# ARTHROPOD COMMUNITIES ON DECOMPOSING FRUIT IN AGRICULTURAL AND FORESTED AREAS ON MOOREA, FRENCH POLYNESIA

GENOA I. STARRS

*Environmental Science Policy and Management, University of California, Berkeley, California 94720 USA*

*Abstract.* A controlled observation study was used to determine differences in athropod communities on fruits introduced to the island of Mo'orea, French Polynesia, approximately 300 and 1000 years ago respectively: papaya (*Carica papaya*) and Tahitian chestnut (*Inocarpus fagifer*), in two regions: an agricultural school and a tropical moist broadleaf forest. Distinct differences in communities existed by fruit and region, and there was interaction between the influence of region and fruit type. Papaya communities showed the most differences by region. Papaya communities had a greater mean number of individuals and taxa than Tahitian chestnut communities. Region did not have a significant effect on the mean number of individuals and taxa, but for both individuals and taxa the forested region showed more variation in the communities found on each fruit than in the agricultural region, perhaps due to greater niche differentiation (competition among species), on the less frequently disturbed site. The most abundant taxa were flies (Diptera) and ants (Hymenoptera: Formicidae). Community differentiation by region appeared to be influenced most strongly by less abundant species, rather than by the most abundant taxa. This study provides groundwork for future studies of tropical relationships between arthropods, land use changes, and fruit, and provides evidence of agricultural impacts on arthropod communities.

*Key words: agriculture; arthropod; community analysis; exotic species; fruit; Moorea, French Polynesia; land use; niche; papaya; Tahitian chestnut; tropical agriculture.*

## INTRODUCTION

Islands are a classic example of areas with high levels of endemism. The process of colonization followed by adaptive radiation is a commonly observed pattern resulting in a diversity of species unique to an island or its archipelago (Grant 1998). Another classic feature of island diversity is taxonomic disharmony, a concept describing the tendency of isolated islands to have skewed representations of taxa as compared to continental source areas, with the overrepresentation of some groups and the absence of others (Gillespie et al. 2007, Gillespie & Roderick 2002).

Taxonomic disharmony can be observed in the Society chain of Islands, where this study was performed. The Society Islands form a relatively young archipelago, with the oldest island, Maupiti, dated at 3.9–4.9 million years old. This represents the upper time limit over which adaptive radiation could occur (Neall & Trewick 2008). As a result, the Society chain has relatively low diversity of native species. This, combined with the taxonomic disharmony prevalent in the Chain results in a system vulnerable to invasion (Paulay 1994).

Mo'orea is the second youngest island in the Society Island chain, and has been subject to two major introduction events. Polynesian voyagers introduced a number of species to the Society Island chain when they arrived approximately 1000 years ago, and European contact led to another influx of new species, beginning with the voyage of Captain Cook who arrived in Tahiti in 1777 (Anderson et al. 1999, Cook 1971). On islands such as Mo'orea, the introduction of agricultural exotics has and continues to have noticeable impacts on the ecosystem. Plants from both the Polynesian and European periods of introduction are present in both agricultural and less frequently disturbed forested settings.

The mid-elevation valleys of Mo'orea have two main categories of land use: forested and agricultural; however, the boundary between the two can be unclear. Naturalized plants, such as the Tahitian chestnut (*Inocarpus fagifer)*—an early Polynesian introduction—are often found growing in forest concurrently with more recently introduced fruit trees, such as papaya (*Carica papaya*). *Inocarpus fagifer* is a member of the Fabacae family that is naturalized in the forests of Mo'orea. Its fruit consists of a fibrous shell over a kernel (Pauku 2006). Papaya exemplifies the fruits that were introduced and cultivated post-European contact—fleshy, sweet, soft, and has its own suite of associated agricultural pests (Pena et al. 2002). The differing characteristics of the fruit, the time since introduction, and the coincident introduction of associated species, may lead to different communities of insects using each fruit even though they occupy the same sites, despite the fact that time since introduction is short.

Agricultural practices can have a wide range of ecological impacts, especially on arthropod communities, and field- and tree-cropping are is practiced extensively in French Polynesia. Mo'orea has already been subject to a number of invasions by agricultural pests, such as the glassy-winged sharpshooter (Grandgirard et al. 2006), the oriental fruit fly *Bractrocera dorsalis* (Vargas et al. 2007), and all ant species present on the island (Wilson & Taylor 1967). Though in the long-term vegetation disturbance from indigenous agriculture is a nearly ubiquitous feature of the island's vegetation, in recent times, the introduction of intensive agriculture and monocultural cropping has potentially had dramatic impacts on abundance and diversity of arthropod taxa and species. Different land uses may influence the types of arthropods available to prey on nearby fruit and to disperse to less cultivated areas, ultimately shifting insect communities on a broad scale and through them, all members dependent upon them in their trophic web.

Arthropods are highly important in almost every ecosystem, with roles as decomposers, pollinators, predators, pests, and perhaps most important, prey (Weisser & Siemann 2004). With the absence of native mammals on Mo'orea, understanding the nature of frugivorous insect communities and what influences their abundance and composition is vital to dealing with issues of conservation and cultivation.

Examining the relationships between arthropod communities, fruit, and land use can help deepen understanding of the impacts that changing land use and agriculture are having on the island. This study used controlled observations to attempt to answer three questions: (1) Do different fruit species attract different insect communities? (2) Does land use have an influence on local insect communities and how they use fruit resources? (3) Can we detect patterns in the types of taxa, species, or communities and their relationship to land use (region) and fruit type?

## METHODS

### *Study sites*

The Opunohu Valley (Fig. 1) is the less developed of the two valleys on Mo'orea. It contains a relatively high abundance of forest compared to its neighboring valley, Paopao (Fig. 1). Due to its interspersion of forested and cultivated areas, the Opunohu valley was chosen as the better site for this study. Maps were made using QGIS and Google Earth (2012).

The two chosen study regions within the valley were chosen to represent forested and agricultural land at similar elevations. Figure 1 shows the location of the two regions on the island. The Three Pines trail sites ranged from 166–176 m in elevation, and were characterized by dense forest cover, with both over- and understory vegetation and with between 1–4cm of leaf litter.

The Agricultural School sites ranged from 72–85 m in elevation, and were heterogeneous in habitats and vegetation. These included pineapple fields, papaya and soursop orchards, and miscellaneous areas bordering fields; each differed in the amount of ground cover and shading.

