

Biogeography of Pacific insects and other terrestrial invertebrates: A status report

Scott E. Miller

Bishop Museum, 1525 Bernice Street, Honolulu, Hawaii 96817, USA

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Abstract

Because of their great diversity, insects and other invertebrates present excellent opportunities for biogeographic studies. Some of the features of insects include generality of distribution, much specialization within the context of overall versatility, many taxa possess rapid responses to environmental perturbation, some taxa are readily identifiable by non-specialists, many taxa are good indicators of areas of endemism, and many taxa are readily sampled with quantitative methods. Despite this, Pacific insect biogeography has advanced little since the now-classic studies by Gressitt and collaborators. Amongst the smaller Pacific islands, there is a basic pattern of depauperate, disharmonic biotas attenuating from west to east. In some cases, modern understandings of speciation processes, as well as tectonic, eustatic and human-induced background changes will require reinterpretation of traditional concepts. Most of the New Guinea insect biota shows closest relationships with that of Asia, with genera perhaps tending to be fewer in number but more species-rich. Most analyses have addressed the overall relationships of the New Guinea fauna, not regional endemism. Large scale experiments by Bishop Museum from 1957-1970 demonstrated the importance of dispersal, which may also be responsible for some distributions commonly considered to be introductions. But recent studies of both geology and biogeography indicate the importance of plate tectonics and rifted terranes as well.

Background

Introduction

Invertebrates and, in particular, insects, offer tremendous potential for the study of biogeography and evolutionary processes on islands. Collectively, they are both abundant and diverse, including groups well suited as indicators of

change across gradients at many scales – geographic across and amongst islands, temporal between seasons and years – as well as across trophic groups and ecological associations. This chapter attempts to provide a context for understanding the state of knowledge of terrestrial and freshwater invertebrates in the Pacific Basin – what we know, what we do not know, some caveats for biogeographic studies, and some opportunities for future studies. This chapter will provide some coverage of terrestrial and freshwater invertebrates in general, but will focus on terrestrial insects in particular. The terrestrial snails are reviewed elsewhere in this book (Cowie) and knowledge of most other taxa is severely limited; for introductions to spiders see Baert and Jocque (1993) and Lehtinen (1993), myriapods see Minelli (1984), isopods see Jackson (1941), and plant parasitic nematodes see Bridge (1988).

Specifically, this chapter will (1) review the history of entomological exploration in the Pacific; (2) list the major published data sources currently available; (3) highlight some of the major studies that have contributed to our knowledge of pattern and process; and (4) note some of the promising directions for future research, including the urgent need for basic inventory of the biotas of the Pacific islands.

Insects possess many positive features for use in biogeographic and conservation studies (see also Brown, 1991; Finnamore, 1996; Holloway and Stork, 1991; Kremen *et al.*, 1993; Rosenberg *et al.*, 1986; Sutton and Collins, 1991): (1) generality of distribution – insects are found in almost

every conceivable habitat and niche; (2) they exhibit much specialization within the context of overall versatility; (3) many taxa show rapid responses to environmental perturbation; (4) some taxa are readily identifiable without specialized training; (5) many taxa are good indicators of areas of endemism; and (6) many taxa are readily sampled with quantitative methods, providing high quality data for statistical analysis. Insect diversity presents many groups that are highly appropriate for mapping patterns of species richness, areas of endemism, or taxic diversity, as well as monitoring environmental quality. Indeed, they are likely to prove more useful than many vertebrate groups, in part because of the statistical implications of their high diversity. But, biogeographers, conservationists, and others have often avoided insects, because of the inherent problems in dealing with them: (1) the tremendous number of species, especially in tropical areas such as New Guinea; (2) the daunting number of individuals in most tropical sites; and (3) because of these, problems in information transfer from the research community to the conservation and agricultural communities. The problems facing invertebrate study in the Pacific Basin involve: (1) lack of synthesis of what is already known but scattered throughout the world biological literature; (2) lack of expertise to study specimens already accumulated in collections; and (3) lack of adequate sampling of many islands and many taxa, especially those requiring specialized sampling techniques. Even where basic knowledge at an alpha taxonomic level is available, the phylogenies and detailed biological data necessary to add depth to biogeographic studies are usually lacking. As shown by the preceding chapters, it is possible to overcome these problems by focusing on a particular geographical region or a narrow taxonomic group, but a cohesive analysis of invertebrates is well beyond the scope of this book. The numbers of species involved in the insects, mites, and snails are so vast that detailed studies must focus on selected taxonomic groups.

