VOLUME 96, NO. 4 DECEMBER 2021

THE QUARTERLY REVIEW
of BIOLOGY

INSECT RADIATION ON ISLANDS: BIOGEOGRAPHIC PATTERN AND EVOLUTIONARY PROCESS IN HAWAIIAN INSECTS

DAVID H. HEMBRY
Department of Entomology, Cornell University
Ithaca, New York 14853 USA
Department of Ecology and Evolutionary Biology, University of Arizona
Tucson, Arizona 85721 USA
Department of Biology, University of Texas Permian Basin
Odessa, Texas 79762 USA
E-MAIL: HEMBRY_D@UTPB.EDU

GORDON BENNETT
Department of Life and Environmental Science, University of California
Merced, California 95343 USA
E-MAIL: GBENNETT2@UCMERCED.EDU

EMILIE BESS
Entomo Farms
Norwood, Ontario K0L 2V0 Canada
E-MAIL: LEE@ENTOMOFARMS.COM

IDELLE COOPER
Department of Biology, James Madison University
Harrisonburg, Virginia 22807 USA
E-MAIL: COOPERIA@JMU.EDU

The Quarterly Review of Biology, volume 96, number 4, December 2021.
https://doi.org/10.1086/717787

Steve Jordan
Department of Biology, Bucknell University
Lewisburg, Pennsylvania 17837 USA
e-mail: sdjordan@bucknell.edu

James Liebherr
Department of Entomology, Cornell University
Ithaca, New York 14853 USA
e-mail: jk15@cornell.edu

Karl N. Magnacca
Department of Natural Sciences, Bernice P. Bishop Museum
Honolulu, Hawai'i 96817 USA
e-mail: knm956@gmail.com

Diana M. Percy
Department of Botany, University of British Columbia
Vancouver, British Columbia V6T 1Z4 Canada
e-mail: diana.percy@botany.ubc.ca

Dan Polhemus
Department of Natural Sciences, Bernice P. Bishop Museum
Honolulu, Hawai'i 96817 USA
e-mail: bugman@bishopmuseum.org

Daniel Rubinoff
Department of Plant and Environmental Protection Sciences, University of Hawai'i at Mānoa
Honolulu, Hawai'i 96822 USA
e-mail: rubinoff@hawaii.edu

Kerry Shaw
Department of Neurobiology and Behavior, Cornell University
Ithaca, New York 14853 USA
e-mail: kls4@cornell

Patrick M. O'Grady
Department of Entomology, Cornell University
Ithaca, New York 14853 USA
e-mail: pmo43@cornell.edu

Dedication

We dedicate this paper to the memory of Vicki Funk (Smithsonian Institution) and Jonathan "Jackie" Brown (Grinnell College), two researchers who have done much to further our understanding of the Hawaiian biota. Vicki specialized on Compositae and did extensive work on the Hawaiian Bidens. She, along with Warren Wagner, literally wrote the book on Hawaiian biogeography (Wagner and Funk 1995). Jackie was an expert on Hawaiian Tephritidae and Megalagrion and was a source of inspiration for us. We will miss their friendship, mentorship, and passion for Hawaiian plants and insects.

KEYWORDS
Hawai'i, insects, adaptive radiation, macroevolution,
oceanic island biogeography, speciation

ABSTRACT
The spectacular adaptive radiations on the Hawaiian Islands offer the tantalizing possibility of ascertaining the predictability of evolution, especially with regard to how the archipelago's dynamic geology suggests a priori hypotheses for evolutionary pattern and process. In the past two decades advances in sequencing and phylogenetics have shed new light on the evolution of this model fauna. Here, we provide an overview of recent research on major endemic Hawaiian insect radiations. We find that, in contrast to earlier views, a substantial fraction of Hawaiian insect clades colonized the archipelago prior to the formation of the current high islands (5.1 Ma) and have persisted through one or more rounds of island formation and subsidence prior to the emergence of the current archipelago. Many Hawaiian insect radiations show elements of the progression rule, a null expectation where biogeographic patterns on the phylogeny mirror the chronological sequence of island formation, but few match its predictions exactly. Diversity in most radiations is shaped by a complicated interplay of among-island dispersal and within-island diversification. Finally, we find a positive relationship between clade age and species richness in Hawaiian insects, but with a great deal of variance that is likely explained by aspects of ecology and clade-specific factors.

Introduction

THE biotas of remote island archipelagos, such as the Galápagos and Hawaiian Islands, have long served as model systems for investigating fundamental evolutionary questions (Darwin 1859; Lack 1947; Carlquist 1974; Simon 1987; Wagner and Funk 1995; Gillespie 2004; Whittaker et al. 2008; Grant and Grant 2014; Warren et al. 2015; Shaw and Gillespie 2016; Patiño et al. 2017). The influential theory of island biogeography proposes that species diversity on island systems is a function of many factors, including island area and distance from the mainland (MacArthur and Wilson 1967). Under this theory, larger islands should support more species than smaller ones because of less extinction. Furthermore, islands that are closer to continental source populations will experience more colonization and, consequently, have higher species numbers than more remote islands. Traditional island biogeography theory, however, downplays the potential for in situ diversification that some lineages possess and the impact that long periods of time might have on island lineages. Indeed, this theory is fundamentally incomplete as a comprehensive framework for predicting biodiversity on remote archipelagos. Dispersal is important in generating the biotas of remote, isolated archipelagos, but their total biodiversity is shaped largely by local speciation such that their faunas and floras are characterized by endemic taxa, including speciose endemic radiations (Wagner et al. 1999; Liebherr 2001; Grant and Grant 2014; Shaw and Gillespie 2016). Furthermore, other factors, such as species interactions and biogeographic complexity, have been suggested to govern species diversity (especially in major radiations) on remote islands (Diamond 1975; Gillespie 2004; Rominger et al. 2016). Accordingly, study of the endemic biodiversity of remote archipelagos has much more to contribute to our understanding of how ecological and evolutionary factors affect rates and patterns of evolutionary diversification (Warren et al. 2015; Patiño et al. 2017).

Hawaiian insects offer an outstanding opportunity to explore factors shaping the evolution of species diversity. The sizes, geological ages, and ecological diversity of the Hawaiian Islands make them a long-held model system for understanding speciation dynamics and taxonomic and ecological diversification. In this review, we use recent molecular phylogenetic studies to examine the roles played by geological history and timing of colonization in the diversification of Hawaiian insects. We specifically cover colonization events that occurred before humans arrived in Hawai'i, as a model for understanding the role of these factors in generating in situ biological diversity. The extensive literature on invasive species and human-mediated introduction events is outside the scope of this review and is covered elsewhere (e.g., Kirch 2000; Gillespie and Roderick 2002).

GEOLOGY OF THE HAWAIIAN ISLANDS

The Hawaiian Archipelago is the most remote high-island group on the planet, located 3200 km from the closest continent (Carson and Clague 1995). This isolation has allowed a few colonizing species to evolve into an impressive biota, with over 1000 species of plants (Wagner et al. 1999) and an estimated 7000 species of insects (Liebherr 2001), roughly 90% of which are thought to be endemic. Nevertheless, these estimates are likely an underestimate of the historical and contemporary endemic insect richness in Hawai'i.

The Hawaiian Archipelago has formed over a more-or-less stationary mantle plume hotspot in the Pacific Plate that has been active periodically for the past 60 million years (Sharp and Clague 2006). Islands form as lava seeps through the hotspot and, over time, breaks the ocean's surface. As islands are transported to the northwest by plate tectonics, they move off the hotspot, volcanic activity declines, and they begin to subside under their own weight. Erosion from wind and water carves deep valleys and removes large amounts of sediment, further reducing island elevation and area, although potentially diversifying habitats. Additionally, landslides during island formation and subsidence radically change island area and complexity (Moore et al. 1989). As the Pacific Plate moves to the northwest, new islands form above the hotspot, creating a conveyor belt-like array with older islands in the northwest of the chain and younger islands in the southeast. Older islands eventually erode completely, becoming atolls, seamounts, and shoals before sinking below sea level and disappearing into the Aleutian Trench. Similar processes elsewhere in the world have produced other oceanic archipelagos, such as the Galápagos, Canary, Society, and Marquesas Islands (Bailey 1976; Duncan and McDougall 1976; Clouard and Bonneville 2005).

All Hawaiian Islands undergo a characteristic history of shield formation, erosion, and subsidence (Figures 1A, B, and C). Figure 1a shows the geological history of the Hawaiian Islands over the past 25 million years based on Price and Clague (2002). Shield formation, maximum island elevation above sea level, and island persistence above 2000 m and 1000 m are shown. These elevations are important biologically because of the interaction of the islands with moisture-laden northeast trade winds. Islands over approximately 1000 m in elevation are high enough to intercept the trade winds, causing cloud formation and heavy rainfall on the windward (northeast) sides of the islands, creating the opportunity for rainforest growth (Figure 1C; Juvik et al. 2000). The upper elevation for such trade wind-fed rainforest is roughly 2000 m. High islands in Hawai'i are, by definition (Carson and Clague 1995), over 1000 m above sea level and are capable of supporting rainforest habitat. The elevation, erosion, and subsidence of these islands produces a dizzying array of habitats and microclimates on each island over the course of its existence. The number of high islands has also varied over time, with some periods characterized by multiple high islands that have persisted for 5–10 million years, and other by reduced volcanic activity and few or no high islands present for periods of 2–5 million years

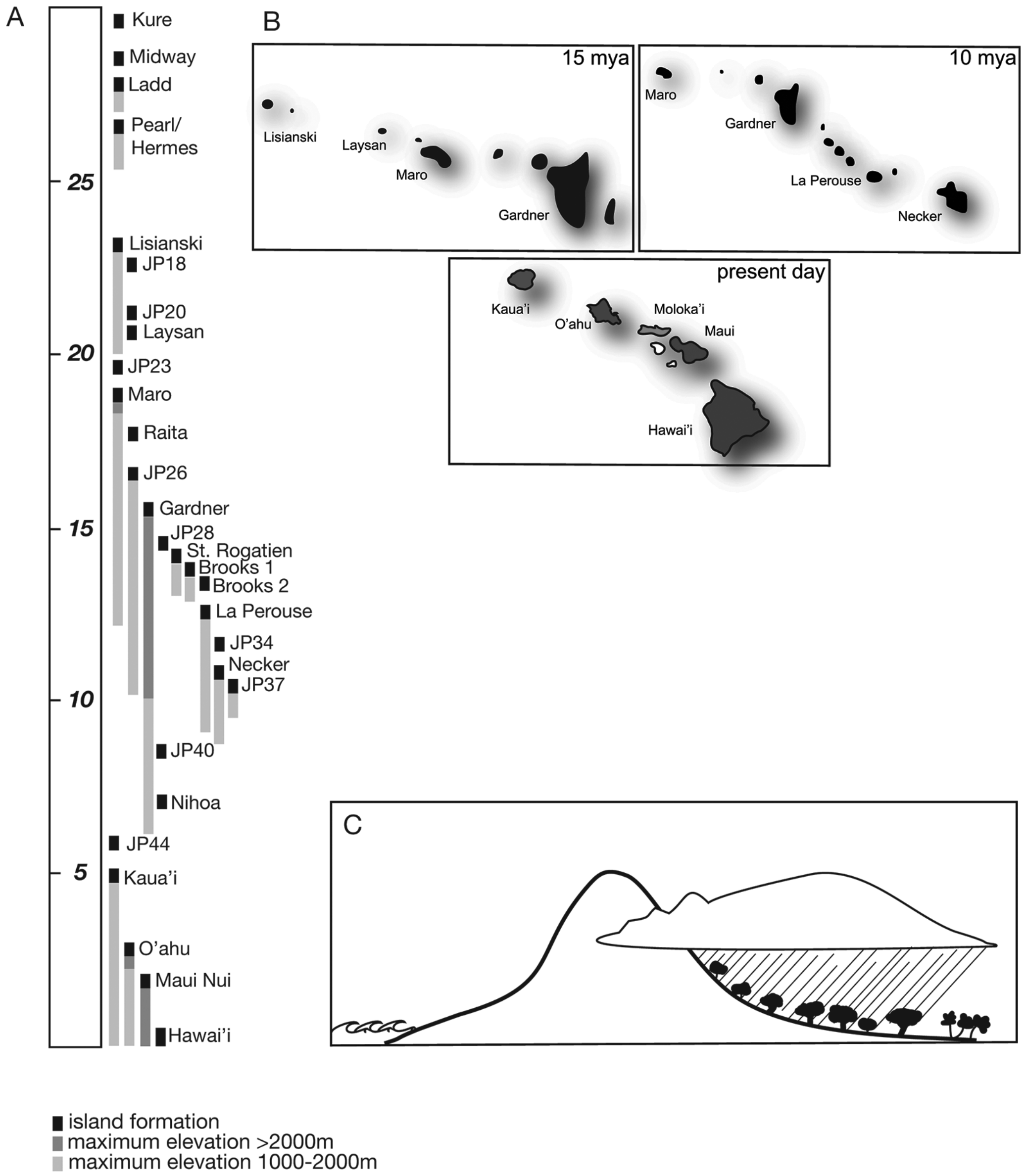

Figure 1. Geography, Geologic History, and Topography of the Hawaiian Islands

A. Timeline depicting the geologic history of the Hawaiian Islands, showing shield formation, maximum elevation, and co-occurrence of islands over the past 30 million years. B. Map of the main Hawaiian Islands in the present day and at 10 and 15 million years ago. C. Diagram depicting the inversion layer and its effects on cloud forest formation. See the online edition for a color version of this figure.

(Figures 1A and B). Taken together, the episodic nature of Hawaiian volcanism and the continuous processes of erosion and subsidence have had a large, and somewhat underappreciated, impact not only on the ability of species to colonize and diversify on this archipelago, but also to persist as rainforest habitats flicker in and out of existence.

HAWAIIAN BIOGEOGRAPHY

The patterns of diversification and biogeography in Hawaiʻi generally result from three distinct phenomena: founding events, interisland diversification, and escape events. Understanding these fundamental biogeographic processes is essential to synthesizing novel data on the processes generating Hawaiian insect diversity.

Arriving in the Hawaiian Archipelago

It is clear that not all species can reach Hawaiʻi, become established, and subsequently persist and diversify. The Hawaiian flora and fauna are disharmonic relative to continental land masses, that is, lacking representatives found on surrounding continental regions (Gillespie and Roderick 2002). This pattern may be due to a number of factors including vagility, desiccation resistance, geographic and host range, generation time, or simply chance. Molecular phylogenetic studies demonstrate that the vast majority of all animal and plant genera native to Hawaiʻi are the products of single, ancient colonization events (Wagner et al. 1999; Liebherr 2001). Humans first arrived in Hawaiʻi approximately 1000 years ago (Kirch 2000, 2011; Athens et al. 2014; Crowe 2018) and the diversity and evolution of plants and animals that have been introduced by humans since that time show distinctly different patterns.

Sources

The endemic Hawaiian biota has been assembled via colonization from a wide variety of source populations across the Pacific Basin, including other Pacific islands, tropical Asia, Australasia (Australia and New Zealand), East Asia, North America, and the Neotropics, as well as possibly Africa (Zimmerman 1948a; Carlquist 1970; Wagner and Funk 1995; Cowie and Holland 2006; Sakai et al. 2006; Price and Wagner 2018). Early authors thought that as much as 90–95% of the Hawaiian insect fauna is of western Pacific origin (Zimmerman 1948a; Carlquist 1970). This category encompasses all lineages that are ultimately of Asian or Australasian origin, many of which may have colonized Hawaiʻi indirectly via the many archipelagos to the west and south of Hawaiʻi in Micronesia, Polynesia, Fiji, or other Pacific island groups. The paucity of American (eastern Pacific) taxa usually is attributed to the extremely low density of islands between Hawaiʻi and the Americas. We now know at least one case, in *Rhyncogonus* weevils, where western Pacific islands have served as stepping stones for colonizing insects (Claridge et al. 2017) and some data suggest other cases as well (long-legged flies and craneflies; Goodman and O'Grady 2013; Goodman et al. 2014).

Our understanding of source areas for the Hawaiian insect fauna remains much less clear than for vascular plants and birds (Cowie and Holland 2006; Price and Wagner 2018). One major reason for the discrepancy is that it is challenging to perform sufficient outgroup sampling around the entire Pacific Basin for many Hawaiian insect radiations, especially since the entomofaunas of those source areas are often incompletely known. Even with extensive outgroup sampling, extinction and the age of some older Hawaiian radiations renders the identification of their source areas challenging (Stalker 1972; Jordan et al. 2003; Wahlberg and Rubinoff 2011; Haines et al. 2014; Johns et al. 2018; Rubinoff et al. 2021). Consequently, identification of origins for the Hawaiian insect fauna remains a major challenge, although increasing opportunities for collaboration between Pacific Rim biologists offers hope for more extensive sampling.

Methods of Dispersal

The native (endemic and indigenous) Hawaiian terrestrial biota has assembled via three primary dispersal mechanisms: wind (including powered flight), attachment to birds or large flighted insects (externally or internally), or by drifting in seawater (Zimmerman 1948a; Carlquist 1970). A large fraction of Hawaiian endemic insects likely arrived via wind dispersal (Zimmerman 1942, 1948a; Carlquist 1970), as is considered to be common in insects and other organisms on other archipelagos (Peck 1994; Gillespie et al. 2012). This conclusion is based both on the small body size of many Hawaiian insects, as well as a spectacular series of studies conducted by the Bishop Museum in Honolulu from 1957–1970, during which nets and traps were towed behind ships and aircraft to sample arthropods in the air column (0–2500 m) over the Pacific (Gressitt and Nakata 1957; Yoshimoto and Gressitt 1959, 1960, 1961, 1963; Holzapfel et al. 1978). These studies collected a wide variety of insects up to several thousands of kilometers from land. Tropical storms may further aid wind dispersal of insects, both through wind currents and increased humidity (Zimmerman 1942, 1948a; Holzapfel et al. 1978). Some large-bodied Hawaiian endemic insects (e.g., dragonflies, butterflies), which are strong fliers, belong to groups that are migratory on continents (Carlquist 1970). Additionally, Zimmerman (1948a) points out that insects may have dispersed via attachment to birds or large flighted insects (either passively or actively), or floating on uprooted trees or rafts of vegetation. Insects, especially flightless ones, may also have been transported between islands via giant landslides in which tracts of forest fell into the ocean and drifted to neighboring islands (Moore et al. 1989, 1994). For some groups, more than one of these dispersal methods is probable, and it can be difficult to distinguish among them using contemporary data. For instance, many small-bodied phytophagous insects could plausibly be dispersed either as larvae via vegetation rafts or as adults via wind.

Patterns of Diversification in Hawai‘i

Once lineages colonize the Hawaiian archipelago, they are able to either back colonize older islands or to forward colonize younger ones as they form. Here, the MacArthur and Wilson (1967) rules of distance from source and island area seem to determine colonization frequency and success, along with ecological and morphological traits. Hawaiian taxa show varying levels of endemism, ranging from broadly distributed on all of the islands to narrowly distributed single volcano endemics. Similar geologic dynamics occur in other oceanic archipelagos, with broadly similar effects on biodiversity dynamics (Juan et al. 2000; Parent et al. 2008; Whittaker et al. 2008; Valente et al. 2014; Hembry 2018). The Hawaiian archipelago thus introduces unparalleled opportunities to study the geographical scales over which different factors are and are not relevant to evolutionary diversification.

Weather events have the potential to influence colonization within Hawai‘i, particularly in flightless or weakly flying insect lineages. Interestingly, the most consistent wind patterns are not expected to aid dispersal within the archipelago. The prevailing trade winds blow from the northeast, meaning that species caught up in them are usually blown out to sea, rather than to another island, with the exception of Lāna‘i (Jones and Jordan 2015). Kona winds blow backward up the chain, from the southeast to northwest and may account for back colonization of small-bodied insects. Kona storms, a different phenomenon from more typical Kona winds, originate in the southwest, bringing rain to the leeward slopes of the islands. Kona storms are unlikely to result in transfer of species from island to island because, in general, they push insects out to sea. However, hurricanes and large winter storms may track up or down the archipelago, either from older to younger islands or vice versa, generating distinct biogeographic patterns of progression or back dispersal. These rare, large-impact events may be responsible for some of the biogeographic patterns we see within the Hawaiian Islands.

Extinction also has an impact on biogeographic patterns observed in various Hawaiian lineages. Unfortunately, fossilization on newly emerged volcanic islands is quite rare. The oldest subfossils known from the Hawaiian Islands are from Makauwahi Cave on Kaua‘i and date to the late Holocene (Liebherr and Porch 2015), placing the fossil record in Hawai‘i on the scale of thousands to tens of thousands of years. This is useful when trying to understand prehuman communities, but it is not useful for investigating older divergences on the scale considered in this review. We can infer that extinctions must have taken place as available net island area has periodically declined throughout the archipelago. This was evident during the period 5–7 Ma, just prior to the formation of Kaua‘i, which was characterized by the elimination of habitats over 1000 m in elevation and is

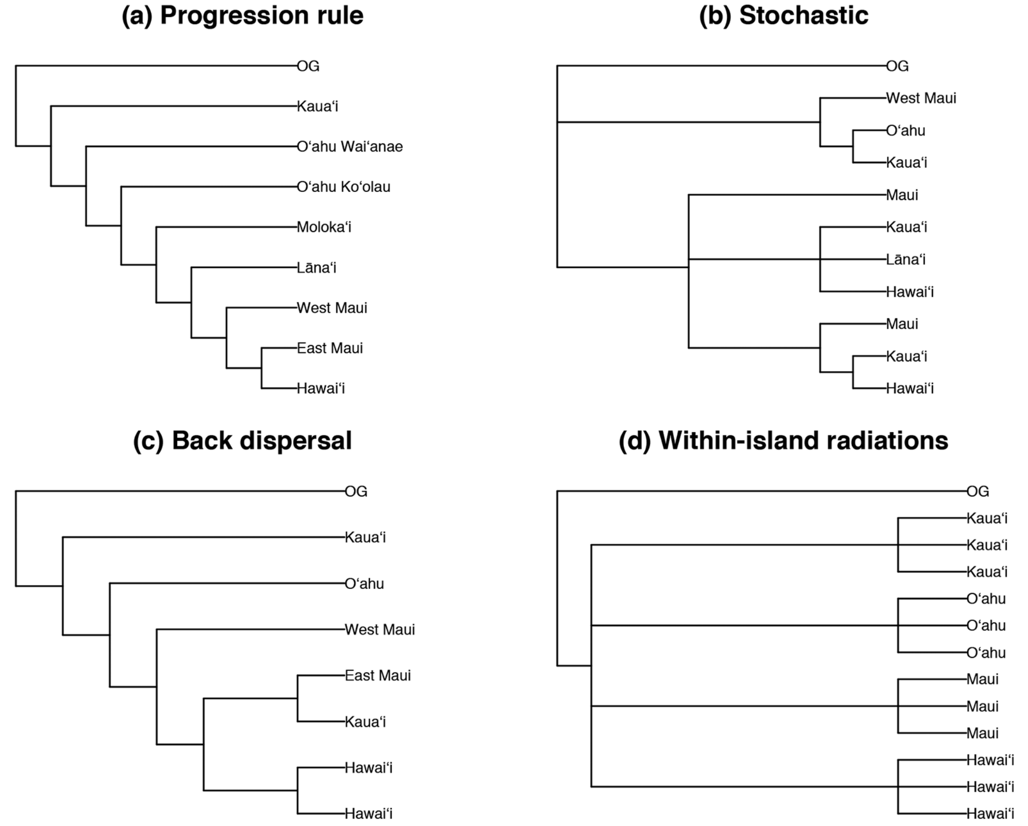

Figure 2. Four Primary Biogeographic Patterns for Hawaiian Radiations Proposed By Funk and Wagner (1995)

a. Progression rule is a pattern in which recently diverged lineages are found on younger islands, and earlier diverging lineages are found on older islands. This type of pattern might be expected from a hot spot archipelago where younger islands are colonized by taxa from nearby older islands (Carson and Clague 1995). Rare storm events may also drive the progression rule pattern because they often move down the island chain perpendicular to both the trade and Kona winds. b. Stochastic patterns, in which island colonization is unrelated to the relative ages of the islands, may be seen in taxa that are highly vagile or that have very recently colonized Hawai'i (Funk and Wagner 1995). c. Back dispersal, in which older islands are colonized by taxa from younger islands, may be driven by storm events. d. Within-island radiations may be driven allopatric speciation across multiple volcanic peaks within a single island, such as the Big Island of Hawai'i or Maui. They may also be potentially driven by isolation in different valleys or watersheds, by ecological heterogeneity of food resources, or by specialization onto different host plants (for phytophagous insects) or host insects (for parasitoids).

thought to have caused the extinction of nearly all of the Hawaiian flora—and probably many of its associated insects (Price and Clague 2002). Nonetheless, we have very little information about extinction rates and events during the pre-Holocene history of the archipelago. Therefore, phylogenies of all Hawaiian lineages should be interpreted with the caveat that modern sampling does not represent the species diversity of the recent past, and any inferred biogeographic patterns may be obscured by missing taxa.

