

A PRELIMINARY SURVEY OF APOIDEA (ANTHOPHILA) AND THEIR USE OF FLORAL RESOURCES ON THE ISLAND OF MO'OREA, FRENCH POLYNESIA

DANIEL H. REJAS

Dept. of Environmental Science, Policy, and Management, University of California, Berkeley, USA

Abstract

The terrestrial biota of the French Polynesian archipelago presents a unique opportunity for study due to a relatively poor understanding of its biology. Among the terrestrial invertebrates, the Apoidea are one of many taxa with incompletely documented biodiversity. This study investigated the diversity of the bees on the island of Mo'orea, part of the Society Islands in French Polynesia. Across a range of elevations, I collected 239 individual bees and observed the floral visits of an additional 266 bees. The visited floral species were recorded to assess apoid use of floral resources, and vegetation surveys of collection sites were conducted to assess the available floral community. A total of five genera of bees were found on Mo'orea, including two which are recorded for the first time in the Society Islands. This study suggests that introduced species, rather than native species, comprise the bee biota of Mo'orea, with the longest established species seemingly introduced at or around the time of colonization by early Polynesians. With the exception of the genera *Lithurgus* and *Megachile*, bee genera were found to rely predominantly on non-native floral resources. Floral visitation predilection by Mo'orean bees may prove to further the spread of introduced and invasive floral species.

Key words: Bee diversity, Apoidea (Anthophila), floral resources, *Lithurgus scabrosus*, *Xylocopa sonorina*, *Megachile umbripennis*, invasive species, Mo'orea, French Polynesia

Introduction

Plant pollination is an essential ecosystem service that serves as a mechanism for the reproduction of most flowering plants. As such, the presence and distributions of flowering plants are the result of successful pollination (Barthell et al. 2001). It is estimated that approximately 60 to 80 percent of the more than 250,000 species of flowering plants on earth depend on animals, primarily insects, for pollination (Kearns & Inouye 1997, Kremen et al. 2007).

Bees, one of the most abundant of floral pollinators, generally are regarded as beneficial for their role in pollination, although negative consequences may exist,

such as pollination of invasive flora and interference with the pollination of native flora (Waser et al. 1996, Simberloff 1999, Richardson et al. 2000, Goulson 2003). Currently, little is known about these potential effects within the French Polynesian archipelago, though studies have been conducted elsewhere in the Pacific, including in New Zealand (Butz Huryn 1997) and Hawaii (Magnacca 2007). The disharmonic nature of island systems of the Pacific, where many important pollinators are absent, can pose challenges for island flora (Gillespie & Roderick 2002, Schueller 2004).

In French Polynesia, the bee fauna is fairly depauperate, due to the relatively

poor dispersal ability of the majority of bee species (Kuhlmann 2006, Michener 2007) and the relative isolation of the Polynesian archipelagos (Gillespie & Roderick 2002). To date, only three species have been quantitatively studied and listed in the Society Islands: *Lithurgus scabrosus* Smith 1853, *Megachile umbripennis* Smith 1874, and *Apis mellifera* Linnaeus 1758 (Michener 1965, Nishida unpubl.). No scientific surveys of Apoidea have been conducted on Mo'orea. However, the apoid taxa of the Pacific islands in general, and French Polynesia more specifically, are generally poorly documented (Kuhlmann 2006, Michener 2007). Comprehensive surveys of bee diversity and biology have been carried out on the Hawaiian islands (Snelling 2003, Magnacca 2007) and the continental landmasses of New Zealand and Australia (Michener 1965, 2007, Goulson & Hanley 2004), but no more than superficial study of the bee fauna has been conducted in the Society Islands since the Bishop Museum's collections in the late 1930's and 1940's (Kuhlmann 2006, pers. comm.).

This study evaluates the apoid biodiversity of Mo'orea, and investigates the use of floral resources by Mo'orea's bees. These preliminary steps toward discerning the roles of Mo'orea's bees in the ecosystem may serve to further planning and conservation efforts for native flora, as well as have implications for our understanding of dispersal and persistence of floral species on islands.

