Hawaiian Terrestrial Arthropods: An Overview

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ABSTRACT

The Hawaiian Islands are the most isolated group of islands in the world. The 8 main southeastern islands, with their sequentially younger ages, great physiographic and climatic variation, and the repetition of climatic regimes and ecosystems on each island, are ideal natural laboratories for evolutionary and ecological research. Few organisms crossed the vast oceanic distances and successfully colonized the islands. About 400 colonizers gave rise to over 5,000 endemic species of arthropods, with probably at least as many more undescribed species awaiting study. This dearth of knowledge of the total fauna makes it difficult to assess their conservation status and formulate conservation programs for native arthropods. Over 3,200 alien species of arthropods have been purposefully or inadvertently introduced by human activities. Possibly 2,500 of these are established residents. Declining populations of native species indicate the impacts of these aliens may be severe. Systematic studies, field surveys, and long-term ecological research programs are needed to determine the status of native and alien species and formulate conservation programs for the remaining native species. Recent biological discoveries demonstrate that no habitat should be excluded from survey.

INTRODUCTION

The Hawaiian Islands, which extend 2,400 km from the northern subtropical to tropical Pacific, are the most isolated high islands on earth (ca. 3,850 km from any continent and about the same distance from the nearest high islands, the Marquesas in French Polynesia). The Hawaiian Islands are the summits of giant submarine volcanoes emanating from a hot spot in the mantle below the Pacific Tectonic Plate. The Hawaiian Hot Spot has been relatively stationary over time, producing volcanoes in assembly-line fashion as the Pacific Plate moved northwest. Each island or island group is progressively older in a northwest direction and each has always been isolated from the others by deep straits 40 km or more wide (Dalrymple, Silver & Jackson 1973).

The island chain originated over 70 million years (ma) ago and is comprised of 3 parts (Fig. 1): the youngest 8 main islands (originated <5.6 ma ago) with their satellite islets at the southeast end, the relict volcanic islands and coral atolls (ca. 6–30 ma) in the middle, and a long chain of progressively more sunken seamounts (35–>70 ma) stretching to the Aleutian Trench. Undoubtedly, additional islands once existed but are now subducted into the trench (Clague & Dalrymple 1987).

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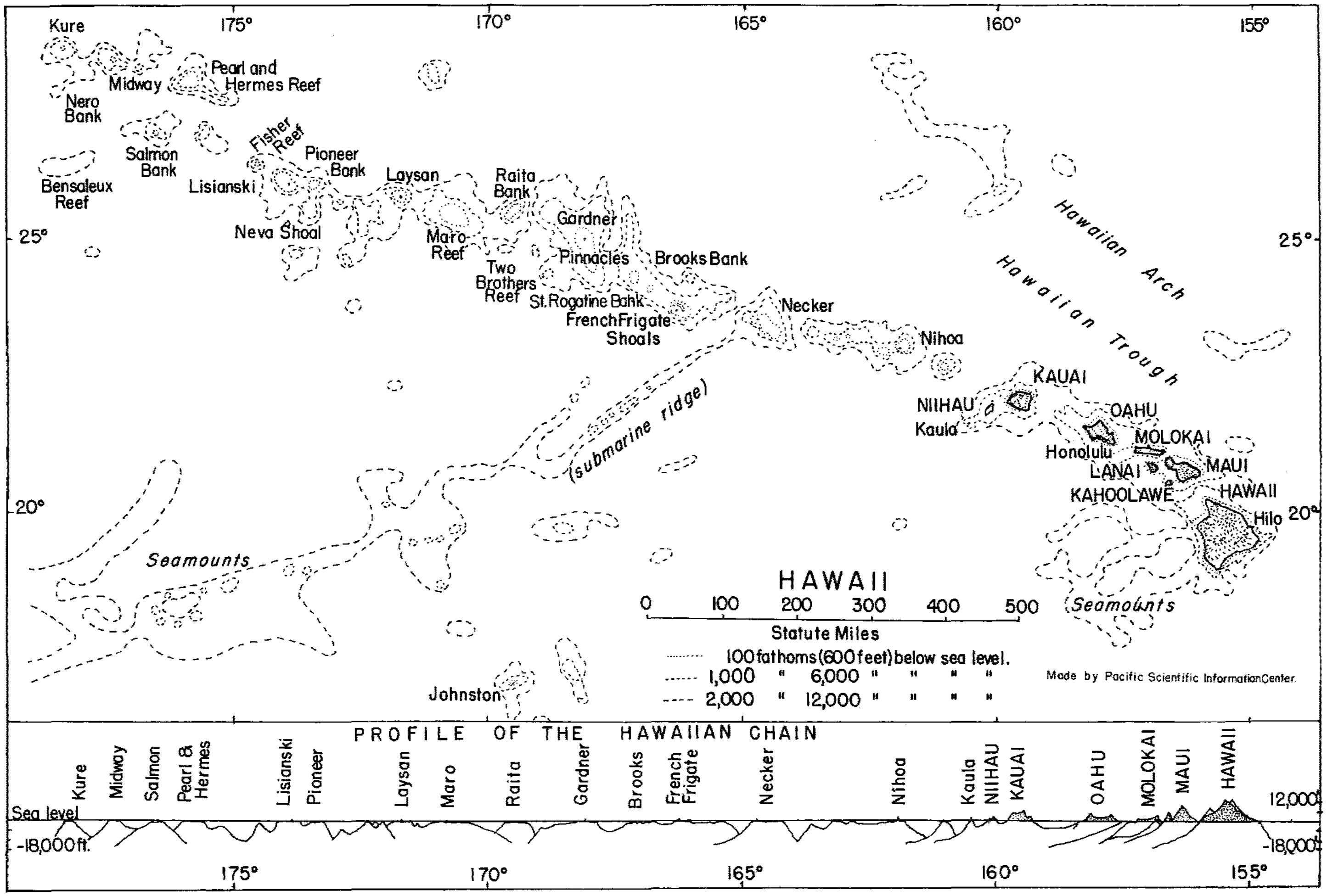

Fig. 1. Map of the Hawaiian Islands, showing both plan and profile view of the island chain. (Copyright Bishop Museum. Geography and Map Collection, Bishop Museum.)

The major ecosystems in the Hawaiian islands are: littoral (on both rocky and sandy shores), strand plant community, lowland dry scrub, desert, grassland, partly deciduous dry forest, mesic forest, and (on the windward sides of some islands) lowland rain forest grading into a montane rain forest near 900 m. On the higher mountains a cool dry forest or savannah (mountain parkland) occurs above 1,500 m, which grades into alpine scrub (above 2,000 m) and a stone desert supporting an aeolian community (above 3,000 m) (Fig. 2). The boundaries of these ecosystems are dictated by climate, local topography, lava morphology, age, soil development, altitude, and degree of human disturbance. These ecosystems have been further subdivided into about 120 different communities on the basis of dominant plants (Gagné & Cuddihy 1990), and all of the world's major plant formations occur within the islands (Mueller-Dombois, Bridges & Carson 1981). Young unvegetated lava flows in each climatic regime also support aeolian communities, and lava tubes and other voids in young lava support diverse communities of cave animals (Howarth 1987). More than 180 distinct natural communities (i.e., discrete groups of interacting species in a common area) are found in the Hawaiian Islands, comparable to the number of communities found in continental areas (Mueller-Dombois, Bridges & Carson 1981; Gagné & Cuddihy 1990; Daws 1988). Part of the reason for this great diversity of habitats and natural communities results from the great rainfall gradients created orographically by the northeast tradewinds. Rainfall varies from between 25 cm on leeward coasts to over 1,000 cm at mid-elevation windward sites.