Recognizing that the real histories of dispersal and speciation of Hawaiian endemic clades vary, Wagner and Funk (1995) classified potential biogeographic scenarios into nine basic and combined patterns, four of which we consider to be primary (progression rule, within-island radiation, stochastic colonization, and back dispersal; Figure 2;

Table 1). We consider the remaining five patterns to either be special cases of the four primary types or to reflect the inherent limitations of phylogenetic inference ("unresolved"). Here, we summarize the four primary patterns and scenarios expected to produce them.

Progression Rule

The progression rule (Figure 2a) is a stepping stone pattern observed in a number of lineages in Hawai'i, as well as in other hotspot oceanic archipelagos (Juan et al. 2000; Parent et al. 2008; Hembry 2018). The progression rule differs from a standard stepping stone model because it takes divergence time into account; recently diverged lineages are found on younger islands, and more anciently diverging lineages are found on older islands. This pattern might be expected in a hotspot archipelago where younger islands are colonized from nearby older islands. It is difficult to overstate the importance of the progression

TABLE 1

Biogeographic patterns seen in selected Hawaiian insect radiations, according to the four primary biogeographic patterns identified by Funk and Wagner (1995) and shown in Figure 4

Clade	**Patterns**					
	Progression	**Radiation**	**Stochastic**	**Back dispersal**	**Reference(s)**	**Notes**
Megalagrion	Yes	Yes	Perhaps	Perhaps	Jordan et al. (2003)	Back dispersal and stochastic hard to distinguish
Laupala	Yes	Yes	No	No	Mendelson and Shaw (2005)	
Banza	Yes	Yes	Yes	Yes	Shapiro et al. (2006)	
Nesophrosyne	Yes	Yes	Yes	Yes	Bennett and O'Grady (2012, 2013)	
Pariaconus	Yes	Yes	No	No	Percy (2017b)	mtDNA data
Swezeyana	No	Yes	Yes	Perhaps	Percy (2018)	mtDNA data
Ptycta	Yes	Yes	Yes	Probably not	Bess et al. (2014)	Dating analyses make assessment difficult
Rhyncogonus	Yes	Yes	Yes	No	Claridge et al. (2017)	Very few species in Hawaiian radiation sampled
Xyleborus	Perhaps	Yes	Yes	Perhaps	Cognato et al. (2018)	Very few species in Hawaiian radiation sampled
Philodoria	Yes	Yes	Yes	Perhaps	Johns et al. (2018)	Back dispersal and stochastic hard to distinguish
Hyposmocoma	Yes	Yes	Yes	Perhaps	Haines et al. (2014)	Back dispersal and stochastic hard to distinguish
Tephritidae	Partial	Yes	Yes	Yes	Viale et al. (2015)	
Drosophila + *Scaptomyza*	Yes	Yes	Yes	Yes	Bonacum et al. (2005); Lapoint et al. (2011, 2013, 2014); O'Grady et al. (2011); Magnacca and Price (2015); O'Grady and DeSalle (2018a)	This is a large radiation, with various lineages showing some or all of these patterns
Campsicnemus	Yes	Yes	Perhaps	Perhaps	Goodman et al. (2014)	Back dispersal and stochastic hard to distinguish, but few putative examples of either
Eurynogaster complex	Yes	Yes	Yes	Probably not	Goodman et al. (2016)	
Dicranomyia	No	No	Yes	Perhaps	Goodman and O'Grady (2013)	Back colonization seems likely but is not clearly demonstrated

rule as an animating hypothesis in the study of the evolution of the Hawaiian biota.

Progression rule patterns can be thought of as strict or relaxed. A strict progression rule would include taxa present on all of the islands. A relaxed progression rule would still show the older-to-younger lineage pattern, but would skip some islands. This might be due to extinction, poor taxon sampling, or because the lineage never actually established on the intervening islands. Large storm events, generating scouring floods with floating vegetation and/or strong winds, occasionally move down the island chain perpendicular to both the trade and Kona windsand may drive a progression rule pattern.

Stochastic Patterns

In contrast to the progression rule, stochastic patterns (Figure 2b) show no relationship with relative island ages and the phylogenetic relationships of taxa on different islands. Funk and Wagner (1995) provide several possible explanations for stochastic biogeographic patterns in Hawai‘i: (a) the taxon is highly vagile, so that dispersal distances are much greater than typical adjacent interisland distances; (b) the taxon has very recently colonized Hawai‘i and has not diversified; or (c) in this taxon, the colonization and speciation history truly is independent with respect to geologic history. Both (a) and (b) can be considered special cases of (c). When examining the phylogeography of island organisms, the null hypothesis that a clade's history of diversification is unrelated to the geologic sequence of island formation should be considered.

Back Dispersal

Some lineages may also disperse from younger to older islands. It is thought that storm events may be primarily responsible for such back-dispersal events (Figure 2c), although attachment to birds or floating debris may also be responsible. Back dispersal may be rare relative to progression rule patterns due to the fact that closely related taxa may already exist on the older islands and any "new" arrival will either hybridize or be outcompeted by their sister taxon. However, if enough time has passed and reproductive isolation and/or ecological differentiation exists, back colonists may be successful and maintained as distinct entities (Lapoint et al. 2011).

Within-Island Radiation

Species may diversify on a single island, particularly if they are narrow geographic or habitat endemics or if they display tight associations with specific host plants. Large islands comprised of multiple volcanic peaks, such as the Big Island of Hawai‘i, may contain enough geographic isolation to generate sibling species on different peaks (Bennett and O'Grady 2013; Haines et al. 2014). Likewise, ecological heterogeneity for feeding and/or oviposition substrate can drive a similar pattern of isolation by distance within the same island. Such within-island radiation (Figure 2d) is a major process underlying adaptive radiations and the diversification of the most species-rich Hawaiian insect clades. Specific hypotheses relating to timing of volcanic emergence, trade and Kona winds, and host plant dispersal may be generated for such events, although these have not been explicitly tested in most groups (but see Jordan et al. 2003; Bennett and O'Grady 2013). Large radiations may be generated by one or more bursts of ecologically driven within-island radiation on an older island followed by progression rule dispersal of each lineage onto succeeding islands, as seen in Hawaiian *Drosophila* (Magnacca and Price 2015).

Maui Nui Patterns

The islands of Maui, Moloka‘i, Lāna‘i, and Kaho‘olawe, often referred to as Maui Nui or "greater Maui," were contiguous at several periods of glacial maxima (i.e., low sea stands) during the Pleistocene (Price and Elliott-Fisk 2004). The islands of Maui Nui often share species (Liebherr 1997; Jordan et al. 2005; O'Grady et al. 2011), even in lineages that are characterized by a high degree of single-island endemism because dispersal was facilitated by past connections between the volcanoes of Lāna‘i, East and West Maui, Moloka‘i, and Kaho‘olawe. This pattern of vicariance is similar to within-island dispersal patterns, only spread across the closely associated Maui Nui islands. Distinguishing the effects of erosion and subsidence from overwater dispersal in the biogeography of Maui Nui taxa is challenging.

Ecological Shifts

Island lineages often evolve ecological niche shifts in situ, some of which rank among the most celebrated examples of evolution (Lack 1947; Carlquist 1974; Losos 2009). Like the radiations of Galápagos finches, West Indian anoles, and Hawaiian silverswords, Hawaiian insect radiations are also replete with examples of ecological or niche shifts. These include habitat shifts in elevation (ground beetles [Coleoptera: Carabidae: *Blackburnia*, *Mecyclothorax*], leafhoppers [Hemiptera: Cicadellidae: *Nesophrosyne*], and planthoppers [Hemiptera: Delphacidae: *Nesosydne*]) to dwelling in lava tube caves (ground beetles [*Blackburnia* and *Mecyclothorax*], assassin bugs [Hemiptera: Reduviidae], water treaders [Hemiptera: Mesoveliidae], planthoppers [Hemiptera: Cixiidae: *Oliarus*], and crickets [Gryllidae: *Thaumatogryllus*, *Caconemobius*]) from aquatic or riparian habitat to terrestrial habitat (the Hawaiian endemic damselflies [Odonata: Coenagrionidae: *Megalagrion*], shore bugs [Hemiptera: Saldidae], and water-scavenging beetles [Coleoptera: Hydrophilidae: *Limnoxenus*]), and from terrestrial to aquatic habitats in *Hyposmocoma* moths (Lepidoptera: Cosmopterigidae) and *Blackburnia* carabid beetles; shifts among host plant species and families (beetles [Coleoptera: Belidae, *Proterhinus*, Cerambycidae: *Plagithmysis*], flies [Diptera: Drosophilidae: *Drosophila*], plant bugs [Hemiptera: Miridae: *Orthotylus*], *Nesophrosyne* leafhoppers, *Nesosydne* planthoppers, and moths [Lepidoptera: Gracillariidae: *Philodoria*, Carposinidae: *Carposina*]), including shifts between angiosperm and fern hosts in *Proterhinus* weevils, shifts to plants introduced by humans in *Omiodes* moths (Lepidoptera: Crambidae), and shifts to novel Hawaiian host plants in the colonizing ancestors of the psyllid genera *Megatrioza* and *Pariaconus* (Hemiptera: Psyllidae); shifts in host-plant tissue use, including the acquisition of galling in tephritid flies (Diptera: Tephritidae) and the leaf-mining habit in *Proterhinus* weevils; shifts from detritivory or herbivory to carnivory in the larvae of the moth genera *Hyposmocoma*, *Agrotis* (Lepidoptera: Noctuidae), and *Eupithecia* (Lepidoptera: Geometridae); the acquisition of the water-skating habit in *Campsicnemus* flies (Diptera: Dolichopodidae); and wing reduction leading to the loss of flightedness in *Limnoxenus* beetles and the ability to make sounds in the cricket genera *Thaumatogryllus* and *Leptogryllus* (Orthoptera: Gryllidae). Many of these examples are discussed in greater detail in the overviews of different insect orders (below).

A handful of endemic Hawaiian insect radiations may have evolved niche shifts that are compatible with the influential taxon cycle hypothesis in island biogeography, which proposes that species' ranges undergo cyclical expansions and contractions associated with ecological shifts (Wilson 1959, 1961; Ricklefs and Bermingham 2002; Economo and Sarnat 2012). The original formulation of the taxon cycle, based on Melanesian ants, is a complex verbal model containing a number of interrelated components (Wilson 1959, 1961). One of these components is the proposition that taxa shift over evolutionary time from variable, lower-elevation habitat to stable, higher-elevation habitats, while undergoing declines in abundance (Wilson 1959, 1961; Economo and Sarnat 2012). It is this element of the taxon cycle that is most relevant to the Hawaiian entomofauna, although it has not been explicitly tested in Hawaiian insects using molecular phylogenetic data. Liebherr and Porch (2015) use morphology-based phylogenetic analyses incorporating extinct subfossil and extant taxa to demonstrate that *Blackburnia* ground beetles have not evolved from low to high elevation habitats on Kaua'i. In contrast, both ephydrid and canacid flies display a phylogenetic pattern of basal, strand-associated, salt-tolerant taxa at low elevations and derived taxa occupying high-elevation freshwater streams (O'Grady et al., unpublished data). In these fly radiations, many of the low-elevation coastal species are widespread, and the high-elevation species are single-island or single-mountain endemics. Such a pattern, analogous to some seen in other coastal and aquatic Hawaiian insect groups, may be consistent with this

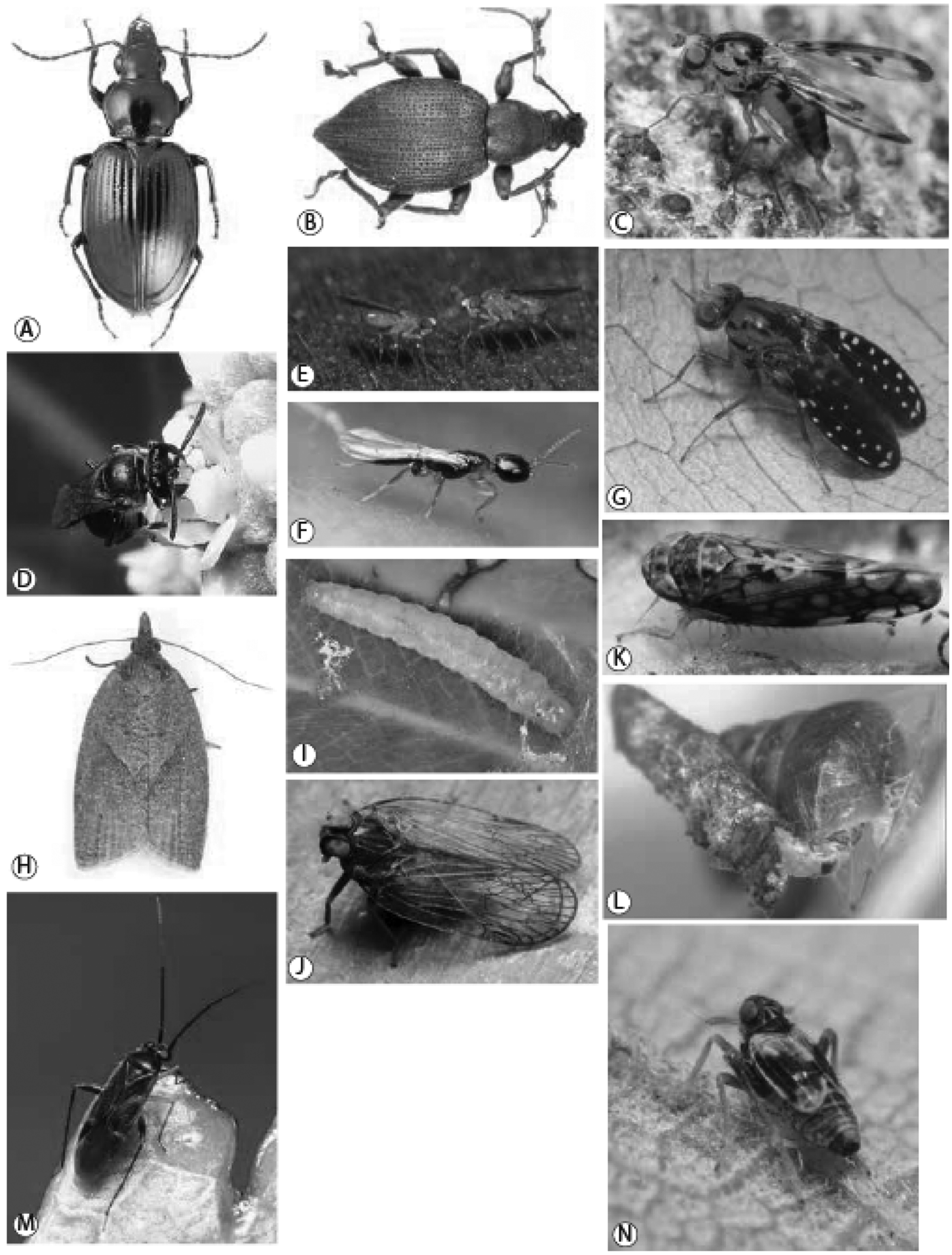

Plate 1. Images of Some Endemic Hawaiian Insects

A. *Mecyclothorax rex* (Carabidae), Koʻolau Forest Reserve, Haleakalā, Maui; B. *Rhycogonus zeta* (Curculionidae), *ex: Freycinetia* axil, Maunalei Arboretum, West Maui, Maui; C. *Drosophila substenoptera* (Drosophilidae), Palikū, Oʻahu; D. *Scaptomyza cyrtandrae* (Drosophilidae), Stainback Highway, Hawaiʻi; E. *Hylaeus longiceps* (Colletidae), Kahuku, Oʻahu; F. *Sierola weawea* (Bethylidae), Kaluaʻa, Oʻahu; G. *Drosophila neogrimshawi* (Drosophilidae), second component of the taxon cycle hypothesis. This phenomenon might also explain the presence of narrow endemics of some lineages (e.g., *Megalagrion* damselflies) in high-elevation bog habitats.

Leaving Hawai‘i

Although species that colonize remote islands may evolve into hyperdiverse lineages, oceanic islands are often considered a “dead end” to colonizing lineages and thus species diversity (Mayr 1942; Wilson 1961; Diamond 1970). Island-adapted taxa are generally poor dispersers (Darwin 1859) and, as an island erodes and submerges, many endemic taxa go extinct, eliminating entire lineages. It is often difficult for island species to compete with more robust taxa introduced from continental sources (Gillespie and Roderick 2002) because island endemics have often lost key defensive traits (e.g., thornless Hawaiian raspberries and mintless Hawaiian mints), have reduced dispersal abilities (e.g., flightless craneflies and moths), or have evolved behaviors that make them less able to escape predation (Carlquist 1974).

This “dead end” idea has been reinforced by the relative difficulty in determining specific sister group relationships of many endemic Hawaiian lineages. For example, the sister taxon of the Hawaiian Drosophilidae is possibly a large clade of species distributed throughout the Holarctic, Neotropical, and Paleotropical regions, although statistical support for this relationship is not particularly strong (Remsen and DeSalle 1998; Remsen and O’Grady 2002; O’Grady and DeSalle 2008, 2018a,b). This phylogenetic ambiguity is likely due to a combination of factors including the rapid burst of diversification that took place at the base of the genus *Drosophila* approximately 30 million years ago, the large divergence time within this genus, and the great degree of evolutionary change along both lineages (Russo et al. 1995, 2013).

Modern phylogenetic studies are overturning much of the dogma against colonization of continental landmasses by island lineages (Heaney 2007; Bellemain and Ricklefs 2008). Several studies have extensively sampled taxa from both island and continental lineages and included sufficient molecular data to resolve deep divergences with statistical power. A number of Hawaiian groups are now known to have successfully colonized other remote archipelagos or even continents, including Hawaiian Drosophilidae (O’Grady and DeSalle 2008; O’Grady et al. 2011; Lapoint et al. 2013), sandalwoods (Harbaugh and Baldwin 2007), *Melicope* (Appelhans et al. 2014, 2018), snails (Rundell et al. 2004), potentially other plant groups (Price and Wagner 2018), and possibly even birds (Filardi and Moyle 2005). There is ample evidence of biotic exchange between remote archipelagos across the Pacific and Indian Oceans (Cibois et al. 2011; Hembry et al. 2013; Le Roux et al. 2014; Andersen et al. 2015), suggesting that the Hawaiian Islands are more likely part of a broader global exchange of species than a turgid backwater.

THE ENDEMIC HAWAIIAN INSECT FAUNA

Many Hawaiian insect lineages are considered examples of adaptive radiation (Kambysellis et al. 1995; Craddock 2000; Gillespie and Roderick 2002). HHere, we provide overviews of Hawaiian diversity within the most species-rich insect orders (Coleoptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera, Odonata, and Orthoptera). Our goal is to draw attention to particular species-rich or evolutionarily interesting taxa, many of which have radiated within Hawai‘i (Plates 1 and 2).

Mt. Ka‘ala, O‘ahu; H. undescribed *Pararrhaptica* sp. (Tortricidae), *ex: Myrsine sandwicensis* (kōlea lau li‘i), Mt. Ka‘ala, O‘ahu; I. unidentified *Spheterista* sp., *ex: Polyscias* (*Tetraplasandra*) *oahuensis* (‘ohe mauka), Ko‘olau Mountains, O‘ahu; J. *Oliarus* sp. (Cixiidae), ‘Ōla‘a Forest, Hawai‘i; K. *Nesophrosyne* sp. (Cicadellidae), Palikea, O‘ahu; L. *Hyposmocoma molluscivora* (Cosmopterygidae), ex: *Tornetellides* sp., Maui; .M. *Orthotylus neoilicis* (Miridae), Stainback Highway, Hawai‘i; N. *Nesosydne pipturi* (Delphacidae), Palikea, O‘ahu. Photo credits: James Liebherr (A, B); Kyhl Austin (H, I); Karl Magnacca (C–G, J–K, M–N); Rubinoff Laboratory (L). See the online edition for a color version of this plate.

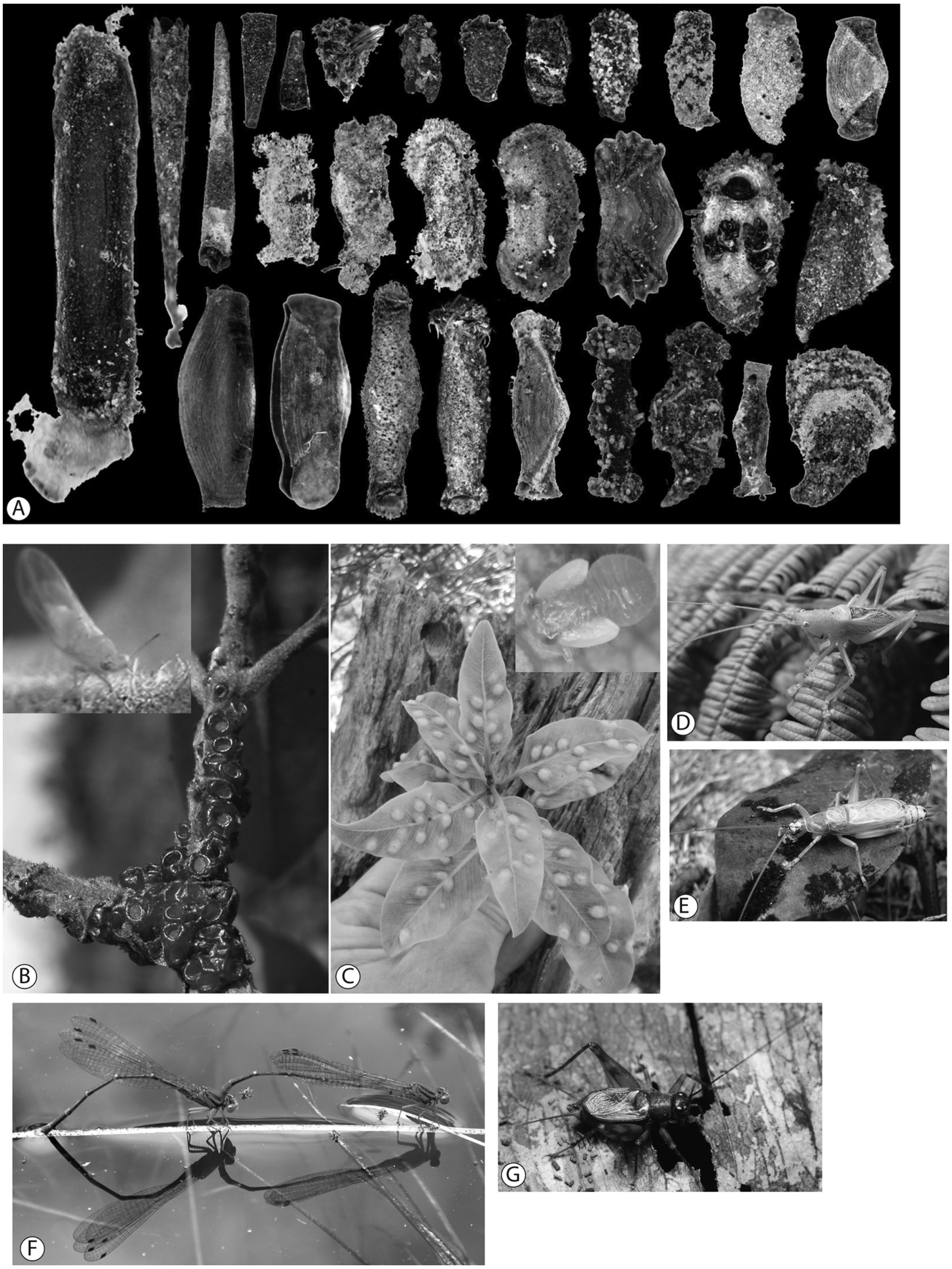

Plate 2. Images of Additional Endemic Hawaiian Insects

A. Montage of various *Hyposmocoma* larval case structures (Cosmopterygidae). Each case represents not just a unique species, but lineage of species, each endemic to a single volcano; B. *Pariaconus crassiocalix* (Triozidae; inset) with cup galls on *Metrosideros polymorpha*, Nuʻalolo Trail, Kauaʻi; C. *Pariaconus ohiacola* (inset) with leaf galls on *Metrosideros polymorpha*, Oʻahu; D. *Banza* sp. (Tettigoniidae); E. *Prognathogryllus mauka* (Gryllidae); F. *Megalagrion calliphya* (Coenagrionidae); G. *Laupala* sp. (Gryllidae), Kaluaʻa, Oʻahu. Photo credits: Rubinoff Laboratory (A); Diana Percy (B, C); Kerry Shaw (D, E); Idelle Cooper (F); Karl Magnacca (G). See the online edition for a color version of this plate.

We highlight what is known about the evolution and biogeography of those radiations that have received phylogenetic or taxonomic attention; the biogeography, speciation, and macroevolution of these groups will be further synthesized in the Discussion section below. Finally, we hope these overviews inspire future work on many poorly known yet interesting Hawaiian insect radiations that have not received recent attention from biologists.

Coleoptera

Coleoptera are the most diverse order of insects in the Hawaiian entomofauna, with roughly 25% (1559) of the 5618 described native Hawaiian insect species placed in this order (Eldredge and Evenhuis 2003). Hawaiian Coleoptera are dominated taxonomically by four major radiations, each comprising more than 100 described species (Liebherr 2001, 2015). These include two phytophagous genera, *Proterhinus* weevils (Belidae) and *Plagithmysus* longhorned beetles (Cerambycidae), and two genera of predaceous Carabidae, *Blackburnia* and *Mecyclothorax*. Interestingly, the beetle clades Carabidae, Cerambycidae, and Curculionoidea (weevils) are among the most species-rich beetle clades on continents. Of these, *Blackburnia* and *Mecyclothorax*, as well as several less diverse radiations (*Rhyncogonus*, *Limnoxenus*, *Bembidion*, and *Xyleborus*), have received molecular phylogenetic attention, thereby adding to our understanding of how and when beetles colonized Hawai‘i, as well the various evolutionary bases underlying beetle diversification (Liebherr 2001).