Materials and Methods

Study sites

A total of six study sites were chosen within a range of elevations and vegetation types on the island of Mo'orea, French Polynesia. Collections and observations were conducted between 09 October 2008 and 10 November 2008. I separated sites into three categories in order to investigate potential elevation-based distributions of the bees of

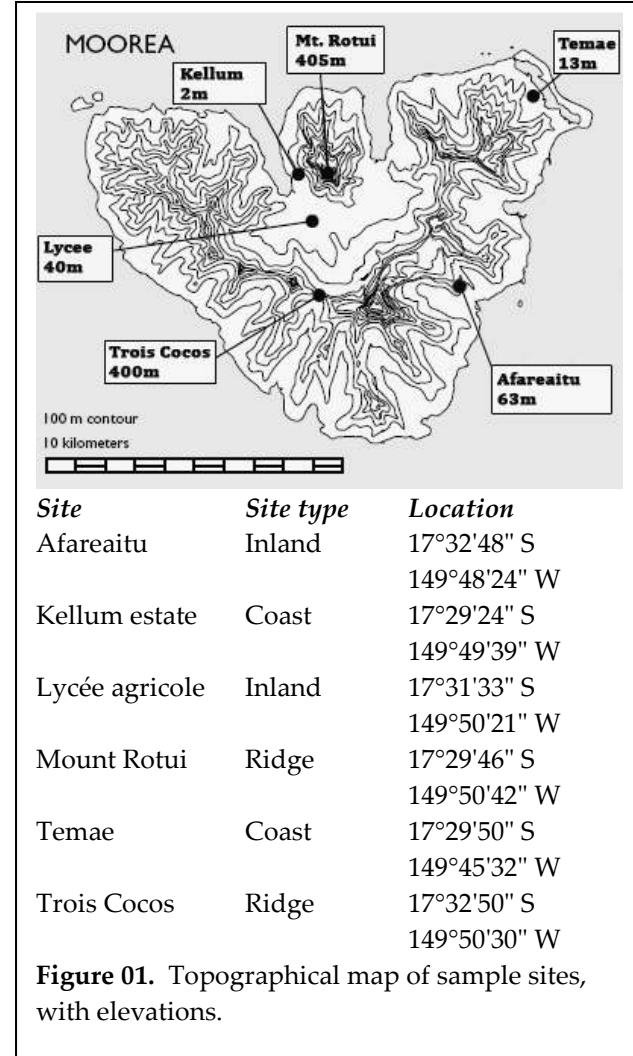


Figure 01. Topographical map of sample sites, with elevations.

Mo'orea. Site categories included low-elevation coastal areas, mid-elevation inland areas, and higher-elevation ridges (Figure 01). At each site, I marked out a 100 meter by 5 meter plot on either side of the access point to the site (e.g. foot trail, path, etc.) within which all floral and hymenopteran specimens were collected and observed.

Vegetation surveys

At each study site, I surveyed the floral species present at each visit within the established plots. Each site survey consisted of 20 one-square-meter quadrats that were evenly spaced across the two plots (Figure 02a), beginning at the edge of the plot and continuing four meters apart. Within each quadrat I documented all floral resources,

identifying to genus and species when possible (Whistler 1996, Welsh 1998, B. Mishler pers. comm.). Flowers were counted individually, except when part of an inflorescence. For floral species with inflorescences, the average number of actual flowers of several inflorescences was counted and multiplied by the number of inflorescences in the quadrat to ascertain the approximate number of flowers.

Specimen collection and observations

I collected bees with a net during a timed one hour period, which occurred predominantly between the hours of 08:30–14:00 at each site. Bees were caught with a net, and transferred into an ethyl acetate kill-jar. The kill-jar was labeled with the floral species the bee was visiting, if applicable. In order to mitigate the transference of pollen between specimens, the kill-jar was lined with a clean kimwipe. Bees were handled and pinned on the same kimwipe, and forceps were cleaned with ethanol between processing of each specimen. Bees were identified to genus, and species if possible (Michener 2007, V. Gonzalez pers. comm.). All insect specimens were sent to and stored at the Essig Museum of Entomology at the University of California, Berkeley.