The Southeastern Hawaiian Islands

Hawai'i Island, locally known and referred to hereinafter as the "Big Island," is the youngest, largest, and highest island in the chain (500,000–700,000 years old, 10,000 km^2 in area, and 4,205 m above sea level). It was formed by the coalescing of 5 volcanoes: Kohala, Mauna Kea, Hualalai, Mauna Loa, and Kīlauea. Mauna Kea (4,205 m) bears the scars of past glaciers and broke the ocean surface at least 380,000 years ago. Mauna Loa (4,170 m) and Kīlauea (1,220 m) are still very active.

Lava flows create continuous strips of new substrates with similar chemical structure for animal and plant succession along altitudinal and climatic gradients. These flows are more or less regular in time and space and cover parts of older flows, allowing comparisons of recolonization and succession on different age lava flows, in different climates. Islands of older vegetation surrounded by younger lava flows, called "kipukas" are abundant on the younger volcanoes. These are often rich in native species and provide benchmarks for later successional stages. In spite of the locally high rainfall, Kīlauea and Mauna Loa lack surface streams because of the high porosity of the young lava. The aquatic fauna of Mauna Loa and Kīlauea is meager and restricted to leaf axils and other small pools in the rain forest and in coastal pools in lava. The oldest volcanoes on the Big Island have young but well-developed streams and a better developed aquatic biota.

Northwest of the Big Island is an island complex, sometimes called Maui Nui, consisting of 6 volcanoes on 4 islands (Maui, Kaho'olawe, Lana'i, and Moloka'i), which have been separated by subsidence and erosion (Clague & Dalrymple 1987). Biologically, they comprise 5 distinct areas: East Maui or Haleakalā (0.8 ma), West Maui (1.3 ma), Kaho'olawe (>1.3 ma), Lana'i (1.3 ma), and Moloka'i (1.3–1.8 ma). Lana'i, West Maui, and Moloka'i are similar biogeographically, sharing many taxa, often with closely related species on neighboring mountains. East Maui (Haleakalā) is younger and higher (3,050 m) than these 3 islands and shares taxa with them but shares more with the Big Island than do the others. Kaho'olawe is the lowest island and has been badly degraded through human disturbance.

The geologically defined cave and aeolian habitats, found on the Big Island, disappear on the older islands, except locally on post-erosional flows and on the younger Haleakalā volcano.

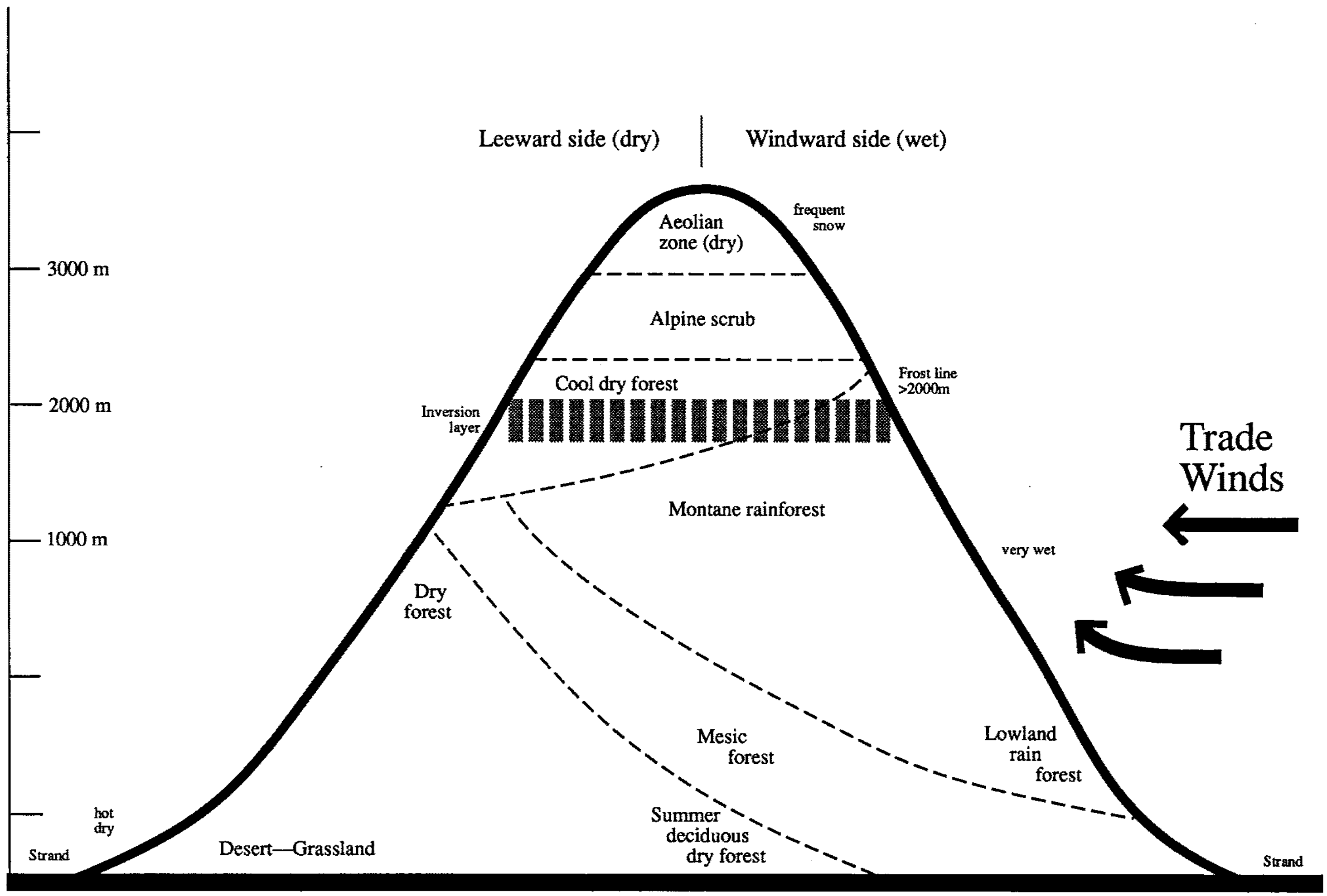

Fig. 2. The major vegetation zones show on a generalized cross-section through a higher Hawaiian mountain. Altitude not to scale.

Table 1. Number of species of selected native insect groups endemic* or (indigenous**) to each island.

	NW	Kaua'i	Oah'u	Maui Nui***	Hawai'i
Diptera:					
Drosophila (all infuscate winged sp.)	0	23(4)	50(7)	70(7)	52(10)
Discritomyia	0	2(3)	4(3)	6(3)	9(3)
Lispocephala	0	12(0)	18(1)	45(3)	28(3)
Campsicnemus	0	6(2)	30(6)	54(12)	31(12)
Eurynogaster	0	14(2)	17(4)	14(4)	5(4)
Scaptomyza (Elmomyza)	0	19(6)	5(6)	25(14)	19(13)
Limonia (Dicranomyia)	0	1(7)	1(8)	3(8)	1(7)
Coleoptera:					
Oodemus	4	20(0)	12(2)	14(6)	6(4)
Plagithmysus	1	19(0)	20(0)	52(0)	44(0)
Mecyclothorax	0	0(0)	6(0)	63(0)	16(0)
Bembidion	0	7(4)	2(3)	3(3)	2(0)
Odonata:					
Megalagrion	0	9(1)	5(4)	5(6)	3(6)
Orthoptera:					
Banza	1	2(0)	2(0)	4(0)	1(0)

* Endemic refers to species naturally occurring only on the listed island.
** Indigenous refers to species naturally occurring on the listed island as well as on other islands.
*** Maui Nui includes the islands of Maui, Lana'i, Moloka'i, and Kaho'olawe.