Blackburnia

This radiation of moderately sized carabid beetles comprises 140 described species (Liebherr and Porch 2015). *Blackburnia* are predaceous as adults and larvae (Liebherr 2000), with species radiating ecologically within many life zones and terrestrial habitats, mesic and wet forests, subalpine and alpine shrublands, riparian and aquatic microhabitats, and caves (Gagné and Cuddihy 1990; Liebherr and Samuelson 1992; Krushelnycky et al. 2005; Liebherr and Short 2006). Some species show fidelity to different plant associations within montane forests, with various species restricted to *Acacia koa*-dominated forest (Polhemus et al. 2003). Nearly all species occupy single islands, although four species range across the now-isolated volcanoes that formed Maui Nui (Liebherr and Zimmerman 2000).

Morphological phylogenetic analysis indicates that the *Blackburnia* radiation is monophyletic (Liebherr and Zimmerman 1998), with the Australian genus *Notagonum* (Liebherr 2005, 2017) the best supported outgroup based on *Notagonum* and *Blackburnia* being mutual members of a clade characterized by monorchy; i.e., presence of only a single male testis (Will et al. 2005). Via morphological and multilocus phylogenetic analysis, Cryan et al. (2001) corroborated monophyly of major lineages within *Blackburnia* and resolved many species triplets occupying Moloka‘i, West Maui, and Haleakalā, the former windward faces of Maui Nui (Liebherr 1997). Based on either outgroup, *Blackburnia* colonized Hawai‘i from Australia via aerial dispersal, with arrival time hypothesized to be 28–30 Ma based on phylogenetic relationships among Pacific platynine taxa constrained by ages of their occupied islands (Liebherr and Zimmerman 1998; Liebherr 2005, 2017).

Mecyclothorax

Mecyclothorax is another large radiation, with at least 239 described species endemic to Hawai‘i. All Hawaiian *Mecyclothorax* species lack flight wings, although the generalized *M. montivagus*, proposed to be the sister taxon to the rest of the Hawaiian radiation, retains brachypterous wing stubs. This vestigial trait suggests that, like *Blackburnia*, colonization was by a winged ancestor that evolved to occupy a diversity of habitats. Close relatives to Hawaiian *Mecyclothorax* include the geographically widespread, ecologically abundant, macropterous, Australian *M. punctipennis*, the brachypterous *M. sculptopunctatus* isolated on St. Paul and Amsterdam Islands of the Indian Ocean, the single macropterous New Zealand species *M. rotundicollis*, the Australian species *M. ambiguus*, and 108 brachypterous to apterous Society Island *Mecyclothorax* (Liebherr 2012, 2013, 2018).

Unlike the other major beetle radiations, which show a progression of colonization from older to younger islands, *Mecyclothorax* first colonized Maui Nui, where at least 189 described species are now endemic. The most diverse *Mecyclothorax* fauna is found in Haleakalā, with representation by 14 of 16 species groups recognized for the Hawaiian fauna. Oʻahu exhibits an attenuated fauna representing only four species groups characterized by derived patterns of setation (Liebherr 2009), and Kauaʻi lacks any species at all. From initial occupation of subalpine mesic shrublands on Haleakalā, a community type shared with its Australian ancestor (Liebherr 2018), species have evolved to occupy lowland to montane mesic and wet forests, alpine shrublands, and lava tube caves on the Big Island (Liebherr 2008a). The 189 described species that occupy Maui Nui display impressive levels of sympatry, with as many as 39 species recorded from a 30 cm × 30 cm quadrangle (Liebherr 2015), and occupy many different microhabitats (streamside riparian, terrestrial, and arboreal epiphytes or bark substrates). Closely related species are allopatrically distributed on different slopes of various Maui Nui volcanoes (Liebherr 2006), as well as stratigraphically isolated in lowland, montane, and subalpine habitats.

Rhyncogonus

The large, flightless *Rhyncogonus* weevils (Curculionidae) constitute a signature radiation within Hawaiʻi and across the Pacific (Claridge et al. 2017). Their large size and low intrinsic vagility belie their broad distributional range that incorporates remote archipelagos from Hawaiʻi southward through the Wake and the Line Islands, and extending throughout French Polynesia to Rapa Iti in the Australs and Henderson Island in the Pitcairns. Hawaiian *Rhyncogonus* number 47 species (Samuelson 2003), with most species endemic to Kauaʻi (14 spp.) or Oʻahu (21 spp.). Single species are found on the Northwest Islands of Laysan, Necker, and Nihoa (Clague and Dalrymple 1989). *Rhyncogonus* weevils are known to be root feeders as larvae, but host associations remain poorly known. The females of Oʻahu's *R. blackburni* lay clusters of eggs on the bases of *Acacia koa* phyllodes that the females may glue together (Giffard 1907). Upon hatching, larvae drop to the soil where they feed on the roots. Yet *R. blackburni* adults have also been recorded feeding on *Elaeocarpus* and *Scaevola* leaves; whether these represent larval hosts remains unknown (Samuelson 2003). Based on a four-gene data set, Hawaiian *Rhyncogonus* are monophyletic, with the colonizing propagule emanating from the Society Islands 5.7–9.0 Ma, a time of origin consistent with *Rhyncogonus* occupation of Necker and Nihoa (Claridge et al. 2017).

Bembidion

A third major carabid beetle radiation comprises 23 *Bembidion* species (Liebherr 2008b) representing two colonization events. The more diverse portion of this fauna constitutes 21 species of subgenus *Nesocidium*, with this lineage colonizing Hawaiʻi from New Zealand (Liebherr and Maddison 2013). *Bembidion* are most diverse on Kauaʻi (13 species), then Oʻahu and Maui Nui (nine species each), with only two species known from Hawaiʻi Island (Liebherr 2008b), and thus their diversity profile complements the Maui Nui-centric distributional profile of *Mecyclothorax*.

Limnoxenus

The Hawaiian hydrophilid beetle fauna comprises seven species of *Limnoxenus* (Short and Liebherr 2007), a genus otherwise including species from Europe, South America, Australia, New Zealand, and New Caledonia (Short et al. 2017; Toussaint and Short 2017). Four Hawaiian *Limnoxenus* have evolved from a fully aquatic lifestyle to occupy either hygropetric substrates adjacent to streams or to a fully terrestrial habitat with both larvae and adults occupying arboreal epiphytic mossmats (Short and Liebherr 2007). Hawaiian *Limnoxenus* have also undergone flight-wing reduction, with only one fully aquatic species polymorphically exhibiting fully functional flight wings. Other characters of body shape, systematic setose dorsal punctures, and tarsal setation transformed congruently with the ecological shift away from water.

Xyleborus

Xyleborus ambrosia beetles (Curculionidae: Scolytinae) are represented by 21 native, precinctive Hawaiian species, 18 of these based on female beetles and three exclusively by males (Samuelson 1981). *Xyleborus* has achieved a pantropical distribution since its origin 20 Ma (Cognato et al. 2018), with six nonnative species complementing the native fauna. *Xyleborus* are haplodiploid, with diploid, mated females establishing a new colony after mating with their haploid brothers. The founding female carries the ambrosia fungus, inoculating her tunnels to provide fungal nutrition for herself, her larvae, and her subsequently emerging progeny. Both distributional and host plant ranges may be broad; e.g., *X. vulcanus* is distributed across all current high islands, while being recorded from hosts including *Perrottetia* (Dipentodontaceae), *Elaeocarpus* (Elaeocarpaceae), *Acacia koa* (Fabaceae), *Syzygium* (Myrtaceae), *Bobea* and *Melicope* (Rubiaceae), and *Pipturus* (Urticaceae; Swezey 1954; Samuelson 1981). Based on a five-gene partition data set, the native Hawaiian radiation is monophyletic with Asia as its geographic source (Cognato et al. 2018). *Xyleborus* colonized the Hawai‘i chain 9.8 Ma—on an island no younger than Necker Island—and must have colonized progressively to the current high islands. However, relationships of currently available species do not support progression rule patterns of island colonization, with back dispersal evident among populations of widespread species.

Rapid ‘Ōhi‘a Death, caused by the pathogenic fungus *Ceratocystis lukuohia*, has recently become an issue in on the Big Island of Hawai‘i where large diebacks have altered the tree communities in many areas. Although ‘ōhi‘a lehua (*Metrosideros polymorpha*, Myrtaceae) is not commonly attacked by native *Xyleborus*, with only the Big Island endemic *X. simillimus* recorded from *Metrosideros* (Samuelson 1981), the nonnative taxon *X. ferrugineus* does vector this pathogen to ‘ōhi‘a (Roy et al. 2019). Continued research on both native and introduced Hawaiian *Xyleborus* is essential, as ‘ōhi‘a is a keystone tree in many Hawaiian forest formations (Gagné and Cuddihy 1990).

Other Coleoptera

Two major Hawaiian beetle radiations, *Proterhinus* weevils (Curculionidae) and the longhorned beetle genus *Plagithmysus* (Cerambycidae), have not yet received molecular phylogenetic attention. Hawaiian *Proterhinus* weevils (Curculionidae) comprise 177 named species and subspecific forms (Nishida 2002). The diverse Hawaiian fauna is complemented across its Pacific Island distribution by depauperate faunas in Samoa, the Society Islands, the Marquesas, Enderbury Island, and Miti‘āro, Cook Islands (Brown 2019). *Proterhinus* larvae feed predominantly under bark or in dead and dying twigs or larger branches of trees and subalpine shrubs (Perkins 1913; Swezey 1954), although several Hawaiian species are leaf miners of *Broussasia* (Hydrangeaceae) and eight species feed on dead frond stipes of *Cibotium* (Cibotiaceae) or *Sadleria* (Blechnaceae) ferns (Perkins 1920; Anderson 1941). *Proterhinus* beetles have been collected in association with 56 native plant genera representing 34 families (Swezey 1954), with host plant preferences ranging from monophagous to highly polyphagous (e.g., species such as *P. angustiformis* that feed on multiple host plant families; Swezey 1954).

The longhorn beetle genus *Plagithmysus* (Cerambycidae), with 142 Hawaiian species, is placed within the tribe Clytini. Gressitt (1978) suggested southern North America as the geographic source for the Hawaiian radiation. *Plagithmysus* exhibits a distinctive distribution pattern relative to most other Hawaiian insect groups. Although they are distributed on all high islands plus Nihoa, they are distinct in that fully 49 of 142 (approximately 35%) named forms (Nishida 2002; Samuelson 2006) are endemic to the youngest island, Hawai‘i. *Plagithmysus* beetles exhibit a broad range of host plants, including 27 flowering plant families. Unlike *Proterhinus*, however, *Plagithmysus* are more commonly associated with primarily woody plants, including 23 species on *Acacia koa* and six on *Sophora* (Fabaceae), 10 species associated with *Metrosideros*, and two with *Syzygium* (Myrtaceae). Although

Gressitt (1978) proposed that *Plagithmysus* exhibit progressive colonization of the island chain, with representatives of various species groups utilizing the same or related hosts as each lineage colonized newly emerging islands, contradictions to this pattern are attested (Samuelson and Davis 1986).

Diptera

Phylogenetic relationships and divergence dates have been inferred for a number of dipteran groups that have radiated within the Hawaiian Islands (Nitta and O'Grady 2008; Lapoint et al. 2011, 2013, 2014; O'Grady et al. 2011; Goodman and O'Grady 2013; Goodman et al. 2014, 2016; Viale et al. 2015). Age of colonization ranges from the oldest known group of Hawaiian taxa, the Hawaiian Drosophilidae at 25 million years old, to groups dating to younger than the age of Kaua'i at 5 million years. Most Diptera families colonized the Hawaiian Islands a single time, although at least one, the Dolichopodidae, has undergone multiple colonization events (Goodman et al. 2014, 2016).

Drosophilidae

The Hawaiian Drosophilidae are the oldest, largest, and perhaps the best studied lineage of endemic Hawaiian taxa. There are an estimated 1000 species, found in two major lineages, the Hawaiian *Drosophila* and genus *Scaptomyza*, each of which is strongly supported as monophyletic and sister to the other (Thomas and Hunt 1993; Kambysellis et al. 1995; Russo et al. 1995, 2013; O'Grady et al. 2011; Yassin 2013; O'Grady and DeSalle 2018a,b). The Hawaiian Drosophilidae arrived in the archipelago approximately 25 million years ago and predate all Hawaiian plant and animal lineages investigated to date. The Hawaiian Islands at that time were very low in elevation (less than 1000 m) and probably lacked any of the rainforest plants or habitats that we observe today (Price and Clague 2002; Price and Wagner 2018). Campanulaceae are one of the only plant lineages that predate Kaua'i, colonizing the archipelago roughly 16 million years ago (Givnish et al. 2009). Although this group is an important Hawaiian *Drosophila* host plant, the flies evolved in the Hawaiian Islands for nearly 10 million years without this resource.

The Hawaiian Drosophilidae have persisted in the islands for 25 million years, colonizing new islands as they emerged and diversifying within the archipelago. Several Hawaiian Drosophilidae groups have well-supported phylogenetic hypotheses available (reviewed in O'Grady et al. 2011; O'Grady and DeSalle 2018b). The most common biogeographic pattern observed is the progression rule, seen in the *antopocerus*, *modified tarsus*, and *picture wing* species groups (Bonacum et al. 2005; Lapoint et al. 2011, 2013, 2014; O'Grady et al. 2011; Magnacca and Price 2015), and in several subgenera of *Scaptomyza* (Lapoint et al. 2013). Lapoint et al. (2011) also observed a back-colonization pattern in the *spoon tarsus* species group, where taxa moved from the youngest island of Hawai'i to the older volcanoes of East Maui, West Maui, and Moloka'i. Some groups of Hawaiian *Drosophila*, such as the *haleakalae* group, are characterized by stochastic pattern of movement from island to island, with little reference to island age (O'Grady and Zilversmit 2004).

Interestingly, members of the genus *Scaptomyza* seem to have escaped from Hawai'i during approximately the last 15 million years and gone on to colonize several continental landmasses (O'Grady and DeSalle 2008; Lapoint et al. 2013). This island-to-continent biogeographic pattern is unique among insects, although has been observed in plant and snail lineages (Rundell et al. 2004; Harbaugh and Baldwin 2007; Appelhans et al. 2014, 2018).

Tephritidae

Native Hawaiian Tephritidae (true fruit flies) constitute 25 described species from three genera: *Trupanea* and *Neotephritis*, both of which are also found outside Hawai'i, and the endemic *Phaeogramma* (Brown et al. 2006; Viale et al. 2015). As larvae, these flies are internal feeders—seed predators inside flower heads, stem miners, or gallers—of native Hawaiian Asteraceae in the silversword alliance, *Bidens*, *Lipochaeta*, and *Artemisia* (Viale et al.

2015). Molecular phylogenetic analyses using mitochondrial loci indicate that *Phaeogramma* falls within a paraphyletic *Trupanea*, and that this Hawai‘i-endemic clade is monophyletic (Brown et al. 2006; Viale et al. 2015). The biogeographic history of both *Trupanea* and *Phaeogramma* in Hawai‘i remains ambiguous because of short branch lengths and low support values in backbone nodes of their current phylogeny. However, molecular phylogenetic analysis shows that these flies originally diversified as flower head feeders, before evolving the galling and stem-mining habits one or more times (Viale et al. 2015). The bulk of this diversification has taken place on *Dubautia*, although the apparent sister (with poor support) to the rest of the Hawaiian endemic clade is a flower head feeder on *Artemisia*. *Trupanea* and *Phaeogramma* also have extracellular bacterial symbionts ("*Candidatus* Stammerula trupaneae") resident in their midgut, which have codiversified with their hosts, although a few instances of horizontal transmission, perhaps mediated by shared host plant substrates, can be identified in the phylogeny (Viale et al. 2015).

Dolichopodidae

Several endemic lineages of Hawaiian long-legged flies (Dolichopodidae) appear to have colonized the archipelago independently of one another (Goodman et al. 2016). Although there are seven dolichopodid genera present in Hawai‘i, only four have been examined in a phylogenetic context. These lineages are: *Campsicnemus*, a genus of 183 species found both within and outside of Hawai‘i; the *Eurynogaster* genus complex, a clade of 66 Hawaiian endemics; six Hawaiian species in the genus *Conchopus*; and a single Hawaiian representative in the genus *Thinophilus*. There are also one-to-two species each in the genera *Asyndetus*, *Hydrophorus*, and *Paraliancalus*, but there is little we can say about their relationships without additional data. Based on phylogenetic analyses (Goodman et al. 2016), there were at least three separate colonization events giving rise to the Hawaiian dolichopodid fauna: one for the *Eurynogaster* complex (approximately 12 Ma), one in *Campsicnemus* (4.5 Ma), and one in *Conchopus* (1.8 Ma). Dolichopodidae are generalist predators, strong fliers, and include many species that skim on the surface of fresh and/or brackish water. Together, these ecological characteristics may indicate good colonizing species and explain the multiple colonizations of the Hawaiian Islands by this family. *Campsicnemus* and *Eurynogaster* taxa have both diversified in the Hawaiian Islands and both genera show support for progression rule patterns (Goodman et al. 2014). Within the *Eurynogaster* complex, island-specific diversification is also observed, with both *Uropachys* (six spp.) and *Arciellia* (seven spp.) having multiple species endemic to Kaua‘i (Goodman et al. 2016).

Limoniidae

Limoniid crane flies are present in a small radiation of 13 endemic species in the genus *Dicranomyia*. Interestingly, this lineage colonized the Hawaiian Islands about 7 million years ago, prior to the formation of Kaua‘i. Unlike most other Hawaiian Diptera lineages, however, these taxa have a relatively low percentage of single-island endemic species, roughly 30% compared to over 90% for Drosophilidae and Dolichopodidae. Consequently, crane fly species tend to be broadly distributed on more than one island and show little evidence of a progression rule pattern within the Hawaiian Islands (Goodman and O'Grady 2013). This is perhaps due to the aquatic and semiaquatic habits that the larvae inhabit and their ability to tolerate brackish and salt water, making dispersal between islands more likely.

Hemiptera

Heteroptera

The native Hawaiian Heteroptera biota currently comprises 382 described species, of which 380 are considered endemic (Zimmerman 1948b; Nishida 2002). The majority of species within this local assemblage are representatives of a limited number of speciose insular radiations, particularly in the families Miridae, Lygaeidae, and Nabidae. Three mirid genera have 40 or more endemic Hawaiian species: *Orthotylus* with 95 species (Polhemus

2002, 2004, 2011, 2013), *Nesiomiris* with 50 species (Gagné 1997), and *Sarona* with 40 species (Asquith 1994). In addition, somewhat smaller insular radiations with at least 20 insular endemic species, many undescribed, are present in the mirid genera *Sulamita*, *Koanoa*, and *Pseudoclerada* (Asquith 1997). Three insular endemic radiations are also present in the lygaeid genera *Nysius* with 28 species (some of these occurring as endemics in the Northwestern Hawaiian Islands), *Oceanides* with 27 species, and *Neseis* with 23 species (Usinger 1942; Ashlock 1966; Polhemus 1998, 2002). Finally, in the family Nabidae the genus *Nabis* has an insular radiation containing 25 currently described endemic species, and another 41 endemics described and figured in manuscript, and nearing publication in a pending monograph (Polhemus, unpublished data).

At least 75 percent of the described native Heteroptera species in the Hawaiian Islands are the products of only 10 insular radiations at the genus level. In addition, the islands' Heteroptera biota is markedly disharmonic, lacking entire families such as Coreidae, Tingidae, and Corixidae that are species rich in continental settings, and with only a limited representation of other such families such as Reduviidae, Pentatomidae, Gerridae, Veliidae, Mesoveliidae, and Saldidae. Among these latter groups the Hawaiian taxa present often exhibit significant ecological shifts, including obligately cavernicolous species of Reduviidae and Mesoveliidae, the presence of only marine species in Gerridae, and transition from riparian to arboreal habitats in Saldidae. Despite the presence of hundreds of perennial freshwater streams, Hawai'i also lacks most families of aquatic and semiaquatic Heteroptera, with representatives of only four out of the world's 22 families in this assemblage present. None of these have undergone significant local radiations in the islands' inland waters.

With the exception of the morphologically based phylogeny for *Sarona* provided by Asquith (1995), none of the insular Hawaiian Heteroptera radiations has been analyzed phylogenetically, using either morphological or molecular data sets. However, given the presence of the radiations noted above, coupled with obligate host plant feeding relationships in many of the mirid genera, this group provides an interesting opportunity for future research of speciation modes and in the study of insect and host plant coevolution. For example, Hawaiian members of the genus *Orthotylus* feed on 45 endemic plant species in 19 genera representing 16 families (Polhemus 2013).

Auchenorrhyncha

The endemic plant-sap feeding insects in the suborder Auchenorrhyncha are among the most diverse and ubiquitous of the Hawaiian insects. Species are found in virtually every habitat type, across the coastal to subalpine gradient with particular abundance in mesic and rainforest habitats. Most species are single-island endemics, showing high levels of host plant specificity, often to a single endemic plant species or lineage (Zimmerman 1948c; Asche 1997; Bennett and O'Grady 2012). Despite their local ubiquity, the endemic Auchenorrhyncha are disproportionately represented by only a few lineages, including the family Cicadellidae (leafhoppers) and infraorder Fulgoromorpha (planthoppers). Several major Auchenorrhyncha lineages are remarkably absent from the Hawaiian biota, despite being well represented in continental systems. These lineages include the spittlebugs (Cercopoidea), cicadas (Cicadoidea), and the relatively diverse sharpshooter leafhoppers (Cicadellidae: Cicadellinae). Interestingly, these absent groups are generally xylem feeding, whereas the Hawaiian Auchenorrhyncha are phloem feeders. Xylem is one of the most nutritionally deficient diets and taxa specializing on xylem are typically larger and have longer feeding times, with species consuming up to 100 times their body mass per hour (reviewed by Redak et al. 2004). Ecological behaviors of these insects are further tied to the daily and seasonal quality of their host plants; the ability of insects to successfully feed on xylem declines with plant quality and health. The absence of xylem feeders in the endemic Hawaiian insects is likely associated with their elevated dietary requirements of abundant and healthy plants—all of which would be lacking in rafting or aerial dispersal scenarios.

Cicadellidae

The Hawaiian cicadellid fauna is strikingly disharmonious with respect to mainland diversity. Only one of the 25 recognized cicadellid subfamilies, Deltocephalinae, is represented in Hawaiʻi. Furthermore, only a few (e.g., *Nesophrosyne* and *Balclutha*) of the over 900 known cicadellid genera are present (Zimmerman 1948c). *Nesophrosyne* is derived from a single introduction and is among the most diverse insect radiations, with more than 200 predicted species, only approximately one-third of which are currently described (Bennett and O'Grady 2011, 2013). *Balclutha*, although commonly found across the archipelago, includes only six described species with more possible. A comprehensive molecular phylogeny exists for *Nesophrosyne* (Bennett and O'Grady 2012) and has revealed a profound, and underdocumented, species diversity. In particular, genetic data for the *Nesophrosyne* demonstrates a large number of cryptic species, diagnosable with 5–10% genetic diversity at the commonly used species marker, mitochondrial cytochrome-oxidase I (COI) locus. Morphologically indistinguishable species maintain the same general ecological and host plant associations, but are restricted to individual volcanoes and long-isolated forests (Bennett and O'Grady 2012).

Cixiidae

Only two of the 20 recognized planthopper families are represented in Hawaiʻi encompassing more than 200 described endemic species (Asche 1997). The endemic Cixiidae include two genera of independent origins, *Oliarus* and *Iolania*. A morphological phylogeny has been produced for the seven known species of *Iolania* (Hoch 2006). *Oliarus* is considerably more diverse, with a total of 58 described species (Zimmerman 1948c; Asche 1997; Hoch 2006). *Oliarus* includes a number of cave-adapted taxa. A remarkable subterranean diversity has been found among isolated cave populations of a troglodytic *Oliarus* species (Hoch and Howarth 1999; Wessel et al. 2013). Wessel et al. (2013) found evidence of cryptic species, suggesting that many more species in this genus are awaiting description.

Delphacidae

In contrast to other Auchenorryncha lineages, the Hawaiian Delphacidae fauna consists of 10 genera with more than 140 described species (Asche 1997). The total number of independent arrivals of delphacids is unclear, but probably fewer than the number of genera as several were described as Hawaiian endemics using a limited set of taxonomic characters (Asche 1997). The largest delphacid genus, *Nesosydne* (82 described species), is perhaps best understood and the focus of recent speciation work (Goodman et al. 2012, 2019). Population genetic approaches suggest that, like *Nesophrosyne*, *Nesosydne* species are at the early stages of divergence along both ecological and geographic axes (Goodman et al. 2019).