Following existing recommended protocol for collection of Apoidea, temperature, wind speed, and sky conditions were recorded, with a baseline temperature for sampling set at 18°C for pan traps and 21°C for netting (McCall & Primack 1992, LeBuhn et al. unpubl.). I set out pan traps for five hours per visit at each site, primarily between the hours of 08:30–13:30. 15 pan traps were placed along one of the 100 meter edges of the plots, starting 5 meters in from one end of the plot and then placed every 6 meters. Pan traps were positioned in alternating colors of white, blue, and fluorescent yellow.

In addition to netting and pan-trapping specimens, I recorded timed observations of

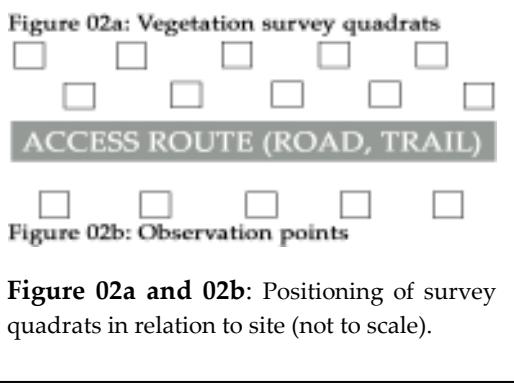


Figure 02a and 02b: Positioning of survey quadrats in relation to site (not to scale).

bee visits to flowers, both before and after the netting period. Observation methods were modified from a standardized protocol (Kearns & Inouye 1993) to facilitate comparison across any future studies. Each observation period was 50 minutes long, during which I observed 5 one-square-meter plots for ten minutes each. I recorded a total of 10 sets of observations per site, per visit. Observation plots began 10 meters in from the edge of the plot and then every 20 meters (Figure 02b). During each observation period, I recorded all floral species present in the observational plot, as well as all bee visits to those flowers.

Results

Vegetation surveys

Vegetation surveys yielded a total of 27 floral species, of which 23 were identifiable to at least genus level. I was unable to identify four surveyed floral species, which are labeled Unknown 002, Unknown 004,

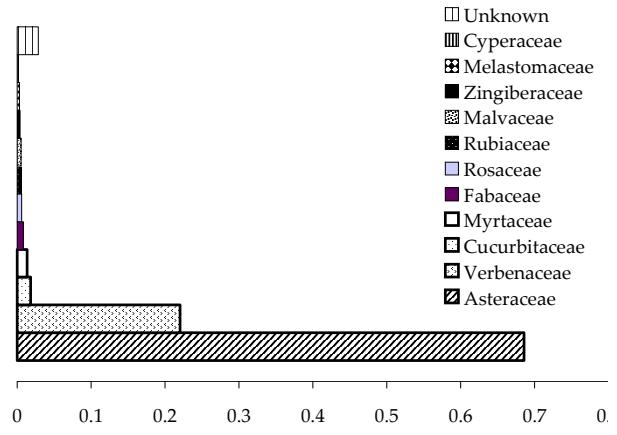


Figure 03: Percentage of flowers surveyed, by Family

Unknown 005, and Unknown 017. The species identified to genus comprised 11 plant Families, (Figure 03).

	Floral community characteristics ^a			Diversity index ^b
Site	Native	Non-native	Unknown	Simpson's index)
Afar	0	269	0	4.108
Kell	0	343	31	3.593
Lycé	0	292	0	4.797
Rotu	12	1	0	1.166
Tema	5	173	6	1.196
Troi	7	289	1	2.537

Table 04: Plant community characteristics.

^aPlant characters measure in number of flowers.

^bDiversity index calculated utilizing all floral species; not a measure of native vs. non-native. The two highest diversity indices are in **bold**.