However, streams are more numerous and the aquatic fauna better developed. Many more groups have colonized Maui Nui than the Big Island, and speciation within this four-island complex gives it the most diverse arthropod fauna in the archipelago (cf. Table 1).

O'ahu was formed by 2 volcanoes 2.6 and 3.7 ma ago, respectively. The highest ridges, though highly eroded, rise up to 1,230 m. Despite the pressures from a metropolitan population, a significant portion of the native biota survives. For example, some of the best remaining lowland dry forests occur on O'ahu because of the greater hunting pressures on alien ungulates than on other islands. Additionally, the stream fauna and bog communities are well developed. However, aeolian and alpine communities have completely disappeared, and the cave fauna is reduced to relictual pockets. The island, along with many habitats, has been reduced in size by subsidence and erosion, but the spectacularly dissected topography and greater age have led to speciation through *in situ* isolation which has resulted in extreme local endemism in some groups.

Kaua'i is the oldest of the main islands but is still a mere 5.1–5.6 ma old. It rises nearly 1,600 m and has one of the wettest spots on earth, with rainfall up to 1,500 cm/yr. Kaua'i is more isolated, being 116 km from Oahu, and supports many relicts and more primitive members within many native groups. Habitats are older and seem to be more mature with more species sharing resources. In relation to land area, the insect fauna of Kaua'i is probably the most diverse but least known of any in the Hawaiian islands. The large central plateau, the Alakai Swamp, has a diverse rain forest biota, but it is threatened by introduced ungulates and invasive weeds. An episode of voluminous post-erosional lava flows rejuvenated the island 0.6–1.4 ma ago, and a small but interesting relictual cave fauna survives.

The Northwest Hawaiian Islands

Most of the northwestern Hawaiian Islands are administered by the U. S. Fish and Wildlife Service as a wildlife sanctuary. However, the main emphasis of management and protection has been devoted to birds and near-shore marine vertebrates (mammals and turtles). The insect faunas of these low islands are still poorly known, yet they offer an exciting opportunity for future research on what was once the lowland insect fauna of the main islands. Insects associated with sea birds and marine littoral habitats on these islands are often widespread. In addition, endemic members of many typical Hawaiian insect groups are, or were at one time, found on these islands, indicating a stepping-stone progression of the fauna along the chain.

Nihoa and Necker islands, 250 km and 540 km northwest of Kaua'i, respectively, are volcanic remnants with relict lowland biotas. Many plant and animal groups still survive on these islands and provide a partial view of what the lowland biota of the main islands was before the arrival of humans (Conant et al. 1983). Necker Island is unique in resting on the shoulders of a much older sea mount (Rotondo et al. 1981), but there is no biological or geological evidence that any part of this sea mount was above sea level or had a terrestrial biota when it joined the Hawaiian chain (Simon et al. 1984). Of special concern to the native and endangered biota on both islands is the recent invasion by several alien insect pests. Some of these immigrants may have arrived by natural dispersal from the main islands, though dispersal as stowaways on landing craft is more likely.

The islands northwest of Necker become successively more eroded and sunken (reduced to lava pinnacles, shoals, and atolls). Early incidental collections indicate they once had a unique Hawaiian biota, but all of them have been more or less disturbed by human intervention (Bryan 1926; Butler & Usinger 1963; Beardsley 1966). The cascading demise of a major portion of the native biota of Laysan after the introduction of rabbits remains one of the best examples of detrimental effects of alien species on an island ecosystem. Many native insect species still survive, however.

Northwest of Kure Atoll, the oldest of the emergent Hawaiian islands, the chain angles northward as the Emperor Sea Mounts. At least some of these are guyots indicating that they were once above sea level. These guyots very likely acted as stepping stones for some of the current Hawaiian biota.

ORIGIN OF THE BIOTA

The biota of the Hawaiian Islands has been constrained by the extreme isolation, youth, and climate of the islands. Only those groups that could disperse across vast oceanic distances and were able to establish viable populations became successful colonizers. Many propagules arrived only to find their beachhead unsuitable or were unable to reproduce, and so they perished. The terrestrial fauna is composed primarily of 3 characteristically vagile groups: arthropods (especially insects), land snails, and birds. Native terrestrial mammals are represented by only 2 bats, 1 of which is extinct (Tomich 1986, Ziegler & Howarth, unpubl. data).

The youth of the islands is reflected in the fauna. Most groups present are young, widespread, successful groups on the continents (e.g., among the insects *Agrotis*, *Nysius*, *Odynerus*, *Crabro*, *Hyleaus*, *Drosophila*, Curculionidae, and Carabidae). Many primitive continental groups are absent, although *Proterhinus* (a primitive weevil that is most speciose in Hawai'i) and others are exceptions.

Those that successfully established evolved to exploit jointly the full range of available habitats. Insects, disproportionately well-represented on oceanic islands, are theoretically among the most important groups in nutrient cycling in most island ecosystems (Howarth 1985; Wilson 1987). Those arriving by air were phoretic on birds, flew themselves, or drifted with wind as aerial plankton. Those arriving by sea swam, drifted with waves, or rode on

Table 2. Tentative summary of Hawaiian terrestrial arthropods.

Order	Endemic* species	Indigenous** species	Alien*** species
Palpigrada			1
Pseudoscorpionida	4		5
Scorpionida			1
Schizomida			1
Acari†	92	6	396
Araneae†	101		73
Amphipoda†	4	1	2
Isopoda†	3	?	17
Diplopoda†	15		10
Chilopoda†	4?		22
Pauropoda			2
Symphyla			4
Protura			1
Diplura			4
Collembola†	9		57
Thysanura	2		5
Ephemeroptera			3
Odonata	31	2	6
Orthoptera†	52		27
Blattaria			21
Mantodea			6
Dermaptera	7	1	11
Isoptera			6
Embioptera			2
Zoraptera			1
Psocoptera†	75	5	41
Mallophaga†	4	15	47
Anoplura			14
Thysanoptera	26		122
Heteroptera†	216	1	100
Homoptera†	385		294
Neuroptera†	51		8
Lepidoptera†	952		194
Trichoptera			3
Coleoptera†	1373	15	610
Strepsiptera			4
Diptera†	1115	10	431
Siphonaptera	1		9
Hymenoptera†	641	16	624
Totals	5163	72	3185

Source: Nishida & Miller 1989.

* Endemic refers to species naturally occurring only in Hawai'i.

** Indigenous refers to species naturally occurring in Hawai'i as well as elsewhere.

*** Alien includes both inadvertent and purposefully introduced species.

† Indicates groups in which significant number of additional species are known, but not yet described.

Table 3. Relative representation of major insect groups in different regions.

Order	Number of species in major insect groups as a percentage of the total regional fauna			
	World (762,659)*	North America (93,728)*	Hawai'i *1948* (3,722)*	Hawai'i *1989* (5005)*
Coleoptera	39	32	37	28
Diptera	16	19	7	22
Lepidoptera	15	12	23	19
Hymenoptera	14	19	17	13
Other Orders	16	18	16	18

Sources: World and North American data from Danks (1988), Hawaiian data from Zimmerman (1948) and Nishida & Miller (1989).

*Number of currently recognized native species.

flotsam (Carlquist 1981). The oceanic distances to Hawai'i have always been so vast that, except for halophilic species, the sea was a poor avenue for the dispersal of arthropods. Wind, especially storms and jet streams, carried most of the successful propagules of arthropods to the isles (cf. Holzapfel, Clagg & Goff 1978).