Careful analysis of previous literature, use of accumulated museum collections, and field work by specialists are all important to the production of sound taxonomic and distributional data for biogeographic studies. For example, Clarke's (1986) masterful monograph of Marquesan moths detailed 260 species, of which 131 species and subspecies were described as new. Most of the new taxa were only recognized because of Clarke's careful collecting and rear-

ing of specimens. Studies based only on literature can be severely limited by poor sampling and perpetuation of taxonomic errors (see for example discussion in Baert and Jocque, 1993 and Lehtinen, 1993). For land snails, path analyses by Cowie (1996 and this volume) showed that collecting effort is a major contributor to recognized species diversity.

Pacific biogeography: The general overview

J. Linsley Gressitt laid out the classic vision of Pacific insect biogeography in a series of papers starting in 1956, with refinements in 1958, 1961, 1971, 1974, and finally restated in 1982a. While many details have been modified or added in the intervening years, the basic pattern remains the same. Revisions of various families and genera provide further data points, but most fit the basic Gressitt model. Studies of *Drosophila* flies and other organisms have also provided better insight into the evolutionary processes on Pacific islands (Carson, this volume).

The primary theme of Gressitt's vision relative to the oceanic Pacific islands (Gressitt, 1982a) was that the major island groups have separate more or less unique insect faunas that have evolved locally from ancestors that successfully colonized at rare intervals by dispersal. Islands more distant from source areas have less harmonic faunas, with fewer families and genera, and often with a great range of form (adaptive radiation) among descendants from a single ancestor. Islands nearer to source areas have more evolutionary lineages represented, and many diverge less from their continental relatives. There is striking reduction in the diversity of families and genera as one proceeds eastward across the Pacific from New Guinea. Wilson and Hunt (1967) discussed the role of small islands as "stepping stones" in facilitating dispersal across the Pacific, while Paulay (1994) provides a modern overview of these processes with many examples from Pacific islands.

Munroe's chapter in this volume provides a clear example of Gressitt's model, using new data on pyraloid moths (Lepidoptera: Crambidae and Pyralidae) for major island groups (focusing on Fiji, Samoa, Rapa, the Society Islands, the Marquesas, and Hawaii). There is a progressive decrease in the number of founding stocks and an increase in the proportion of radiating speciation with distance from Papuan source areas. Numbers of species show more relationship to area than distance, because local

speciation has compensated for a lack of colonizers. The cicada data summarized in the chapter by de Boer and Duffels shows a more severe faunal attenuation; the cicadas did not penetrate eastward past Samoa, presumably because vicariance was more important than dispersal in their distribution.

Another theme in Gressitt's vision was that the New Guinea insect fauna was dominated by Oriental elements (Gressitt, 1974): "For many insects it is more realistic to include the Papuan area ... and all of Melanesia, Micronesia, and Polynesia in the Oriental Region, with a zone of overlap with the Australian Region in southern New Guinea and northeastern Australia. ...insects and plants rather freely entered [the Papuan area] at various periods from the west, giving New Guinea and nearby islands a dominance of Oriental elements over Australian."

History of entomological surveys

Although early European explorers collected a few invertebrate specimens around the Pacific, the first comprehensive and well documented surveys for invertebrates were not made until the mid to late 1800s. The *Fauna Hawaiiensis* collections between 1892 and 1913 were probably the most significant entomological collections from the smaller Pacific islands up to that time. A series of subsequent major expeditions were undertaken by the Bishop Museum and collaborators between 1923 and 1940, including the Tanager, Whippoorwill, Whitney South Seas, Mangarevan, and Lapham Expeditions, and the Pacific Entomological Survey (Gressitt and Quate, 1958). See Frodin and Gressitt (1982) for a detailed review of biological exploration of New Guinea.