Over 90% of floral resources surveyed (slightly over 1300 flowers) were from the two plant families Asteraceae (68.6%) and Verbenaceae (22.1%). Floral species known to be native only accounted for 1.8% of floral resources present across all sites, with 95.3% known to be non-native and 2.9% unknown. Simpson's index of diversity [$\frac{1}{D}$, where $D = \frac{\sum_{i=1}^s n_i(n_i - 1)}{N(N - 1)}$] was calculated to determine a metric to describe floral species abundance in relation to the total species. From these calculations, the inland sites of Afareaitu and Lycé agricole ranked highest in diversity, though the flora surveyed at

these sites was composed entirely of non-native species (Table 04). For a full list of floral species surveyed, see Appendix A.

The calculation of Simpson's diversity index by site classification type (coastal lowlands, inland mid-elevations, and higher-elevation ridges) yielded the highest index assigned to the inland, mid-elevation sites of Lycé agricole and Afareaitu. The number of native and non-native floral resources did not show significant statistical differences by site type.

Bee collection and observation

Data on a total of 505 bees was collected from pan traps, timed netting, and observations. The apoid biota recorded included five genera in the two families Apidae and Megachilidae. In Apidae (Apinae), the European honeybee, *Apis mellifera* Linnaeus 1758, was present at all sites sampled. Sampling yielded specimens of *Xylocopa sonorina* Smith 1874, in the family Apidae (Xylocopinae), which was previously unrecorded in the Society Islands. Similarly, the presence of bees in the genus *Ceratina* Latrielle 1802 was recorded for the first time. The two bees in the family Megachilidae, *Lithurgus scabrosus* Smith 1859 and *Megachile umbripennis* Smith 1853, occurred in the lowest numbers, and at the least number of sites (Table 05).

In total, bees utilized 24 different floral species, of which 20 were identified to genus

Site type	Afar	Kell	Lycé	Moun	Tema	Troi
Elevation (m)	Inland	Coast	Inland	Ridge	Coast	Ridge
Species						
<i>Apis mellifera</i> [254]	X	X	X	X	X	X
<i>Ceratina</i> [223]	X	X	X		X	X
<i>Lithurgus scabrosus</i> [10]					X	
<i>Megachile umbripennis</i> [3]			X	X		
<i>Xylocopa sonorina</i> [15]	X	X	X		X	

Table 05: Distribution of bees on Mo'orea. Total number of bees of each genus and/or species collected and observed indicated in brackets. Codes for abbreviations are as follow: Afar: Afareaitu, Kell: Kellum Estate, Lycé: Lycée Agricole, Moun: Mount Rotui, Tema: Temae, Troi: Trois Cocos.

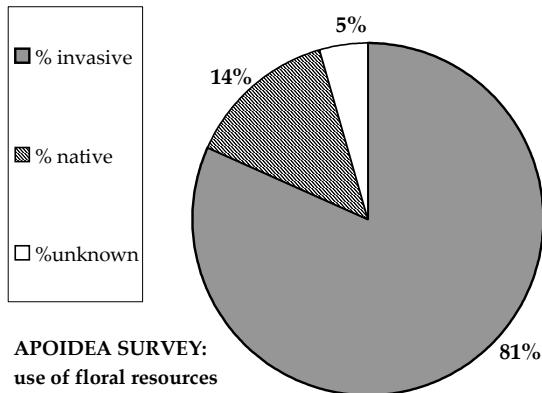


Figure 06: Use of native and non-native floral resources by Mo'orea's Apoidea

and then to species, when possible. Four species that were utilized by bees were not able to be identified, and were labeled as Unknown 002, Unknown 013, Unknown 015, and Unknown 018. The identified plants constituted nine plant families, of which Asteraceae was most heavily utilized by the bee fauna, with 62.6% of all visits occurring on a floral species in Asteraceae.