Biologists visiting the islands are at first struck by what is not present because relatively few colonizers succeeded in becoming established. Only about 50% of the known orders and just 15% of the known families of insects are represented in the native fauna (Table 2). Only 350–400 separate colonizations can account for the total estimated insect fauna (ca. 10,000 endemic species), an average of 25 species per colonization (Zimmerman 1948; Gagné 1988; Nishida & Miller 1989). Over the 70 ma age of the islands only 1 long-distance dispersal event every 175,000 years could account for the current fauna. Even if they all arrived during the age of the present high islands, only 1 arrival every 12,750 years would account for just the insect fauna. The specific numbers are less extreme for other groups, but the pattern of only a few colonizers giving rise to many closely related species is a characteristic of the Hawaiian biota (Zimmerman 1948; Howarth, Sohmer & Duckworth 1988; Wagner, Herbst & Sohmer 1990).

Most native insects are representatives of modern, small, vagile groups that are often found dispersing as aerial plankton on the continents and over the oceans (Gressitt & Yoshimoto 1963; Hespenheide 1977; Holzapfel, Clagg & Goff 1978). These include small flies, beetles, wasps, moths, bugs, leafhoppers, and planthoppers. Large showy insects and the primitive, flightless, moisture-loving soil forms are poorly represented. Many groups important in continental areas are missing. There are no native chrysomelid, scarabaeid, or buprestid beetles, swallowtail butterflies, termites, short-horned grasshoppers, cockroaches, mayflies, stoneflies, horse and deer flies, bumblebees, sawflies, ants, and only one flea. Beetles, flies, moths, and bugs are perhaps proportionately better represented in Hawai'i than elsewhere (Table 3).

Each island received propagules from neighboring older islands with the infusion of rarer colonizers from greater distances. Hawai'i, being in the northern mid-Pacific, has received these long-distance propagules from all points of the compass, but unfavorable equatorial ocean and air currents greatly restricted groups from crossing the equator (Armstrong 1983; Hourigan & Reese 1987). The majority arrived from the Oriental region and could have island-hopped across part of the western Pacific. A large percentage belong to Holarctic groups and could have come from the north, east, or west. The *Drosophila* most likely came from north Asia

(Carson 1987a), the butterflies *Udara* and *Vanessa* from the west, the *Manduca* hawkmoth from the east, and *Hyles* hawkmoths from the east, west, or north. Some representatives, such as *Plagithmysus* beetles, are from the Nearctic region (Gressitt 1978) and a few, such as the prognathogrylline crickets and the *Oodemus*, *Rhynchogonus* and *Proterhinus* weevils, are characteristic Hawaiian or Pacific groups without clear continental affinities.

HISTORY

Polynesians knew the native insects and developed cultural and verbal traditions concerning the native insect fauna of the Hawaiian Islands. Unfortunately, little of this oral tradition was recorded by westerners before this aspect of Hawaiian culture was lost. Some of the Hawaiian insect names are listed in Kent (1986).

Scientific knowledge of Hawaiian biology developed during 3 periods: the exploration period (1778–1850), the resident naturalist period (1820–1900), and the modern period (1900 to the present) (Kay 1976). Unfortunately, arthropods were neglected by most of the early explorers, and even specimens brought back were ignored by the scientists in Europe and North America. Insects were collected by the naturalists on Cook's initial voyage to Hawai'i in 1778 and 1779, but only 2 wasps were described from the material. Plants, snails, and birds captured the curiosity of the early naturalists, and a myth developed (which at first proved hard to break) that insects were uncommon or rare on oceanic islands.

Entomological studies began in earnest late in the resident naturalist period with the arrival of the 1st resident naturalist to concentrate on insects, the Reverend Thomas Blackburn who lived in Hawai'i for 6 years (1877–1883). He supplied scientists at the British Museum (Natural History) and elsewhere with a steady stream of specimens, finally dispelling the myth that insects were poorly represented in Hawai'i. Unfortunately, many of Blackburn's species have not been recollected. Human activities and invasions of alien biota, especially cattle and other ungulates, destroyed much of the native biota before insects were seriously collected. We owe much of our understanding of the native lowland insect fauna to Blackburn's work.

The modern period of Hawaiian entomology began just before the turn of the century with the arrival of professionally trained scientists. At about this time plantation agriculture was growing as the principal economic base. Newly arriving alien insect pests were a continual concern, especially to sugar cane crops. In 1893 the Hawai'i National government hired Albert Koebele, who had just established a successful pest control program in California using alien insect predators. Koebele traveled throughout the world sending alien species to Hawai'i and is credited with introducing hundreds of beneficial species for biological control (Swezey 1931; Funasaki et al. 1988). It was a grandiose experiment in ecology, but, unfortunately, accurate records of specific introductions, their fate, and resultant impacts on the native biota were not kept. Additionally, important questions on the impact on nontarget organisms were never researched or answered.

Growing awareness of the diverse and unique fauna of Hawai'i, as well as the specter of extinctions, led to the commissioning of a faunal survey sponsored jointly by the Royal Society of London and the British Association for the Advancement of Science in collaboration with the Bishop Museum, Honolulu. They hired the British entomologist R.C.L. Perkins for the formidable task of conducting the survey's fieldwork that eventually resulted in the *Fauna Hawaiiensis* (Sharp 1899–1913; Perkins 1913). From 1892 to the early 1900s, he made truly remarkable collections of many groups, concentrating especially on Coleoptera, Lepidoptera, Hymenoptera, Odonata, and some minor orders. Only a few groups, including the Diptera and Heteroptera, were less well covered. His ability to procure good material and identify species in the field is now legendary, and his accounts include a wealth of biological information

(Manning 1986). The 3 volumes of *Fauna Hawaiiensis* (Sharp 1899–1913) remain as the baseline of our knowledge of many arthropod groups.

Early successes with biological control encouraged further development of the program. In 1904 the Hawaiian Sugar Planters' Association (HSPA) commenced with its program of biological control. For more than half a century, HSPA was the largest employer of entomologists in Hawai'i. A number of prominent entomologists passed through their ranks, including R.C.L. Perkins, O. H. Swezey, F. X. Williams, and E. C. Zimmerman. Swezey (1931), listed 300 species purposefully introduced up until 1929, of which 92 definitely established. He lamented the fact that perhaps another 3,000 species were experimented with but were not recorded! Most of these 3,000 species did not become established, but many of our currently established immigrant insect predators and parasitoids may have arrived in this way. The biocontrol program in Hawai'i continues today under the aegis of the State Department of Agriculture (Funasaki et al. 1988). Between 1890 and 1985, the documented intentional introductions and releases into the state totalled 639 species of arthropods, of which 230 became established (Funasaki et al. 1988).

In addition to his duties at the HSPA, O. H. Swezey conducted studies on the biologies of native Hawaiian insects, especially moths. Most of what is known on this subject is the result of his work, which spanned 50 years. His notes were collated in *Forest Entomology in Hawaii* (Swezey 1954), which continues as the primary source of host data for many Hawaiian groups.