Beginning in 1953, J. Linsley Gressitt led massive entomological survey operations throughout the Pacific Basin, resulting in the most comprehensive collections ever assembled. This introduced a major era of intensive sampling, as well as detailed study of many aspects of Pacific entomology. In order to place the faunas of the small Pacific islands into a broader context, Gressitt expanded studies into New Guinea and Asian source areas, as well as Antarctica. Although Bishop Museum fieldwork continues, the pace slowed in the late 1970s. From the mid 1980s to the present, the Museum instead focused on rehousing, sorting, and curating previously collected material to maximize its usefulness for systematic and biogeographic studies.

In addition, from 1974 to 1978, the United Nations (United Nations Development Programme and the Food and Agriculture Organization) sponsored an agricultural pest and disease survey of American Samoa, Cook Islands, Fiji, Kiribati, Niue, Tonga, Tuvalu, and Western Samoa. The entomological survey was coordinated by the New Zealand Department of Scientific and Industrial Research (now LandCare), and resulted in the collection of some 500,000 specimens (Maddison, 1989). Although focused on agricultural issues, not biogeographic questions, this survey represents a rich source of biogeographic data. Unfortunately, very little has yet been published on these collections (Maddison, 1989; Dale and Maddison, 1984).

Major published sources of knowledge

Because the literature on Pacific biodiversity is very scattered, and the level of knowledge across the various island groups is very uneven, it is important to review the major sources (or recent papers that provide entry into the key literature) of entomological knowledge for the major island groups. Major sources for most islands are the now defunct serials *Pacific Insects* (1959-1985) and *Pacific Insects Monographs* (1961-1986), formerly published by Bishop Museum. The following list will focus on entomology; see Cowie (this volume) and Cowie *et al.* (1995) for background on land snails.

Cook Islands: No general review.

Easter Island (Isla de Pascua): Campos and Peña (1973); Holloway (1990b).

Fiji: There is no general summary, but see Robinson (1975) for Lepidoptera and biogeography, and Snow (1969) for further references.

Hawaii: The major series is *Insects of Hawaii* (Zimmerman *et al.*, 1948-1992). A checklist of terrestrial arthropods was published by Nishida (1994) and is available in updated form on Internet. See also Howarth (1990).

Henderson: Benton (1995); Benton and Lehtinen (1995).

Marquesas: Adamson (1935, 1936, 1939); Mumford (1936); Pacific Entomological Survey (1932, 1935b, 1939); see also Clarke (1986), Perrault (1978).

Micronesia, including Guam: The major series is *Insects of Micronesia* (1954-present), originally an independent serial published by Bishop Museum, now published within the journal *Micronesica*; also Samuelson and Nishida (1987), Swezey (1942, 1946).

New Caledonia: Chazeau (1993, 1995); see also Holloway (1979).

New Guinea: See many papers in Gressitt (1982b) and also papers cited in Gressitt and Szent-Ivany (1968) and Sekhran and Miller (1996).

Rapa: Clarke (1971); Paulay (1985).

Samoa: The major series is *Insects of Samoa* (9 volumes, 1927-1935), published by the British Museum (Natural History). See also the bibliography by Holmes (1984: 307-329). The Bishop Museum is currently producing checklists of the terrestrial arthropods and non marine snails.

Society Islands: Pacific Entomological Survey (1935a).

Solomon Islands: Greenslade (1969) and Bigger (1988); also many papers in the Rennell Island series (Wolff, 1958-1991).

Tokelau: Hinckley (1969).

Tonga: No general review, but see Snow (1969) for references.

Vanuatu (New Hebrides): Gross (1975), Robinson (1976).

Studies of Pacific Insect Biogeography

Although the literature on distribution of insects in the Pacific is vast, there are relatively few studies that have assembled comprehensive distributional data across many or most islands for taxa that include enough species from which to generalize patterns. Some of the more significant studies that have mapped diverse groups across the Pacific Basin include the following. In general, they reveal the typical pattern of faunal attenuation from west to east.