Similar to the large presence of non-native floral species in the vegetation surveys, non-native species accounted for the bulk of floral visits by the bees of Mo'orea. Of all floral visits recorded by netting from flowers or through observations, a total of 81% of visits occurred on a floral species known to be non-native to the Society Islands, while 14%

of visits occurred on native vegetation (Figure 06). For the genera *Apis* and *Ceratina*, this was found to be statistically significant when examined by a one-way ANOVA performed in JMP version 7.0.2 (*Apis* $p=0.0001$, *Ceratina* $p=0.0072$). For all other genera, sample size did not allow for statistical analysis. Qualitatively, however, use of native and non-native species had significant correlations based on bee genera (Figure 07). Additionally, the overall number of floral visits to non-native species, based on number of floral units present, was found to be statistically significant ($p=0.0382$).

Diagrams of pollinator-plant utilization from the bees collected and observed on Mo'orea indicated high generalization in floral resource use by the bee genera *Apis* and *Ceratina* (Appendix B). The remaining three genera, *X. sonorina*, *L. scabrosus*, and *M. umbripennis*, though collected in relatively low numbers, indicated a stronger specialization in their use of floral resources, with *X. sonorina* collected from two floral species, *M. umbripennis* from two floral species, and *L. scabrosus* solely collected from the native *Hibiscus tiliaceus* (Malvaceae). While low sample size prevented statistical comparison, both *M. umbripennis* and *L. scabrosus* were collected solely on native floral species, while *X. sonorina* was collected solely on non-native floral species.

Simpson's diversity index ranked inland

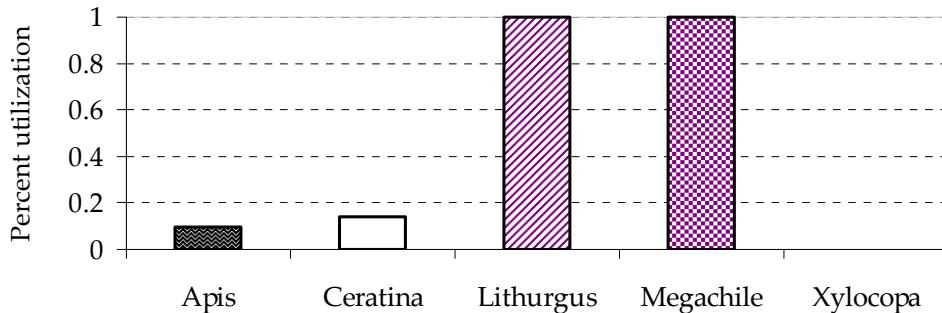


Figure 07: Percentage of time bee genera collected or observed on native floral species.

sites highest in terms of diversity of bees by site type (Coast 1.509, Inland 3.427, Ridge 1.819). Overall, this correlated with plant diversity, with overall bee diversity highest at sites that were ranked highest in overall plant diversity. Despite low sample size, which prohibited statistical comparison, the general trend existed where greater floral diversity at a survey site corresponded with both greater diversity and higher number of bees at the site.

Bee biology and distribution

Apis mellifera Linnaeus 1758

Distribution: Worldwide. Introduced to the Society Islands (Michener 1965, Kuhlmann 2006, Nishida unpubl.). Collected at all study sites on Mo'orea.

Biology: Eusocial and polylectic. Raised commercially and kept by hobby apiarists on Mo'orea (H. Murphy pers. comm.); feral colonies mostly crevice nesting (Michener 2007).

Lithurgus scabrosus Smith 1853

Distribution: Present in Southeast Asia and through the Pacific Islands to Hawai'i (Michener 1965, Snelling 2003, Kuhlmann 2006). Purportedly a Polynesian introduction to the Polynesian islands (Kuhlmann 2006, Michener 2007).

Biology: Solitary bee that nests primarily in wood of trees, and appears to have narrowly oligoleptic relationships with flora in the families Malvaceae and Convolvulaceae (Snelling 2003, Kuhlmann 2006, Michener 2007). Collected solely at Temae from *Hibiscus tiliaceus* (Malvaceae) on Mo'orea.

Megachile umbripennis Smith 1874

Distribution: Present in Southeast Asia and through the Pacific Islands to Hawaii (Michener 1965, 2007, Snelling 2003, Kuhlmann 2006). Suggested to be a Polynesian introduction (Kuhlmann

2006, Michener 2007). Collected at Lycée Agricole and Mount Rotui on Mo'orea.