Auchenorrhyncha—General Trends

When considering the Hawaiian Auchenorrhyncha, it is important to note that comparison of raw species numbers provides little insight into the actual diversity and evolution of these insects. Robust and consistent systematic treatments are largely lacking. Some groups, such as the Cixiidae, have been described to include relatively large numbers of subspecies, although this practice has not been used for the leafhoppers or other delphacid planthoppers (Zimmerman 1948c; Asche 1997). Species descriptions among these groups have further received differing levels of attention and detail, with many species described using inconsistent and unreliable criteria (e.g., nymphs and variable external characters; reviewed by Zimmerman 1948c).

Despite gaps in our taxonomic and systematic knowledge, recent work on particular elements of the Hawaiian Auchenorrhyncha have made important contributions to our understanding of how geography and ecology can broadly shape insect diversity (Goodman et al. 2012, 2015, 2019; Bennett and O'Grady 2013; Wessel et al. 2013). For example, host plant associations are a major driver in shaping insect diversity in *Nesophrosyne* and *Nesosydne*

(Bennett and O'Grady 2012; Goodman et al. 2019). After initial adaptation to particular host plant lineages, these insects tend to diversify in parallel with plants as they disperse and establish throughout the archipelago (Bennett and O'Grady 2013). However, more recently established host plants (e.g., *Dodonaea* that established since 1.2 Ma) can provide novel ecological opportunities on older islands permitting successful back dispersals.

In other remarkable cases, Auchenorrhyncha species show transitions to the more extreme ecosystems found in Hawai'i. Both *Nesophrosyne* and *Nesosydne* include species adapted to host plant species that occur in the arid and cool summit ranges of Haleakalā and Mauna Kea (Zimmerman 1948c). In contrast, *Oliarus* species have adapted to strict root-feeding among lava tube and cave environments across the archipelago; these species further exhibit typical cave-adapted traits such as reduced or absent eyes and loss of pigmentation (Hoch and Howarth 1999; Wessel et al. 2013). The evolutionary patterns observed in Auchenorryncha may be explained by low dispersal rates between replicated habitats within a single island, an inability for species to admix or successfully compete with already established populations, or challenges that gravid migrants face in finding high-quality host plants after dispersal. Thus, it is likely that cryptic diversity is common among not only the Auchenorrhyncha lineages, but also in other Hawaiian insect lineages with narrow habitat specialization and low rates of dispersal.

Sternorrhyncha

All Sternorrhyncha are obligate plant-feeders with piercing mouthparts evolved to feed on plant sap (xylem and phloem). Approximately 375 species of Sternorrhyncha are recorded for the Hawaiian Islands. A little over 70% are considered introduced (including some serious pests), in many cases via agricultural or horticultural imports, and just under 30% are endemic; all native species are endemic to the archipelago. Sternorrhyncha comprises five superfamilies but only two superfamilies have endemic Hawaiian species: Coccoidea and Psylloidea. In terms of dispersal ability, these two groups represent opposite ends of a spectrum, with low dispersal/sedentary life stages in Coccoidea, and moderate dispersal with all adults winged in Psylloidea. None of the Sternorrhyncha are strong dispersers capable of reaching the archipelago independently so abiotic and biotic dispersal agents are therefore key, but little is known about these agents, the frequency of events, mechanics of transportation, or rates of successful colonization. Together, it is not clear that either dispersal ability, mobility traits, or selective dispersal agents can explain why there are no native lineages of Aphidomorpha or whiteflies in the Hawaiian Islands, or why many families in Coccoidea and Psylloidea did not colonize the archipelago. For instance, all independent colonizations of the Hawaiian Islands (≥ 8) by Psylloidea are from just one family (Triozidae; Percy 2017b; Percy et al. 2018) despite adjacent Pacific island regions having members of all eight psyllid families. Similarly, the estimated number of independent colonizations for Coccoidea (approximately five to six; Beardsley 1997) are from only two of the more than 20 recognized families. Psylloidea has the largest number of endemic Hawaiian taxa (74 spp. in 11 genera), with fewer endemic Coccoidea (34 spp. in 14 genera). Strikingly, the ratio of native to adventitious taxa in these two superfamilies is markedly different: less than 20% of the 172 Coccoidea species, but more than 90% of the 81 Psylloidea species are native.

Endemism in Coccoidea and Psylloidea is often coupled with absence of identifiable relatives elsewhere in the Pacific (Beardsley 1997; Percy 2017b). Limited and disharmonic representation of taxa suggests long-distance dispersal to the archipelago is rare but typical for these small insects. Divergent morphologies in many taxa make systematic affiliations outside the archipelago challenging, although for at least some endemic Pseudococcidae, Beardsley (1997) posited Australian and Pacific island origins. Our knowledge of the specific source faunas for most endemic lineages of Coccoidae and Psylloidea is scant. Due to the central location of the Hawaiian archipelago in the Pacific, the number of potential source faunas is large, and these faunas are often less well studied than the Hawaiian fauna. Historic taxonomic placement of endemic species can also be misleading in cases where artificial generic placements were used for convenience (Percy 2017b). Host plant specialization in Sternorrhyncha varies from broad generalists to extreme host specialists. Interestingly, Psylloidea, which exhibit the highest plant specialization, also comprise the largest endemic Hawaiian fauna, implying that observed specialization is not a barrier to island colonization. However, for most colonization events little is known about ancestral biologies or host plants, and therefore the size of a host leap required to successfully establish remains unmeasurable. The available molecular phylogenetic data for Sternorrhyncha, critical to answering many of the questions relating to systematic placement, ancestral affiliations, and patterns of dispersal and divergence within the archipelago, are all in Psylloidea.

Pariaconus

The most thoroughly examined and species-rich lineage of Psylloidea in the Hawaiian Islands is the endemic genus *Pariaconus*, with 36 described species, 33 of which (92%) are single-island endemics (Percy 2017b). Molecular systematics has established the most likely source region as Australasia-Asia based on the closest outgroups, and there are no close relatives currently known from other Pacific islands, implying a single long-distance colonization event. All species of *Pariaconus* are known to feed on a single host plant, *Metrosiderospolymorpha*, and molecular dating evidence suggests the initial immigrant arrived soon after colonization of the Hawaiian Islands by *Metrosideros* (3–5 Ma; Percy et al. 2008; Percy 2017b). Interestingly, the source regions are not the same for plant and insect. Although originally both are Australasian-Asian, *Metrosideros* colonized various islands across the Pacific before reaching Hawaiʻi, whereas psyllids on these other islands feeding on *Metrosideros* represent a monophyletic Pacific lineage separate from *Pariaconus*. Within the Hawaiian archipelago both *Pariaconus* and *Metrosideros* have early colonization and divergence events on the oldest extant island of Kauaʻi, and there is evidence that both psyllid and plant lineages colonized Kauaʻi before colonizing younger islands in keeping with the progression rule. In *Pariaconus* there is no evidence of back dispersal from younger to older islands; the *kamua* species group (10 spp.) is endemic to Kauaʻi, and within-island divergence is found on Oʻahu, Maui, and Hawaiʻi in the *bicoloratus* and *ohialoha* species groups (Percy 2017b). Most of the speciation events (particularly within-island events) can be correlated with a biological shift to galling different parts of the host plant or generation of different gall phenotypes, implying shifts in resource use may have occurred in sympatry (i.e., on the same host within islands). In general, the patterns in *Pariaconus* are consistent with progressive colonization and repeated resource optimization shifts (Percy 2017b).

Other Psylloidea

Although less species rich than *Pariaconus*, there is now some molecular data for all of the other endemic Psylloidea lineages except *Paurotriozana* (Percy 2017a, 2018; Percy et al. 2018). Among these, within-island divergence is evident in *Hevaheva*, *Swezeyana*, and *Kuwayama*. As with *Pariaconus*, divergence in *Swezeyana* also occurs on a single host plant (*Planchonella sandwicensis*, Sapotaceae) again within islands, and again suggestive of sympatric divergence (Percy 2018). *Swezeyana* appears to be a slightly older lineage than *Pariaconus*, with fewer taxa and more stochastic divergence patterns.

The ancestral host plants for most of the Psylloidea lineages remain unknown, but in one case, in *Megatrioza*, an unusual host switch to *Pritchardia* palms (monocot host plants are extremely unusual in Psylloidea) may have occurred with colonization of the islands, and specificity to this host genus has subsequently been maintained during speciation events across the archipelago. A wide host leap on colonization may also have occurred in *Pariaconus* whose closest outgroup does not occur on *Metrosideros* or other Myrtaceae hosts (Percy 2017b). These cases suggest that long-distance dispersal to the Hawaiian Islands may require the ability to establish on unfamiliar hosts, a substantial filter to colonizing psyllids that may explain why only Triozidae taxa have established on the islands (Percy 2017b). Conservation of host preference post-establishment is typical in Psylloidea, even during interisland colonization and speciation, and therefore a relatively small portion of the Hawaiian flora hosts psyllids. In a recent Psylloidea phylogeny (Percy et al. 2018), Hawaiian taxa in *Hevaheva, Trioza, Megatrioza*, and *Crawforda* come out as potential sister groups, which would require some broader host leaps to have taken place post colonization during divergence in the Hawaiian Islands. However, deep divergences between these genera suggest more outgroup sampling will likely reveal non-Hawaiian ancestors, increasing the estimated number of independent colonizations to the archipelago.

Lineage diversity in both Coccoidea and Psylloidea is strongly influenced and constrained by diversity and divergence in native host plants, a general feature shared with several Auchenorrhyncha taxa. Highly specific associations with currently rare and threatened endemic plants raise serious conservation concerns, even greater than for the threatened host plants, because extirpation of the insect taxa is likely to precede that of the plant. In the case of the two species of *Stevekenia* (Psylloidea), both single-island endemics on *Nothocestrum* host plants that have been added to the IUCN Red List, there were less than a handful of individuals known at the time these species were described (Percy 2017a).

Hymenoptera

Hymenoptera, with about 33 lineages represented by over 650 described species and hundreds more undescribed, are one of the more diverse orders in Hawai‘i. However, they have been understudied relative to Diptera and Hemiptera. For example, many groups have not been revisited since they were originally described in *Fauna Hawaiiensis* (Perkins 1899, 1910; Ashmead 1901). The endemic chalcidoids, with at least 150 species across five families (Encyrtidae, Eulophidae, Eupelmidae, Mymaridae, and Pteromalidae), are particularly poorly known since the original descriptions are often inadequate and old specimens are in poor condition. Several large-to-moderate radiations—*Nesodynerus* (Vespidae, 111 species), *Hylaeus* (*Nesoprosopis*; Colletidae, 63 species), *Enicospilus* (Ichneumonidae, 24 species), and *Ectemnius* (Crabronidae, 21 species)—are relatively well characterized, but phylogenetic analysis has only been done for *Hylaeus* (Magnacca and Danforth 2006, 2007). The largest hymenopteran genus, *Sierola* (Bethylidae), has 212 endemic species described and probably 400–500 total, but is only beginning to be studied taxonomically and little is currently known. The great diversity of Hawaiian bethylids exemplifies the disharmonic nature of the Hawaiian fauna. In most continental areas, where the parasitoid fauna is dominated by Ichneumonidae and Braconidae, Bethylidae are a relatively small and overlooked group. The enormous radiation of *Sierola* in Hawai‘i, in contrast, makes up close to half of all native Hymenoptera species, with ichneumonids and braconids together totaling barely 5% of native species diversity.

Bethylidae

Aside from a small radiation of *Sclerodermus* (12–20 species), the Hawaiian bethylid fauna is dominated by a very large radiation of *Sierola*. The genus is widespread and abundant from Australia across nearly all Pacific island groups, with a few uncommon species in mainland South and Southeast Asia and Sundaland. This group is understudied, with nearly all known species awaiting description and the bulk of described species represented by the poorly known Hawaiian radiation. Within Hawai‘i, understanding of the bethylid fauna is heterogeneous—the O‘ahu species have been recently revised (Magnacca 2020), and those of the island of Hawai‘i partially described, while the faunas of Kaua‘i, Maui, and Moloka‘i are almost entirely unknown. No phylogenetic study has been conducted, but a few patterns are evident. *Sierola* appears to have originated in Australia, where the greatest morphological diversity occurs and where species appearing intermediate with the sister genus *Goniozus* occur. The monophyly of the Hawaiian *Sierola* is unclear, particularly given their ready dispersal across the Pacific and lack of morphological characters distinguishing them as a group from those found elsewhere. The non-Australian species are derived from a morphological subset of the Australian taxa, but also contain a number of morphological innovations, particularly in Hawaiʻi, such as the development of extremely modified mandibles, pale brown to yellow coloration, and deep, often ventrally angulate head shapes. Interestingly, all of these are paralleled in *Goniozus*. Within the Hawaiian Islands, these extreme forms are more commonly found on the older islands of Kauaʻi and Oʻahu (both in terms of numbers of species and abundance in the landscape), while the species present on younger islands such as Hawaiʻi tend to be more generalized. However, on Oʻahu many of the species are known from very few specimens—often only one—despite intensive collecting, suggesting that rare species with unusual forms may be missed on the other islands because they have not been the subject of similar collecting efforts. The degree of divergence among the species, and between the Hawaiian and the rather monotonous Pacific species, suggests that the group has been in Hawaiʻi at least since the origin of Kauaʻi, and possibly longer.

Colletidae

The sole lineage of native bees is also the only native hymenopteran group that has been analyzed phylogenetically. The 63 endemic *Hylaeus* belong to the subgenus *Nesoprosopis*, an otherwise obscure clade found in the eastern Palearctic and Oriental regions, with one species extending to western Europe (Daly and Magnacca 2003). A number of interesting undescribed species are found in China and Southeast Asia, but the closest relatives of the Hawaiian species are probably those from Japan. The Hawaiian taxa are derived from a single, relatively recent introduction between 0.5–1 million years ago (Magnacca and Danforth 2006). The major species groups diverged first on Hawaiʻi or possibly Maui, followed by stochastic dispersal to older islands—the relationships consist mainly of species pairs or triads, with one found on Hawaiʻi and one or two on another island, with more or less random distribution of the latter. This pattern is reflected not only in the tree but in the number of species. Unlike in most groups, the native *Hylaeus* are most diverse and have the most island endemics on Hawaiʻi Island, and have the fewest species on Kauaʻi and Oʻahu.

Lepidoptera

Hawaiʻi hosts over 1000 endemic moth species, but only two native butterflies (Nishida 2002), a common but still mysterious phenomenon of taxonomic disproportionality on islands (e.g., Clarke 1971). The actual number of moth species could easily be 50% higher since virtually every molecular study (Rubinoff and Schmitz 2010; Schmitz and Rubinoff 2011a,b; Haines et al. 2014), even of well-known large moths, reveals undescribed species (Rubinoff et al. 2021). There are at least 58 independent lineages (each likely an independent colonization event) hailing from 19 different families. Native species diversity is a highly disharmonic representation of global taxa, with many lepidopteran families never reaching the islands and many lineages that did still being relatively species poor; 16 lineages are represented by a single species, and about 40 lineages have fewer than 10 species (Haines 2011). Thus, whether due to timing or inherent limitations, relatively few lineages have radiated, but those that did make up most of the species diversity.

Interestingly, many Hawaiian Lepidoptera boast global evolutionary anomalies with regard to their ecologies. Carnivory within Lepidoptera globally is rarer than in any other insect order, with only 0.13% of all caterpillar species eating other animals, and all of those (outside Hawaiʻi) attack other insects (Pierce 1995). However, in Hawaiʻi, several independent origins of carnivory have occurred. For example, there are two species of alpine, diurnal *Agrotis* (Noctuidae) moth species restricted to stone deserts above 3000 m, both with semipredacious larvae (Medeiros et al. 2019). Furthermore, Hawaiian members of the globally distributed genus *Eupithecia* (Geometridae) include 21 species, all but one of which are ambush predator caterpillars, a characteristic not observed in the family anywhere else on the planet. Finally, although the majority of species in the genus *Hyposmocoma* (Cosmopterigidae) are probably scavengers or herbivores, there is a carnivore lineage with over 12 species, including some that specialize on hunting tree snails (Rubinoff and Haines 2005). The forces driving the adaptation to gastropod-feeding in *Hyposmocoma* remain unclear but may be linked to the abundance of snails in the Hawaiian Archipelago and the relatively unexploited nature of this resource.

Adaptation to and diversification on specific host plants is a characteristic observed in many Hawaiian Lepidoptera lineages. Larvae of the over 41 species of endemic *Carposina* have diversified to use at least 12 different host plant families, and a range of feeding modes, representing a remarkable ecological radiation (Medeiros et al. 2016). The Tortricidae contain over 70 endemic species from at least 10 separate colonization events, but little is known about most of their ecologies and phylogenetic relationships. The endemic genus *Philodoria* (Gracillariidae) has over 30 leaf mining species, including some that may have gone extinct along with their host plants, with their existence only evidenced by the distinctive larval mines preserved in herbarium specimens (Johns et al. 2014, 2016, 2018). Another ecological adaptation unique to Hawai‘i is seen in the Crambidae, where the 185 species are typical plant feeders. Interestingly, the larvae of some species hide underground when not feeding, a factor that might have helped them avoid predation by native predators and parasitoids, as well as weather the onslaught of invasive hymenopteran predators (King and Rubinoff 2008; King et al. 2010). This adaptation may also have allowed Crambidae to diversify more rapidly than their sister lineage, the Pyralidae, which includes only six native species.

Xylorictidae

Although globally somewhat obscure, the Xylorictidae have diversified into 32 species in Hawai‘i (Medeiros 2009), all part of the endemic genus *Thyrocopa*, which has independently evolved flightless, jumping adults on Maui and Hawai‘i Island; both such species are restricted to alpine environments above 3000 m (Medeiros and Gillespie 2011). The scavenger larvae are present throughout most rainforest and alpine ecosystems. *Thyrocopa* also exemplify niche conservatism, with species from the remote, low elevation, dry, windy Northwest Hawaiian Islands being closely related to the high elevation flightless species living in similarly dry and windy habitats (Medeiros et al. 2015).

Cosmopterigidae

The most extreme example of taxonomic disharmony in Hawai‘i is in the Cosmopterigidae, which include a little over 1800 species globally (van Nieukerken et al. 2016). *Hyposmocoma*, the endemic Hawaiian genus in the family, has exploded with at least 600 species, including hundreds that are recognized but not described, making up not only a preponderance of the overall family’s diversity but also 30–40% of *all* Lepidoptera species in Hawai‘i.

Several lineages in *Hyposmocoma* have independently evolved an aquatic lifestyle and are found residing in and along streams (Rubinoff and Schmitz 2010; Schmitz and Rubinoff 2011b). Although only 0.5% caterpillars on the planet are aquatic (Mey and Speidel 2008), this trait has evolved independently in *Hyposmocoma* at least four times (Rubinoff and Schmitz 2010). Almost all *Hyposmocoma* are restricted to single volcanoes within islands, and quite frequently sister taxa in this genus are found on different islands, not on adjacent volcanoes on the same island (Rubinoff and Schmitz 2010; Haines et al. 2014). Many species are highly specialized in their ecologies. For example, some reside only on the lichen-covered root tips of fallen ‘ōhi‘a (*Metrosideros*) trees in rainforests (Schmitz and Rubinoff 2011a), others only in the dead bracts of tree ferns. Perhaps their most puzzling feature is the ornate silk cases the larvae spin and inhabit throughout their development. Almost every lineage has a unique, signature case structure, with occasional instances of convergent evolution (Schmitz and Rubinoff 2011a; Kawahara and Rubinoff 2013). The reasons for these unprecedented evolutionary bursts of diversification and evolutionary novelties are unclear, but they may be related to the age of the colonization. The ancestor of *Hyposmocoma* arrived approximately 15 million years ago and nearly all major ecological/case lineages in the genus were present before Kauaʻi arose five million years ago, meaning there were at least 20 independent dispersal events from the older northwest islands down to the current main islands (Haines et al. 2014). Although in some *Hyposmocoma* lineages there is adherence to the progression rule, in others there is a pandemonium of interisland dispersal (including from younger to older islands) confirming the potential vagility inherent in the group. This ancient origin for the 20 species groups in *Hyposmocoma* also suggests that conditions on the now-receding dry, low atolls of the Northwest Hawaiian Islands may have, when those islands were younger and higher, resembled the diverse forests and climates present on the current islands, including resident tree snails and a diversity of plants and ecosystems.

It is likely that continued research will reveal additional evolutionary surprises in the Hawaiian Lepidoptera. For example, the monotypic sphingid genus *Tinestoma* is endemic to Kauaʻi, known only from 18 specimens and remains a complete mystery. Despite being the second largest native moth, even the larval host plant is unknown and may reflect a currently unimagined ecology. However, extinction looms for it and many other Lepidoptera. The original diversity of Hawaiian Lepidoptera was undoubtedly far greater than what remains, and extinction is rife in the group (e.g., Johns et al. 2014). The constant introduction of invasive species, including ants (King et al. 2010), habitat destruction, and a lack of basic distribution data (Medeiros et al. 2013) preclude meaningful conservation measures, and many species are likely on the verge of extinction but could be saved with concerted action (Kawahara and Rubinoff 2012).

Odonata

The majority of Hawaiian Odonata belong to the endemic radiation of *Megalagrion* damselflies. Only a few species of dragonflies (Anisoptera) are native to Hawaiʻi. The indigenous *Pantala flavescens* (Libellulidae) and green darner *Anax junius* (Aeshnidae) are also widely distributed outside Hawaiʻi, where some populations are migratory. The only endemic Hawaiian dragonflies are *Anax strenuus* (Aeshnidae) and *Nesogonia blackburni* (Libellulidae; Howarth and Mull 1992).

The 23 endemic Hawaiian *Megalagrion* damselflies are a spectacular example of adaptive radiation, exhibiting dramatic variation in larval and adult morphology as well as breeding habitats. *Megalagrion* breeding ecology includes fully aquatic larvae in basal springs, brackish anchialine pools, streams, acidic bogs, and anthropogenic aquatic structures, semiaquatic larvae in films of water and damp moss on waterfall faces and seeps, or in small pockets of water in plant leaf axils and, extraordinarily, terrestrial larvae in damp leaf litter beneath fern banks.

Adaptive radiation of *Megalagrion* was driven primarily by colonization of new volcanoes and ecological opportunities in larval habitats (Jordan et al. 2003). Exploitation of these habitats was surely facilitated by a lack of natural predators and competitors. Molecular data suggest that *Megalagrion* arrived in Hawaiʻi about 11 Ma, perhaps as a single gravid female, although her point of origin is unknown. At that time, none of the current high islands existed, so *Megalagrion* probably became established on Gardner, La Perouse, or Necker Islands, all of which overlapped temporally with Kauaʻi (Price and Clague 2002). Single-island endemics likely arose and went extinct over the life span of islands that are now largely eroded. Today, *Megalagrion* includes generalist species found on multiple islands as well as single-island endemics restricted to specialized habitats. The radiation appears to have followed three of the four main diversification patterns outlined above, dependent on species plasticity and vagility (Jordan et al. 2003). First, the progression rule clearly applies to clades that breed in fast streams, pools, and plant leaf axils. Second, *Megalagrion* underwent a dramatic within-island radiation on Kauaʻi beginning about 1.9 Ma, finely partitioning bog-associated habitats in close geographical proximity. Third, *M. hawaiiense* may have dispersed back up the chain from a source on Hawaiʻi Island. More localized patterns can also be seen within species of *Megalagrion*, including dispersal periodically interrupted by ephemeral sea channels or facilitated by wind or human activities (Jordan et al. 2005, 2007; Jones and Jordan 2015).

Recent studies have begun to examine how selection pressures experienced in different habitats lead to phenotypic variation and adaptation. Adult damselflies exhibit extensive color variation, but there is no phylogenetic signal for color (Cooper et al. 2016). Instead, a single ecological variable, exposure to solar radiation, predicts body color variation among and within species. Specifically, redder coloration is associated with more exposure to solar radiation. Many species have vivid red coloration, particularly in males, but this pigmentation is not a sexual signal (Cook et al. 2018). Rather, the bright red color characteristic of many *Megalagrion* functions as an antioxidant in habitat with high UV exposure (Cooper 2010). The adult environment is linked to larval habitat, but there is little research on larval adaptation. Gill shape is correlated with larval habitat type and may have enabled ecological transitions during adaptive radiation (Polhemus 1997). Because this radiation contains more variation in larval habitats than all other odonates worldwide, this system provides a unique opportunity to study how selection may lead to morphological, physiological, and behavioral adaptations across ecological gradients and between islands.

Ten *Megalagrion* species are considered threatened, endangered, or possibly extinct (Polhemus 2004; IUCN 2021). Perhaps because of their close association with aquatic habitat, *Megalagrion* are threatened by introduced alien invasive fishes (Englund 1999), stream diversion for agriculture and urban development (Polhemus 1993), physical destruction of habitat, and degradation of stream catchments by feral ungulates, particularly pigs (Nogueira-Filho et al. 2009). These damselflies may also be affected by changes to water availability due to climate change. For several decades, Hawaiʻi has been experiencing more frequent and prolonged droughts, especially at high elevations (Longman et al. 2015).