The Bernice P. Bishop Museum (BPBM), founded in 1889, was instrumental in providing local support for Perkins and the *Fauna Hawaiiensis* and in encouraging other biological surveys of the islands. It remains the premier natural history institution in the islands. The Hawaiian Entomological Society was founded in 1906 and is one of the oldest entomological societies in the country. The *Proceedings of the Hawaiian Entomological Society* and publications by Bishop Museum Press and the University of Hawaii Press, have been the principal outlets for Hawaiian entomological research since *Fauna Hawaiiensis.*

E. C. Zimmerman at BPBM and HSPA began cataloging the Hawaiian fauna and describing new species in 1934. He also began a long-term project documenting the insect fauna in the monumental series, *Insects of Hawaii.* The 1st of 14 currently-produced volumes was published in 1948. Only the large orders Hymenoptera and Coleoptera have not been treated. D. Elmo Hardy at the University of Hawaii joined the project in 1949 and published accounts of the Diptera as volumes 10-14 (1960-1981). Tenorio (1969) added a supplement on the Dolichopodae. The 300% increase in relative representation of Diptera in the fauna between 1948 and 1989 (Table 3) resulted from Hardy's encouragement of systematic studies. Volume 1 (Zimmerman 1948) remains the best overall treatment of the natural history of Hawai'i to date. The earlier systematic volumes are 40 years out of date but remain useful compilations. Except for those in Hardy's Diptera volumes, few new species were described, hence there is a large accumulation of undescribed taxa in collections.

Systematics Resources

Steffan (1976) reviewed the systematics resources in Hawai'i. The premier collection of arthropods from Hawai'i and the Pacific is housed at the Bishop Museum. The Hawaiian insect collection consists of nearly 1 million specimens, representing more than ¾ of the described species. The collection houses early historical material, especially from *Fauna Hawaiiensis,* which mirrors the fauna as it was at the time of collection in the early 1900s, and a wealth of newer material, some unworked from biosurveys and environmental impact statement assessments. Amy Suehiro maintained a card catalog of Hawaiian entomological literature and taxa from 1928 to 1968. This card file has served as the foundation for the database of Nishida & Miller (1989). Additional significant collections are housed at the State Department of Agriculture (DOA) and the University of Hawaii at Manoa. The DOA collection includes valuable historical material from the former HSPA collection and vouchers of biological control programs. Primary type specimens formerly in HSPA are now in the Bishop Museum. Significant historical collections are also housed at the British Museum (Natural History), which was the primary depository for voucher material from the *Fauna Hawaiiensis* survey.

HAWAIIAN INSECT EVOLUTION

The isolation of the Hawaiian Islands from each other, their sequential ages, and the repetitive occurrence of similar climatic zones, habitats, and ecosystems on each island, along with the formation of isolating barriers within each island by erosion, have favored speciation.

Most speciation events are hypothesized to follow founding of new isolated populations (Carson 1987b). The founding cohort was often small, sometimes only a single gravid female, which could carry only a subset of the genetic repertoire of its parental population, changing gene frequencies and fixing some alleles (Carson 1987b). As the founder population expanded and adapted to its new surroundings, it could diverge from its parental population. This process was repeated on each island with less frequent return of a derived species to its ancestral home (Carson 1987a). On top of this pattern has been an incredible array of adaptive shifts, wherein a subpopulation of a successful population exploits a totally new resource or habitat. Again it may have been a small closely related cohort, possibly a single female, within the population that made the switch. Not all of these would give rise to new species, and it is not known at what stage the speciation event occurs.

These adaptive shifts placed the new population under the influence of new selective pressures, leading to surprisingly rapid morphological changes. In many cases the degree of change has been so great that the original describers placed many species in endemic genera, either to highlight the spectacular changes or to indicate that the affinities to other species were so obscure. For example, the 5 beetlelike flightless lacewings were placed in 2 endemic genera (*Pseudopsectra* and *Nesothauma*), yet Zimmerman (1957) concluded that each flightless species evolved independently from a separate flighted ancestral species in the genus *Nesomicromus*. Therefore *Pseudopsectra*, with 4 described species, is polyphyletic and not a good genus. Also, native *Drosophila* were placed by Hardy (1965) in 3 endemic genera and a number of subgenera before modern work showed them to all belong to the subgenus *Drosophila*; yet according to Kaneshiro (1976), the degree of morphological change within this group far exceeds the range for the whole family Drosophilidae outside of Hawai'i! Furthermore, the native *Plagithmysus* beetles were placed in 6 genera until Gressitt (1978) showed them to represent a single closely related group.

An epitome of rapid morphological change associated with adaptive shifts is exhibited by some of the cave species. The cave fauna contains examples of macro-evolution on micro-continents in mini-time. For example, there are 80 described endemic species in the worldwide cixiid planthopper genus, *Oliarus*. Most *Oliarus* are big-eyed, flighted, somber colored denizens of forests, but no less than 5 evolutionary lines have independently invaded caves and are now obligate subterranean species with reduced or absent eyes, wings, and body pigment. One line occurs on Moloka'i, 2 on East Maui, and 2 occur on the Big Island. The 4 lines (with 5 species) on Maui and the Big Island all evolved within the last million years. The degree of convergence shown by the different cave species on different islands is striking. Despite the complete change in life style and morphology, characters of the male genitalia place them within the native complex of surface species. At least 1 line containing 2 cave species on the Big Island can be placed in a known group of big-eyed surface species (Howarth 1988).

A new population created by an adaptive shift may disperse up or down the chain, becoming the ancestor to additional species (Carson 1987a; Gagné 1983). These 2 phenomena, founder events and adaptive shifts, have been reoccurring down and up the chain in parallel, creating swarms of closely related species within many native groups. Hawai'i is the premier locality for study of the results of this process, called adaptive radiation. Hawaiian *Drosophila* (more than 450 species) and *Hyposmocoma* (350–500 species) head a list of 9 genera that each contain more than 100 described native species (i.e., the beetles *Proterinus* and *Plagithmysus*, the flies *Campsicnemus*, *Scaptomyza*, and *Lispocephala*, and the wasps *Sierola* and *Odynerus*). This list will expand greatly as additional systematic studies are completed. The vast majority of Hawaiian invertebrate species are endemic to a single island (e.g., Table 1).

Adaptive radiation may fill available niches in a brief time. In fact, evidence from the Big Island suggests that ecological niches (defined as functional roles in ecosystems) become occupied in ecological time, like succession, rather than evolutionary time as is commonly assumed (Mueller-Dombois & Howarth 1981, Howarth 1987).

The evolutionary processes in Hawai'i have great predictive value. One can find new species on an unusual host or in an unusual habitat and successfully predict that a close relative exploits a similar niche on the neighboring islands. This has been done on several occasions with the cave fauna and aeolian communities (Howarth 1987) and in studies on specific groups (e.g., in cerambycids *Plagithmysus* [Gressitt 1978], in mirids *Nesiomiris* [Gagné, unpublished data], in geometrids *Eupithecia* [Montgomery 1983], and with flies *Drosophila* [Montgomery 1975]). In each of these groups it was correctly predicted that one would find a new species in a given habitat, based on the ecology of the group on another island.

On the oldest islands of Kaua'i and O'ahu are representatives of taxa that have not yet dispersed down the chain to the younger islands and species believed to be close to the ancestors of taxa found on the younger islands. On Kaua'i one finds the hawkmoth *Tinostoma*, and the lucanid beetle *Apterocyclus*, and the most primitive species of many speciose Hawaiian lineages (e.g., *Drosophila* [Carson 1987a], the mirids *Nesiomiris* [Gagné 1983], and the damselflies *Megalagrion*). In *Megalagrion* the species on the younger islands from O'ahu to the Big Island, inclusive, can be placed easily into 4–5 distinct species-groups, with usually a single species of each group on each island. However, on Kaua'i these species groups blend into a confusing array of mixed morphological traits among the 9 endemic species. Many of the individual species endemic to O'ahu and Maui can be traced back to presumed ancestral species on Kaua'i, but these ancestors on Kaua'i cannot be so easily placed in species groups (Zimmerman 1948, Maciolek & Howarth 1978). In 1–2 million years, O'ahu will be faunistically like Kaua'i once additional Kaua'i species jump to O'ahu and more autochthonous O'ahu species evolve. In a few groups (e.g., *Banza* [katydids] and *Plagithmysus* [beetles]), the hypothesized primitive species occur on the even older island of Nihoa.