### *Study design*

This study was performed with a randomized block design. Five blocks were located in each region, with ten blocks total (Fig. 2). Exclosures (Fig. 3) comprised of a cylindrical wire cage (1.27 by 1.27 cm) wire mesh) designed to exclude mammals and birds, were placed within the blocks. Each block consisted of three exclosures (Fig. 4). Each exclosure contained flypaper and one of the following: half a Tahitian chestnut, an equivalently sized piece of papaya fruit, or flypaper without fruit. Papaya was used if it appeared orange and was fragrant when uncut. Tahitian chestnut was used when it was ripe enough to fall from the tree but not yet brown, desiccated, or chewed. Flypaper was cut into 4 by 6.5 cm rectangles and stapled to the fruit, with one half covering of the exposed flesh, and excess paper wrapping around the rind (Fig. 3). In the flypaper alone cage flypaper was placed face up on the

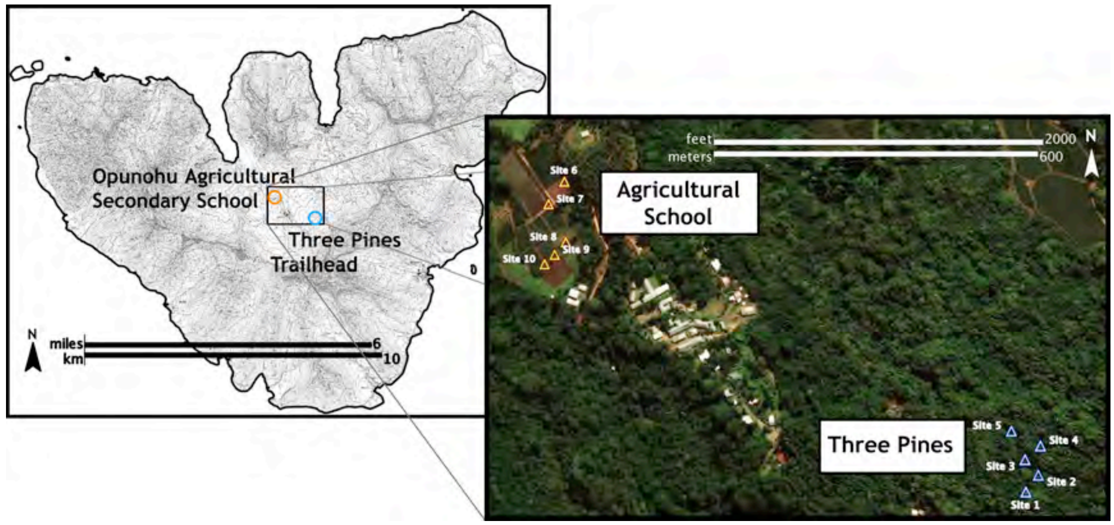



FIG. 1. The locations of the study regions on Mo'orea. The Opunohu valley is the western part of the island interior. Pao Pao is the eastern valley (QGIS 2012).

FIG. 2. The two regions, with the location of field sites. This photo shows the differences in land use. Each triangle represents a block/site. Blue triangles indicate blocks located in Three Pines, while orange triangles indicate blocks in the Agricultural School (Google Earth 2009).

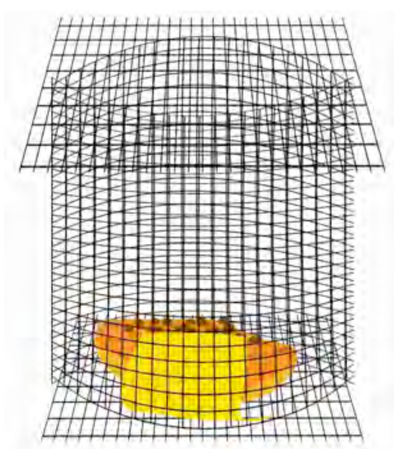


FIG. 3. A fruit exclosure shown with a quarter of a papaya and flypaper. Not shown to exact scale—wire mesh was 1.27 by 1.27 cm squares (a larger mesh). The top and bottom were zip-tied on. Cages were tagged and numbered.

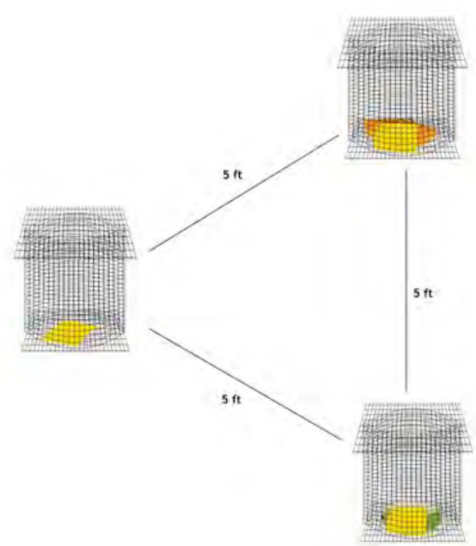



FIG. 4. A block, consisting of three cages five feet (3.1 m) apart. At each site, one contained papaya, one contained Tahitian chestnut, and one contained flypaper alone.

bottom of the cage. The three cages in a block were arranged in an equilateral triangle, with each exclosure 1.5 m from the others (Fig. 4).

Blocks were placed a minimum of 31 m apart. After walking 31 m, a die was rolled twice, and the product of the numbers would be an additional distance walked. This was repeated to determine the distance off the trail. Values could range from 1.5–24 m. Placement off the trail alternated between the left and right side. The experiment was repeated three times (October 17–19, 24–26, and 28–30, 2012).

Discriminant analyses were used to determine differences between communities, and to visually detect patterns in the data. A two-way ANOVA was used to examine the relationship between region, fruit type, and the response variables of number of arthropod individuals and number of arthropod taxa. Taxa with more than 20 individuals sampled were analyzed using a MANOVA test comparing fruit type and region combined against each individual species. All statistical tests were performed in JMP 10.0. For all statistical analyses, a p value of <0.05 was deemed significant.

*Collection and identification*

Flypaper and fruit were collected two days after placement. Flypaper was removed from the fruit, and the sticky side was sealed using cellophane to prevent additional insects from sticking after collection, and to minimize the mangling or mixing of samples. Samples were set in labeled plastic bags along with their fruit, and placed in a freezer until they could to be examined under a dissecting scope. Voucher pictures were taken using a microscope camera. The samples were identified using a using dichotomous keys and the Mo'orea Biocode Project (Paulian 1998, Triplehorn & Johnson 2005).