Biology: Solitary, wood nesting bee proposed to be narrowly oligoleptic on Fabaceae by Kuhlmann (2006). Although one specimen of this species was collected on *Metrosideros collina* (Myrtaceae) at Mount Rotui, specimen was not sampled for *M. collina* pollen.

Xylocopa sonorina Smith 1874

Distribution: Believed to be from the Americas, and species originally described from specimen collected in Hawai'i (Snelling 2003). Present from China, Japan, the Philippines, and through the Pacific islands (Gerling 1983). Not previously described in the Society Islands. Found in coastal and inland elevation sites including Temae, Kellum Estate, and Lycée agricole.

Biology: Solitary to communal nesting bee, making nests in wood (Gerling 1983). Based on foraging behavior on Mo'orea, species may be oligoleptic on Verbenaceae and Melastomaceae.

Ceratina Latreille 1802

Distribution: Unlike the other species collected on Mo'orea, I was unable to identify *Ceratina* specimens to species. Two different morphospecies, one or both of which may prove to be *Ceratina dentipes*. Morphospecies 01 larger in size (4-5mm), with two submarginal cells. Facial markings characteristically triangular to hourglass shaped. Morphospecies 02 smaller in size (3.5-4.5mm), with three submarginal cells. Facial markings characteristic rectangular stripe. Specimens of the genus *Ceratina* were collected at all sites except Mount Rotui, though morphospecies varied in collection location (see Appendix B).

Biology: Solitary bees nesting in pithy stems. Nests collected at Afareaitu and Trois Cocos.

A key to the Apoidea of the island of Mo'orea is included in Appendix C.

Discussion

Bee diversity on Mo'orea

The rather depauperate bee biota of Mo'orea includes just five genera, of which four are represented by a single species. Of pollinators, the introduced European honeybee, *A. mellifera*, was the most abundant and ubiquitous of bees, followed closely by those in the genus *Ceratina*. Based on collected and observed specimens both appear fairly cosmopolitan in distribution on the island. Though relatively small numbers of *Xylocopa*, *Lithurgus*, and *Megachile* were collected and observed, certain trends existed in their occurrence. *Xylocopa* occurred in all sites except the high elevation sites, which *Lithurgus* and *Megachile* appeared primarily restricted by the availability of floral resources.

The relatively small number of bee species meshes well with the coupling of the generally poor dispersal ability of bees (Michener 2007) and the effects of the high isolation of islands such as those in French Polynesia (Gillespie & Roderick 2002, Meyer unpubl.). While some of the isolated Polynesian islands have seen adaptive radiation of bee fauna, such as in the native *Hylaeus* (Colletidae) of Hawai'i (Snelling 2003, Magnacca 2007), Mo'orea's bees do not seem to have followed that path. Insular radiations tend toward evolutionary disharmony, skewed by attenuation of solely a few lineages (Gillespie & Roderick 2002). The makeup of Mo'orea's bees, however, is a patchwork of fairly distant and unrelated genera, with the oldest colonizers probably arriving within the last 2000 years.

The diversity of bees was greatest in areas with the highest ranked diversity of plant species. This may be due to the fact that higher floral diversity serves to facilitate pollination through competition for pollinators, thereby drawing a greater number and diversity of bee species (Ghazoul 2006). Sites that were ranked highest in floral diversity generally had the highest number of floral visitors, though this was most often skewed by the generalist *Apis* and *Ceratina* species. As a generalist pollinator, a site with a diverse floral community may allow for a higher degree of resilience in both bee and flora species, and may equalize the pollen and nectar reward in relation to the cost of travel to other resources (Waser 1996).

