). This compares with 1,600 in California, 3,600 from the U.S., and 20,000 worldwide.

There are interesting stories of urban bee-flower relationships, and we experienced considerable interest when these stories were mentioned to residents whose gardens we observed and/or collected bees from during the extensive survey. Some of these stories are reported in Zuchowski (2007) and included food and fiber products that urban residents come into contact with frequently in cities. Examples include avocados, tamarind, coffee, berries, watermelons, cashew fruits/nuts, annatto (*Bixa orellana*) plant dye, chayote, etc. Urban residents were only vaguely familiar with some of these stories (Frankie, unpublished).

Native Bee Nesting in Urban Areas

A variety of native bee species have been regularly observed nesting in urban Bagaces and Liberia. Ground-nesting species have been observed in several gardens, with or without bee-attractive plants in close proximity. For example, the large *Centris flavifrons* has been observed nesting together in groups of 20-50 individuals in small garden plots in Bagaces. One of the sites was active yearly during the summer months (January through March in Costa Rica) in bare soil at a local grade school site (removed from children's access). Another group of *C. flavifrons* was observed nesting in a tiny front yard garden, densely filled with ornamental flowers that were not attractive to bees. On rare occasions this species nested singly in grassy areas of the central park of Bagaces. It is also known to nest singly in wild grassy areas (Frankie and Coville, pers. obser.).

Centris heithausii has been observed nesting in soil within piles of debris adjacent to buildings (Coville *et al.* 1986). This is a relatively rare species visiting flowers in wild areas. Nothing is known of its nesting habits in the wild. *Centris adani* and *C. aethyctera* have been observed nesting singly in large flower pots in urban Bagaces. Both of these species have been observed nesting commonly in open grass fields in wild areas (Vinson and Frankie 1977, Frankie pers. obser.).

In a rare adobe building in Bagaces, which is 100+ years old, its north facing wall is home to several nesting bee species (Fig. 3). *Centris trigonoides* uses the wall for nesting, as well as two species of *Megachile* and a *Melitoma* sp.. *Melitoma* sp. makes a small turret for its entrance and does the same on open ground as well. Cleptoparasitic bees, *Coelioxys chichimeca* and *Mesoplia* are frequent visitors to the holes, presumably to parasitize *Centris* and perhaps *Megachile* species.

Native bees also nest in preexisting cavities in urban areas. Stingless bees such as *Nannotrigona perilampoides* can be observed in some old trees that have large dead branches and dead portions of trunks where there are beetle-emergences holes (Fig. 4). Some species such as *Centris analis*, *C. bicornuta*, and the rare *C. nitida* nest in holes in wood of old buildings. This activity is easily documented by placing wooden trap-nest blocks under the eaves of roofs or on the sides of large ornamental shade trees such as *Tamarindus indica*, a common tree in urban Bagaces. These *Centris* species readily occupy the trap nests (Frankie and Vinson, pers. obser.).



FIGURE 3. L. E. S. Martinez pointing at holes made by bees nesting in adobe wall in Bagaces.

Some Conclusion of Bee-Flower Ecological Studies

Many native bee species live, reproduce, and survive in urban areas of the NW Guanacaste region and of the greater upland Central Valley of the country.

Numerous plant species, native and nonnative, growing in urban areas, provide ample pollen and nectar for native bees. Most of these plant species are in common between the lowland urban areas of Guanacaste and upland areas in the Central Valley, as are the bee species (Frankie and Coville, unpublished).

Urban areas also provide nesting resources for many bee species. Some of these are protected soil areas, and some are cavities in wood and other substrates.

Taken as a whole, floral and nesting resources combined provide for a new constructed habitat for native bees, and this habitat is increasing as human populations increase in many regions of Costa Rica.

Native bees also pollinate food plants such as squash, watermelons, various other melon varieties, coffee, some beans, and tomatoes, but information on this ecosystem service is lacking.