Flightlessness

A conspicuous theme among island insects is the evolution of flightlessness. The Hawaiian fauna contains some of the finest examples: flightless beetlelike lacewings, moths, beetles, flies, bugs, planthoppers, leafhoppers, crickets, katydids, and wasps. In fact of the 11 orders of alate insects that dispersed to the islands, only 1, the odonates (dragonflies and damselflies), has not evolved flightless species.

Flightlessness is not unique to islands or to wind-swept, harsh environments, but is common in every ecosystem, including competitive continental ones. In fact, at nearly every trophic level, most resource exploitation is carried out by flightless organisms. Furthermore, nearly all insects spend the majority of their active lives in flightless stages. Consider the ants, termites, cockroaches, scales, springtails, silverfish, etc., of the home and garden. Since most of the dominant flightless continental groups did not disperse to Hawai'i, many of the alate Hawaiian natives have evolved to fill these roles. What makes this process exciting in Hawai'i is that alate and flightless sibling species often live side-by-side and that sometimes intermediate forms are also extant. With the generally young and less complex geological history of Hawai'i, the pieces to such interesting evolutionary puzzles as flightlessness still exist and can be evaluated. Independent adaptive radiation has occurred on each island. Often flightlessness has evolved within each group independently from separate ancestral species on each island (e.g., hemerobiids [Zimmerman 1957], dolichopodids [Hardy & Delfinado 1974], cixiids [Howarth 1988], and tipulids [Byers 1985]).

Evolutionary Ecology Laboratory

The evolution of the Hawaiian fauna has paralleled the geological evolution of the islands. The 6 largest inhabited islands, with their great diversity of habitats and species, present almost ideal evolutionary laboratories. Each island acts as a mini-continent, having obtained its biota from trans-oceanic dispersal. Each is a microcosm of evolutionary and ecological processes on the continents. The isolation and youth make these processes especially clear. A series of similar habitats has developed sequentially on each island down the chain. The repetition of habitats with regularly varying ages allows one to study the role of time in both evolution and ecology.

The Hawaiian biota has been locked in a series of differently aged and isolated "laboratories" for hundreds of thousands to millions of years, where intricate substantive evolutionary ecology "experiments" have been carried out. Each experiment was established at regular intervals on the newer islands and then allowed to run under similar constraints of climatic, geologic, and biological parameters.

The Hawaiian *Drosophila* has been studied more than any other taxon, but other opportunities exist, especially among other speciose groups. In addition, species of the native cutworms, *Agrotis* and *Peridroma*, and the corn earworm complex, *Helicoverpa*, represent unique and valuable resources in applied evolutionary biology. Since each of these groups is closely related to important continental pest species, there is an opportunity to conduct genetic research and find genetic controls for pest species. Such a project is now under way with the corn earworm complex. The Hawaiian species of *Agrotis* and *Peridroma* range from widespread successful species to rare precinctive species and would be good candidate groups for determining the comparative ecological genetics of rarity and extinction. They are also conspicuous and would be good indicator species of the status of many native species in reserves. Similarly, the 22 closely related species in the pyralid genus *Omiodes* range from endemic agricultural pests to endangered or extinct species.

CONSERVATION STATUS OF HAWAIIAN ARTHROPODS

The conservation status of a few groups will be described to illustrate major problems and indicate possible solutions. Some of the major problems affecting conservation biology of Hawaiian arthropods include (1) taxonomic ignorance, (2) small geographic ranges, (3) impacts of invasive alien species, (4) loss of habitat from agricultural conversion, (5) fire, (6) land clearing, (7) military maneuvers, (8) pollution, (9) water diversion, and (10) mining.

Taxonomic Ignorance

The most serious problem is the taxonomic impediment (Ramsay 1986), which results from the lack of both information on invertebrates and trained personnel to obtain that knowledge. Some Hawaiian groups are so poorly known taxonomically that they currently cannot be identified; thus their management is largely ignored. For example, the 3 major terrestrial crustacean groups, the crabs, amphipods, and isopods, were recognized as components of the native fauna only within the past 2 decades. They remain largely unstudied. Native terrestrial crabs are now all extinct and known only from fossil remains. The native terrestrial amphipods are represented in collections by over 30 species, but only 4 have been described. These amphipods represent a number of different founders and separate adaptive radiations (Bousfield 1984). The situation is even worse with isopods, in which only 3 native species have been described, but the total fauna is known to consist of over 60 species, most of them recently established aliens (Taiti & Ferrara, in press). The populations of some of these alien species occasionally reach phenomenal levels, but their ecological effects are unknown.

The situation among the insects is similar. Zimmerman (1978) lamented that the paratype series of the endemic moth genus *Hyposmocoma* with ca. 350 described species sometimes contained a mix of up to 10 closely related species. Many of these are synonyms, but clearly this exciting native group is badly in need of revision. More telling is the fact that Perkins, who collected for the *Fauna Hawaiiensis* survey, never had a chance to collect Lepidoptera and some other invertebrate groups on West Maui or portions of the other islands. Not a single microlepidopteran has been described from West Maui! Based on what is known of the island distribution of species of *Hyposmocoma*, at least 80 new species in this genus alone are presumed to live on West Maui. Described species of native leaf bugs (Miridae) now total almost 50 species, but a manuscript by Gagné (1983) will double that number with a revision of only 1 genus (*Nesiomiris*). An additional 100 to 200 new species wait in collections for a trained taxonomist's eye. The group is undoubtedly the largest native heteropteran family in the islands.

In nearly every native group that has been studied using modern methods new species are recognized. The best example is clearly the *Drosophila*, the number of known endemic species of which has risen from 48 in 1948 to over 400 under the University of Hawaii *Drosophila* Project, and the asymptote of new species has not yet been reached (Kaneshiro & Boake 1987). The percentage representation given in Table 3 reflects more the level of systematic effort devoted to each group.

The lesson for conservation biology is that it is the population that must be saved. There is a human bias toward saving rare things, and conservationists often exploit this trait to save unique rare species. However, for both scientific reasons and conservation goals, it is also important to save the numerous closely related populations of a widespread variable species. The more populations of endemic species we can preserve for future studies, the greater their combined value is to science and the better our understanding will be of evolutionary ecology, behavior, and biology in general.

Cultural Problems

There are cultural problems that hinder conservation programs. The primary problem concerns the advertising industry's view that the only good bug is a dead one. The public is continually being bombarded with the idea that all insects are harmful and should be killed. This is so persuasive that even many applied insect textbooks imply that all predators of insects are beneficial regardless of their prey. The second problem results from the great cultural diversity of Hawai'i. Each immigrant ethnic group has brought to Hawai'i a portion of its natural world, especially organisms considered "useful" or aesthetic. Often invertebrates ride as hitchhikers on these introductions or find suitable hosts when they finally get here by other means. With the introduction of each new alien, the chance of its associated biota becoming established increases (Howarth 1985). Humans are homogenizing the world's biota.

There is also a cultural bias that species are discrete units in nature. However, the more critical our studies become, the less support such a thesis engenders. If conservation biologists are successful in saving only "good species," then the resultant research is a priori biased and the resources to disprove the myth are lost. Current reserve management, with its emphasis on rare unique distinct species may mean our understanding of evolution will be an artificial result of biased management rather than good science.