Pollinator-plant relationships

The relationship between pollinator and plant carries implications for the persistence and community structure of an ecosystem's flora (Kearns & Inouye 1993, 1997, Ghazoul 2006, Michener 2007). The majority of floral visits by the bees of Mo'orea occurs on non-native plants, and thus may have direct and indirect negative effects on the native flora, either due to competition for pollinators or through synergistic effects among native species. Such synergistic effects, such as invasive "meltdowns," allow facultative exclusion of native species through positive interactions between invasive species. These interactions may include higher levels of pollination or development of floral constancy between or among non-native species (Simberloff & Von Holle 1999, Barthell et al 2001).

While it may be the case that Mo'orea's floral communities originally were predominantly self-pollinated, as is the case in many island systems (Barrett et al. 1996, Schueller 2004), the presence of bees now appears to favor some plant families and species unequally. The generalist bees in high abundance, the genera *Apis* and *Ceratina*, are predominantly visiting non-

native flora, while the Megachilid bees in low abundance, *Lithurgus* and *Megachile*, seem to obligately pollinate native flora. It remains to be seen what the effects of these visits are on actual plant reproduction and dispersal.

Studies in other ecosystems have documented the ability of *Apis* and generalist bees to act in mutualistic associations with invasive floral species, significantly furthering the spread of invasive species (Howarth 1985, Goulson 2003, Ghazoul 2006). At the same time, however, *Apis* has not been shown to negatively affect the spread of native species (Butz Huryn 1997). In the case of Mo'orea, it may be that, due to the large proportion of non-native floral species present and actively visited by *Apis* and *Ceratina*, these facultative pollination effects and potential mutualistic "meltdowns" may be possible. While visitation of a flower may not necessarily mean pollination occurs, the significantly larger number of non-native species visited may lead to continued or increased dominance of non-native floral species on Mo'orea. Both the abundance and presence of these two bee genera in all types of sites also may indicate that higher elevation refugia for native flora may face further threat from expanding populations of non-native floral species.

The observed use of floral resources by both *Apis* and *Ceratina* greatly outnumbered all other bee species. Patterns of very generalist floral resource use existed – with *Apis* visiting 18 different floral species and *Ceratina* visiting 14 different floral species – may have important ramifications for plant communities on Mo'orea, especially the aforementioned potential for facultative spreading of non-native flora. The two genera in the family Megachilidae, *Lithurgus* and *Megachile*, appear to be narrowly oligoleptic on floral species native to the Polynesian islands (Kuhlmann 2006). As such, they may play an important role in the

persistence of native floral species, including *Hibiscus tiliaceus* and *Vigna* species.

Future directions

Present and future interactions between the bee genera and native and non-native floral species carry ramifications for the future structure of the flowering plant communities of Mo'orea. A thorough understanding of the pollination systems present, such as what bees are carrying what pollens, what rates of visitation and pollination success are, and bee population and community structure, must be discerned in order to appropriately conserve Mo'orea's native floral communities and deal with the threat of non-native and invasive flora. Further study is needed to discern the roles of Mo'orea's bee species on these issues, and their place within the ecosystem.

Acknowledgements

I am deeply indebted to the professors, graduate student instructors, and my classmates for their constant support and for providing valuable information and suggestions that greatly shaped this project. Special thanks to the staff of the University of California at Berkeley and the Richard P. Gump South Pacific Research Station who contributed much to the Mo'orea class. Hinano Murphy provided valuable insight into the history of Mo'orea. Genera and species identifications were graciously verified by Dr. Victor Gonzalez (USDA) and from specimens at the Essig Museum of Entomology.

Literature Cited

- Arthur, W. (1995). Wayside plants of the islands: a guide to the lowland flora of the Pacific Islands. University of Hawaii Press. Honolulu HI.
Barrett, S.C.H., Emerson, B., and Mallet, J. (1996). The reproductive biology and