During several years of gathering data for our urban bee paper (Frankie *et al.* 2013), we interacted with numerous urban residents who wanted to know what we were doing, studying, and collecting in their gardens and in public gardens. Conversations with these urban residents were plentiful and “teachable moments” abounded. Some were even afraid of us and would later cut down plants that were attracting bees. At some point, it became clear that we should better prepare to respond to these inquiries. But how? Should we refer them to website, books, extension literature, etc.? Not really, as none of these reference materials exist in Spanish for the lay person in Costa Rica. And, public gardens, native plant societies, and pollinator institutions where this information might be found, did not exist. Furthermore, the vast majority of the people we conversed with did not know of any bee species beyond the honey bee, and rarely stingless bees. They were amazed when we would tell them that the country had 700+ species of bees.



FIGURE 4. *Nannotrigona perilampoides* worker bees lined around nest entrance in tree trunk of old *Tamarindus indica* in urban Bagaces.

As we became aware of this lack of information on bees and other flower visitors and their value to the environment, which many of us now take for granted in the U.S., we also began to seriously wonder how we could transfer some of our pollinator knowledge to urban audiences. We especially wanted to share images of the amazing and diverse bee species and some of their stories (Fig. 5). As biologists we gave occasional talks to local school children and a few adult groups, but always without follow-up reference materials in Spanish (Frankie *et al.* 2004). This also raised the larger question of whether research biologists should invest some of their precious time in outreach and conservation projects. What would be the rewards?

In late 2013, we were invited to present a paper on our Costa Rican bee research to the VIII Congreso de Abejas Nativas held in Heredia, Costa Rica. During the meetings we met an enthusiastic honey bee and stingless beekeeper, Ana Chassoul, who wanted to know more about our work so that she could share it with local school children that she was teaching at the time. We began working with Ana in 2014 and her new NGO (Asociación de Apicultores y Meliponicultores Independientes de Costa Rica) and sharing a wealth of written and photographic information with her, almost all of which was in English (she is bilingual). She shared that knowledge as a volunteer directly with children in four grade schools around the capital city of San Jose for most of 2014 (Fig. 6).

In 2015, she and one of her NGO colleagues began working with the Ministry of Education on a videoconferencing project to extend bee pollinator information to twelve schools throughout the country. The work consisted of preparing a 4-hour monthly lecture on native bees, honey bee and stingless bee beekeeping, horticulture, and conservation to grade school students over a year-long program. The government program was well received by the Minister of Education, and she was invited to return in 2016 to repeat the program to a new and expanded group of students throughout the country, using the same videoconferencing equipment. However, priorities abruptly changed for the Minister, and in March 2016 the limited video conferencing equipment was unexpectedly shifted to another project. Regardless, the extension information from 2014-2015 yielded encouraging results and demonstrated that school children represent a receptive audience to this kind of information. Follow-up questionnaires indicated that students had retained a considerable amount of

information and could repeat it. We recognized these positive responses as indicators of our effectiveness in transmitting knowledge that perhaps someday could be put to practical use (see below).



FIGURE 5. A: *Epicharis elegans* visiting legume flower. B: *Tetragnisca angustula* on *Antigonon leptopus*.

Despite the setback of not being able to continue videoconferencing in 2016, several important results and many ideas were generated for future outreach work. First, in 2014-2015, ~3,500 school children were exposed to native bees, honey bees/beekeeping, pollination of wild and food crop plants, horticulture and how to develop home pollinator gardens through outreach opportunities that Ana Chassoul took advantage of. Second, she also evaluated some of her work through a casual questionnaire. Although the time frame for teaching was relatively short, many students retained the main outreach messages and could later repeat many details about bees, other flower visitors, pollination, and the important services provided by these floral visitors to wild and crop flowers. There is reason and hope that pollinator/pollination messages will persist with some students in the long-term as the case history below suggests.