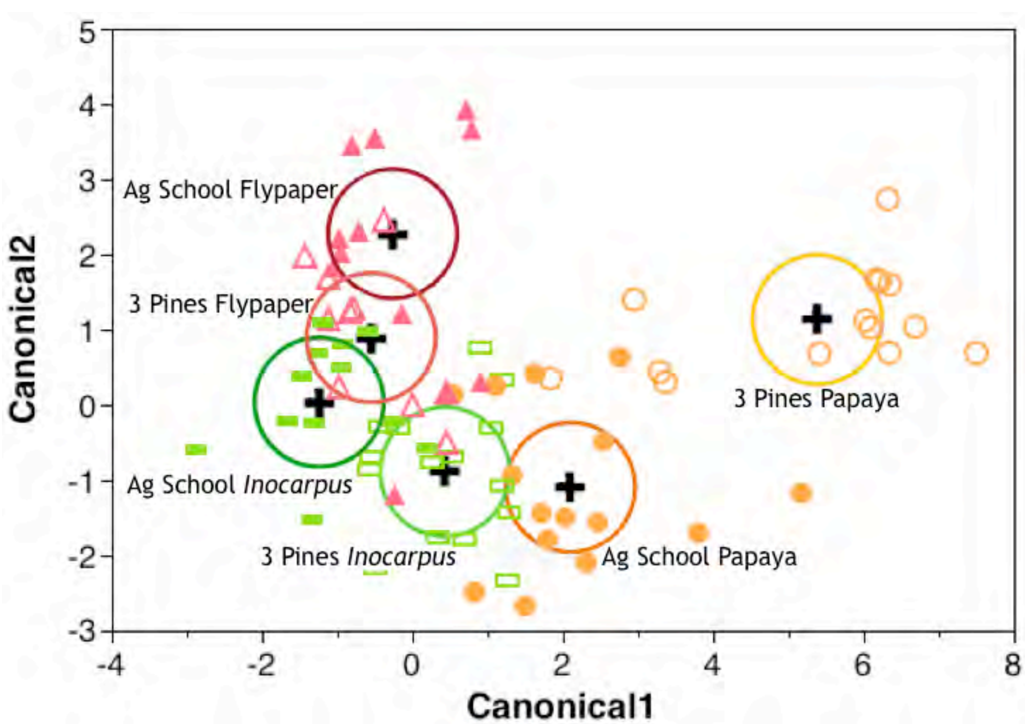



FIG. 5. A canonical plot showing the results of a discriminant analysis of arthropod communities (species composition) by region and fruit. Centroids (the larger circles) represent a 95% confidence limit around the multivariate mean (the cross). If centroids do not overlap, it indicates a significant difference between them significant at $p<0.05$. Circles are papaya samples, rectangles are *Inocarpus* samples, and triangles are flypaper alone. Outline symbols are from the Three Pines region, while filled shapes are from the Agricultural School. The communities on papaya show the largest difference by region, but both *Inocarpus* and papaya communities are significantly different by region within each fruit. Within each location, *Inocarpus* and papaya communities differ significantly from those found on the flypaper.

## RESULTS

There was diversity in taxa and species found. Fifty-two different taxa were recorded, with thirteen different orders of arthropod represented, and a total of 1643 individuals sampled.

*Community patters: Discriminant analysis*

Discriminant analysis was used to examine overall community patterns on the two fruits (*Inocarpus* and papaya) and flypaper in the two regions (Fig. 5). The communities on *Inocarpus* and papaya were significantly different within regions, and the communities on each fruit type differed between regions. The communities on papaya showed the largest variation between regions, and communities on fruit were further apart at Three Pines. In each region, *Inocarpus* and papaya communities also differed significantly from those found on the flypaper, but the communities on flypaper were not significantly different by region. An examination of the loadings on each axis indicates that Hemiptera A and Hymenoptera B were influential along the x-axis, while Larva B and Hymenoptera B were most influential in community differentiation along the y-axis. The interaction of fruit and site is illustrated by the overlap in communities occupying *Inocarpus* at Three Pines and Papaya at the Agricultural School.

Separate discriminant analyses were then performed by fruit type and site to investigate them separately. The communities were shown to be different by both fruit type and site when considered independently (Fig. 6a &b). Hemiptera A and Hymenoptera B were most heavily weighted on the x-axis, and Coleoptera E and Formicidae F on the y-axis, for fruit type. For region, Hymenoptera B and Hemiptera A were most heavily weighted.

*Region and fruit type: Analysis of variance*

Analysis of Variance was used in order to look more specifically at sources of variation in insect taxa and abundance between sites at each site. The effects of region (Three Pines and the Agricultural School) and fruit (*Inocarpus*, papaya, and flypaper alone) were examined in relation to the response variables of average arthropod frequency and average number of arthropod taxa. The average number of arthropods varied by fruit type, with the greatest number of individuals on papaya, followed by Tahitian chestnut, and the lowest number on flypaper alone (two-way ANOVA, p<0.0001, $F_{3,86}$=24.6) (Fig. 7a). The average number of taxa followed the same pattern, with the greatest number of taxa on papaya and the least on the flypaper (two-way ANOVA, p<0.0001, $F_{3,86}$=11.1) (Fig. 7b). The number of taxa varied much less between the fruits at the Agricultural School sites than at the Three Pines sites (Fig. 7b). Fruit type was significant on the treatment level (when regions were combined) ($p_{\# individuals}$<0.0001, $p_{\# taxa}$<0.0001), but region was not was not significant when fruit results were combined ($p_{\# individuals}$=0.3, $p_{\# taxa}$=0.4).

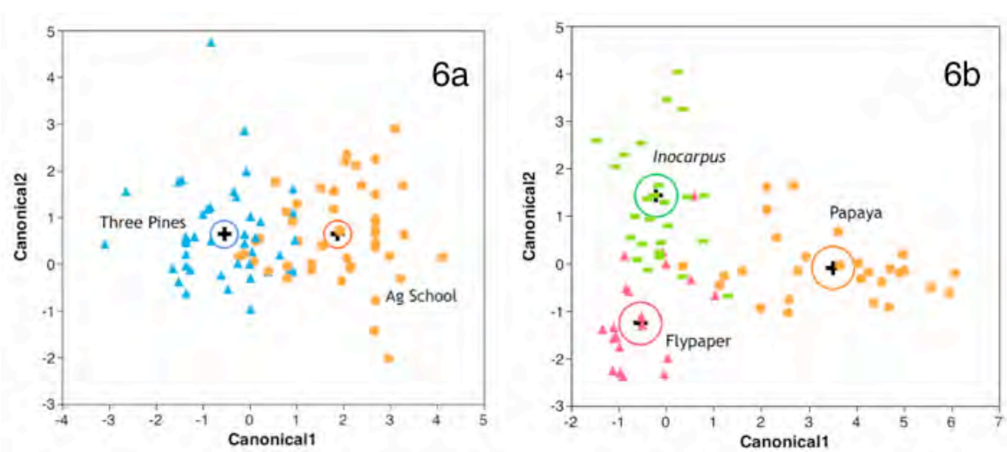



FIG. 6a & b. Canonical plots produced by discriminant analyses showing the differences in communities (species composition) by region regardless of fruit type (6a) and fruit type regardless of region (6b). 6a: Three Pines = blue (dark) triangles, Agricultural School = orange (light) circles. 6b: Papaya = orange circles, *Inocarpus* = green rectangles, flypaper alone = red triangles. The circles are 95% confidence intervals around the multivariate mean.