Small Geographic Range

Many Hawaiian species have extremely restricted geographic ranges. For example, the cave wolf spider (*Adelocosa anops*) is restricted to caves within a single small lava flow on Kaua'i. Its entire known range is threatened by urbanization and recreational developments (Wells, Pyle & Collins 1983). The Big Island species of *Rynchogonus* weevils (*giffardi*) is known from a dry gulch barely 100 m X 10 m—an oasis within a sea of barren pastureland. The once widespread coastal species on O'ahu, *R. simplex*, is now restricted to a few hectares on the southeast tip of that island and possibly some offshore islets (R.C.A. Rice, pers. comm.).

Impacts of Invading Species

Humans have ruined the splendid isolation that allowed the evolution of these spectacular island species. Biological pollution (the impact of invading alien species) is the most insidious, pervasive, and perhaps the most serious conservation threat. Biological pollution is virtually irreversible and has the potential to undo all other conservation programs. Alien species do not respect human boundaries, but can invade all suitable habitats within their dispersal range. The destruction caused by ungulates, rabbits, and certain other vertebrates is well known (Tomich 1986; Vitousek, Loope & Stone 1987), but invertebrates can also be terribly destructive.

About 3,200 species of alien arthropods have been either intentionally or unintentionally introduced to Hawai'i (Table 2). However, the present status of most of these in the islands is unknown. Many populations did not survive to become permanent residents. Some populations subsequently died out for the same reasons that some native populations are declining. Currently there may be 2,500 species of alien arthropods successfully established in Hawai'i (Funasaki et al. 1988). Some alien invertebrates (including both intentionally and unintentionally introduced species) can now be found in virtually all habitats from sea level to the summits of the highest mountains. They have become pests and threaten native species (Howarth 1983, 1985; Gagné & Howarth 1985).

Social and colonial alien insects historically have had far greater adverse effects than most other invertebrates (Howarth 1985). Ants have been strongly implicated in the extinction or extirpation of many native species. Ants with large aggressive colonies, such as the big-headed ant, Argentine ant, long-legged ant, and 2 fire ants, have been the most damaging (Zimmerman 1948; Medeiros, Loope & Cole 1986). In 1977 an aggressive race of the yellowjacket (*Paravespula pennsylvanica*) became established in Hawai'i and quickly spread throughout suitable habitats on all the main islands. Its phenomenal population explosion and spread corresponded with an alarming decline in many native arthropods and may have affected native bird numbers (Gambino, Medeiros & Loope 1987).

The effects of alien species is often unpredictable. Alien invertebrates prey on or parasitize native plants and animals, spread diseases or toxins among native species, supply food or shelter for and help disperse other invading organisms, and alter soils. The reduction of insect prey by alien predators during the critical nesting period of the native forest birds is considered a major factor in the decline of these endangered avian species. Alien parasites, especially mosquitoes, are also considered a major problem in the conservation of native birds (van Riper et al. 1986). Earthworms and termites drastically alter soil structure and nutrient cycling and probably adversely affect regeneration of native plants. Alien seed predators and alien pollinators (especially the honey bee) also restrict regeneration of native plants and favor establishment and spread of alien plant species. Some invertebrate species are food for detrimental vertebrates (e.g., dung beetles for mongooses; slugs and earthworms for pigs) and thereby support greater numbers of these animals than otherwise would be the case (Howarth 1985; Vitousek, Loope & Stone 1987).

Many parasites and predators purposefully introduced for biological control of pest species have expanded their diets to include native species and even alien plant-feeding species introduced to control weeds (Howarth 1983, 1985; Funasaki et al. 1988). The endemic pentatomid stink bugs (*Oecalia* with 14 described endemic species and *Coleotichus* with 1 specie) are disappearing with alarming rapidity. Their demise appears to be the result of parasitism by the biological control agents introduced against the southern green stink bug. Two well-established agents, a scelionid wasp and a tachinid fly, are known to attack *Coleotichus* and other pentatomids (Funasaki et al. 1988). Some native moths, scale insects, and psyllids may also be at special risk from biological control introductions (Howarth 1985) because alien species in these groups have been common targets for biological control (Funasaki et al. 1988).

Land Conversion

Land conversion was begun by the early Hawaiians (Kirch 1982) and is a continuing process, often with devastating effects on the native biota (Gagné 1988). The current land tax structure favors clearing native forests for pasture, plantations, and other ventures. Some prime native habitats have recently been cleared for dubious economic reasons. Fire, wood chipping for biomass energy and for pressed board manufacture, silviculture, mining, pollution, military bombing and resultant fires, geothermal development, and powerline construction also take their toll (Gagné 1988).

Many Hawaiian insects are extremely host specific. In some groups related sympatric species (e.g., *Drosophila* [Montgomery 1975], Cerambycidae [Gressitt 1978], and many Lepidoptera and Homoptera [Swezey 1954]) even divide up the resources of a single host species. As their host plants become rarer and more scattered, these host specific species become vulnerable to extinction. Most of the native leafhoppers (Cicadellidae) and planthoppers (Delphacidae) remain undescribed and many may be going extinct without any documentation. Say "aloha" to the planthoppers in the genus *Aloha*. Most of the species in the endemic moth genus *Mapsidius* are of special concern because their known tree host (*Charpentiera*) is now rare.

The freshwater aquatic fauna is being impacted by stream channelization, impoundments, diversion, pollution, and alien introductions. The last includes introductions for control of mosquitoes and snails as well as escapees from the aquarium trade.

Some moth groups demonstrate the full range of conservation problems. Gagné and Howarth (1985) assessed the native macrolepidoptera and listed 6 major perturbations, not mutually exclusive, that were important in the extinction of 27 species. They are, in order of importance, introductions for biological control, habitat loss, alien mammals, host loss, alien arthropods, and hybridization with an invading alien relative. The native *Hypena* appear to be entirely extinct. Except for the Laysan species, the reasons for their demise are obscure. Their undocumented extinction underscores the vulnerability of some Hawaiian groups and the urgency of beginning a conservation biology program for invertebrates. A large segment of our native fauna may be lost. This loss could have repercussions in other groups.

SOLUTIONS

Recent interdisciplinary evolutionary biology programs have generated considerable publicity and interest in the native Hawaiian biota, and numerous smaller studies were created as spin-offs of these larger ones. The 2 larger studies are the University of Hawaii's *Drosophila* Project, which since the 1950s has been studying the genetics and evolution of the remarkable Hawaiian Drosophilidae (Carson 1987a; Kaneshiro & Boake 1987), and the International Biological Program (IBP) sponsored by NSF and jointly administered by the University of

Hawaii and the Bishop Museum in the 1970s (Mueller-Dombois, Bridges & Carson 1981). This growth in interest, along with the realization that the native biota is at extreme risk, has led to conservation biology initiatives, which have been encouraged by exposure in special issues of scientific and popular conservation and natural history magazines devoted to the Hawaiian biota (Barrett 1975; Dodge 1982; Ternes & Simon 1982; Simon & Sugden 1987; Miller 1988). Leading agencies involved in this shift of emphasis and in the development of a conservation biology program are the U.S. National Park Service, the U.S. Fish and Wildlife Service, The Nature Conservancy of Hawai'i, the Natural Area Reserves System, the Bishop Museum, and the University of Hawaii.

Recent biological discoveries, including new species (even a new genus of living bird), new caterpillars with a unique feeding strategy, and surprising new ecosystems in caves and lava flows, show that there is a great deal remaining in Hawai'i, which is worth saving, and that island biology is not yet fully known. Discoveries in ecology and evolutionary biology demonstrate that the Hawaiian islands are ideal laboratories and can elucidate how fundamental life processes work. Potential for further programs is great, especially in conservation biology. For here we can, unfortunately, examine all stages in the extinction process, assess the role of invading species, and study in isolation the effects of various novel perturbations (Vitousek, Loope & Stone 1987).