FIGURE 6. Ana Chassoul presenting talks to children in a grade school near city of Escazu, Central Valley of Costa Rica.

From 1986 to 1997 our research group developed a conservation and environmental education NGO in Costa Rica to outreach natural history information to local school children (ages 8 – 12) in Bagaces (Frankie and Vinson 2004). All aspects of the natural world in Costa Rica and Latin America were presented through an environmental education (EE) center in the town. The center was open all day 5 days a week and offered literature (almost 900 volumes collected over a 12-year period), field trips, games, local speakers and professional speakers from San Jose and beyond, and finally a place where kids could relax and learn about the environment and conservation in their country. Interestingly, we never had to solicit kids for the offerings at the Center. Over the 12-year period, the Center attracted slightly more than 1,000 children.

Our program officially ended in 1997 as we were unable to find funds to continue the EE work. Further, we had accomplished all of our original outreach goals (Frankie and Vinson 2004). Then, in 2005, Susannah Herbert from Oxford, England heard about our work and followed-up with a questionnaire to see if the

students in our program had retained some of the information we had presented in the Center after several years. Her study compared students who were in our program with students who had not participated. Her overall findings indicated that the students in our program did retain a significant amount of information and could repeat it. All of the findings were statistically significant (Herbert 2006).

Since then, we had been looking to develop publications in Spanish about pollinators (especially bees) and pollination. We are currently writing two books for the lay public; one in Spanish and one in English with colleagues from the University of Costa Rica and the National University of Costa Rica on common native bees and their urban garden flowers. We are also developing a plan for distribution of the books in Costa Rican schools and beyond.

Conclusions

Bees are considered the most important pollinator of plants in Costa Rica and all of Latin America. Yet, little is known about the native species to most urban residents that we interacted with.

As urban areas grow in Latin America and around the world, so do constructed environments grow and diversify, offering numerous opportunities for a wide variety of organisms, including bees, to reproduce and survive (Hall *et al.* 2016).

There is a growing scientific interest in studying these urban organisms worldwide. There is also a lag in transferring this knowledge into useful information that urban residents can understand and come to appreciate.

Institutions and professionals that can transfer bee knowledge are largely lacking in Costa Rica.

There are several factors inhibiting the transfer of scientific information into forms that can be useful for everyday citizens. One of these (mentioned above) is pressure on professional biologists to publish papers in peer-reviewed journals by home institutions. Thus, there is a tradition that dictates this “route” for professionals (see O’Meara 2003). Another factor is lack of incentives to do a combination of research and outreach, giving about equal weight or value to each activity. This combination would probably require researchers to work at the onset with outreach specialists. Other factors include how to connect citizens with bees and other pollinators through appropriate and affordable literature and community activities. This would involve informed community activists taking ownership of pollinator information and distributing it in a usable form through a variety of channels. The outreach work of Ana Chassoul offers a model for this kind of outreach.

Finally, a very recent paper by Keeler and 21 co-authors (2017) provides an important perspective on relationships of research and outreach that address many of the case-history issues raised in this paper, and also offers “five key areas” that must be undertaken to promote what they refer to as, “... a new kind of science.” The key areas are: 1. Produce not only professors but also future environmental leaders; 2. Cultivate a culture that values use-inspired research; 3. Move ideas into action faster; 4. Put people at the center of environmental science; 5. Reimagine academic structures to encourage innovation. Their paper was inspired by a 1998 essay in *Science* by Jane Lubchenco (1998) who called for a “New Social Contract for Science.”

Acknowledgements

We thank the California and Texas Agricultural Experiment Stations for their support of the research and outreach projects. Partial support was also provided by the National Geographic Society of Washington, DC. Peter Ronchi, Tim McMahon and Sara Leon Guerrero assisted with collections of bee-flower frequency data in Bagaces and Liberia. David and Gary Stewart provided logistic support to conduct research on their respective wild land properties near Bagaces in Guanacaste. The Hilda Sandoval family in Bagaces offered logistic and moral support for the project. We thank Ana Chassoul for her story on extending information on bees and other pollinators to children in several Costa Rican schools. Paul Hanson, Sara Galbraith, and Robbin Thorp kindly read an early draft of the paper.