Belkin (1962): mosquitoes (Diptera: Culicidae)

Cassola (1990): tiger beetles (Coleoptera: Carabidae: Cicindelini)

Drew (1975): fruit flies (Diptera: Tephritidae)

Duffels and collaborators (1986, etc.); de Boer (1995); de Boer and Duffels (this volume): cicadas (Homoptera: Cicadidae)

Evenhuis (1982): bee flies (Diptera: Bombyliidae)

Gressitt (1956, 1961, 1971, 1982a): beetles (Coleoptera: Chrysomelidae, Cerambycidae)

Holloway (1983, etc.): moths (Lepidoptera: various families)

Muona (1991): beetles (Coleoptera: Eucnemidae)

Olmi (1990): parasitic wasps (Hymenoptera: Dryinidae)

Schuh and Stonedahl (1986): plant bugs (Hemiptera: Miridae)

Wilson (1959a); Wilson and Taylor (1967a): ants (Hymenoptera: Formicidae)

Zimmerman (1942): various (Hymenoptera: Mutillidae; Coleoptera: Curculionidae; etc.)

Gressitt (1956: 13) mapped a faunal subdivision of the Pacific area. While such maps are convenient tools for organizing biogeographic concepts, the boundaries are highly dependant upon the history and biology of the taxa chosen for mapping, as well as what assumptions are made for defining areas (overall similarity or other criteria). Stoddart (1992) criticized such maps of the Pacific for including heterogenous islands in artificial map units; he suggested focusing instead on typology: atolls, elevated limestone (makatea) islands, and high (often volcanic) islands. Van Balgooy *et al.* (this volume) encountered similar problems with Pacific plant distribution maps; also see comments in Schuh and Stonedahl (1986) about the limitations of concepts of biotic regions based on overall similarity.

The biogeography of butterflies of 26 archipelagos in the Pacific was recently addressed in a multiple regression analysis by Adler and Dudley (1994). They found that the total area of an archipelago and its distance from other land masses were important predictors of the number of butterfly species within an archipelago. Endemism was promoted by the number of large islands within an archipelago. It is worth

noting, however, that all their species numbers were derived from literature, which may be a serious limitation. Miller and Miller (1993), in a detailed paper not cited by Adler and Dudley, reported 24 species from Tonga, while Adler and Dudley reported 28 (perhaps synonyms were counted multiple times?).

Present

Status of taxonomic knowledge

Detailed estimates of the numbers of species known have only been undertaken for Hawaii (Eldredge and Miller, 1995; Miller and Eldredge, 1996), New Caledonia (Chazeau, 1993), and New Guinea (Sekhran and Miller, 1996: table 6.1). Other sources include R.H. Cowie (this volume – mollusks), L.G. Eldredge (pers. comm. – decapods), P.N. Turner (pers. comm. – rotifers), and Bridge and Page (1984 – plant parasitic nematodes). These figures are summarized in table 1. The figures in the table are generally numbers of species (including non-native) recorded in the literature, which sometimes greatly under represents the true number of species that will eventually become known. The figure for insects of New Guinea is an estimate of the eventual total. Gressitt (1958) provided estimates for numbers of insects on other Pacific islands and Cowie (this volume) provides estimates for land snails from some Pacific islands. The only large group of invertebrates for which a modern taxonomic catalog exists for the entire Pacific region is the flies (Evenhuis, 1989). Sadly, knowledge of many of the more obscure non-

marine invertebrate groups (e.g., Porifera, Coelenterata, Rotifera, Bryozoa), as well as the free-living protists, has advanced little since the review of Mumford (1940).

As noted by Holloway (1991), a further impediment to biogeographic studies in the Pacific, as well as Asian source areas, is the paucity of well resolved phylogenetic hypotheses (cladograms). Many of those that do exist have features that render them uninformative for biogeographic analysis, such as poor cladistic resolution, a large number of uninformative widespread taxa coincident over all or part of the range of the genus, or a high degree of localized sympatry. Schuh and Stonedahl (1986) provided one of the few cladistic biogeographic analyses of terrestrial insects in the Pacific Basin, but their analysis included few islands beyond New Guinea.