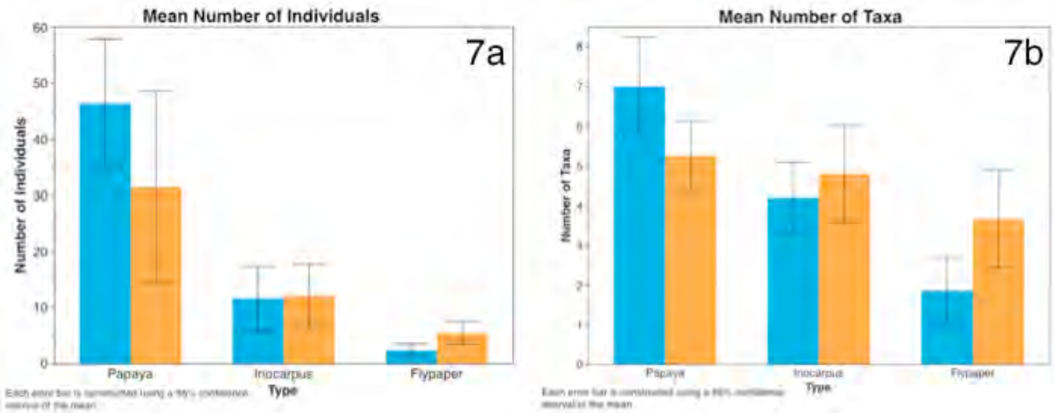



FIG. 7a &b. The average number of individuals (7a) and taxa (7b) present on each fruit type at each site. Fruit type differed in both mean number of individuals and taxa (two-way ANOVA, p<0.0001, $F_{3,86}$=24.6, two-way ANOVA, p<0.0001, $F_{3,86}$=11.1). Region did not. Error bars indicate that for each fruit and flypaper, the number of individuals and taxa is significantly different at the Three Pines site, but not at the Agricultural School. Color codes for region. Three Pines = Blue/dark bars, Agricultural School = light/yellow bars.

*Species composition*

The most frequently occurring arthropod species were examined more closely. Eight taxa had more than twenty total individuals across all samples (Table 1), all either Dipterans or Formicidae (Hymenoptera: Formicidae). Diptera B (*Drosophila sp.)* had the largest number of individuals, and most occurrences in every category except on flypaper alone. Diptera B, Formicidae A, Formicidae C, and Formicidae D all had the most occurrences on papaya, and the least on flypaper. Most exhibited little difference between region, except for Diptera A and Formicidae D, which appeared more at the Agricultural School, and Diptera H, J, and Formicidae C, which occurred more at Three Pines. Significance of MANOVAs of these eight species versus fruit and region is reported in Table 1.

| | **Total** | | **Fruit (# occurrences)** | | | **Region (# occurrences)** | |
|---|---|---|---|---|---|---|---|
| **Taxa** | **# of Occurrences** | **# of Individuals** | **Papaya** | ***Inocarpus*** | **Flypaper** | **Agricultural School** | **Three Pines** |
| **Diptera A** | 21 | 27 | 5 | 11 | 5 | 14 | 7 |
| **Diptera B**** | **55** | **542** | **28** | **22** | 4 | **24** | **30** |
| **Diptera H** | 26 | 73 | 10 | 16 | 0 | 10 | 16 |
| **Diptera J*** | 15 | 48 | 6 | 8 | 0 | 5 | 9 |
| **Formicidae A**** | 22 | 130 | 14 | 4 | 4 | 11 | 11 |
| **Formicidae B** | 14 | 27 | 6 | 1 | **7** | 8 | 6 |
| **Formicidae C**** | 44 | 521 | 25 | 12 | 6 | 20 | 23 |
| **Formicidae D*** | 10 | **39** | 8 | 1 | 1 | 7 | 3 |

TABLE 1. Examining all taxa with more than 20 individuals sampled reveals that several taxa showed distinct differences in use of fruit and/or region. Number of occurrences in each category of fruit and taxa are reported. Diptera B (*Drosophila sp.*) has the most overall occurrences, individuals sampled, and occurrences in every category except on flypaper alone. Asterisks indicate significance of a MANOVA with fruit type and region vs. species. ** indicates p<0.01, * indicates p<0.05. Bolded text shows the largest value in each column. Shaded cells are the lowest values in each category, on a gradient from low to high, dark to light. Diptera B was the most commonly occurring insect on all fruit at each location, and had a high number of individuals.

## DISCUSSION

### *Community Patterns*

Fruits were utilized by different arthropod communities. When grouped across regions, fruits exhibited different communities (Fig. 6b). Papaya attracted the largest numbers of individuals and taxa. Communities on papaya also showed the largest variation by site (Fig. 5). Papaya attracted larger numbers of fruit flies (*Drosophila* sp.), and had the most occurrences of three of the four most prevalent ant species. These taxa (Diptera, Formicidae) are commonly associated with agricultural crops and fruits with high sugar content (Pena et al. 2002).

Though the study sites were in contrasting environments (farm and forest), region only distinguished communities as a whole, not species abundance or taxa. Land use differences between agricultural and forested regions have been shown to have effects on the insect and ant communities present (Neves et al. 2012). Similarly, when fruit types were grouped, the communities were differentiated by region (Fig. 6a). However, the lack of a significant effect of region on mean number of individuals and taxa was somewhat surprising (Fig. 7). Table 1 shows larger differences in occurrences of the eight most abundant taxa by fruit than by region, showing that the more common taxa play larger role in distinguishing communities by fruit type than by region. These results suggest community differentiation by region may be due to combinations of species or more rarely occurring species rather than the presence of any site specific or common taxa.

In combination, fruit type and region had some obfuscating effects. The clear differentiations seen in figures 6a and b were less clear when an overall discriminant analysis was performed (Fig. 5), suggesting interactions between communities, regions, and fruit type.

### *Site and Fruit Type*

The Agricultural School showed less variation in average number of individuals and taxa using each fruit than Three Pines (Fig. 6a &b). This supports the theory of niche differentiation, which posits that over time species evolve to utilize different niches, minimizing overlap in resource use and interspecific competition (Schoener 1989). Niche differentiation occurs over time in stable ecological conditions; however, in non-equilibrium sites, it has been suggested that dispersal ability becomes a more valuable trait, as niches may not be consistently available and new niches may appear, allowing competing species to co-occur (Hutchinson 1953). The lower variation in taxa and number of species using different fruits at the agricultural site may reflect this, as farming involves constant ecological disturbance. The relatively undisturbed forest site provides a longer period of more stable habitat in which niche differentiation might occur.

The role of fruit in freshwater systems bears examining as well, as the high-energy input of fruit could potentially be affecting the streams on the island. A preliminary freshwater study was performed in the Three Pines region. Four fruits were placed in the Opunohu creek (two papaya, two *Inocarpus*). One papaya and one *Inocarpus* had one *Melanoides* sp. snail each on them after 48 hours. Though inconclusive, further research should look into fruit utilization in Mo'orea's streams.