Orthoptera

Endemic Hawaiian Orthoptera are represented by two families within the suborder Ensifera (long-horned grasshoppers). The other major suborder of the Orthoptera, the Caelifera (short-horned grasshoppers) are not represented by any endemic lineages in Hawaiʻi, although introduced species are known (Nishida 2002). The endemic Hawaiian Ensifera derive from four separate colonizations, including the katydids (Family Tettigoniidae) and the crickets (family Gryllidae; Otte 1994). The genus *Banza* contains all of the endemic katydid species known in Hawaiʻi (Shapiro et al. 2006), totaling nine described species. Phylogenetic analysis of these rainforest-dwelling species (Shapiro et al. 2006) suggests the emergence of two major clades in the evolutionary history of *Banza*, each showing a general progressive biogeographical pattern from older to younger islands.

The endemic crickets (family Gryllidae) are considerably more diverse than the katydids in Hawaiʻi, likely deriving from four subfamily-level colonizations, including the tree crickets (Oecanthinae), the swordtail crickets (Trigonidiinae), and the ground crickets (Nemobiinae). Together, Otte (1994) recognizes these radiations as approximately 300 endemic species within five endemic genera (the tree crickets *Prognathogryllus*, *Leptogryllus*, and *Thaumatogryllus*; and the swordtail crickets *Laupala* and *Prolaupala*) and three nonendemic genera (*Trigonidium, Caconemobius*, and *Thetella*). Two ground crickets (*Caconemobius sandwichensis* and *Thetella tarnis*) are indigenous but not restricted to Hawaiʻi, being found throughout the northern Pacific region (although further taxonomic treatment may recognize additional diversity within each).

Taxonomic and limited phylogenetic treatments show that all native crickets, save the two ground crickets mentioned above, are geographically restricted to single islands and often single volcanoes (Otte 1994; Shaw 1995, 1996, 2000, 2002; Mendelson and Shaw 2005). Single-island endemism is likely tied to lifestyle and the ubiquitous pattern of flightlessness among the endemic cricket fauna (Otte 1994), minimizing participation in common modes of insect dispersal. Nearly all species in the swordtail and tree cricket radiations are restricted to mid-elevation rainforests (*Thaumatogryllus conanti*, a relict from rainforestless Nihoa being the only known exception to this pattern), where they appear dependent on high humidity and buffered temperature ranges. The geographic consequence of rainforest requirements likely depresses oceanic dispersal between islands. The two species with more widespread distributions, *Caconemobius sandwichensis* and *Thetella tarnis*, both inhabit the coastal splash zone of rocky beaches on multiple islands, probably due to greater opportunity for oceanic dispersal.

Endemism appears to extend to single volcano endemism in some cases, as exemplified by some species of the genus *Laupala*. Insight is greatest with this group due to extensive genetic and molecular phylogenetic analyses. A molecular phylogeny (Mendelson and Shaw 2005) shows a strong progression pattern where Kaua‘i taxa form a monophyletic group that is sister to the remaining *Laupala* clade. Two species groups are evident in the non-Kaua‘i sister group, each showing an older to younger island biogeographic progression (Mendelson and Shaw 2005; Shaw and Gillespie 2016). Lineages from these two species groups have speciated into the same habitats, leading to sympatric communities on each of the younger islands, comprised of representative species from each species group. The most conspicuous aspect of community assembly is the acoustic diversity (Otte 1994; Shaw 2000), as all sympatric species sing different songs, likely to facilitate conspecific mate pairing. Although all species of *Laupala* are very closely related, with divergence times apparently dating to no earlier and often much younger than the age of Kaua‘i (Mendelson and Shaw 2005), sympatric species are generally not sister species.

In general, ecological diversity among the most closely related forms is lacking, and this ecological similarity can extend deep into evolutionary history. Closely related species of *Laupala* of the same species group are similarly dark brown to black and lack conspicuous coloration, cannot be distinguished by male genitalia or other categorical features of morphology, and likewise are similar in displaying a lack of host plant dependency. About the endemic swordtail crickets, and especially *Laupala*, Otte (1994) remarks that an unusual ecological shift to a ground-dwelling habit characterizes some species (e.g., as described in Shaw 2000) or groups of species. This pattern appears somewhat plastic depending on congeneric community composition, with some species possibly showing spatial displacement or ecological release in response to the presence of absence of other species. It appears possible that sympatric species at times compete, but no conspicuous ecological divergence arises from it. Other phenotypes such as cuticular hydrocarbons (Mullen et al. 2007), songs, and acoustic preferences (Otte 1994; Shaw 1996; Mendelson and Shaw 2005) do vary substantially at the species level.

Other lineages of endemic crickets display more exciting ecological diversity, although research has only scratched the surface and further work would likely be very productive (deCarvalho and Shaw 2010; Brown 2016). Color pattern diversity is more pronounced and sometimes elegantly cryptic in some species of swordtail and tree crickets. The Moloka‘i swordtail endemic *Trigonidium atroferriginium* is bright green in immature nymphal stages but molts into a black cricket with red legs and yellow wings as an adult. Such patterning, in both life stages, makes it highly cryptic in the foliage of *Metrosideros polymorpha*. In the tree cricket radiation, two genera have lost both fore- and hindwings, making them mute. They have likewise evolved fossorial (genera *Leptogryllus* and *Thaumatogryllus*) and sometimes troglobitic (*Thaumatogryllus*) lifestyles. Morphological changes accompanying these shifts include limb elongations and, in the case of obligate lava tube species, eye reduction and the loss of pigment (Otte 1994). The endemic ground cricket radiation of the genus *Caconemobius* has also colonized cavernous and lava tube habitats on younger islands, showing similar adaptations to the lava tube tree crickets, such as loss of pigment, eye reduction, and limb elongations (Gurney and Rentz 1978; Howarth 2019). The time frames of these radiations are likely on par with those of the extant high islands, but definite answers must wait for phylogenetic evidence of relationships among the many species in these groups.

Psocoptera

Psocids are bark-dwelling insects that feed on fungus and lichen from the surface of trees. These cryptic, *Drosophila*-sized insects are not strong fliers, and are often reluctant to fly even when pursued. Wind dispersal has been proposed as their primary means of movement between islands (Thornton and Harrell 1965). Psocids were found consistently in aerial plankton surveys around Hawai‘i (Yoshimoto and Gressitt 1960, 1963), and showed themselves to be reliable early colonists that quickly built up large populations in the classic island biogeography experiments by Simberloff and Wilson (1969).

Three endemic Psocoptera lineages are present in the Hawaiian Islands. There are two genera in the family Elipsocidae, *Palistreptus* (20 species) and *Kilauella* (seven described species; Thornton 1990), and a single genus, *Ptycta* (51 described species), representing the family Psocidae (Thornton 1984). *Ptycta* is a relatively large genus, with some 170 species worldwide (Bess and Yoshizawa 2007). Both *Kilauella* and *Ptycta* appear to have many undescribed morphospecies in collections (Emilie Bess, pers. obvs., Bishop Museum, Australian Museum), and the total diversity of endemic *Ptycta* is estimated at 100 species. In addition to the endemic taxa, about 50 nonnative psocid species, representing 20 genera, have also been found on the islands (Lienhard and Smithers 2002).

Psocidae

The monophyly of the Hawaiian *Ptycta* was strongly supported in phylogenetic analyses of four genes from 101 individuals of Hawaiian *Ptycta* and 18 geographically diverse outgroup species, and the presence of two distinct Hawaiian clades was also strongly supported (Bess et al. 2014). Clade A is present on all four of the main Hawaiian Island groups (Kaua‘i, O‘ahu, Maui Nui, and Hawai‘i) and Clade B is present on only the three youngest island groups and is particularly diverse on Maui Nui and the island of Hawai‘i. Morphologically, two synapomorphies distinguish structures of the male genitalia between the two groups: Clade B species have more complex structures of the phallosome and hypandrium.

Time-calibrated phylogenetic reconstruction indicates that the endemic Hawaiian *Ptycta* began their radiation pre-Kaua‘i, roughly 7.14 Ma, a date that corresponds closely with the age of the oldest current island of Nihoa (7.2 Ma) and overlaps with the 10.3 Ma habitable age of Necker Island (Bess et al. 2014). The estimated ages of Clade A (2.62 Ma) and Clade B (3.24 Ma) are not significantly different and represent an origin slightly after the formation of O‘ahu (3.7 Ma). Interestingly, taxa from the youngest island are sister to the other taxa in both Clades A and B, suggesting multiple dispersal events from the island of Hawai‘i westward. Furthermore, taxa from Kaua‘i form a clade embedded within Clade A, suggesting back-colonization events within *Ptycta*. However, this pattern could also be the result of extinction of older lineages or failure to sample some lineages. Clearly, there appears to be extensive movement and diversification of *Ptycta* within and between islands following the initial colonization event. The crown age of 7.2 Ma, in combination with inter- and intraisland dispersal and possible extinction events lends support to the progression model for the diversification of Hawaiian *Ptycta*.

DISCUSSION

Phylogenetics have advanced considerably in the 25 years since Wagner and Funk’s (1995) review of Hawaiian biogeography and species evolution, particularly in our ability to computationally infer phylogenies with hundreds of taxa, to easily sequence entire genomes, and to test sophisticated models of evolutionary and biogeographic history. With the larger, more complete phylogenetic trees of Hawaiian insect radiations now available (more than 100–200 terminals in the case of *Ptycta* and *Nesophrosyne*; Bennett and O’Grady 2012; Bess et al. 2014), we find that many Hawaiian insect radiations show a mixture of the four primary biogeographic patterns first identified by Funk and Wagner (1995; Table 1). These new data illustrate the complex and historical interplay of these processes with increased clarity while creating a more comprehensive picture of how the endemic Hawaiian biota was assembled.

The Hawaiian entomofauna is characterized by a number of general, as well as idiosyncratic, biogeographic patterns. Here, we aim to synthesize general patterns in the biogeography and macroevolution of Hawaiian insects. First, we examine the colonization sequence and timing of the various independent Hawaiian lineages. Although there is much to be said about colonization times and temporal patterns within Hawaiian radiations, determining the exact source areas for many taxa remains elusive due to issues with sampling. Then, we consider the general applicability of each of the four primary mechanisms of within-Hawaiʻi diversification identified by Funk and Wagner (1995). Finally, we discuss additional drivers of diversification found across the Hawaiian insect fauna, beginning with a critical assessment of the progression rule hypothesis, and followed by discussion of some factors that might lead to large radiations.

COLONIZATION SEQUENCE

One of the enduring questions in Hawaiian biogeography is the age of its biota. The fact that the Hawaiian hotspot has been geologically active for approximately 80 million years suggests the intriguing hypothesis that some Hawaiian-endemic clades may be far older than Kauaʻi or even the Northwestern Hawaiian Islands, representing relicts of an ancient biota present for tens of millions of years in this remote part of the North Pacific. As a corollary, such great age for Hawaiian lineages would suggest that time has been a significant factor in generating Hawaiian endemic biodiversity.

Price and Clague (2002) used bathymetric measurements to estimate maximum heights of the Northwestern Hawaiian Islands and present-day habitat type distributions (e.g., rainforest greater than 1000 m) to infer past Hawaiian flora. They demonstrated that there was a period of approximately 2 million years prior to the formation of Kauaʻi in which the only subaerial islands were small, spaced apart, and likely less than 1000 m elevation. They then reviewed all of the available dated molecular phylogenies and found that 12 out of 15 Hawaiian multispecies lineages had crown ages less than 5 Ma, indicating that they might be no older than Kauaʻi. Of the three exceptions, two, the Hawaiian *Drosophila* and *Megalagrion* damselflies (Russo et al. 1995, 2013; Jordan et al. 2003), were insect clades and the third, the lobeliad radiation, was a plant lineage (Givnish et al. 1996, 2009). Subsequent phylogenetic studies added a few more examples (*Hyposmocoma*: Haines et al. 2014; the bird family Mohoidae: Fleischer et al. 2008) to this short list of exceptions, suggesting that the erosion of the Northwestern Hawaiian Islands caused the extinction of much of the ancient Hawaiian biota, and thus the bulk of the modern Hawaiian biota is post-Kauaʻi in age.

But Price and Clague's data set included very few insect taxa. Here, synthesizing data across more recent studies, we find that a notable fraction (12 of 17) of estimated ages of insect radiations predate Kauaʻi (5.1 Ma; Table 2; Figure 3), adding seven additional examples of pre-Kauaʻi lineages to their 2002 totals (this total does not include *Rhyncogonus*, which is inferred to be post-Kauaʻi using geologic calibrations but pre-Kauaʻi using molecular clocks; Claridge et al. 2017). These estimated ages range from 25 Ma in *Drosophila*+*Scaptomyza*, 21 Ma in *Philodoria*, and 15 Ma in *Hyposmocoma* to 7 Ma in *Ptycta*, roughly 5–7 Ma in the main Hawaiian *Dicranomyia* clade, 6 Ma in *Thyrocopa*, and 5.9 Ma in *Swezeyana*. In those 13 studies where authors report 95% highest posterior density intervals for clade ages, six radiations unambiguously are pre-Kauaʻi (Drosophilidae, *Hyposmocoma*, *Philodoria*, the *Eurynogaster* complex, *Xyleborus*, and *Limnoxenus*, but also the molecular clock *Rhyncogonus* estimate). These results suggest that an important and possibly a major fraction of the Hawaiian insect fauna initially colonized the archipelago before and persisted through the bottleneck preceding the emergence of the existing high islands.

These findings have two important implications for macroevolutionary dynamics of the Hawaiian insect fauna. First, the range of colonization dates are spread across a

TABLE 2

Published divergence time estimates for the ages (crown ages) for Hawaiian insect radiations

Group	Species	Age (Ma)	Range (Ma)[1]	Reference(s)
COLEOPTERA				
Curculionidae				
Rhynocogonus	34	4.8 (geologic) 7.3 (molecular)	3.5–6.2 (geologic); 5.7–9.0 (molecular) (both 95% CI)	Claridge et al. (2017)
Hydrophilidae				
Limnoxenus	3	19.48	11.3–29.74	Toussaint and Short (2017)
Scolytidae				
Xyleborus	21	9.8	6–14	Cognato et al. (2018)
DIPTERA				
Drosophilidae	566 (1000)	25.15	(23.9–27.46)	Russo et al. (1995, 2013); Lapoint et al. (2014)
Hawaiian *Drosophila*		9.14	6.57–11.82	Lapoint et al. (2014)
AMC Clade	91	4.4	3.45–5.45	Lapoint et al. (2014)
antopocerus group	15	2.48	1.81–3.24	Lapoint et al. (2014)
modified tarsus group	76	3.69	2.9–4.51	Lapoint et al. (2014)
picture wing	120	6.0	4.5–7.3	Magnacca and Price (2015)
haleakalae	51	9.9	9.8–10 (composite)	O'Grady and Zilversmit (2004)
Scaptomyza	267	23.3	18.2–29.3	Lapoint et al. (2013)**
Dolichopodidae				
Campsicnemus	183	4.58	4.15–5.01	Goodman et al. (2014)
Eurynogaster	66	11.8	9.08–15.04	Goodman et al. (2016)
Ephydridae				
Scatella	15	10.8		O'Grady and Stepaniak (unpublished)
Limoniidae				
Dicranomyia	13	6.9 (16)*	4.96–8.8	Goodman and O'Grady (2013)
Tephritidae				
Trupanea	21	not estimated	N/A	Viale et al. (2015)
HEMIPTERA				
Cicadellidae				
Nesophrosyne	69 (200)	3.2	2.75–3.74	Bennett and O'Grady (2013)
Triozidae				
Pariaconus	36	5	3.5–6.5	Percy (2017b)
Swezeyana	9	5.9	4–7.7	Percy (2018)
HYMENOPTERA				
Colletidae				
Hylaeus	60	0.5–0.7 (geologic)		Magnacca and Danforth (2006)
LEPIDOPTERA				
Cosmopterigidae				
Hyposmocoma	~400	14.8	10.5–19.6	Haines et al. (2014)
Gracillariidae				
Philodoria	32	21**	17.37–26.30	Johns et al. (2018)
Xyloryctidae				
Thyrocopa	39	5.94 (geologic)	Not provided	Medeiros and Gillespie (2011)
ODONATA				
Coenagrionidae				
Megalagrion	25	9.6 (mean)	3.9–16.0 (composite)	Jordan et al. (2003)

TABLE 2
Continued

Group	Species	Age (Ma)	Range (Ma)^1	Reference(s)
PSOCOPTERA				
Psocidae				
Ptycta	50	7.14	4.73–10.05	Bess et al. (2014)

*First age represents the age of the main Hawaiian radiation of *Dicranomyia*. Second age in parentheses represents the age of the common ancestor of all Hawaiian *Dicranomyia*, including the aberrant Hawaiian endemic *D. inquispina*, which may represent an independent colonization of the archipelago.

**Authors conducted many different divergence time estimates, most of which were in close agreement; presented here are the ones in which the authors stated they had the most confidence.Range (Ma)^1 is 95% HPD unless otherwise noted.

period of 25 Ma to the present, rather than being clustered around a particular window. This pattern has been seen in some other insular biotas (e.g., the Marquesas endemic fauna and flora, Hembry 2018; southeastern Polynesian and Galápagos birds, Thibault and Cibois 2017; Valente et al. 2015), but not in all insular biotas (e.g., the Society Islands biota, Hembry and Balukjian 2016; Macaronesian birds, Illera et al. 2012). This strongly suggests that early-colonizing lineages did not fully preempt later colonization and radiations by other lineages, meaning there is little evidence for a priority effect. It also suggests there was not a single period that was especially conducive to colonization, either due to global conditions or local ones in the Hawaiian Islands. Both *Campsicnemus* and *Nesophrosyne* have undergone spectacular diversification despite colonizing less than 5 Ma. The hypothesis that colonization is not preempted by earlier colonizing lineages is best demonstrated by Dolichopodidae flies, which colonized at least three times over the past 12 Ma and radiated twice independently (*Campsicnemus* and the *Eurynogaster* complex; Goodman et al. 2016). Second, diversification in the Hawaiian Islands before the formation of Kaua‘i did contribute to extant lineage diversity in these radiations since each of these anciently colonizing clades are inferred to have colonized the main Hawaiian Islands at least twice from the Northwestern Hawaiian Islands.

A larger fraction of early-colonizing insect lineages relative to plant lineages suggests that some aspects of insect and plant macroevolutionary dynamics may be decoupled across the history of the Hawaiian Archipelago, despite current evidence of host plant specialization (Price and Clague 2002; Bennett and O'Grady 2012; Price and Wagner 2018). Six of the 12 pre-Kaua‘i insect clades use plant resources directly or indirectly as food, and all of these use multiple host plant families in Hawai‘i. *Drosophila* feed on yeasts and other microbes that grow on decomposing plant tissues (Magnacca et al. 2008). *Ptycta* bark lice live on plants but feed on fungi and algae growing on tree trunks (Bess et al. 2014). *Philodoria* are leaf miners; Johns et al. (2018) argue compellingly that they may have persisted through periods of low-elevation islands by feeding on Malvaceae, a major component of lower elevation habitats. *Rhyncogonus* are chewers that consume host plant leaves as adults but host plant roots as larvae (Claridge et al. 2017); in French Polynesia, where Hawaiian congeners originated, some species live at sea level and consume leaves of Malvaceae (*Hibiscus tiliaceus*, which is native there) and introduced woody plants (such as *Psidium guajava*; David Hembry, unpublished notes, 2008; Claridge et al. 2017). *Xyleborus* beetles cultivate fungi in wood of several host plant families but many Hawaiian species are highly specialized (Cognato et al. 2018). *Swezeyana* psyllids, which may just slightly predate Kaua‘i, are exclusively phloem feeders of *Planchonella sandwicensis* (Percy 2018). This suggests that these older, specialist, lineages either dynamically adapted to a wholesale shift in plant and animal biotas, despite their current specialization (e.g., *Xyleborus*, *Philodoria*, certain *Drosophila*, lineage of snail-eating *Hyposmocoma*), or that many of the plant and

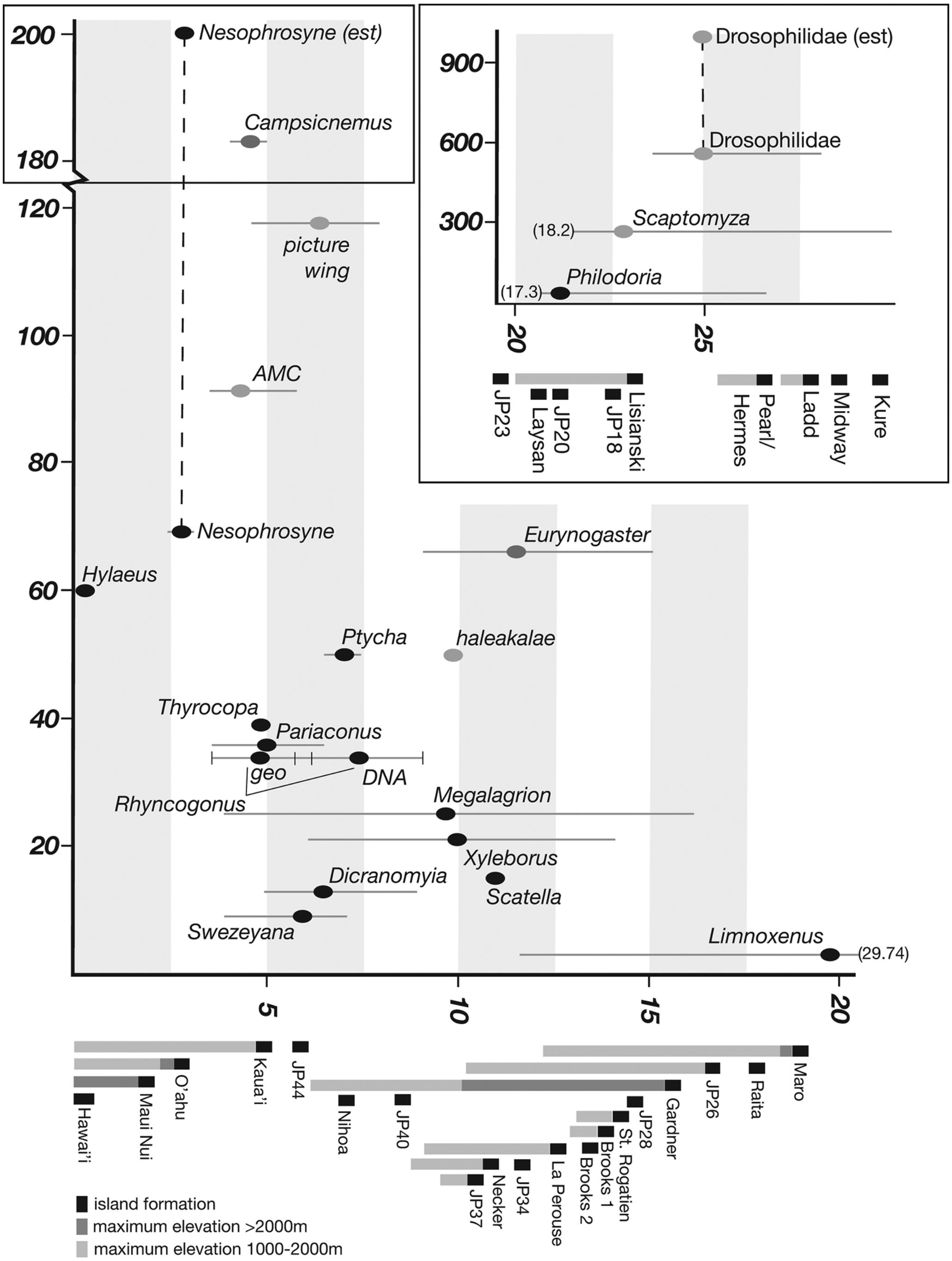

FIGURE 3. ESTIMATED DATES OF COLONIZATIONS OF THE HAWAIIAN ISLANDS BY DIFFERENT INSECT CLADES (FROM PREVIOUSLY PUBLISHED STUDIES) PLOTTED AGAINST PRESENT SPECIES RICHNESS

Dots indicate dates of colonization obtained through divergence time estimation; horizontal lines indicate 95% highest probability density for date of colonization for studies in which Bayesian divergence time estimation (Drummond and Rambaut 2007; Drummond et al. 2012; Bouckaert et al. 2014) was used. For certain radiations, such as Drosophilidae and *Nesophrosyne* (Cicadellidae), both number of currently described species and estimated total species richness are plotted separately. See the online edition for a color version of this figure.

some animal lineages are older than currently understood and, in some cases, these specialized interactions have been maintained since before Kauaʻi formed. In contrast, among herbivorous insect clades, *Nesophrosyne* and *Pariaconus* (phloem feeders) are post-Kauaʻi in age. It will be interesting to examine the age of additional phytophagous Hawaiian insect clades to see whether there are general patterns in ecology that are correlated with dates of colonization.

Additionally, the range of colonization dates across the age of the archipelago is consistent with colonization occurring in temporal windows in which there were large "target" islands such as Gardner, La Perouse, Kauaʻi, and Maui Nui, in line with MacArthur and Wilson's predictions (1967). This mechanism may be why some of the recent groups are probably Maui Nui in origin—since that island complex has occupied a large area for roughly the last one million years. Older groups, such as *Drosophila*+*Scaptomyza*, might have established on a relatively small target 25 Ma, but subsequently had multiple lineages go through rounds of diversification and colonization once the much larger Gardner complex began to form. Temporal sequences of island colonization remain a poorly understood area of island biogeography, so further investigation of the chronological assembly of the Hawaiian entomofauna likely will be of broad interest to evolution and biogeography generally (Warren et al. 2015; Patiño et al. 2017).