Literature

- Adler, F.R. & Tanner, C.J. (2013) *Urban Ecosystems, Ecological Principles for the Built Environment*. Cambridge University Press, 345 pp.
- Alvos-Dos-Santos, I. (2003) Trap-nesting bees and wasps on the University Campus in São Paulo, southeastern Brazil (Hymenoptera: Aculeata). *Journal of Kansas Entomological Society*, 76, 328–334.
- Bawa, K.S. (1974) Breeding systems of tree species of a lowland tropical community. *Evolution*, 28, 85–92.
<https://doi.org/10.2307/2407241>
- Bawa, K.S. (2004) Impact of global changes on the reproductive biology of trees in tropical dry forests. In: Frankie, G.W., Mata, A. & Vinson, S.B. (Eds.), *Biodiversity Conservation in Costa Rica: Learning the Lessons in a Seasonal Dry Forest*, University of California Press, Berkeley, pp. 38–47.
<https://doi.org/10.1525/california/9780520223097.003.0004>
- Bogner, F.X. (2010) The influence of short-term outdoor ecology education on long-term variables of environmental perspective. *The Journal of Environmental Education*, 29.4 (1998), 17–29.
- Cane, J.H. (2005) Bees' needs challenged by urbanization. In: Johnson, E.A. and Klemens, M.W. (Eds.), *Nature in Fragments: The Legacy of Sprawl*. Columbia University Press, pp. 109–124.
- Coville, R.E., Frankie, G.W., Buchmann, S.L., Vinson, S.B. & Williams, H.J. (1986) Nesting and male behavior of *Centris heithausi* (Hymenoptera: Anthophoridae) in Costa Rica with chemical analysis of the hindleg glands of males. *Journal of the Kansas Entomological Society*, 59, 325–336.
- Farmer, J., Knapp, D. & Benton, G.M. (2010) An elementary school environmental education field trip: Long-term effects on ecological and environmental knowledge and attitude development. *The Journal of Environmental Education* 38.3 (2007), 33–42.
- Forman, R.T.T. (2014) *Urban Ecology; Science of Cities*. Cambridge University Press, 462 pp.
- Frankie, G.W., Baker, H.G. & Opler, P.A. (1974) Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. *Journal of Ecology*, 62, 881–919.
<https://doi.org/10.2307/2258961>
- Frankie, G.W., Opler, P.A. & Bawa, K.S. (1976) Foraging behavior of solitary bees: Implications for outcrossing of a neotropical forest tree species. *Journal of Ecology*, 64, 1049–1057.
<https://doi.org/10.2307/2258824>
- Frankie, G.W., Haber, W.A., Opler, P.A. & Bawa, K.S. (1983) Characteristics and organization of the large bee pollination system in the Costa Rican dry forest. In: Jones, C.E. & Little, R. (Eds.), *Handbook of Experimental Pollination Biology*, Van Nostrand-Reinhold, New York, pp. 411–447.
- Frankie, G.W. & Haber, W.A. (1983) Why bees move among mass flowering neotropical trees. In: Jones, C.E. and Little, R. (Eds.), *Handbook of Experimental Pollination Biology*. Van Nostrand-Reinhold, New York, pp. 361–372.
- Frankie, G.W. & Thorp, R.W. (2003) Pollination and Pollinators. In: Resh, V.H. & Carde, R.T. (Eds.), *Encyclopedia of Insects*. Academic Press, pp. 919–926.
- Frankie, G.W. & Vinson, S.B. (2004) Conservation and environmental education in rural Northwestern Costa Rica. In: Frankie, G.W., Mata, A. & Vinson, S.B. (Eds.), *Biodiversity Conservation in Costa Rica, Learning the Lesson in a Seasonal Dry Forest*. University of California Press, Berkeley, pp. 247–256.
- Frankie, G.W., Rizzardi, M.A., Vinson, S.B., Griswold, T.L. & Ronchi, P. (2005a) Changing bee composition and frequency on a flowering legume, *Andira inermis* (Wright) Kunth ex DC. during El Niño and La Niña years (1997-1999) in northwestern Costa Rica. *Journal of Kansas Entomological Society*, 78, 100–117.
- Frankie, G.W., Rizzardi, M.A., Vinson, S.B. & Griswold, T.L. (2009a) Decline in bee diversity and abundance from 1972-2004 on a flowering leguminous tree, *Andira inermis* in Costa Rica at the interface of disturbed dry forest and the urban environment. *Journal of Kansas Entomological Society*, 82, 1–20.
- Frankie, G.W., Thorp, R.W., Coville, R.E. & Ertter, B. (2014) *California Bees and Blooms, A Guide for Gardeners and Naturalists*. Heyday, Berkeley, California, 300 pp.
- Galt, R.E. (2014) *Food Systems in an Unequal World, Pesticides, Vegetables, and Agrarian Capitalism in Costa Rica*. University of Arizona Press, Tucson, 292 pp.
- Gentry, A.H. (1974) Coevolutionary patterns in Central American Bignoniaceae. *Annals of Missouri Botanical Garden*, 61, 728–759.
<https://doi.org/10.2307/2395026>
- Grissell, E. (2001) *Insects and Gardens*. Timber Press. Portland, Oregon, 345 pp.
- Grissell, E. (2010) *Bees, Wasps and Ants, The Indispensable Role of Hymenoptera in Gardens*. Timber Press, Portland, Oregon. 335 pp.
- Griswold, T., Parker, F.D. & Hanson, P.E. (2000) An inventory of the bees of Costa Rica: The myth of the depauperate tropics.