### *Species composition*

The eight most abundant taxa were ants and flies (Hymenotpera: Formicidae, Diptera), typical fruit predators. *Drosophila* sp. was the most prevalent species, with the largest number of individuals and the greatest number of occurrences. These taxa contain species that are cosmopolitan and notorious for their dispersal and invasion abilities. Overall, though many taxa were identified to genus or species level, the conditions of samples were not good enough for complete accuracy (Appendix A, B).

## CONCLUSIONS

To answer the three research questions, first, there are distinct differences in the patterns of insect taxa and communities in each region that may reflect differences in land use. Second, different fruit communities attract different insect communities, and this is influenced by region, perhaps due to different land use, time since introduction, or the concurrent introduction of accompanying insect species. Third, one possible explanation for locational differences in the species abundance and taxa in on the fruit that fits with ideas about niche differentiation is the difference in rates of disturbance at each site, but the types of plant species in the local environment, elevational differences, and other factors might also be responsible.

The effects of agriculture and development on an island ecosystem could have vital conservation implications. This study showed a higher diversity of arthropods than was expected, and that agriculture is associated with different arthropod communities. Arthropod communities on islands are subjected to different selective pressures than those in continental habitats (Gillespie & Roderick 2002, Grant 1998). This can lead to the evolution of unique, endemic species not seen on continental landmasses, as well organization of novel combinations of organisms into communities. Protecting and understanding these systems is important to understanding evolution and adaptive radiation, especially in regions such as Mo'orea, where projects like the Biocode project are making it a model system for ecological and biological research. As rates of agricultural expansion are increasing in tropical regions, understanding the potential effects of land use change is vital, hopefully before they occur (Houghton 1994). The introduction of new vegetation (crops) as well as their associated pests makes agriculture an activity of high ecological risk in environments vulnerable to invasion.

The results of this study are preliminary, but produced results on landscape, community, and individual taxa levels, providing groundwork for future studies. Though communities were differentiated by fruit type and region, when combined, patterns were less clear. Examining what species are responsible, and how environment and competition can affect a single species' fruit preference and the organization of communities provides ample topics for future research. The lessened variation in number of individuals and taxa by fruit type in the agricultural area could be a platform from to study the implications of niche differentiation and the effects of land use change.

The lack of similar studies is notable. Although research on arthropod succession in fruit has been done in temperate zones (Hui 1990, Jianrong et al. 1996), relatively little has been done in the tropics, on islands, or as a comparison across fruit species. The implications of these results make this area of study worthwhile already; however, expanding the types of fruits and regions could broaden the implications considerably.

The addition of fruits to the ecosystem of Mo'orea provided a nutrient and carbohydrate rich source of food for any arthropod able to use it. With a surprising number of arthropod taxa found, understanding the relationship between land, crops, and arthropods should be a priority: For ecologists, it is the bottom line of the trophic web, for farmers, it is a product and food source, and for scientists, it is a model system, set on Mo'orea, a biological and ecological sandbox.

## ACKNOWLEDGMENTS

I thank Professors George Roderick, Vincent Resh, Brent Mishler, and Jonathon Stillman for their ample assistance on every part of this project. I thank Rosemary Romero, Darcy Ernst, and Matthew Luskin for their help as well. Finally, I am grateful to my classmates for field assistance and proofreading, and my family for funding and support. This research benefited from the support and services of UC Berkeley's Geospatial Innovation Facility (GIF), gif.berkeley.edu.

## LITERATURE CITED

Anderson, A. J., Conte, E., Clark, G. R., Sinoto, Y. and F. J. Petchey, 1999. Renewed excavations at Motu Paeao, Maupiti Island, French Polynesia: preliminary results. New Zealand Journal of Archaeology **21:**47–66.

Triplehorn, C. A., and N. F. Johnson. 2005. Borror and DeLong's introduction to the study of insects. Thompson Brooks/Cole, Belmont.

Cook, J. 1971. The explorations of Captain James Cook in the Pacific, as told by selections of his own journals, 1768-1779. Dover Publications, New York.

Gillespie, R. G., Claridge, E. M., and G. K. Roderick. 2007. Biodiversity dynamics in isolated island communities: interaction between natural and human-mediated processes. Molecular Ecology **17:**45-57.

Gillespie, R. G., and G. K. Roderick. 2002. Arthropods on islands: colonization, speciation, and conservation. Annual review of entomology **47:**595-632.

Google Earth 6.1. 2012. Moorea, French Polynesia 17°31'59.81"S and 149°49'54.18"W. Map. Google, June 3, 2009. Web. November 14, 2012.

Grandgirard, J., Hoddle, M. S., Roderick, G. K., Petit, J. N., Percy, D., Putoa, R., and N. Davies. 2006. Invasion of French Polynesia by the glassy-winged sharpshooter, *Homalodisca coagulata* (Hemiptera: Cicadellidae): A new threat to the South Pacific. Pacific Science **60:**429-438.

Grant, P. R., editor. 1998. Evolution on islands. Oxford University Press, Oxford.

Houghton, R. A. 1994. The worldwide extent of land-use change. Bioscience **44:**305-313.

Hui, S. W. L. X. X. 1990. A preliminary study on pest control and succession of insect community in apple orchards. Journal of Southwest Agricultural University **12:**137-144.

Hutchinson, G. E. 1953. The concept of pattern in ecology. Proceedings of the Academy of Natural Sciences of Philadelphia **105**:1-12.

Jianrong, L., Waneheng, S., and L. Xu. 1996. Study of the ecological dominance of insect communities in apple plantations. Chinese Journal of Ecology **1:**20-23.

JMP, Version 10.0. 2012. SAS Institute Inc., Cary, NC, 1989-2012.

Moorea Biocode Project. 2012. mooreabiocode.org.

Neall, V. E., and S. A. Trewick. 2008. The age and origin of the Pacific islands: a geological overview. Philosophical Transactions of the Royal Society B: Biological Sciences **363:**3293-3308.

Neves, F. S., Braga, R. F., Araújo, L. S., Campos, R. I., and M. Fagundes. 2012. Differential effects of land use on ant and herbivore insect communities associated with Caryocar brasiliense (Caryocaraceae). Revista de Biología Tropical **60**:1065-1073.

Pauku, R. L. 2006. *Inocarpus fagifer* (Tahitian chestnut). Growth **5:**14.

Paulian, R. 1998. Les insectes de Tahiti. Boubée, Paris.

Pena, J., Sharp, J., and M. Wysoki, editors. 2002. Tropical fruit pests and pollinators: biology, economic importance, natural enemies and control. CABI Publishing, Wallingford.

Paulay, G. 1994. Biodiversity on oceanic islands: its origin and extinction. American Zoologist **34**:134-144.