PROGRESSION RULE

A number of Hawaiian groups (*Nesophrosyne*, *Pariaconus*, *Ptycta*, *Campsicnemus*, *Laupala*, *Eurynogaster*+*Arciellia*+*Uropachys*) show an overall progression rule from Kauaʻi or older islands to younger ones, either via biogeographic reconstruction of the whole radiation or in one or more subclades (Table 1). Notably, *Hyposmocoma* shows a progression rule pattern that encompasses both the Northwestern Hawaiian Islands and main Hawaiian Islands (Haines et al. 2014). Nearly all groups show an older-to-younger pattern somewhere in their phylogeny, although in some groups this pattern is clearer than in others, and only in some cases has it been assessed via a statistical biogeographic reconstruction approach. The only three exceptions are the main clade of *Dicranomyia* craneflies, most flighted species of which are indigenous to more than one island, and for which historical biogeographic reconstruction generates equivocal results at all major nodes (Goodman and O'Grady 2013); *Xyleborus* wood-boring beetles, for which a formal biogeographic reconstruction may find evidence for progression (Cognato et al. 2018); and *Swezeyana* psyllids, for which only a mitochondrial DNA tree is available at present (Percy 2018).

WITHIN-ISLAND RADIATION

All Hawaiian radiations examined here, with the exception of *Dicranomyia*, show within-island radiation (Table 1). Such radiation can occur within any of the major islands (Kauaʻi, Oʻahu, Maui Nui, or Hawaiʻi). Within-island radiation thus appears to be a major and underappreciated mechanism for diversification in Hawaiian insects, possibly even accounting for the majority of diversification in adaptive radiations such as *Nesophrosyne* (Bennett and O'Grady 2013), *Mecyclothorax* (Liebherr 2006, 2015), and *Hyposmocoma* (Haines et al. 2014). Such diversification is often clearly associated with allopatric isolation on different volcanoes on larger, younger islands such as Hawaiʻi and the historically linked Maui Nui complex. At least a few Hawaiian insect radiations, such as *Hyles* (Sphingidae) may have diversified without within-island radiation (Hundsdoerfer et al. 2009). Future work to examine whether diversification is driven strictly by biogeography or if, instead, there is also ecological speciation onto different host plants in herbivorous taxa or onto different host insects in parasitoid taxa (Patiño et al. 2017) will be of great interest.

STOCHASTIC AND BACK DISPERSAL

Stochastic and back-dispersal patterns are, in practice, hard to distinguish in groups such as *Banza*, *Megalagrion*, *Campsicnemus*, *Philodoria*, and *Hyposmocoma* (Jordan et al. 2003; Shapiro et al. 2006; Rubinoff and Schmitz 2010; Goodman et al. 2014; Haines et al. 2014;

Johns et al. 2018; Table 1). Distinguishing them may require formal biogeographic reconstruction, as in cases of back colonization demonstrated in *Nesophrosyne* (Bennett and O'Grady 2013) and *Drosophila* (Lapoint et al. 2011, 2014). In the former case, back colonization appears to have been permitted by the recent arrival of new host plant resources creating newly available niches on older islands. Most groups show evidence for either stochastic, back colonization, or both patterns, with the caveat that the patterns are difficult to distinguish rigorously in many cases. The clearest example of a stochastic pattern is probably in *Dicranomyia* craneflies, described above. In *Hylaeus* bees, the stochastic pattern is back dispersal by definition since the center of origin is on the youngest island of Hawai'i (Magnacca and Danforth 2006). *Xyleborus* wood-boring beetles are another likely candidate for back colonization (Cognato et al. 2018). Back colonization is of great interest ecologically since it implies that island communities do not completely fill (in an ecological niche sense) in the initial period of dispersal and diversification that follows island formation. These patterns also reveal that island ecology has been dynamic over time, with new niches opening on older islands. Consequently, we encourage entomologists studying insular faunas to use biogeographic reconstruction methods to attempt to test for it more generally. The only radiation to not show evidence for either of these stochastic or back-colonization patterns is *Laupala* crickets, which appear to follow a progression rule almost perfectly (Mendelson and Shaw 2005).

CRITICAL ASSESSMENT OF HAWAIIAN BIOGEOGRAPHIC HYPOTHESES

The progression rule has been an influential hypothesis in Hawaiian biogeography (Wagner and Funk 1995), and has been applied to other oceanic archipelagos (Parent et al. 2008; Hembry and Balukjian 2016; Hembry 2018). The fact that geologic history could be known in such detail and have such a cleanly predictable effect on speciation and phylogenetic branching (Carson 1997) was a remarkable insight that doubtless had a salutary effect on research into the evolution of Hawaiian endemic biodiversity. Some radiations, such as *Laupala* and *Drosophila*, show patterns recognizably similar to a straightforward progression rule (Bonacum et al. 2005; Mendelson and Shaw 2005). However, many other radiations show either a progression rule or patterns consistent with a partial progression rule (not including all main islands) in some of their subclades, alongside stochastic, back-dispersal, and within-island radiation patterns (e.g., *Nesophrosyne*, *Campsicnemus*, *Eurynogaster+Arciellia+Uropachys*, *Philodoria*, *Hyposmocoma*). Explicit biogeographic inferences (e.g., Bennett and O'Grady 2013; Bess et al. 2014; Haines et al. 2014) indicate that some of these progression patterns are consistent with the hypothesis of dispersal from older islands to younger islands. In some cases, biogeographic inferences in conjunction with divergence time estimation can lend greater support for the progression rule than biogeographic analyses alone (*Ptycta*; Bess et al. 2014).

Testing a strictly defined progression rule (Figures 2a, 4a) is quite challenging from a computational standpoint. The progression rule is both highly complex and specific compared to most hypotheses tested using phylogenetic comparative methods. The progression rule is more parameter rich than those that test monophyly of an ingroup or hypotheses about the frequency of transitions between character states of interest, and is merely one of a very large number of possible tree topologies that can be shown within a Hawaiian radiation. In a likelihood framework, it is not clear that testing a strict progression rule using a model comparison approach is actually meaningful given this reality. We further lack any kind of agreement about what a statistical "threshold" would be above which a Hawaiian phylogeny would be significantly consistent with a progression rule (e.g., Figures 4b and c) and distinguishable from a stochastic pattern (Figure 4d). A strict progression rule in these respects may be an unworkable hypothesis, especially as we gain data on larger and messier Hawaiian radiations. However, a relaxed form of the progression rule (Hembry and Balukjian 2016;

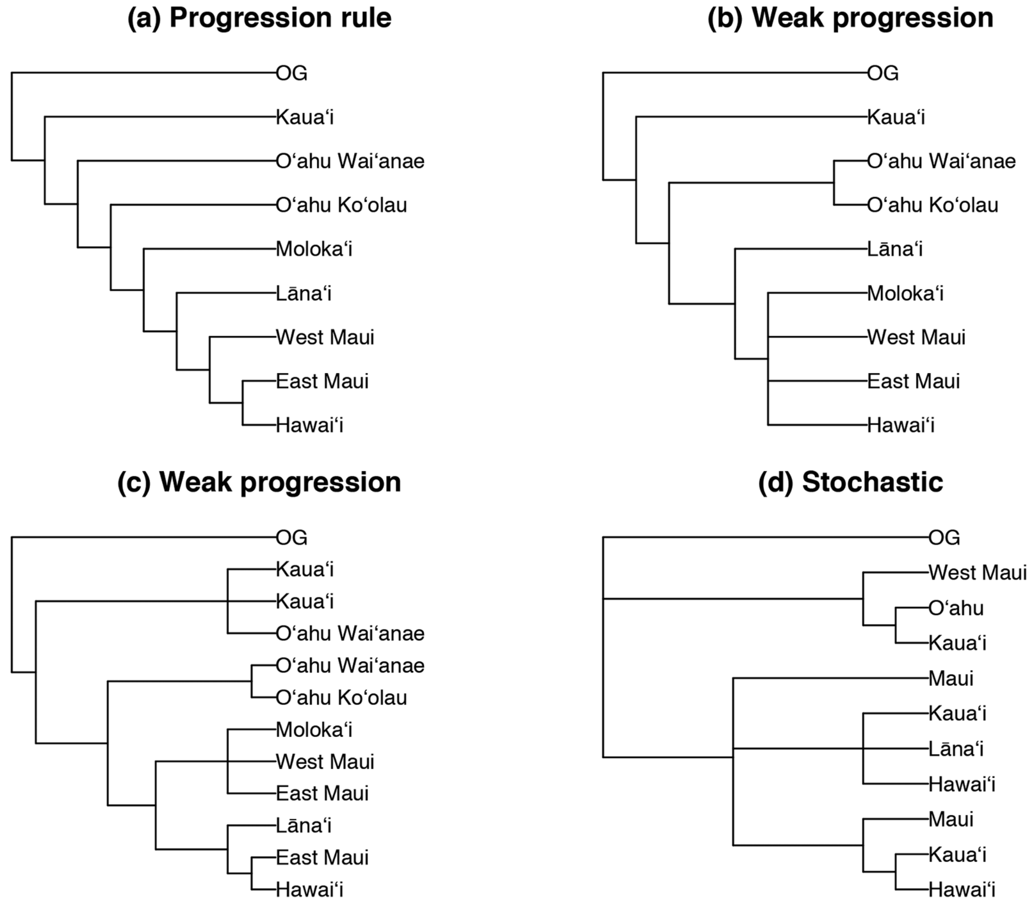

Figure 4. Strong and Weak Progression Rules

a. Progression rule as presented in Funk and Wagner (1995), here referred to as a “strong” progression rule. b. Hypothetical example of a “weak” progression rule: O‘ahu taxa are monophyletic, Lāna‘i rather than Moloka‘i is sister to the rest of Maui Nui, and Moloka‘i, Maui, and Hawai‘i taxa form a polytomy, but the general pattern of early-diverging lineages on older islands and younger-diverging lineages is apparent. c. Second hypothetical example of a “weak” progression rule in which generally early-diverging lineages from older islands (Kaua‘i and O‘ahu) form a basal grade within which is nested a derived clade of taxa from younger islands (Maui Nui and Hawai‘i). d. Stochastic pattern as presented in Funk and Wagner (1995); here, no pattern of early-diverging lineages on older islands and later-diverging lineages on younger islands is apparent.

Hembry 2018), defined as a pattern (or mechanism) in which earlier diverging lineages are found on older islands and younger lineages are found on younger islands (Figures 4b and c), is still useful, and describes aspects of many Hawaiian radiations. We must continue to recognize, however, that not all radiations follow even a relaxed progression rule, as is the case in the Hawaiian entomofauna as well as in the biota of the Galápagos and Society Islands (Parent et al. 2008; Hembry and Balukjian 2016).

Furthermore, despite the historical focus on the progression rule per se in Hawaiian biogeography and evolution, we suggest a conceptual reframing of this problem as one in which the spatial configuration of islands, volcanoes, and habitat patches in Hawai‘i is

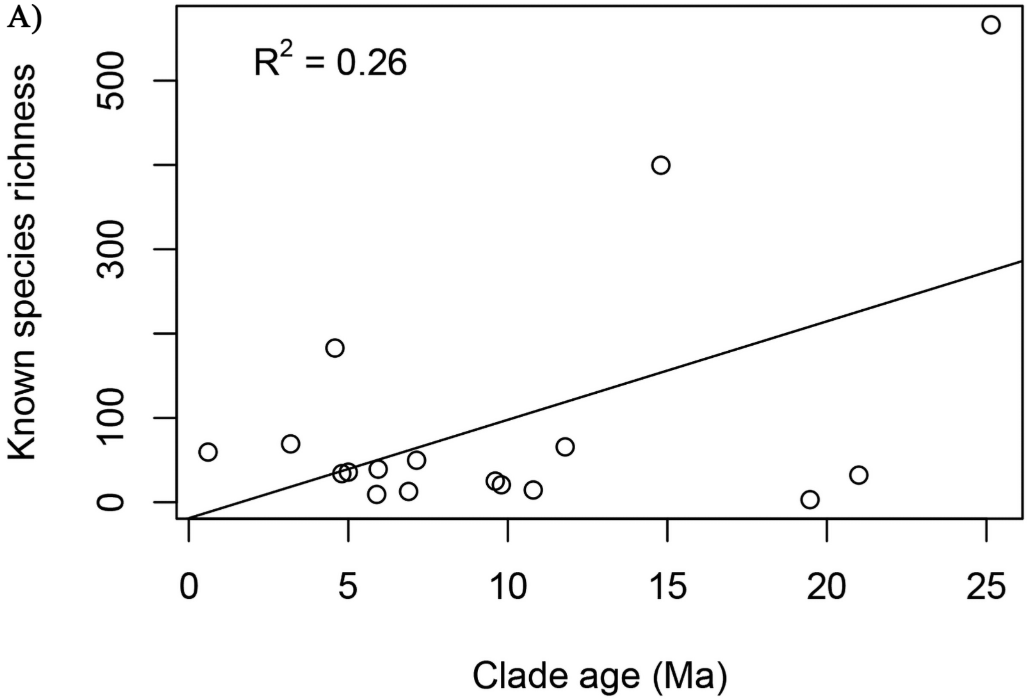

FIGURE 5. CLADE AGE-SPECIES RICHNESS RELATIONSHIPS FOR ALL HAWAIIAN INSECT RADIATIONS CONSIDERED IN THIS STUDY

Plotted R^2 value represents a least-squares linear regression. a. Age-richness relationship using known species richnesses ($R^2 = 0.26$, $p = 0.036$). b. Age-richness relationship using estimated species richnesses for Drosophilidae and *Nesophrosyne* ($R^2 = 0.29$, $p = 0.026$).

an especially amenable model system for investigating the scales at which habitat discontinuity is relevant to metapopulation dynamics, speciation, hybridization, community assembly, and macroevolution. Such an approach may also provide a coherent framework into which many of the other factors considered in Hawaiian biogeography—such as dispersal mechanisms, interisland distances, and island size—can be integrated, thus providing further general insights to evolutionary biologists in many different disciplines.

WHAT MAKES A LARGE RADIATION?

Lineage Age

Comparison of colonization dates with extant species richness reveals a positive relationship between the two with a great deal of variance (known species richnesses: $R^2 = 0.26$, $p = 0.036$; estimated species richnesses: $R^2 = 0.29$, $p = 0.026$; Figure 5). Unsurprisingly for a heterogeneous assortment of clades of varying ages, known species richnesses are not normally distributed (Shapiro-Wilk normality test, $p < 0.001$), although *ln*-transformed known species richnesses are approximately normally distributed (Shapiro-Wilk test, $p = 0.72$). A Dixon outlier test of these *ln*-transformed richnesses fails to find any outlier radiations ($p = 0.73$). Thus, diversity is positively correlated with date of colonization—but many other factors are important in determining what makes a large Hawaiian insect radiation, including the varying criteria and rigor applied to the definition of species across generations of entomologists working on various groups and the susceptibility of those groups to extinction and diversification.

As an aside, we note that a positive relationship between clade age and richness is frequently observed when comparing multiple clades from the same biogeographic region (Li and Wiens 2019), and that using

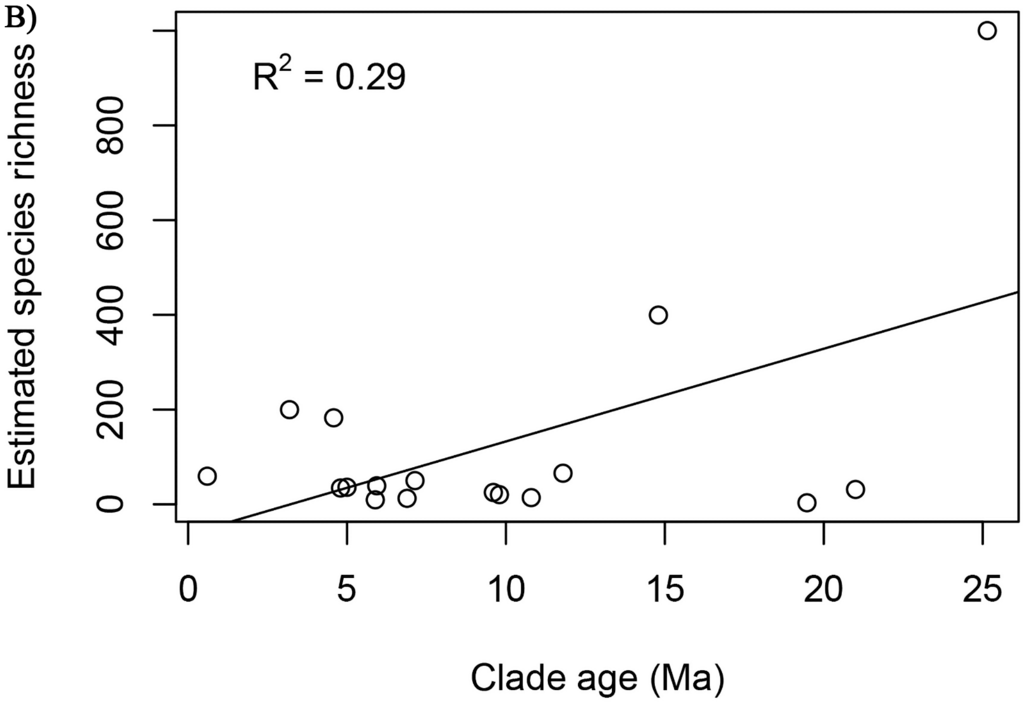

Figure 5. (*Continued*)

Hawaiian endemic clades as the units of analysis avoids some pitfalls associated with using ranked higher taxa in these kinds of analyses (e.g., Stadler et al. 2014). However, given the exceptional aspects of the Hawaiian environment and these insect clades—particularly that all of these clades have diversified on young islands with many vacant niches and that the land area of these islands has varied dramatically over the past 25 Myr—we caution against drawing general inferences about the relationship between clade age and species richness across the Tree of Life from these data alone.

Dispersal Ability

Several other factors can be hypothesized that may determine the size of Hawaiian insect radiations, and different radiations are likely diversifying for different reasons and under different dynamics (Valente et al. 2015). For instance, it seems plausible that vagility may be negatively correlated with diversity. Radiations such as *Scatella* and *Dicranomyia* are relatively species poor. Species in both genera are found in coastal habitats where larvae and/or pupae develop in and are adapted to brackish water. Dispersal across water as immatures may be likely in these saline tolerant taxa, leading to the widespread distribution of some species (only approximately 30% of species in each lineage are single-island endemics). Alternately, taxa found in habitats where adults are prone to being blown by winds, as is the case in *Dicranomyia* (Nitta and O'Grady 2008), may also explain widespread distribution patterns. Likewise, strong flyers like lycaenid and nymphalid butterflies, and dragonflies are represented in Hawai'i by singletons (Zimmerman 1948a).

Ecological Factors

Perhaps most importantly, very species-rich lineages also show a great deal of ecological diversity (e.g., *Drosophila+Scaptomyza* feeding substrates and behaviors; *Hyposmocoma* cases and foods; host plants in *Nesophrosyne*, *Nesosydne*, and *Orthotylus*; host caterpillars and feeding sites in *Sierola*; and habitat in *Campsicnemus*). Similar patterns are seen across insects globally (e.g., Wiens et al. 2015). The absence of other competing taxa—presumably those less able to disperse over such long distances or simply not as successful by chance—is a major factor in driving diversification of large island radiations, particularly in creating the imbalance between continental and Hawaiian patterns of diversity. For example, the absence in Hawai‘i of the myriad saprophagous fly families such as Neriidae, Lauxaniidae, and Heleomyzidae may have led to the impressive radiation of Drosophilidae in Hawai‘i. Likewise, the absence or reduced diversity of small lepidopteran parasitoids such as Ichneumonidae, Braconidae, and Pteromalidae have undoubtedly been key to the extraordinary radiation of *Sierola*. Understanding the drivers of insular diversity has recently been recognized as a major open area in island biogeography research (Warren et al. 2015; Patiño et al. 2017).

Microbial Symbiosis

Symbiosis is now recognized as a key evolutionary driver of insect diversity. It is estimated that 10–20% of all insects (up to one million species) may rely on beneficial symbionts for essential benefits (Douglas 2011). Prominent and illustrative examples can be found among the lineages of the Auchenorrhyncha (Hemiptera), where symbioses with microbes have played fundamental roles in their ecological and evolutionary diversification. In Hawai‘i, an intriguing aspect of the Auchenorrhyncha is that most species rely on ancient, obligate associations with microbial symbionts (Moran et al. 2005). Because their plant-sap diets are limited in essential nutrition (amino acids and vitamins), insects depend on microbes to provide them. In Hawai‘i, colonizing lineages have carried with them these associations. Both the endemic Hawaiian cixiids and cicadellids maintain the two ancestral bacterial symbionts of the suborder, *Sulcia* and a *Betaproteobacteria* (Bennett and Mao 2018). In contrast, the delphacids (e.g., *Nesosydne*) are predicted to rely on a fungal yeast-like symbiont, which is found widely throughout the family. Recent work has further revealed that symbioses are important to several other significant Hawaiian insect radiations, including seed bugs in the genus *Nysius* (Hemiptera: Heteroptera: Lygaeidae; Stever et al. 2021). Genomic and molecular verification of symbionts in Hawaiian insects is mostly lacking (but see Bennett and O'Grady 2012; Bennett and Mao 2018). However, these symbiotic systems can provide fertile grounds for understanding the role of symbioses in the biology and diversification of insects more generally (Poff et al. 2017).

Conclusions

Hawai‘i has long been held as an evolutionary model system because it offers the possibility of understanding which aspects of evolution are predictable, especially with regard to how the archipelago's (and, by extension, the Earth's) dynamic geology is the engine of diversification and species richness. New data from the past two decades of research illustrates clearly the extent to which Hawai‘i's unique hotspot geology has shaped the evolution of Hawaiian insects. Although the progression rule is one of the most frequently predicted and observed biogeographic patterns on hotspot archipelagoes like Hawai‘i, perfect adherence to a progression rule is rare and perhaps should not be the default expectation. Many Hawaiian insect radiations have diversified according to a complex mixture of progression, stochastic, back-dispersal, and within-island patterns of speciation and dispersal. In contrast to previously held views about the age of the Hawaiian biota, we find here that a substantial fraction of Hawaiian insect clades for which data are available predate the formation of current high islands. These lineages have likely persisted through geologically and biotically dynamic periods of island erosion and subsidence and habitat and species extinction.

The Hawaiian entomofauna continues to open the door to a broad range of possible insights into the patterns and mechanisms of evolution, including relationships between clade age and species richness and plant and insect macroevolution as we have discussed here. Hawai‘i offers unparalleled opportunities to study speciation and gene flow, repeated, convergent patterns in evolution, and the deep macroevolutionary history of adaptive radiations. Within the detailed known context of the archipelago's geology, disentangling abiotic (geology, climate) and biotic (plants, symbionts) drivers of animal diversity becomes possible in Hawai‘i to a degree that is difficult elsewhere. Our hope is that this review will inspire the next generation of evolutionary biologists studying the Hawaiian biota and its conservation.

ACKNOWLEDGMENTS

We thank J. Wiens for helpful discussion and K. Austin, B. Burgunder, C. Doorenweerd, M. Medeiros, L. Noronha, K. O'Hearn, L. Pineiro, S. Pote, and A. Santos Rampasso for helpful feedback. Daniel Rubinoff acknowledges funding from NSF grant #DEB-0918341, the United States Department of Agriculture (USDA) and USDA State Research, Education and Extension project HAW00942-H, administered by the College of Tropical Agriculture and Human Resources, University of Hawai‘i at Mānoa. Patrick M. O'Grady acknowledges funding from NSF grants DEB2030129, DEB1839598, and DEB1241253. None of this work would have been possible without the permits, land access, and logistical support that has been generously provided to the authors during the past several decades of fieldwork. We would like to thank the following institutions and individuals: State of Hawai‘i, Department of Land and Natural Resources (Cynthia King and Betsy Gagné), Mahi Pono, LLC, formerly East Maui Irrigation (Garret Hew and Mark Vaught), Mauna Kahālāwai Watershed Partnership (Randy Bartlett), Hawai‘i Volcanoes National Park (David Foote, Rhonda Loh, and Darcy Hu), Haleakalā National Park, Nature Conservancy of Hawai‘i (Trae Menard), Paul Krushelnycky, and Steven Montgomery.

REFERENCES

Andersen M. J., Hosner P. A., Filardi C. E., Moyle R. G. 2015. Phylogeny of the monarch flycatchers reveals extensive paraphyly and novel relationships within a major Australo-Pacific radiation. *Molecular Phylogenetics and Evolution* 83:118–136.

Anderson W. H. 1941. On some larvae of genus *Proterhinus* (Coleoptera: Aglycyderidae). *Proceedings of the Hawaiian Entomological Society* 11:25–35.

Appelhans M. S., Wen J., Wood K. R., Allan G. J., Zimmer E. A., Wagner W. L. 2014. Molecular phylogenetic analysis of Hawaiian Rutaceae (*Melicope*, *Platydesma* and *Zanthoxylum*) and their different colonization patterns. *Botanical Journal of the Linnean Society* 174:425–448.