Patterns of endemism across various taxa appear to be correlated with dispersal capabilities. There is a high degree of endemism in many groups of insects and land snails. On the other hand, there appears to be relatively low endemism amongst the tiny invertebrates that presumably disperse as aerial plankton, such as tardigrades and rotifers. Some groups like mites are simply too poorly known to assess, because many species are known only from one sample. Similar patterns occur in plants, with relatively high endemism amongst flowering plants, contrasted with lower endemism rates amongst ferns and bryophytes, which disperse more readily. Further sampling and taxonomic refinement will be necessary before the patterns are really clear (Eldredge and Miller, 1995; Miller and Eldredge, 1996).

Table 1. Numbers of terrestrial and freshwater invertebrates known from Hawaii, New Caledonia, and New Guinea (see text for explanation).

Taxon	Hawaii	New Caledonia	New Guinea
Porifera (sponges)	1	2	?
Cnidaria (hydra)	2	?	?
Platyhelminthes (flatworms)	47	39	3 (not including parasites)
Acanthocephala (spiny-headed worms)	2	?	?
Nemertinea (ribbon worms)	2	?	?
Rotifera (rotifers)	41	?	140
Nematoda (nematodes)	237	2	63 (plant parasites only)
Bryozoa (moss animals)	2	?	?
Mollusca (mollusks)	896	213	1000
Annelida (worms)	29	44	47
Tardigrada (tardigrades)	21	?	?
Arthropods (other than insects and decapods)	897	506	500?
Decapod Crustacea (shrimps and crabs)	13	33	29
Insects	7862	3512	300000

Contributions of Pacific invertebrates to evolutionary theory

As noted earlier in this volume by Hampton Carson, the natural laboratory represented by the many iterations of island archipelagos throughout the Pacific Basin has provided fertile ground for the creation and testing of theories in evolutionary biology and biogeography. For instance, the Hawaiian *Drosophila* fruit flies are renowned for their importance as models of genetic processes in island biology (Carson, this volume and included references), and land snails, especially *Partula* in French Polynesia have also provided an important model system (Cowie, 1992). Some of the first ideas of stochastic evolution were based on little known studies on Hawaiian land snails by John Gulick (Carson, this volume; several essays in MacLeod and Rehbock, 1994).

Invertebrates on Pacific islands, especially ants, have been important in the development of biogeographic and ecological theory, primarily because of the interests of P.J. Darlington and E.O. Wilson. MacArthur and Wilson's (1967) book on the equilibrium theory of island biogeography, for instance, includes many ant examples. It is an interesting aside to note that Brown and Lomolino (1989) described the earlier independent, but unpublished, formulation of the equilibrium theory by E.G. Munroe, who went on to work on Pacific moths (this volume). Wilson (1959a, b, 1961) also proposed the taxon cycle based on his observations of Melanesian ants; see Darlington (1971a, b) and Bickel (this volume) for further discussion of taxon cycles in the region. Wilson and Hunt (1967) and Wilson and Taylor (1967b) further expanded on these models of the dispersal and evolution of species on Pacific islands (see also Dlusskiy, 1993).

Even so, much remains to be learned about the pervasive ecological interactions of ants and other social insects on islands (e.g., Cole *et al.*, 1992; Gillespie and Reimer, 1993; Reimer, 1994). Wilson (1990, 1996) pointed out that the lack of native social insects in Hawaii and several other Pacific islands is a rare experiment in the ecological importance of social insects. Specifically, he has suggested that this lack of native social insects "was a major contributor to some of the tendencies characterizing the Hawaiian biota as a whole, including flightlessness, lack of evasive behavior, increased abundance and diversity of carabid beetles and spiders, adaptive shift to predation in some terrestrial insect groups, and the loss of extrafloral nectaries in flowering plants" (Wilson, 1990, 1996).