Quantum GIS Development Team. 2012. Quantum GIS Geographic Information System. Open Geospatial Foundation Project. http://qgis.osgeo.org.

Schoener, T. W. 1989. The ecological niche. Pages 79-113 *in* Cherrett, J. M. editor. Ecological concepts: The contribution of ecology to an understanding of the natural world. Blackwell Scientific Publications, Oxford.

Vargas, R. I., Leblanc, L., Putoa, R., and A. Eitam. 2007. Impact of introduction of *Bactrocera dorsalis* (Diptera: Tephritidae) and classical biological control releases of *Fopius arisanus* (Hymenoptera: Braconidae) on economically important fruit lies in French Polynesia. Journal of Economic Entomology **100**:670-679.

Weisser, W. W. and E. Siemann. 2004. Insects and ecosystem function. Springer, Berlin.

Wilson, E. O. and R. W. Taylor. 1967. The ants of Polynesia (Hymenoptera: Formicidae). Pacific Insects Monographs **14**:1–109.

## APPENDIX A

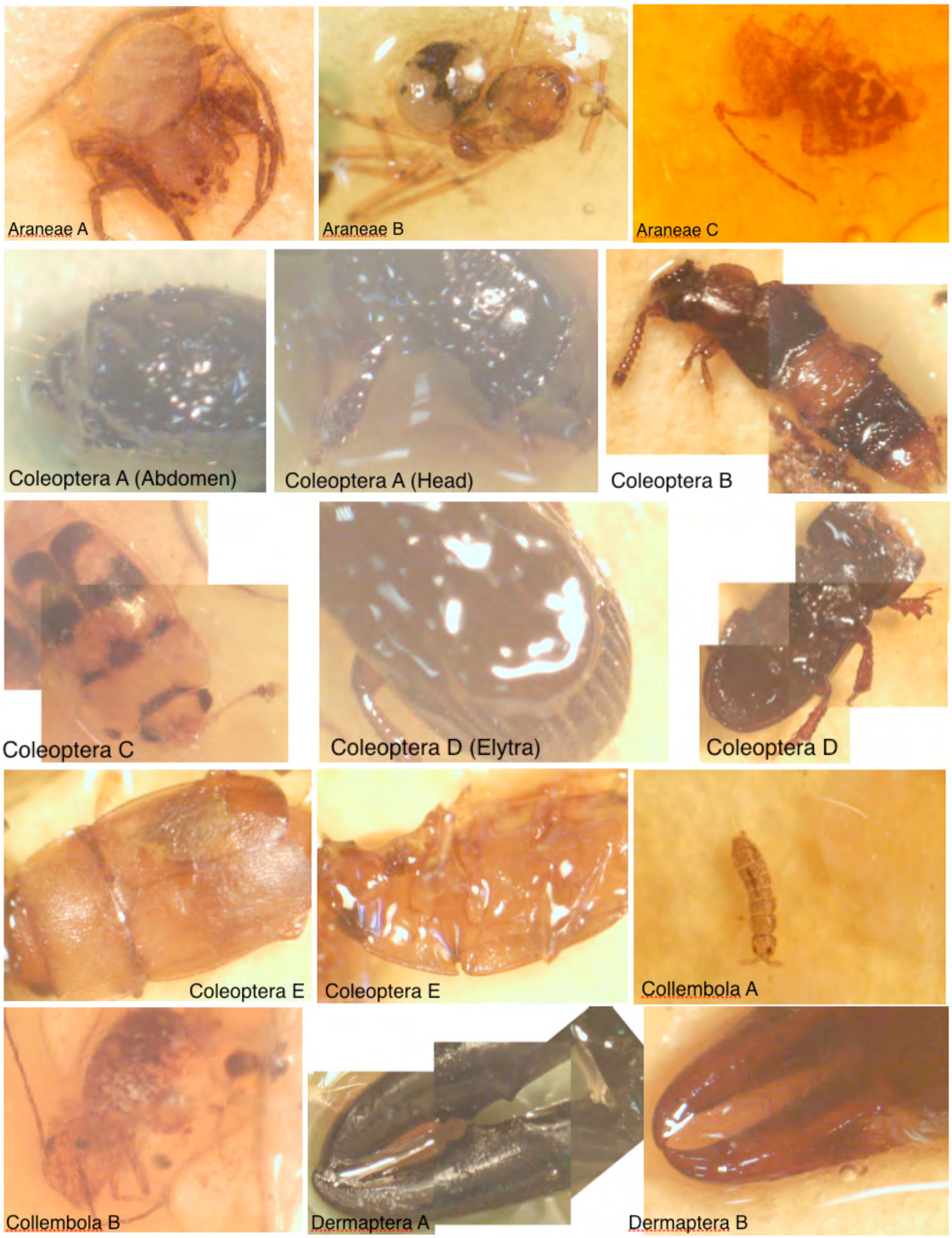
Preliminary identifications of taxa and cross-references to the Mo'orea Biocode Project specimens. The title "larva" was given to any juvenile arthropod, regardless of whether they are homometabolous or hemimetabolous.

| | Biocode ID | Family | Binomial | Notes |
|---|---|---|---|---|
| **Araneae A** | | | | |
| **Araneae B** | | | | |
| **Araneae C** | | | | |
| **Larva A** | | | | Diptera? |
| **Larva B** | | | | Hemiptera? |