- In: Proceedings of the Sixth International Conference on Apiculture in Tropical Climates*, Costa Rica. International Bee Research Association, San Jose, pp. 152–16.
- Hall, D.M., Camilo, G.R., Tonietto, R.K., Ollerton, J., Ahrné, K., Arduser, M., Ascher, J.S., Baldock, K.C.R., Fowler, R.E., Frankie, G.W., Goulson, D., Gunnarsson, B., Hanley, M.E., Jackson, J.I., Langellotto, G., Lowenstein, D., Minor, E.S., Philpott, S.M., Potts, S.G., Sirohi, M.H., Spevak, E.M., Stone, G. & Threlfall, C. (2017) The city as a refuge for insect pollinators. *Conservation Biology*, 31(1).
- Heithaus, E.R. (1974) The role of plant-pollinator interactions in determining community structure. *Annals of Missouri Botanical Garden*, 61, 675–691.
<https://doi.org/10.2307/2395023>
- Heithaus, E.R. (1979a) Community structure of neotropical flower visiting bees and wasps: diversity and phenology. *Ecology*, 60, 190–202.
- Heithaus E.R. (1979b) Flower-feeding specialization in wild bee and wasp communities in seasonal neotropical habitats. *Oecologia*, 42, 179–194.
- Herbert, Susannah (2006) *An Evaluation of the Long-term Effects of an Environmental Education Program in Costa Rica*. Diss. Centre for the Environment, Oxford University.
- Hernandez, J., Frankie, G.W. & Thorp, R.W. (2009) Ecology of urban bees: A review of current knowledge and directions for future study. *Cities and the Environment* 2 (1): article 3, 15 pp. Available from: <http://digitalcommons.lmu.edu/cate/vol2/iss1/3> (accessed 31 October 2013)
- Holdridge, L.R., Grenke, W.C., Hatheway, W.H., Liang, T. & Tosi, Jr, J.A. (1971) *Forest Environments in Tropical Life Zones: a Pilot Study*. Pergamon Press, Oxford.
- Janzen, D.H. (1967) Synchronization of sexual reproduction of trees within the dry season in Central America. *Evolution*, 21, 620–637.
<https://doi.org/10.2307/2406621>
- Janzen, D.H. (1971) Euglossine bees as long-distance pollinators of tropical plants. *Science*, 171, 203–205.
<https://doi.org/10.1126/science.171.3967.203>
- Keeler, B.L., Chaplin-Kramer, R., Guerry, A.D., Addison, P.F.E., Bettigole, C., Burke, I.C., Gentry, B., Chambliss, K., Young, C., Travis, A.J., Darimont, C.T., Gordon, D.R., Hellmann, J., Kareiva, P., Monfort, S., Olander, L., Profeta, T., Possingham, H.P., Slotterback, C., Sterling, E., Ticktin, T. & Vira, B. (2017) Society Is Ready for a New Kind of Science – Is Academia? *Bioscience*, 67, 591–592.