Appelhans M. S., Wen J., Duretto M., Crayn D., Wagner W. L. 2018. Historical biogeography of *Melicope* (Rutaceae) and its close relatives with a special emphasis on Pacific dispersals. *Journal of Systematics and Evolution* 56:576–599.

Asche M. 1997. A review of the systematics of Hawaiian planthoppers (Hemiptera: Fulgoroidea). *Pacific Science* 51:366–376.

Ashlock P. D. 1966. New Hawaiian Orsillinae (Hemiptera-Heteroptera: Lygaeidae). *Pacific Insects* 8:805–825.

Ashmead W. H. 1901. Hymenoptera Parasitica. Pages 277–364 in *Fauna Hawaiiensis or the Zoology of the Sandwich (Hawaiian) Isles, Volume I, Part III*, edited by D. Sharp. Cambridge (United Kingdom): Cambridge University Press.

Asquith A. 1994. *Revision of the Endemic Hawaiian Genus* Sarona *Kirkaldy (Heteroptera: Miridae: Orthotylinae).* Bishop Museum Occasional Papers, Volume 40. Honolulu (Hawai‘i): Bishop Museum Press.

Asquith A. 1995. Evolution of *Sarona* (Heteroptera, Miridae): speciation on geographic and ecological islands. Pages 90–120 in *Hawaiian Biogeography: Evolution on a Hot Spot Archipelago*, edited by W. L. Wagner, V. A. Funk. Washington (DC): Smithsonian Institution Press.

Asquith A. 1997. Hawaiian Miridae (Hemiptera: Heteroptera): the evolution of bugs and thought. *Pacific Science* 51:356–365.

Athens J. S., Rieth T. M., Dye T. S. 2014. A paleoenvironmental and archaeological model-based age estimate for the colonization of Hawai‘i. *American Antiquity* 79:144–155.

Bailey K. 1976. Potassium-argon ages from the Galápagos Islands. *Science* 192:465–467.

Beardsley J. W. 1997. Hawaiian Pseudococcidae (Hemiptera): a group that Perkins missed. *Pacific Science* 51:377–379.

Bellemain E., Ricklefs R. E. 2008. Are islands the end of the colonization road? *Trends in Ecology and Evolution* 23:461–468.

Bennett G. M., Mao M. 2018. Comparative genomics of a quadripartite symbiosis in a planthopper host reveals the origins and rearranged nutritional responsibilities of anciently diverged bacterial lineages. *Environmental Microbiology* 20:4461–4472.

Bennett G. M., O'Grady P. M. 2011. Review of the native Hawaiian leafhopper genus *Nesophrosyne* (Hemiptera: Cicadellidae: Deltocephalinae) with description of eight new species associated with *Broussaisia arguta* (Hydrangeaceae). *Zootaxa* 2805:1–25.

Bennett G. M., O'Grady P. M. 2012. Host–plants shape insect diversity: phylogeny, origin, and species diversity of native Hawaiian leafhoppers (Cicadellidae: *Nesophrosyne*). *Molecular Phylogenetics and Evolution* 65:705–717.

Bennett G. M., O'Grady P. M. 2013. Historical biogeography and ecological opportunity in the adaptive radiation of native Hawaiian leafhoppers (Cicadellidae: *Nesophrosyne*). *Journal of Biogeography* 40:1512–1523.

Bess E. C., Yoshizawa K. 2007. Redefinition of *Ptycta* Enderlein (Psocodea: "Psocoptera": Psocidae) and taxonomic revision of the Japanese species. *Entomological Science* 10:279–290.

Bess E. C., Catanach T. A., Johnson K. P. 2014. The importance of molecular dating analyses for inferring Hawaiian biogeographical history: a case study with bark lice (Psocidae: *Ptycta*). *Journal of Biogeography* 41:158–167.

Bonacum J., O'Grady P. M., Kambysellis M., DeSalle R. 2005. Phylogeny and age of diversification of the *planitibia* species group of the Hawaiian *Drosophila*. *Molecular Phylogenetics and Evolution* 37:73–82.

Bouckaert R., Heled J., Kühnert D., Vaughan T., Wu C.-H., Xie D., Suchard M. A., Rambaut A., Drummond A. J. 2014. BEAST 2: a software platform for Bayesian evolutionary analysis. *PLOS Computational Biology* 10:e1003537.

Brown J. M., Todd-Thompson M., McCord A., O'Brien A., O'Fallon B. 2006. Phylogeny, host association, and wing pattern variation in the endemic Hawaiian fruit flies (Diptera, Tephritidae). *Instrumenta Biodiversitatis* 7:1–16.

Brown S. D. J. 2019. A new species of *Proterhinus* Sharp, 1878 (Coleoptera: Curculionoidea: Belidae) from Miti'aro, Cook Islands, South Pacific. *Zootaxa* 4664: 481–496.

Brown W. D. 2016. Mating behavior of the endemic Hawaiian cricket *Leptogryllus elongatus* (Orthoptera: Gryllidae: Oecanthinae). *Journal of Insect Behavior* 29:449–458.

Carlquist S. 1970. *Hawaii: A Natural History: Geology, Climate, Native Flora and Fauna Above the Shoreline*. Garden City (New York): American Museum of Natural History/Natural History Press.

Carlquist S. 1974. *Island Biology*. New York: Columbia University Press.

Carson H. L. 1997. Sexual selection: a driver of genetic change in Hawaiian *Drosophila*. *Journal of Heredity* 88:343–352.

Carson H. L., Clague D. A. 1995. Geology and biogeography of the Hawaiian Islands. Pages 14–29 in *Hawaiian Biogeography: Evolution on a Hot Spot Archipelago*, edited by W. L. Wagner and V. A. Funk. Washington (DC): Smithsonian Institution Press.

Cibois A., Beadell J. S., Graves G. R., Pasquet E., Slikas B., Sonsthagen S. A., Thibault J.-C., Fleischer R. C. 2011. Charting the course of reed-warblers across the Pacific islands. *Journal of Biogeography* 38:1963–1975.

Clague D. A., Dalrymple G. B. 1989. Tectonics, geochronology, and origins of the Hawaiian-Emperor volcanic chain. Pages 187–217 in *The Geology of North America*, Volume N, edited by E. L. Winterer, D. M. Hussong, and R. W. Decker. Boulder (Colorado): Geological Society of America.

Claridge E. M., Gillespie R. G., Brewer M. S., Roderick G. K. 2017. Stepping-stones across space and time: repeated radiation of Pacific flightless broad-nosed weevils (Coleoptera: Curculionidae: Entiminae: *Rhyncogonus*). *Journal of Biogeography* 44:784–796.

Clarke J. F. G. 1971. The Lepidoptera of Rapa Island. *Smithsonian Contributions to Zoology* 56:1–282.

Clouard V., Bonneville A. 2005. Ages of seamounts, islands, and plateaus on the Pacific Plate. *Special Papers-Geological Society of America* 388:71–90.

Cognato A. I., Jordal B. H., Rubinoff D. 2018. Ancient "wanderlust" leads to diversification of endemic Hawaiian *Xyleborus* species (Coleoptera: Curculionidae: Scolytinae). *Insect Systematics and Diversity* 2:1.

Cook P., Rasmussen R., Brown J. M., Cooper I. A. 2018. Sexual conflict does not maintain female colour polymorphism in a territorial damselfly. *Animal Behaviour* 140:171–176.

Cooper I. A. 2010. Ecology of sexual dimorphism and clinal variation of coloration in a damselfly. *American Naturalist* 176:566–572.

Cooper I. A., Brown J. M., Getty T. 2016. A role for ecology in the evolution of colour variation and sexual dimorphism in Hawaiian damselflies. *Journal of Evolutionary Biology* 29:418–427.

Cowie R. H., Holland B. S. 2006. Dispersal is fundamental to biogeography and the evolution of biodiversity on oceanic islands. *Journal of Biogeography* 33:193–198.

Craddock E. M. 2000. Speciation processes in the adaptive radiation of Hawaiian plants and animals. Pages 1–53 in *Evolutionary Biology*, Volume 31, edited by M. K. Hecht, R. J. Macintyre, and M. T. Clegg. Boston (Massachusetts): Springer.

Crowe A. 2018. *Pathway of the Birds: The Voyaging Achievements of Māori and Their Polynesian Ancestors*. Honolulu (Hawai'i): University of Hawai'i Press.

Cryan J. R., Liebherr J. K., Fetzner J. W. Jr., Whiting M. F. 2001. Evaluation of relationships within the endemic Hawaiian Platynini (Coleoptera: Carabidae) based on molecular and morphological evidence. *Molecular Phylogenetics and Evolution* 21:72–85.

Daly H. V., Magnacca K. N. 2003. Hawaiian *Hylaeus* (*Nesoprosopis*) bees (Hymenoptera: Apoidea). *Insects of Hawaii* 17:1–234.

Darwin C. 1859. *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*. London (United Kingdom): John Murray.

deCarvalho T. N., Shaw K. L. 2010. Divergence of courtship and mating behaviors among endemic Hawaiian swordtail crickets. *Behaviour* 147:479–504.

Diamond J. M. 1970. Ecological consequences of island colonization by southwest Pacific birds, II. The effect of species diversity on total population density. *Proceedings of the National Academy of Sciences of the United States of America* 67:1715–1721.

Diamond J. M. 1975. Assembly of species communities. Pages 342–444 in *Ecology and Evolution of Communities*, edited by M. L. Cody, R. H. MacArthur, and J. M. Diamond. Cambridge (Massachusetts): Belknap Press of Harvard University Press.

Douglas A. E. 2011. Lessons from studying insect symbioses. *Cell Host & Microbe* 10:359–367.

Drummond A. J., Rambaut A. 2007. BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evolutionary Biology* 7:214.

Drummond A. J., Suchard M. A., Xie D., Rambaut A. 2012. Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Molecular Biology and Evolution* 29: 1969–1973.

Duncan R. A., McDougall I. 1976. Linear volcanism in French Polynesia. *Journal of Volcanology and Geothermal Research* 1:197–227.

Economo E. P., Sarnat E. M. 2012. Revisiting the ants of Melanesia and the taxon cycle: historical and human-mediated invasions of a tropical archipelago. *American Naturalist* 180:E1–E16.

Eldredge L. G., Evenhuis, N. L. 2003. *Hawaii's Biodiversity: A Detailed Assessment of the Numbers of Species in the Hawaiian Islands*. Bishop Museum Occasional Papers, Volume 76. Honolulu (Hawai'i): Bishop Museum Press.

Englund R. E. 1999. The impacts of introduced poeciliid fish and Odonata on the endemic *Megalagnon* (Odonata) damselflies of Oahu Island, Hawaii. *Journal of Insect Conservation* 3:225–243.

Filardi C. E., Moyle R. G. 2005. Single origin of a pan-Pacific bird group and upstream colonization of Australasia. *Nature* 438:216–219.

Fleischer R. C., James H. F., Olson S. L. 2008. Convergent evolution of Hawaiian and Australo-Pacific honeyeaters from distant songbird ancestors. *Current Biology* 18:1927–1931.

Funk V. A., Wagner W. L. 1995. Biogeographic patterns in the Hawaiian Islands. Pages 379–419 in *Hawaiian Biogeography: Evolution on a Hot Spot Archipelago*, edited by W. L. Wagner and V. A. Funk. Washington (DC): Smithsonian Institution Press.

Gagné W. C. 1997. *Insular Evolution, Speciation, and Revision of the Hawaiian Genus* Nesiomiris *(Hemiptera: Miridae)*. Bishop Museum Bulletins in Entomology, Volume 7. Honolulu (Hawai'i): Bishop Museum Press.

Gagné W. C., Cuddihy L. W. 1990. Vegetation. Pages 45–114 in *Manual of the Flowering Plants of Hawai'i*, Volume 1, edited by W. L. Wagner, D. R. Herbst, and S. H. Sohmer. Honolulu (Hawai'i): University of Hawai'i Press.

Giffard W. M. 1907. Breeding experiments and some observations on the life history of *Rhyncogonus blackburni* Sharp. *Proceedings of the Hawaiian Entomological Society* 1:127–129.

Gillespie R. 2004. Community assembly through adaptive radiation in Hawaiian spiders. *Science* 303:356–359.

Gillespie R. G., Roderick G. K. 2002. Arthropods on islands: colonization, speciation, and conservation. *Annual Review of Entomology* 47:595–632.

Gillespie R. G., Baldwin B. G., Waters J. M., Fraser C. I., Nikula R., Roderick G. K. 2012. Long-distance dispersal: a framework for hypothesis testing. *Trends in Ecology and Evolution* 27:47–56.

Givnish T. J., Sytsma K. J., Patterson T. B., Hapeman J. R. 1996. Comparison of patterns of geographic speciation and adaptive radiation in *Cyanea* and *Clermontia* (Campanulaceae) based on a cladistic analysis of DNA sequence and restriction-site data. *American Journal of Botany* 83(Supplement):159.

Givnish T. J., Millam K. C., Mast A. R., Paterson T. B., Theim T. J., Hipp A. L., Henss J. M., Smith J. F., Wood K. R., Sytsma K. J. 2009. Origin, adaptive radiation and diversification of the Hawaiian lobeliads (Asterales: Campanulaceae). *Proceedings of the Royal Society B: Biological Sciences* 276:407–416.

Goodman K. R., O'Grady P. M. 2013. Molecular phylogeny and biogeography of the Hawaiian craneflies *Dicranomyia* (Diptera: Limoniidae). *PLOS ONE* 8: e73019.

Goodman K. R., Welter S. C., Roderick G. K. 2012. Genetic divergence is decoupled from ecological diversification in the Hawaiian *Nesosydne* planthoppers. *Evolution* 66:2798–2814.

Goodman K. R., Evenhuis N. L., Bartošová-Sojková P., O'Grady P. M. 2014. Diversification in Hawaiian long-legged flies (Diptera: Dolichopodidae: *Campsicnemus*): biogeographic isolation and ecological adaptation. *Molecular Phylogenetics and Evolution* 81: 232–241.

Goodman K. R., Kelley J. P., Welter S. C., Roderick G. K., Elias D. O. 2015. Rapid diversification of sexual signals in Hawaiian *Nesosydne* planthoppers (Hemiptera: Delphacidae): the relative role of neutral and selective forces. *Journal of Evolutionary Biology* 28:415–427.

Goodman K. R., Evenhuis N., Bartošová-Sojková P., O'Grady P. M. 2016. Multiple, independent colonizations of the Hawaiian archipelago by the family Dolichopodidae (Diptera). *PeerJ* 4:e2704.

Goodman K. R., Prost S., Bi K., Brewer M. S., Gillespie R. G. 2019. Host and geography together drive early adaptive radiation of Hawaiian planthoppers. *Molecular Ecology* 28:4513–4528.

Grant P. R., Grant B. R. 2014. *40 Years of Evolution: Darwin's Finches on Daphne Major Island.* Princeton (New Jersey): Princeton University Press.

Gressitt J. L. 1978. Evolution of the endemic Hawaiian cerambycid beetles. *Pacific Insects* 18:137–167.

Gressitt J. L., Nakata S. 1957. Trapping of air-borne insects on ships on the Pacific. *Proceedings of the Hawaiian Entomological Society* 16:363–365.

Gurney A. B., Rentz D. C. 1978. The cavernicolous fauna of Hawaiian lava tubes. 10. Crickets (Orthoptera, Gryllidae). *Pacific Insects* 18:85–103.

Haines W. P. 2011. The biogeography, phylogenetics and population structure of Hawaiian Lepidoptera, with a focus on the genus *Omiodes* (Crambidae). PhD diss., University of Hawai'i at Mānoa.

Haines W. P., Schmitz P., Rubinoff D. 2014. Ancient diversification of *Hyposmocoma* moths in Hawaii. *Nature Communications* 5:3502.

Harbaugh D. T., Baldwin B. G. 2007. Phylogeny and biogeography of the sandalwoods (*Santalum*, Santalaceae): repeated dispersals throughout the Pacific. *American Journal of Botany* 94:1028–1040.

Heaney L. R. 2007. Is a new paradigm emerging for oceanic island biogeography? *Journal of Biogeography* 34:753–757.

Hembry D. H. 2018. Evolutionary biogeography of the terrestrial biota of the Marquesas Islands, one of the world's remotest archipelagos. *Journal of Biogeography* 45:1713–1726.

Hembry D. H., Balukjian B. 2016. Molecular phylogeography of the Society Islands (Tahiti; South Pacific) reveals departures from hotspot archipelago models. *Journal of Biogeography* 43:1372–1387.

Hembry D. H., Kawakita A., Gurr N. E., Schmaedick M. A., Baldwin B. G., Gillespie R. G. 2013. Non-congruent colonizations and diversification in a coevolving pollination mutualism on oceanic islands. *Proceedings of the Royal Society B: Biological Sciences* 280:20130361.

Hoch H. 2006. Systematics and evolution of *Iolania* (Hemiptera: Fulgoromorpha: Cixiidae) from Hawai'i. *Systematic Entomology* 31:302–320.

Hoch H., Howarth F. G. 1999. Multiple cave invasions by species of the planthopper genus *Oliarus* in Hawaii (Homoptera: Fulgoroidea: Cixiidae). *Zoological Journal of the Linnean Society* 127:453–475.

Holzapfel E. P., Clagg H. B., Goff M. L. 1978. Trapping of air-borne insects on ships on the Pacific, part 9. *Pacific Insects* 19:65–90.

Howarth F. G. 2019. Adaptive shifts. Pages 47–55 in *Encyclopedia of Caves,* Third Edition, edited by W. B. White, D. C. Culver, and T. Pipan. London (United Kingdom): Elsevier.

Howarth F. G., Mull W. P. 1992. *Hawaiian Insects and Their Kin.* Honolulu (Hawai'i): University of Hawai'i Press.

Hundsdoerfer A. K., Rubinoff D., Attié M., Wink M., Kitching I. J. 2009. A revised molecular phylogeny of the globally distributed hawkmoth genus *Hyles* (Lepidoptera: Sphingidae), based on mitochondrial and nuclear DNA sequences. *Molecular Phylogenetics and Evolution* 52:852–865.

Illera J. C., Rando J. C., Richardson D. S., Emerson B. C. 2012. Age, origins and extinctions of the avifauna of Macaronesia: a synthesis of phylogenetic and fossil information. *Quaternary Science Reviews* 50:14–22.

IUCN (International Union for Conservation of Nature). 2021. *The IUCN Red List of Threatened Species, Version 2021-2.* https://www.iucnredlist.org. (Accessed 18 October 2021).

Johns C. A., Tangalin N., Bustamente K., Kawahara A. Y. 2014. Evidence of an undescribed, extinct *Philodoria* species (Lepidoptera: Gracillariidae) from Hawaiian *Hesperomannia* herbarium specimens. *Proceedings of the Hawaiian Entomological Society* 46:55–57.

Johns C. A., Moore M. R., Kawahara A. Y. 2016. Molecular phylogeny, revised higher classification, and implications for conservation of endangered Hawaiian leaf-mining moths (Lepidoptera: Gracillariidae: *Philodoria*). *Pacific Science* 70:361–372.

Johns C. A., Toussaint E. F. A., Breinholt J. W., Kawahara A. Y. 2018. Origin and macroevolution of micro-moths on sunken Hawaiian islands. *Proceedings of the Royal Society B: Biological Sciences* 285: 20181047.

Jones B. R., Jordan S. 2015. Genetic consequences of Pleistocene sea-level change on Hawaiian *Megalagrion* damselflies. *Journal of Heredity* 106:618–627.

Jordan S., Simon C., Polhemus D. 2003. Molecular systematics and adaptive radiation of Hawaii's endemic damselfly genus *Megalagrion* (Odonata: Coenagrionidae). *Systematic Biology* 52:89–109.

Jordan S., Simon C., Foote D., Englund R. A. 2005. Phylogeographic patterns of Hawaiian *Megalagrion* damselflies (Odonata: Coenagrionidae) correlate with Pleistocene island boundaries. *Molecular Ecology* 14:3457–3470.

Jordan S., Barruet E., Olaf M., Parsons B., Simon C. 2007. Blue *Hawaiiense* and beyond: conservation genetics and comparative phylogeography of four Hawaiian *Megalagrion* damselfly species (Odonata: Coenagrionidae). Pages 247–260 in *Biology of Hawaiian Streams and Estuaries,* edited by N. L. Evenhuis and J. M. Fitzsimons. Bishop Museum Bulletin in Cultural and Environmental Studies, Volume 3. Honolulu (Hawai'i): Bishop Museum Press.

Juan C., Emerson B. C., Oromí P., Hewitt G. M. 2000. Colonization and diversification: towards a phylogeographic synthesis for the Canary Islands. *Trends in Ecology and Evolution* 15:104–109.

Juvik J. O., Paradise T. R., Juvik S. P. 2000. *Student Atlas of Hawai'i.* Honolulu (Hawai'i): Bess Press.

Kambysellis M. P., Ho K.-F., Craddock E. M., Piano F., Parisi M., Cohen J. 1995. Pattern of ecological shifts in the diversification of Hawaiian *Drosophila* inferred from a molecular phylogeny. *Current Biology* 5:1129–1139.

Kawahara A. Y., Rubinoff D. 2012. Three new species of fancy case caterpillars from threatened forests of Hawaii (Lepidoptera, Cosmopterigidae, *Hyposmocoma*). *ZooKeys* 170:1–20.

Kawahara A. Y., Rubinoff D. 2013. Convergent evolution of morphology and habitat use in the explosive Hawaiian fancy case caterpillar radiation. *Journal of Evolutionary Biology* 26:1763–1773.

King C., Rubinoff D. 2008. First record of fossorial behavior in Hawaiian leafroller moth larvae, *Omiodes continuatalis* (Lepidoptera: Crambidae). *Pacific Science* 62:147–150.

King C. B. A., Haines W. P., Rubinoff D. 2010. Impacts of invasive parasitoids on declining endemic Hawaiian leafroller moths (*Omiodes*: Crambidae) vary among sites and species. *Journal of Applied Ecology* 47:299–308.

Kirch P. V. 2000. *On the Road of the Winds: An Archaeological History of the Pacific Islands Before European Contact*. Berkeley (California): University of California Press.

Kirch P. V. 2011. When did the Polynesians settle Hawai‘i? A review of 150 years of scholarly inquiry and a tentative answer. *Hawaiian Archaeology* 12:3–26.

Krushelnycky P. D., Gillespie R. G., Loope L. L., Liebherr J. K. 2005. Rediscovery and uncertain future of high-elevation Haleakalā carabid beetles (Coleoptera). *Pacific Science* 59:399–410.

Lack D. L. 1947. *Darwin's Finches: An Essay on the General Biological Theory of Evolution*. Gloucester (Massachusetts): P. Smith.

Lapoint R. T., Gidaya A., O'Grady P. M. 2011. Phylogenetic relationships in the spoon tarsus subgroup of Hawaiian *Drosophila*: conflict and concordance between gene trees. *Molecular Phylogenetics and Evolution* 58:492–501.

Lapoint R. T., O'Grady P. M., Whiteman N. K. 2013. Diversification and dispersal of the Hawaiian Drosophilidae: the evolution of *Scaptomyza*. *Molecular Phylogenetics and Evolution* 69:95–108.

Lapoint R. T., Magnacca K. N., O'Grady P. M. 2014. Phylogenetics of the *Antopocerus-modifiedtarsus* clade of Hawaiian *Drosophila*: diversification across the Hawaiian Islands. *PLOS ONE* 9:e113227.

Le Roux J. J., Strasberg D., Rouget M., Morden C. W., Koordom M., Richardson D. M. 2014. Relatedness defies biogeography: the tale of two island endemics (*Acacia heterophylla* and *A. koa*). *New Phytologist* 204:230–242.

Li H., Wiens J. J. 2019. Time explains regional richness patterns within clades more often than diversification rates or area. *American Naturalist* 193:514–529.

Liebherr J. K. 1997. Dispersal and vicariance in Hawaiian platynine carabid beetles (Coleoptera). *Pacific Science* 51:424–439.

Liebherr J. K. 2000. The unity of characters: ecological and morphological specialisation in larvae of Hawaiian platynine Carabidae (Coleoptera). *Invertebrate Taxonomy* 14:931–940.

Liebherr J. K. 2001. Preface. Pages v–xv in *Insects of Hawaii*, Volume 1, edited by E. C. Zimmerman. Honolulu (Hawai‘i): University of Hawai‘i Press.

Liebherr J. K. 2005. Platynini (Coleoptera: Carabidae) of Vanuatu: Miocene diversification on the Melanesian arc. *Invertebrate Systematics* 19:263–295.

Liebherr J. K. 2006. Taxonomic revision of the *Mecyclothorax* beetles (Coleoptera: Carabidae, Psydrini) of Molokai, Hawaii and recognition of areas of endemism on Kamakou Volcano. *Journal of the New York Entomological Society* 114:179–281.

Liebherr J. K. 2008a. Taxonomic revision of Hawaiian *Bembidion* Latreille (Coleoptera: Carabidae, Bembidiini) with a discussion of their reductive and derivative evolutionary specializations. *Annals of Carnegie Museum* 77:31–78.

Liebherr J. K. 2008b. Taxonomic revision of *Mecyclothorax* Sharp (Coleoptera, Carabidae) of Hawaii Island: abundant genitalic variation in a nascent island radiation. *Deutsche Entomologische Zeitschrift* 55:19–78.