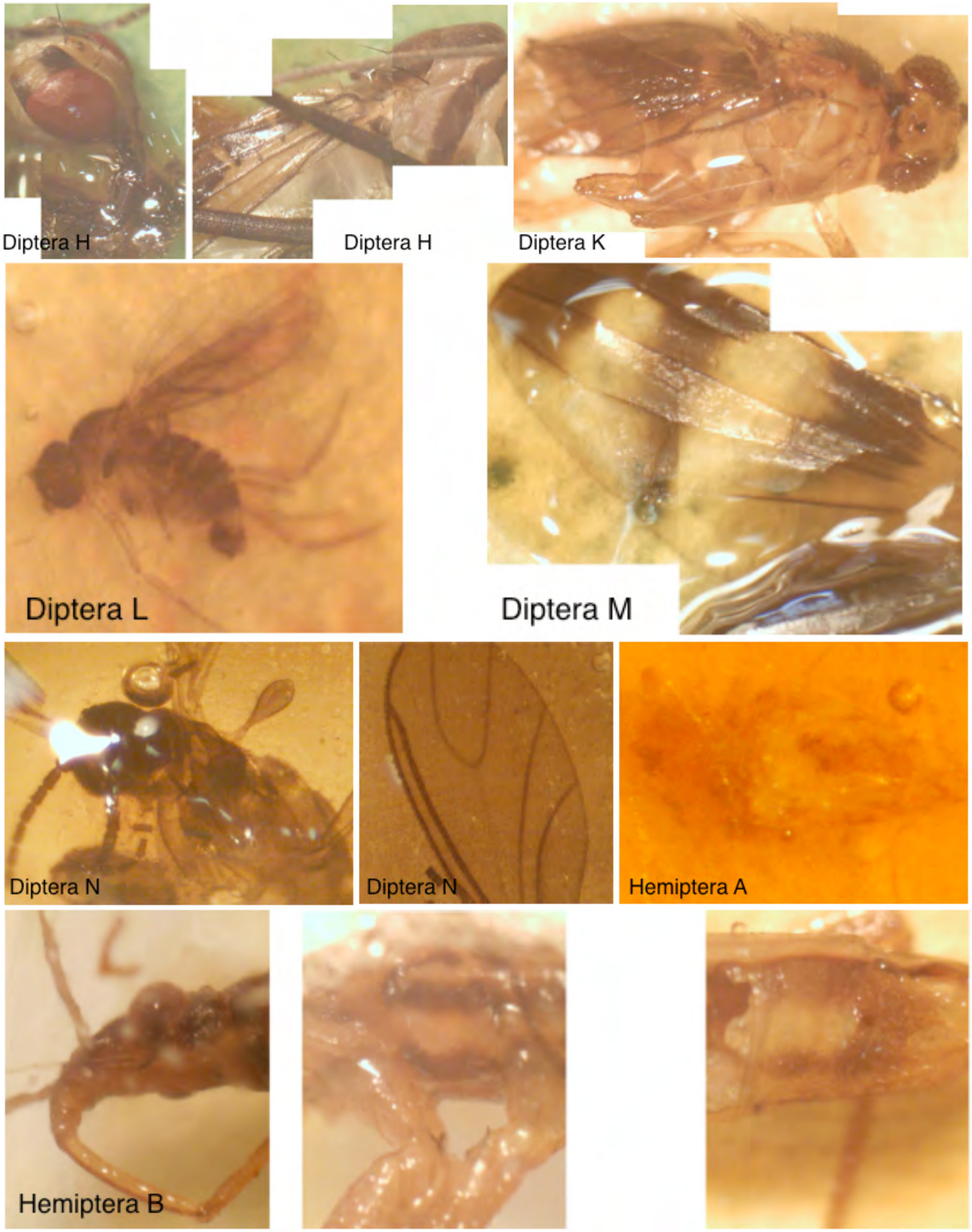
| | | | | |
|---|---|---|---|---|
| **Larva C** | | | | |
| **Larva D** | | | | Dermaptera |
| **Coleoptera A** | 4444 4444 0110 0297 | Staphylinidae | | |
| **Coleoptera B** | 4444 4444 0510 0869 | Staphylinidae | | |
| **Coleoptera C** | 4444 4444 0211 5359 | Nitidulidae | *Carpophilus* sp. | |
| **Coleoptera D** | | Scolytidae? | | |
| **Coleoptera E** | 4444 4444 0311 2811 | Nitidulidae | *Carpophilus* sp. | Tentative |
| **Collembola A** | | | | |
| **Collembola B** | | | | |
| **Dermaptera A** | | Chelisochidae | *Chelisoches morio* | |
| **Dermaptera B** | | Labiidae | *Spirolabia pilicornis* | |
| **Dermaptera C** | | Chelisochidae | *Chelisoches morio* | |
| **Diptera A** | | Phoridae | | |
| **Diptera B** | 4444 4444 0310 0080 | | *Drosophila* sp. | |
| **Diptera C** | | | | |
| **Diptera D** | | | | |
| **Diptera E** | | Dolichopodidae? | | |
| **Diptera F** | | | | |
| **Diptera H** | 4444 4444 0310 0084 | Neriidae | *Telostylinus lineolatus* | Tentative |
| **Diptera I** | | | | |
| **Diptera J** | | | | |
| **Diptera K** | | | | |
| **Diptera L** | | Phoridae | | |
| **Diptera M** | | Platystomatidae | | |
| **Diptera N** | | Sciaridae | *Sciara* sp. | |
| **Diplopoda A** | 4444 4444 0110 0455 | | | |
| **Formicidae A** | | Formicidae | | |
| **Formicidae B** | | Formicidae | | |
| **Formicidae C** | | Formicidae | *Pheidole fervens* | Tentative |
| **Formicidae D** | | Formicidae | *Technomyrmex albipes* | Tentative |
| **Formicidae E** | | Formicidae | *Monomorium floricola* | Tentative |
| **Formicidae F** | | Formicidae | *Anoplolepis gracilipes* | Tentative |
| **Formicidae G** | | Formicidae | *Cardiocondyla* sp. | Tentative |
| **Hemiptera A** | | | | |
| **Hemiptera B** | | Coreidae | *Leptoglossus australis* | |
| **Hymenoptera A** | 4444 4444 0211 4954 | | | |
| **Hymenoptera B** | | | | |
| **Hymenoptera C** | 4444 4444 0211 3878 | | | |
| **Hymenoptera D** | | Apidae | *Apis mellifica* | |
| **Hymenoptera E** | 4444 4444 0211 7260 | | | |
| **Lepidoptera A** | | | | |
| **Orthoptera A** | | | | |
| **Unidentified B** | | | | |
| **Unidentified C** | | | | Acari? |
| **Unidentified D** | | | | |
| **Unidentified E** | | | | Thysanura? |
| **Unidentified F** | | | | Acari |