- genetics of island plants. *Philosophical Transactions of the Royal Society of London* 351:725-733.
- Barthell, J.F., Randall, J.M., Thorp, R.W., and Wenner, A.W. (2001). Promotion of seed set in yellow star-thistle by honeybees: evidence of an invasive mutualism. *Ecological Applications* 11(6): 1870-1883.
- Butz Huryn, V.M. (1997). Ecological impacts of introduced honey bees. *The Quarterly Review of Biology* 72: 275-297.
- Ghazoul, J. (2006). Floral diversity and the facilitation of pollination. *Journal of Ecology* 94:295-304.
- Gillespie, R.G., and Roderick, G.K. (2002). Arthropods on islands: colonization, speciation, and conservation. *Annual Review of Entomology* 47:595-632.
- Goulson, D. (2003). Effects of introduced bees on native ecosystems. *Annual Review of Ecology and Evolutionary Systems* 34:1-26.
- Howarth, F.G. (1985). Impacts of alien land arthropods and mollusks on native plants and animals in Hawai'i. C.P. Stone & J.M. Scott (eds.). Hawai'i's Terrestrial Ecosystems. 149-173. University of HI Press. Honolulu, HI.
- Kearns, C.A. and Inouye, D.W. (1993). Techniques for pollination biologists. University Press of Colorado. Niwot, Colorado.
- Kearns, C.A., and Inouye, D.W. (1997). Pollinators, flowering plants, and conservation biology. *BioScience* 47(5):297-307.
- Kremen, C., Williams, N.M., Aizen, M.A., Gemmill-Herren, B., LeBuhn, G., Minckley, R., Packer, L., Potts, S.G., Roulston, T., Steffan-Dewenter, I., Vasquez, D.P., Winfree, R., Adams, L., Crone, E.E., Greenleaf, S., Keitt, T.H., Klein, A., Regetz, J., and Ricketts, T.H. (2007). Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. *Ecology Letters* 10:299-314.
- Kuhlmann, M. (2006). Fauna and biogeography of the bees and wasps of the Cook Islands (Hymenoptera aculeata). *Journal of Hymenoptera Research* 15(1):26-37.
- LeBuhn G., Griswold, T., Minckley, R., Droege, S., Roulston, T., Cane, J., Parker, F., Buchmann, S., Tepedino, V., Williams, N., Kremen, C., and Messenger, O. (unpublished). A standardized method for monitoring bee populations – the Bee Inventory (BI) plot. Available at: <http://online.sfsu.edu/~beeplot/>.
- Magnacca, K. (2007). Conservation status of the endemic bees of Hawaii, *Hylaeus* (*Nesoprosopis*) (Hymenoptera: Colletidae). *Pacific Science* 61(2):173-190.
- McCall, C. and Primack, R.B. (1992). Influence of flower characteristics, weather, time of day, and season on insect visitation rates in three plant communities. *American Journal of Botany* 79(4):434-442.
- Meyer, J-Y. (unpublished). Conservation of terrestrial biota in French Polynesia: needs and priorities for research and management.
- Michener, C.D. (1965). A classification of the bees of the Australian and South Pacific regions. *Bulletin of the American museum of Natural History* 130: 1-362.
- Michener, C.D. (2007). Bees of the world, 2nd ed. The Johns Hopkins University Press. Baltimore, Maryland.
- Nishida, G.M. (unpublished). French Polynesia ants, bees, and wasps checklist (preliminary), updated 2007. Available: <http://essigdb.berkeley.edu/checklists/>. Accessed: 26 April 2008.
- Richardson, D.M., Allsop, N., D'Antonio, C.M., Milton, S.J., Rejmanek, M. 2000. Plant invasions – the role of mutualisms. *Biological Review* 75:65-93.

- Schueller, S.K. 2004. Self-pollination in island and mainland populations of the introduced hummingbird-pollinated plant, *Nicotiana glauca* (Solanaceae). *American Journal of Botany* 91: 672-681.
- Simberloff, D., and Von Holle, B. (1999). Positive interactions of nonindigenous species: invasional meltdown? *Biological Invasions* 1:21-32.
- Snelling, R.R. (2003). Bees of the Hawaiian Islands, exclusive of Hylaeus (Nesopropis) (Hymenoptera: Apoidea). *Kansas Journal of Entomology* 76(2):342-356.
- Welsh, S.L. (1998). Flora Societensis: a summary revision of the flowering plants of the Society Islands. EPS Inc. Orem, Utah.