New Guinea: mobile organisms in a geologically complex area

New Guinea and surrounding islands provide major challenges for understanding the complex interrelationships of "mobile organisms in a geologically complex area" (Holloway, 1982). The island of New Guinea has evolved as a major land area only over the past ten or so million years through fusion and compression of inner and outer Melanesian island arcs between the northward moving Australian continent on the Indian Ocean tectonic plate and the westward moving margin of the Pacific tectonic plate. Only in the Pliocene and Pleistocene have its mountain ranges been uplifted to the snow line, to be glaciated extensively during the latter period. Despite this geological youth, the insect fauna has attained a diversity that appears to be equivalent to that of the much older tropical lands of Southeast Asia (Gressitt, 1982b). The majority of this fauna has its closest relationships with that of Asia, with the genera tending to be fewer in number but more species-rich. For instance, the majority of moth genera endemic to Melanesia are restricted to, or have their species richness strongly centered in, New Guinea (Holloway, 1984b: 159). Rapid development of high diversity in a geologically unstable environment with high relief is counter to some hypotheses of tropical diversity, particularly those based on environmental stability over long periods of geological time. Therefore studies of the biogeographic origins of the New Guinea fauna and speciation patterns within it are likely to throw considerable light on the process of increase in species richness (Holloway, 1982, 1990a).

Although many authors have addressed the biogeographic relationships of the New Guinea fauna to those of adjacent regions, particularly in regard to the importance of Australian versus Oriental elements, few authors have attempted analyses of biogeography within New Guinea (especially patterns of regional endemism). The paucity of data for regionalization of New Guinea became very clear in an extensive literature survey for the *Papua New Guinea Conservation Needs Assessment* – an attempt to identify the areas within the country of greatest importance to biodiversity conservation. Even amongst the relatively well known ground beetles (Coleoptera: Carabidae), patterns based only on literature records proved misleading. For example, of 11 carabids that were known only from the Northern Province Lowlands (putative regional endemics), four were repre-

sented in the Bishop Museum by specimens from outside of the Northern Province Lowlands (Miller, 1993). Thus, previously unpublished data from museum collections will be important to a comprehensive view of invertebrate biogeography in New Guinea. The best analyses of regional patterns are those for cicadas (Duffels and de Boer, 1990; de Boer, 1995; de Boer and Duffels, this volume and references therein) and aquatic insects (Polhemus, 1993 and this volume). There are relatively few modern revisions (*e.g.*, those applying modern species concepts to adequate samples) of speciose groups in New Guinea. Among the taxa for which such data exist are some groups of mosquitoes, sarcophagid flies, aquatic bugs, ground beetles, chrysomelid beetles, pyraloid moths, butterflies, and cicadas.

A particular problem in New Guinea biogeography remains the continuum in species distribution across the Torres Straits between Australia and New Guinea. Little has been published on the subject since Taylor (1972) concluded that the "Torres Strait itself has had little apparent influence on the patterns and does not seem to be a significant barrier to dispersal in most insect groups nor, perhaps, is it a notable discontinuity [in distribution patterns]." Major problems remain in lack of data (particularly sampling of the savannah element in Papua New Guinea), as well as lack of taxonomic concordance between the faunas, since the Australian and Papuan faunas tend to be studied as isolated units.

Dispersal and vicariance in the distribution of terrestrial arthropods

Much of the Pacific Basin was colonized primarily from New Guinea and adjacent areas via over-water dispersal. However, it is now becoming clear that some taxa colonized islands of the Southwest Pacific via island arcs, some quite ancient, formed along dynamic plate boundaries (*e.g.*, Polhemus, this volume). Thus the distribution of invertebrates represents a mixture of dispersal and vicariance (for example, the flies discussed by Bickel in this volume show both patterns). Even so, the islands north and east of Samoa apparently originated from isolated volcanic hotspots and would have been accessible only to species capable of crossing large water gaps. Because of the extensive discussion of vicariance and underlying geology elsewhere in this volume (Polhemus, de Boer and Duffels,

Kroenke), the remainder of this section will review current ideas about dispersal.