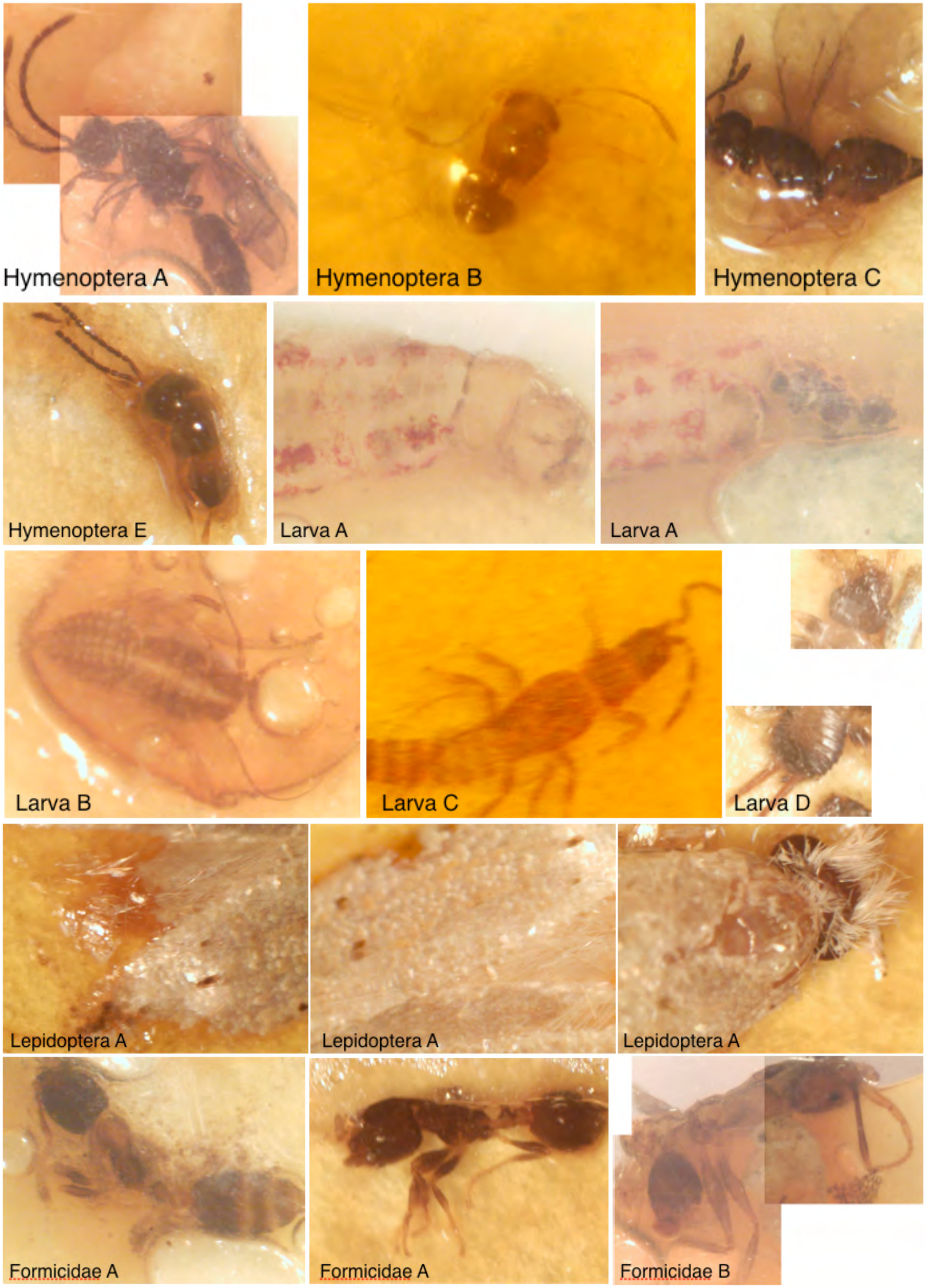
## APPENDIX B

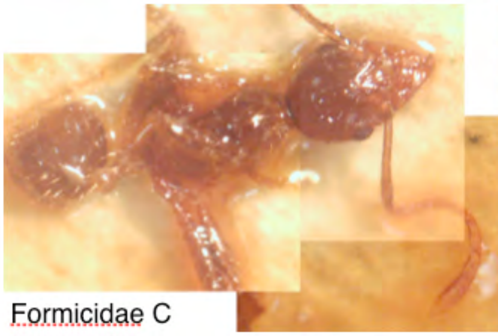
Photographic vouchers taken of each taxa on Mo'orea, corresponding with Table 2. The majority were taken under 20x magnification.

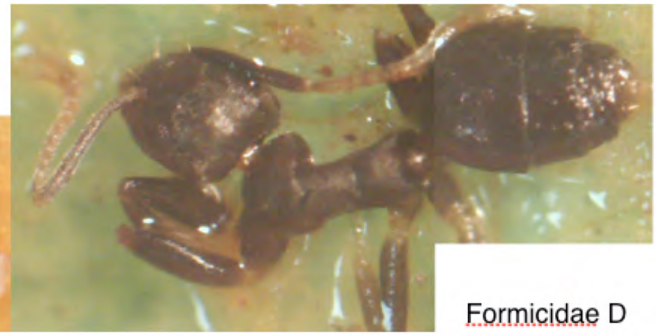



Dermaptera C
Diplopoda A
Diplopoda A
Diptera A
Diptera A
Diptera C
Diptera B
Diptera B
Diptera B
Diptera D
Diptera E
Diptera E
Diptera F
Diptera F
Diptera I


Diptera H
Diptera H
Diptera K
Diptera L
Diptera M
Diptera N
Diptera N
Hemiptera A
Hemiptera B


Hymenoptera A
Hymenoptera B
Hymenoptera C
Hymenoptera E
Larva A
Larva A
Larva B
Larva C
Larva D
Lepidoptera A
Lepidoptera A
Lepidoptera A
Formicidae A
Formicidae A
Formicidae B

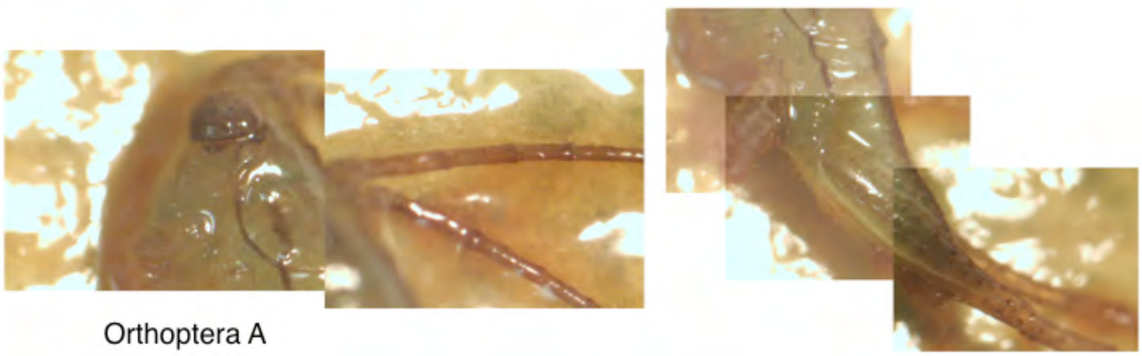

Formicidae C

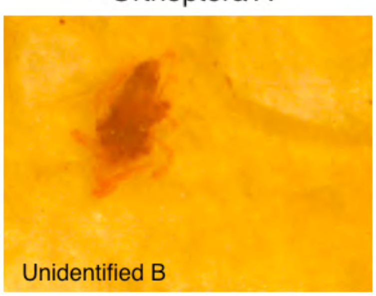

Formicidae D

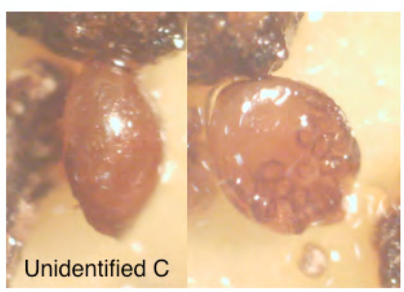

Formicidae E


Formicidae F


Formicidae G


Orthoptera A


Unidentified B


Unidentified C


Unidentified D


Unidentified E


Unidentified F