- Lubchenco, J. (1998) Entering the Century of the Environment: A New Social Contract for Science. *Science*, Vol. 279, 491–497.
<https://doi.org/10.1126/science.279.5350.491>
- Nates-Parra, G., Para, A., Rodriguez, A., Baquero, P. & Velez, D. (2006) Wild bees (Hymenoptera: Apoidea) in urban ecosystems: Preliminary survey in the city of Bogota and its surroundings. *Revista Colombiana de Entomología*, 32, 77–84.
- Nemésio, A. & Silveira, F.A. (2007) Orchid bee fauna (Hymenoptera: Apidae: Euglossina) of Atlantic forest fragments inside an urban area in southeastern Brazil. *Neotropical Entomology*, 36, 186–191.
<https://doi.org/10.1590/S1519-566X2007000200003>
- O'Meara, K. (2003) Reframing incentives and rewards for community service-learning and academic outreach. *Journal of Higher Education Outreach and Engagement*, 8 (2), 201–220.
- Owen, J. (2010) *Wildlife of a Garden, a Thirty-Year Study*. Royal Horticultural Society, London, UK, 261 pp.
- Roubik, D.W. (1989) *Ecology and Natural History of Tropical Bees*. Cambridge University Press, Cambridge, New York. 514 pp.
- Tallamay, D. (2009) *Bringing Nature Home: How You Can Sustain Wildlife with Native Plants, Updated and Expanded*. Timber Press; Expanded Edition, 360 pp.
- Terbough, J. (1999) *Requiem for Nature*. Island Press, 234 pp.
- Vaughan, C., Gack, J., Solorazano, H. & Ray, R. (2003) The effect of environmental education on schoolchildren, their parents, and community members: A study of intergenerational and intercommunity learning. *The Journal of Environmental Education*, 34 (3), 12–21.
<https://doi.org/10.1080/00958960309603489>
- Viana, B.F., Costa de Melo, A.M. & Dias Drumond, P. (2006) Variation in the structure of habitat affecting solitary bees and wasps composition in urban forest fragments of Atlantic forestry in northeastern Brazil. *Sitientibus serie Ciencias Biologica*, 6, 282–295.
- Vinson, S.B. & Frankie, G.W. (1977) Nests of *Centris aethytera* (Hymenoptera: Anthophoridae) in the dry forest of Costa Rica. *Journal of the Kansas Entomological Society*, 50, 301–311.
- Zanette, L.R.S., Martins, R.P. & Ribeiro, S.P. (2005) Effects of urbanization on Neotropical wasp and bee assemblages in a Brazilian metropolis. *Landscape and Urban Planning*, 71, 105–121.
<https://doi.org/10.1016/j.landurbplan.2004.02.003>
- Zuchowski, W. (2007) *Tropical Plants of Costa Rica, A Guide to Native and Exotic Flora*. Cornell University Press, 531 pp.