Large scale experiments by the Bishop Museum from 1957-1970 in air screening over the oceans produced thousands of specimens. Nets were attached to ships and airplanes transverseing the Pacific Ocean. Results of this trapping show a very good correlation, with some exceptions, between the types and proportions of insects trapped and the make-up of faunas on isolated oceanic islands (Holzapfel and Harrell, 1968; Holzapfel *et al.*, 1978). Peck (1994a) performed similar experiments with aerial nets on boats traveling between the Galapagos Islands, and also examined the arthropods on the surface of the water (pleuston) (Peck, 1994b). These studies all demonstrated that, at least for many arthropod taxa, aerial dispersal is possible, although none of these studies were able to differentiate specimens that were collected in good health from those that were dead or dying.

The pervasive influence of humans in both active and passive assistance to the movement of organisms in the Pacific is still under appreciated. Especially among the tiny species, like thrips, it can be hard to separate the effects of wind transportation from movement by commerce, including very early events in human history such as Polynesian voyaging canoes and the advent of European explorers and colonists in the Pacific (*e.g.*, Mound, 1983; Dale and Maddison, 1984).

In a review of moss-inhabiting mites of the Pacific islands, Hammer (1982) discounted movement with humans. She suggested that moss mites spread across the ocean by rafting. She noted striking similarities in the faunas of Fiji, Tonga, and Samoa, but a major lack of shared species between Hawaii and the other Polynesian islands. But, a different group of soil mites studied by Niedbala (1994) showed close relationships between Hawaiian and other Pacific islands. Schatz (1991) felt that rafting and transport on other organisms, especially birds, are the most important means of dispersal of mites to oceanic islands, although he also discussed the unknown magnitude of transportation via human commerce.

Ferguson (1991) published a fascinating essay on the long-range dispersal and biogeography of Lepidoptera that may change the way we think about widespread species on islands. He found that aggressive, widely distributed migrants dominate the moth fauna of many oceanic islands. When the islands are considered on an individual basis, these species are gener-

ally considered to be non-native and to have been passively transported by human activities. However, many of these species and genera are widespread on islands worldwide, suggesting that they may disperse by themselves, although the spread of their weedy hostplants by human activities may also benefit them. Ferguson goes on to document the migratory abilities of many moths of eastern North America. Similar observations in the Pacific have been made by Gregg *et al.* (1994), Farrow (1984), Fox (1978), and Holloway (this volume).

The rapid spread across the Pacific of *Marcia abydata* Guenée (Lepidoptera: Geometridae) and *Heteropsylla cubana* Crawford (Homoptera: Psyllidae) since 1970, presumably following their host *Leucaena leucocephala* (Lam.) de Wit., shows how rapidly insects can disperse and become established (Muddiman *et al.*, 1992; Holloway, 1993).

The future

Challenges for further study

Non-indigenous species (also known as adventive, alien, immigrant, non-native, or introduced [in the broad sense] species) are a major focus of concern for agriculture; forestry, public health, and conservation (U.S. Congress Office of Technology Assessment, 1993, 1995). Many Pacific islands have been deluged with non-indigenous species as a by-product of commerce. Although this began with the earliest human voyages, the scale of transportation first seen in World War II, followed by the advent of commercial air travel, brought the transport of organisms to epidemic levels. Another wave of non-indigenous species has come with intentional introductions for biological control of both invertebrate and weed pests. Hawaii is probably the extreme example: it currently hosts over 3000 species of non-indigenous terrestrial arthropods, of which over 400 were introduced for biological control (Nishida, 1994). Quarantine regulations that are both well designed and consistently implemented remain important in slowing the spread of non-indigenous species (Miller, 1994).

The Pacific islands, especially Hawaii, have hosted a tremendous number of organisms introduced for biological control (Waterhouse and Vargo, 1993; Waterhouse and Norris, 1987, 1989; Waterhouse, 1993). Although some of these introductions have been successful at controlling pest organisms, others have had signifi-

cant unintended impacts on non-target organisms (Howarth, 1991; Nafus, 1993). For instance, the predatory snail *Euglandina rosea* is a major threat to native land snails (Cowie, this volume). It is therefore imperative that future biological control projects follow well designed guidelines to assure the environmental and economic success of the enterprise (Waterhouse, 1991).

What are the conservation issues facing invertebrates? Some of the issues, such as the impacts of invasive alien species are becoming clear (Howarth and Ramsey, 1991; Cowie, this volume). Given the immense ecological importance of invertebrates, as well as the vast portion of overall biodiversity that they represent, how then can they be taken into account in conservation management (New and Yen, 1995)?