Species diversity in Hawai'i is so high that conservation efforts in selected areas will save many endangered species. The Hawaiian fauna is not inherently fragile. Recent conservation efforts have clearly demonstrated that native species respond remarkably to appropriate management actions (Mueller-Dombois, Bridges & Carson 1981; Stone & Scott 1985). Species do recover. However, small population size, the severity of the novel perturbations, and the close interrelationships within native groups act in concert to increase their vulnerability to extinction.

Establish Reserves

To prevent this extinction, each of the distinct habitats needs to be identified and as many examples as possible protected. However, setting aside reserves does not guarantee the long-term survival of the ecosystems unless biological surveys and long-term ecological studies of selected invertebrate and vertebrate groups are initiated. As the knowledge base on biodiversity and the ecology and systematics of arthropod groups grows, management requirements will become more clear.

Determine Indicator Species

To solve the taxonomic impediment, Ramsay (1986; 1989) suggested the identification of a few invertebrate indicator species for each reserve. These indicator species should be chosen on the basis of ease of sampling and recognition as well as their vulnerability to disturbance. Land managers could then be trained to recognize and monitor the indicator species on their reserves to assess the health of invertebrate populations in general. Coupled with knowledge of ecosystem processes, such a system should work.

In other habitats, knowledge of key host plants and appropriate associated invertebrate herbivores could be used as indicator species. The moth genus *Tamsica* occurs mostly in lowland dry habitats and many species may already be extinct. Good populations still exist on some of the small offshore islets around the main islands and on Nihoa. Arthropods should be a recognized resource of these small offshore islands, and the appropriate invertebrate biosurveys and management recommendations for the native invertebrates should be initiated. *Tamsica* would make good indicator species for other possible surviving arthropods on the islets. Many of these offshore islets are sea bird refuges, where management is currently strongly biased and strictly for the birds. Arthropods are given scarce mention or consideration.

Other potential indicator species can be found in the native Amphipoda, Aranae, Odonata, Orthoptera, Neuroptera, Heteroptera, Homoptera, Lepidoptera, Diptera, Coleoptera, and Hymenoptera. In fact, nearly every speciose native group contains appropriate indicator species, if there are trained systematists and ecologists available to identify them.

Biological Survey of Hawaiian Invertebrates

The biological survey of Hawaiian invertebrates is woefully incomplete. Less than ½ to perhaps ⅓ of the native species are described, making it virtually impossible to recognize problems or to formulate effective conservation management plans. Avise (1989) reviewed several examples where inadequate knowledge of systematics led to inappropriate endeavors to save endangered vertebrates. Such problems are more acute among the less well known invertebrates. It cannot be overemphasized that studies in conservation biology, like all other biological disciplines, can only be as good as the systematics research upon which they are based (Wilson 1985; Avise 1989). Whether a population under study represents an alien species or an endemic species, and whether the population represents one or 20 or 200 closely related species, all have direct bearing on valid management recommendations.

Ecological Research

The role of invertebrates, including alien species, in ecosystems is less understood than is the role of vertebrates. In part, this results from our human bias toward being able to recognize the activities of larger organisms, while not noticing the smaller creatures until the damage is done and the causes obscure. Long-term ecological studies are needed to find better management strategies for mitigating the harmful impacts of aliens and to better assess and predict the impacts of intentional introductions. This research is imperative because increasing world commerce continually worsens the problem. We must revise several myths in ecology, especially concerning unfilled niches, immigration potential, ecosystem fragility, etc. This research should be done in both natural and seminatural areas and on key invertebrate species.

Currently, our knowledge of the status of native groups is anecdotal at best. Several native groups of Hawai'i disappeared alarmingly fast: *Megalagrion* damselflies, *Dyscritomyia* flies, and *Achatinella* snails on O'ahu, Collembola, Vespidae, Sphecidae, and Colletidae on most islands. Some of these groups still have good populations on 1 or more islands. These present a once-in-a-species lifetime opportunity for conservation biology. By monitoring these surviving populations in a long-term effort, there is an excellent chance to recognize the beginning stages of decline and their causes and to develop ameliorating strategies.

Reducing Foreign Species Introductions

Strictly enforced quarantines, regulating potentially harmful introductions, are highly cost-effective in preventing undesirable invasions. Quarantine programs are not only effective against the intended organisms but also have 2 very important side benefits: interception of a great number of other intentional and unintentional introductions and, most importantly, impressing on the public that introductions are potentially harmful.

Persons or agencies desiring to introduce an alien species, including those for biological control, must convincingly demonstrate in a critical open public review process that the alien species poses little potential risk to native species, human health, and the local economy. This review should be modeled after environmental impact studies. Organisms introduced for biological control should be monitored with long-term ecological studies to determine the true fate of these species and make applied ecology a predictive science.

Develop Environmentally Sound Pest Controls

In the political and economic arenas, both real and perceived pests are often controlled by whatever arsenal seems expedient, with often detrimental effects on the native biota. It should be clear that there are no panaceas in pest control. Any action to kill or limit one species must also impact other species.

High priority should be given to separating the serious pests requiring control from innocuous species causing no damage or minor damage. Review of pest status would facilitate development of environmentally sound control methods for bona fide pests, while innocuous species and less serious pests could be dealt with more pragmatically. Biological control, being largely irreversible, unpredictable, and self-dispersible, should be used only in exceptional circumstances.

Conflicts of interests arise in identifying pests. One state agency has imported predators to reduce insect damage to the legume, haole koa *(Leucaena leucocephala)*, while many land managers expend considerable resources to control this major alien weed. Even now, public agencies are planting lantana, several melastomas, and other weeds in public places, while other government agencies introduce alien herbivores to control them.

Environmental Education

Successful educational programs that overcome the public's fear of the perplexing array of strange invertebrates and instill an appreciation of the aesthetics and importance of invertebrates for human welfare should be encouraged and developed. These programs would make many environmentally risky control procedures unnecessary. The western cultural bias and fear of invertebrates needs to be changed. The media's message that "the only good bug is a dead bug" does a great disservice to the natural world.

CONCLUSIONS

The Hawaiian fauna is in transition, as profound changes are now occurring in its composition. Many native groups are declining, with concurrent population explosions of alien species. Is it cause and effect and replacement of one group by another? Or is it coincidence, and the native species declining from some unrecognized cause or change in the environment? Most extinction studies are done in hindsight, after the game is lost. Conservation biologists must act now and get into the field to study population dynamics of native species in natural settings in order to understand extinctions and to develop valid conservation strategies. We presently have that opportunity in Hawai'i and urgently need to field a team of biologists to monitor populations of selected native groups.

Long-term ecological studies are needed to separate population fluctuations from irreversible changes, to assess the impacts of aliens, and to develop mitigative measures. Unfortunately, research on the role of invertebrates lags far behind that for the vertebrates, despite the theoretical importance of invertebrates in maintaining the health of ecosystems. In addition, old assumptions concerning island biology must be thrown out.

Some 2,500 different kinds of alien arthropods are believed to be established in Hawai'i, and probably no native species of plant or animal escapes the effects of this biological pollution. Furthermore, control programs, including biological control, aimed at aliens may adversely affect nontarget native species. More effective quarantine measures and more effective review and regulation of importations of living organisms are desperately needed. Society must discourage alien introductions.

The biological survey of Hawai'i should be completed. Perhaps ⅔ of Hawaiian invertebrates remain unknown, making it difficult to develop appropriate conservation programs. As demonstrated in young Hawaiian caves and on the cold stone desert on Mauna Kea (Howarth 1987), one has to actually search all potential habitats for native species before writing them off as devoid of life.

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