Despite the popular conception that many island archipelagos that are "well known" (*e.g.*, Hawaii and Galapagos), there is still a great need for basic data on the distribution, systematics, and ecology of island invertebrates. Evaluation of MacArthur and Wilson's equilibrium theory of island biogeography requires census data over time, which are available only in rare cases (Gilbert, 1980). Conservation applications now being attempted on many islands demand quality data on current distribution and status of populations. Interpretation of evolution and biogeography requires a firm understanding of geography (especially tectonic and eustatic changes over time) and human induced changes.

What triggers the evolution of species-rich groups and adaptive radiations? While groups that have undergone major adaptive radiations may be less common than was once thought (*e.g.*, Peck, 1991, this volume; see also Cowie, 1996), some studies are recognizing presumed polymorphic "species" as new species-rich groups, especially when modern species concepts and novel character states are used (*e.g.*, Hoch and Howarth, 1993; Otte, 1994; Thornton, 1990). This parallels the situation in herpetology where application of new species concepts to what were previously considered widespread species are revealing whole new biogeographic patterns (Allison, this volume; Radtkey *et al.*, 1995).

The rugged topography of some Pacific islands, coupled with the poor dispersal abilities of some insects and snails, has promoted spectacular radiations on small islands. For example, Paulay (1985) documented 67 species of the weevil genus *Miocalles* on the island of Rapa which has an area of only 40 km². Cowie (this volume) notes a similar situation in land snails.

But in other cases, colonizing lineages have not speciated, resulting in a single endemic species within a genus that is widespread through an island archipelago, such as the butterfly *Vanessa tameamea* in Hawaii (Carson, 1987). Different levels of endemism amongst different higher taxa present related questions (see discussion above; Cowie, 1996).

Although Becker (1975, 1992) has examined the ratios of herbivorous and carnivorous insects on many islands, his ideas have not yet been evaluated on Pacific islands other than the Galapagos. This is basically because of lack of suitable inventory data.

The way forward

Given the daunting diversity of Pacific invertebrates, how can progress be made in answering some of these research questions? Several new initiatives may provide more effective ways to proceed in cooperative research endeavors.

The Hawaii Biological Survey was founded at the Bishop Museum in 1992 to address many of the issues discussed above in relation to Hawaii. The strategy of the Hawaii Biological Survey is to do the following for each major group of plants and animals, in collaboration with a variety of other agencies (Allison *et al.*, 1995): (1) develop a computerized database of the literature; (2) prepare a taxonomic checklist based on the literature, collections, and consultation with experts; (3) database Bishop Museum's extensive collections; (4) database information from other collections or other organizations conducting biological surveys (or establishing computer linkage to this information); (5) fill gaps in information through additional fieldwork and research; and (6) make this information widely available to users, in both traditional (*e.g.*, printed) and non-traditional (*e.g.*, Internet World Wide Web) forms. Because of the long history of research in Hawaii, we have initially emphasized the synthesis and dissemination of existing knowledge, in the belief that it is more cost effective to recognize what is already known than to have to discover it again. The Hawaii Biological Survey strategy has now been tested in Hawaii, and provides a useful model that may be applied more broadly within the region (Mlot, 1995).

The problems of lack of information, as well as challenges in the synthesis and dissemination of the information that does exist on Pacific invertebrates, led to the formation of the Pacific

Biosystematics Network (PACINET), under the auspices of BioNet International and the South Pacific Commission as this book was being completed (February 1996). It appears that one of the first activities of PACINET, in cooperation with the Pacific Science Association and many systematics research institutions, will be a symposium and publication bringing together a broad range of expertise to tabulate the status of knowledge of all the invertebrates.

Hopefully this will be the beginning of a new era in the understanding of these fascinating and important creatures. Biodiversity information initiatives such as these promise to strengthen the basic infrastructure of science in the Pacific, providing new opportunities to address the research questions outlined here and many others. It is especially important to return information to the islands themselves, to enable the local residents to understand and manage their own biotas.

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