Liebherr J. K. 2009. Taxonomic revision of the *Mecyclothorax* beetles (Coleoptera: Carabidae) of Oahu: epithets as epitaphs for an endangered fauna? *Systematic Entomology* 34:649–687.

Liebherr J. K. 2012. The first precinctive Carabidae from Moorea, Society Islands: new *Mecyclothorax* spp. (Coleoptera) from the summit of Mont Tohiea. *ZooKeys* 224:37–80.

Liebherr J. K. 2013. The *Mecyclothorax* beetles (Coleoptera: Carabidae, Moriomorphini) of Tahiti, Society Islands. *ZooKeys* 322:1–170.

Liebherr J. K. 2015. The *Mecyclothorax* beetles (Coleoptera: Carabidae, Moriomorphini) of Haleakalā, Maui: keystone of a hyperdiverse Hawaiian radiation. *ZooKeys* 544:1–407.

Liebherr J. K. 2017. *Bryanites graeffii* sp. n. (Coleoptera, Carabidae): museum rediscovery of a relict species from Samoa. *Zoosystematics and Evolution* 93:1–11.

Liebherr J. K. 2018. Taxonomic review of Australian *Mecyclothorax* Sharp (Coleoptera, Carabidae, Moriomorphini) with special emphasis on the *M. lophoides* (Chaudoir) species complex. *Deutsche Entomologische Zeitschrift* 65:177–224.

Liebherr J. K., Maddison D. R. 2013. Colonisation of the Pacific by *Bembidion* beetles (Coleoptera: Carabidae), with description of *Bembidiontahitiense*, sp. nov., from Tahiti, French Polynesia. *Invertebrate Systematics* 27:439–449.

Liebherr J. K., Porch N. 2015. Reassembling a lost lowland carabid beetle assemblage (Coleoptera) from Kauai, Hawaiian Islands. *Invertebrate Systematics* 29: 191–213.

Liebherr J. K., Samuelson G. A. 1992. The first endemic troglobitic carabid beetles in Hawaiian lava tubes (Coleoptera: Carabidae). *Pan-Pacific Entomologist* 68:157–168.

Liebherr J. K., Short A. E. Z. 2006. *Blackburnia riparia*, new species (Coleoptera: Carabidae, Platynini): a novel element in the Hawaiian riparian insect fauna. *Journal of the New York Entomological Society* 114:1–16.

Liebherr J. K., Zimmerman E. C. 1998. Cladistic analysis, phylogeny and biogeography of Hawaiian Platynini (Coleoptera: Carabidae). *Systematic Entomology* 23:137–172.

Liebherr J. K., Zimmerman E. C. 2000. *Insects of the Hawaii, Volume 16: Hawaiian Carabidae (Coleoptera), Part 1: Introduction and Tribe Platynini.* Honolulu (Hawai'i): University of Hawai'i Press.

Lienhard C., Smithers C. N. 2002. *Psocoptera (Insecta): World Catalogue and Bibliography*. Geneva (Switzerland): Muséum d'Histoire Naturelle de Genève.

Longman R. J., Diaz H. F., Giambelluca T. W. 2015. Sustained increases in lower-tropospheric subsidence over the central tropical north Pacific drive a decline in high-elevation rainfall in Hawaii. *Journal of Climate* 28:8743–8759.

Losos J. B. 2009. *Lizards in an Evolutionary Tree: Ecology and Adaptive Radiation of Anoles.* Berkeley (California): University of California Press.

MacArthur R. H., Wilson E. O. 1967. *The Theory of Island Biogeography.* Princeton (New Jersey): Princeton University Press.

Magnacca K. N. 2020. *Review of* Sierola *Cameron (Hymenoptera: Bethylidae) of the Hawaiian Islands. Part 1 : O'ahu.* Bishop Museum Bulletin in Entomology, Volume 14. Honolulu (Hawai'i): Bishop Museum Press.

Magnacca K. N., Danforth B. N. 2006. Evolution and biogeography of native Hawaiian *Hylaeus* bees (Hymenoptera: Colletidae). *Cladistics* 22:393–411.

Magnacca K. N., Danforth B. N. 2007. Low nuclear DNA variation supports a recent origin of Hawaiian *Hylaeus* bees (Hymenoptera: Colletidae). *Molecular Phylogenetics and Evolution* 43:908–915.

Magnacca K. N., Price D. K. 2015. Rapid adaptive radiation and host plant conservation in the Hawaiian picture wing *Drosophila* (Diptera: Drosophilidae). *Molecular Phylogenetics and Evolution* 92:226–242.

Magnacca K. N., Foote D., O'Grady P. M. 2008. A review of the endemic Hawaiian Drosophilidae and their host plants. *Zootaxa* 1728:1–58.

Mayr E. 1942. *Systematics and the Origin of Species from the Viewpoint of a Zoologist.* New York: Columbia University Press.

Medeiros M. J. 2009. A revision of the endemic Hawaiian genus *Thyrocopa* (Lepidoptera: Xyloryctidae: Xyloryctinae). *Zootaxa* 2202:1–47.

Medeiros M. J., Gillespie R. G. 2011. Biogeography and the evolution of flightlessness in a radiation of Hawaiian moths (Xyloryctidae: *Thyrocopa*). *Journal of Biogeography* 38:101–111.

Medeiros M. J., Eiben J. A., Haines W. P., Kaholoaa R., King C. B. A., Krushelnycky P. D., Magnacca K. N., Rubinoff D., Starr F., Starr K. 2013. The importance of insect monitoring to conservation actions in Hawaii. *Proceedings of Hawaiian Entomological Society* 45:149–166.

Medeiros M. J., Goldberg I., Gillespie R. G. 2015. Geographic exploration within a highly niche-conserved moth in the Hawaiian archipelago. *Biological Journal of the Linnean Society* 116:495–506.

Medeiros M. J., Bianchi G. L., Taschetta L. R., Oboyski P. T. 2016. A review of Polynesian *Carposina* Herrich-Schäffer (Lepidoptera: Carposinidae), with descriptions of four new species. *Zoological Journal of the Linnean Society* 177:135–146.

Medeiros M. J., Kirkpatrick J., Elliott C. H., Prestes A., Eiben J., Rubinoff D. 2019. Two new day-flying species of *Agrotis* Ochsenheimer (Lepidoptera: Noctuidae) from the alpine summit of the Maunakea volcano. *Zootaxa* 4545:277–285.

Mendelson T. C., Shaw K. L. 2005. Rapid speciation in an arthropod. *Nature* 433:375–376.

Mey W., Speidel W. 2008. Global diversity of butterflies (Lepidoptera) in freshwater. *Hydrobiologia* 595:521–528.

Moore J. G., Clague D. A., Holcomb R. T., Lipman P. W., Normark W. R., Torresan M. E. 1989. Prodigious submarine landslides on the Hawaiian ridge. *Journal of Geophysical Research: Solid Earth* 94:17465–17484.

Moore J. G., Normark W. R., Holcomb R. T. 1994. Giant Hawaiian landslides. *Annual Review of Earth and Planetary Sciences* 22:119–144.

Moran N. A., Tran P., Gerardo N. M. 2005. Symbiosis and insect diversification: an ancient symbiont of sap-feeding insects from the bacterial phylum Bacteroidetes. *Applied Environmental Microbiology* 71:8802–8810.

Mullen S. P., Mendelson T. C., Schal C., Shaw K. L. 2007. Rapid evolution of cuticular hydrocarbons in a species radiation of acoustically diverse Hawaiian crickets (Gryllidae: Trigonidiinae: *Laupala*). *Evolution* 61:223–231.

Nishida G. M. 2002. *Hawaiian Terrestrial Arthropod Checklist.* Fourth Edition. Bishop Museum Technical Report Number 22. Honolulu (Hawai'i): Hawai'i Biological Survey.

Nitta J. H., O'Grady P. M. 2008. Mitochondrial phylogeny of the endemic Hawaiian craneflies (Diptera, Limoniidae, *Dicranomyia*): implications for biogeography and species formation. *Molecular Phylogenetics and Evolution* 46:1182–1190.

Nogueira-Filho S. L. G., Nogueira S. S. C., Fragoso J. M. V. 2009. Ecological impacts of feral pigs in the Hawaiian Islands. *Biodiversity and Conservation* 18: 3677–3683.

O'Grady P., DeSalle R. 2008. Out of Hawaii: the origin and biogeography of the genus *Scaptomyza* (Diptera: Drosophilidae). *Biology Letters* 4:195–199.

O'Grady P., DeSalle R. 2018a. Hawaiian *Drosophila* as an evolutionary model clade: days of future past. *BioEssays* 40:1700246.

O'Grady P. M., DeSalle R. 2018b. Phylogeny of the genus *Drosophila*. *Genetics* 209:1–25.

O'Grady P. M., Zilversmit M. 2004. Phylogenetic relationships within the *Drosophila haleakalae* species group inferred by molecular and morphological characters (Diptera: Drosophilidae). Pages 117–134 in *Contributions to the Systematics and Evolution of Diptera*, edited by N. L. Evenhuis and K. Y. Kaneshiro. Bishop Museum Bulletin in Entomology, Volume 12. Honolulu (Hawai'i): Bishop Museum Press.

O'Grady P. M., Lapoint R. T., Bonacum J., Lasola J., Owen E., Wu Y., DeSalle R. 2011. Phylogenetic and ecological relationships of the Hawaiian *Drosophila* inferred by mitochondrial DNA analysis. *Molecular Phylogenetics and Evolution* 58:244–256.

Otte D. 1994. *The Crickets of Hawaii: Origin, Systematics, and Evolution*. Philadelphia (Pennsylvania): Orthopterists' Society and the Academy of Natural Sciences.

Parent C. E., Caccone A., Petren K. 2008. Colonization and diversification of Galápagos terrestrial fauna: a phylogenetic and biogeographical synthesis. *Philosophical Transactions of the Royal Society B: Biological Sciences* 363:3347–3361.

Patiño J., Whittaker R. J., Borges P. A. V., et al. 2017. A roadmap for island biology: 50 fundamental questions after 50 years of *The Theory of Island Biogeography*. *Journal of Biogeography* 44:963–983.

Peck S. B. 1994. Aerial dispersal of insects between and to islands in the Galápagos archipelago, Ecuador. *Annals of the Entomological Society of America* 87:218–224.

Percy D. M. 2017a. A new endemic psyllid genus, *Stevekenia* gen. nov. (Hemiptera: Psylloidea, Triozidae), from the Hawaiian Islands with two new and rare species on threatened host plants in the endemic genus *Nothocestrum* (Solanaceae). *Zootaxa* 4286:370–380.

Percy D. M. 2017b. Making the most of your host: the *Metrosideros*-feeding psyllids (Hemiptera, Psylloidea) of the Hawaiian Islands. *ZooKeys* 649:1–163.

Percy D. M. 2018. Revision of the Hawaiian psyllid genus *Swezeyana*, with descriptions of seven new species (Hemiptera, Psylloidea, Triozidae). *ZooKeys* 758:75–113.

Percy D. M., Garver A. M., Wagner W. L., James H. F., Cunningham C. W., Miller S. E., Fleischer R. C. 2008. Progressive island colonization and ancient origin of Hawaiian *Metrosideros* (Myrtaceae). *Proceedings of the Royal Society B: Biological Sciences* 275:1479–1490.

Percy D. M., Crampton-Platt A., Sveinsson S., Lemmon A. R., Moriarty Lemmon E. M., Ouvrard D., Burckhardt D. 2018. Resolving the psyllid tree of life: phylogenomic analyses of the superfamily Psylloidea (Hemiptera). *Systematic Entomology* 43:762–776.

Perkins R. C. L. 1899. Hymenoptera Aculeata. Pages 1–115 in *Fauna Hawaiiensis or the Zoology of the Sandwich (Hawaiian) Isles*, Volume 1, edited by D. Sharp. Cambridge (United Kingdom): Cambridge University Press.

Perkins R. C. L. 1910. Supplement to Hymenoptera. Pages 600–686 in *Fauna Hawaiiensis or the Zoology of the Sandwich (Hawaiian) Isles*, Volume 6, edited by D. Sharp. Cambridge (United Kingdom): Cambridge University Press.

Perkins R. C. L. 1913. Introduction, being a review of the land-fauna of Hawaii. Pages xv–ccxxviii in *Fauna Hawaiiensis or the Zoology of the Sandwich (Hawaiian) Isles*, Volume 1, edited by D. Sharp. Cambridge (United Kingdom): Cambridge University Press.

Perkins R. C. L. 1920. Some new Hawaiian Coleoptera. *Proceedings of the Hawaiian Entomological Society* 4:341–359.

Pierce N. E. 1995. Predatory and parasitic Lepidoptera: carnivores living on plants. *Journal of the Lepidopterists' Society* 49:412–453.

Poff K. E., Stever H., Reil J. B., Seabourn P., Ching A. J., Aoki S., Logan M., Michalski J. R., Santamaria J., Adams J. W., Eiben J. A., Yew J. Y., Ewing C. P., Magnacca K. N., Bennett G. M. 2017. The Native Hawaiian Insect Microbiome Initiative: a critical perspective for Hawaiian insect evolution. *Insects* 8:130.

Polhemus D. A. 1993. Damsels in distress: a review of the conservation status of Hawaiian Megalagrion damselflies (Odonata: Coenagrionidae). Aquatic Conservation: Marine and Freshwater Ecosystems 3:343–349.

Polhemus D. A. 1997. Phylogenetic analysis of the Hawaiian damselfly genus *Megalagrion* (Odonata: Coenagrionidae): implications for biogeography, ecology, and conservation biology. *Pacific Science* 51:395–412.

Polhemus D. A. 1998. *Nysius AA* (Heteroptera: Lygaeidae), a new species of micropterous Weiku Bug from the summit of Mauna Loa volcano, Hawaii. *Proceedings of the Entomological Society of Washington* 100:25–31.

Polhemus D. A. 2002. An initial review of *Orthotylus* in the Hawaiian Islands, with descriptions of twenty-one new species (Heteroptera: Miridae). *Entomologica Americana* 110:270–340.

Polhemus D. A. 2004. Further studies on the genus *Orthotylus* (Heteroptera: Miridae) in the Hawaiian Islands, with descriptions of thirty-four new species. *Entomologica Americana* 112:227–333.

Polhemus D. A. 2011. Continuing studies on the genus *Orthotylus* in the Hawaiian Islands (Heteroptera: Miridae), with descriptions of thirty-two new species. *Entomologica Americana* 117:37–109.

Polhemus D. A. 2013. A fourth contribution to the study of Hawaiian *Orthotylus* (Heteroptera: Miridae): new species, addenda, revised checklist, and key to the *Perrottetia*-feeding species. *Entomologica Americana* 119:30–41.

Polhemus D. A., Ewing C. P., Kaholoa‘a R., Liebherr J. K. 2003. Rediscovery of *Blackburnia anomala* (Coleoptera: Carabidae), in East Maui, Hawai‘i, after a 107–year hiatus. *Pacific Science* 57:161–166.

Price J. P., Clague D. A. 2002. How old is the Hawaiian biota? Geology and phylogeny suggest recent divergence. *Proceedings of the Royal Society B: Biological Sciences* 269:2429–2435.

Price J. P., Elliott-Fisk D. 2004. Topographic history of the Maui Nui complex, Hawai‘i, and its implications for biogeography. *Pacific Science* 58:27–45.

Price J. P., Wagner W. L. 2018. Origins of the Hawaiian flora: phylogenies and biogeography reveal patterns of long-distance dispersal. *Journal of Systematics and Evolution* 56:600–620.

Redak R. A., Purcell A. H., Lopes J. R. S., Blua M. J., Mizell R. F. III, Andersen P. C. 2004. The biology of xylem fluid–feeding insect vectors of *Xylella fastidiosa* and their relation to disease epidemiology. *Annual Reviews of Entomology* 49:243–270.

Remsen J., DeSalle R. 1998. Character congruence of multiple data partitions and the origin of the Hawaiian Drosophilidae. *Molecular Phylogenetics and Evolution* 9:225–235.

Remsen J., O’Grady P. M. 2002. Phylogeny of Drosophilinae (Diptera: Drosophilidae), with comments on combined analysis and character support. *Molecular Phylogenetics and Evolution* 24:249–264.

Ricklefs R. E., Bermingham E. 2002. The concept of the taxon cycle in biogeography. *Global Ecology and Biogeography* 11:353–361.

Rominger A. J., Goodman K. R., Lim J. Y., Armstrong E. E., Becking L. E., Bennett G. M., Brewer M. S., Cotoras D. D., Ewing C. P., Harte J., Martinez N. D., O’Grady P. M., Percy D. M., Price D. K., Roderick G. K., Shaw K. L., Valdovinos F. S., Gruner D. S., Gillespie R. G. 2016. Community assembly on isolated islands: macroecology meets evolution. *Global Ecology and Biogeography* 25:769–780.

Roy K., Ewing C. P., Hughes M. A., Keith L., Bennett G. M. 2019. Presence and viability of *Ceratocystis lukuohia* in ambrosia beetle frass from Rapid ‘Ōhi‘a death-affected *Metrosideros polymorpha* trees on Hawai‘i Island. *Forest Pathology* 49:e12476.

Rubinoff D., Haines W. P. 2005. Web-spinning caterpillar stalks snails. *Science* 309:575.

Rubinoff D., Schmitz P. 2010. Multiple aquatic invasions by an endemic, terrestrial Hawaiian moth radiation. *Proceedings of the National Academy of Sciences of the United States of America* 107:5903–5906.

Rubinoff D., San Jose M., Hundsdorfer A. 2021. Cryptic diversity in a vagile Hawaiian moth group suggests complex factors drive diversification. *Molecular Phylogenetics and Evolution* 155:107002.

Rundell R. J., Holland B. S., Cowie R. H. 2004. Molecular phylogeny and biogeography of the endemic Hawaiian Succineidae (Gastropoda: Pulmonata). *Molecular Phylogenetics and Evolution* 31:246–255.

Russo C. A. M., Takezaki N., Nei M. 1995. Molecular phylogeny and divergence times of drosophilid species. *Molecular Biology and Evolution* 12:391–404.

Russo C. A. M., Mello B., Frazão A., Voloch C. M. 2013. Phylogenetic analysis and a time tree for a large drosophilid data set (Diptera: Drosophilidae). *Zoological Journal of the Linnean Society* 169:765–775.

Sakai A. K., Weller S. G., Wagner W. L., Nepokroeff M., Culley T. M. 2006. Adaptive radiation and evolution of breeding systems in *Schiedea* (Caryophyllaceae), an endemic Hawaiian genus. *Annals of the Missouri Botanical Garden* 93:49–63.

Samuelson G. A. 1981. A synopsis of Hawaiian *Xyleborini* (Coleoptera: Scolytidae). *Pacific Insects* 23:50–92.

Samuelson G. A. 2003. *Review of* Rhyncogonus *of the Hawaiian Islands (Coleoptera: Curculionidae).* Bishop Museum Bulletin in Entomology, Volume 11. Honolulu (Hawai‘i): Bishop Museum Press.

Samuelson G. A. 2006. *New Species of Plagithmysines from Maui and Hawai‘i Plus a Significant New Plant Host Record for a Previously Described Species from Hawai‘i (Coleoptera: Cerambycidae).* Pages 37–44 in *Records of the Hawaii Biological Survey for 2004–2005, Part 2: Notes*, edited by K. R. Wood. Bishop Museum Occasional Papers, Volume 88. Honolulu (Hawai‘i): Bishop Museum Press.

Samuelson G. A., Davis C. J. 1986. A new *Euphorbia*-sssociated plagithmysine from Maui (Coleoptera: Cerambycidae). *Proceedings of the Hawaiian Entomological Society* 27:125–128.

Schmitz P., Rubinoff D. 2011a. Ecologically and morphologically remarkable new cosmet moth species of the genus *Hyposmocoma* (Lepidoptera: Cosmopterigidae) endemic to the Hawaiian Islands with reference to the spectacular diversity of larval cases. *Annals of the Entomological Society of America* 104:1–15.

Schmitz P., Rubinoff D. 2011b. The Hawaiian amphibious caterpillar guild: new species of *Hyposmocoma* (Lepidoptera: Cosmopterigidae) confirm distinct aquatic invasions and complex speciation patterns. *Zoological Journal of the Linnean Society* 162:15–42.

Shapiro L. H., Strazanac J. S., Roderick G. K. 2006. Molecular phylogeny of *Banza* (Orthoptera: Tettigoniidae), the endemic katydids of the Hawaiian archipelago. *Molecular Phylogenetics and Evolution* 41:53–63.

Sharp W. D., Clague D. A. 2006. Age determination and argon geochemistry of Hawaiian Emperor seamounts. Supplement to: Sharp W. D., Clague D. A. 2006. 50-Ma initiation of Hawaiian-Emperor bend records major change in Pacific Plate motion. *Science* 313:1281–1284.

Shaw K. L. 1995. Biogeographic patterns of two independent Hawaiian cricket radiations (*Laupala* and *Prognathogryllus*). Pages 39–56 in *Hawaiian Biogeography:*

Evolution on a Hot Spot Archipelago, edited by W. L. Wagner and V. A. Funk. Washington (DC): Smithsonian Institution Press.

Shaw K. L. 1996. Sequential radiations and patterns of speciation in the Hawaiian cricket genus *Laupala* inferred from DNA sequences. *Evolution* 50:237–255.

Shaw K. L. 2000. Further acoustic diversity in Hawaiian forests: two new species of Hawaiian cricket (Orthoptera: Gryllidae: Trigonidiinae: *Laupala*). *Zoological Journal of the Linnean Society* 129:73–91.

Shaw K. L. 2002. Conflict between nuclear and mitochondrial DNA phylogenies of a recent species radiation: what mtDNA reveals and conceals about modes of speciation in Hawaiian crickets. *Proceedings of the National Academy of Sciences of the United States of America* 99:16122–16127.

Shaw K. L., Gillespie R. G. 2016. Comparative phylogeography of oceanic archipelagos: hotspots for inferences of evolutionary process. *Proceedings of the National Academy of Sciences of the United States of America* 113:7986–7993.

Short A. E. Z., Liebherr J. K. 2007. Systematics and biology of the endemic water scavenger beetles of Hawaii (Coleoptera: Hydrophilide, Hydrophilini). *Systematic Entomology* 32:601–624.

Short A. E. Z., Cole J., Toussaint E. F. A. 2017. Phylogeny, classification and evolution of the water scavenger beetle tribe Hydrobiusini inferred from morphology and molecules (Coleoptera: Hydrophilidae: Hydrophilinae). *Systematic Entomology* 42:677–691.

Simberloff D. S., Wilson E. O. 1969. Experimental zoogeography of islands: the colonization of empty islands. *Ecology* 50:278–296.

Simon C. 1987. Hawaiian evolutionary biology: an introduction. *Trends in Ecology and Evolution* 2:175–178.

Stadler T., Rabosky D. L., Ricklefs R. E., Bokma F. 2014. On age and species richness of higher taxa. *American Naturalist* 184:447–455.

Stalker H. D. 1972. Intergroup phylogenies in *Drosophila* as determined by comparisons of salivary banding patterns. *Genetics* 70:457–474.

Stever H., Eiben J., Bennett G. M. 2021. Hawaiian *Nysius* insects rely on an obligate symbiont with a reduced genome that retains a discrete nutritional profile to match their plant seed diet. *Genome Biology and Evolution* 13:evab189.

Swezey O. H. 1954. *Forest Entomology in Hawaii: An Annotated Check-list of the Insect Faunas of the Various Components of the Hawaiian Forests*. Bernice P. Bishop Museum Special Publication, Number 44. Honolulu (Hawai‘i): Bishop Museum.

Thibault J.-C., Cibois A. 2017. *Birds of Eastern Polynesia: A Biogeographic Atlas*. Barcelona (Spain): Lynx Edicions.

Thomas R. H., Hunt J. A. 1993. Phylogenetic relationships in *Drosophila*: a conflict between molecular and morphological data. *Molecular Biology and Evolution* 10:362–374.

Thornton I. W. B. 1984. Psocoptera of the Hawaiian Islands. Part III: The endemic *Ptycta* complex (Psocidae): systematics, distribution, and evolution. *International Journal of Entomology* 26:1–128.

Thornton I. W. B. 1990. *Psocoptera of the Hawaiian Islands. Part IV: The Endemic Genus* Palistreptus *(Elipsocidae): Systematics, Distribution, and Evolution*. Bishop Museum Bulletin in Entomology, Volume 4. Honolulu (Hawai‘i): Bishop Museum Press.

Thornton I. W. B., Harrell J. C. 1965. Air-borne Psocoptera trapped on ships and aircraft, 2 – Pacific ship trappings, 1963–64. *Pacific Insects* 7:700–702.

Toussaint E. F. A., Short A. E. Z. 2017. Biogeographic mirages? Molecular evidence for dispersal-driven evolution in Hydrobiusini water scavenger beetles. *Systematic Entomology* 42:692–702.

Usinger R. L. 1942. *Genus* Nysius *and Its Allies in the Hawaiian Islands: Hemiptera, Lygaeidae, Orsillini*. Bernice P. Bishop Museum Bulletin, Volume 173. Honolulu (Hawai‘i): Bishop Museum Press.

Valente L. M., Etienne R. S., Phillimore A. B. 2014. The effects of island ontogeny on species diversity and phylogeny. *Proceedings of the Royal Society B: Biological Sciences* 281:20133227.

Valente L. M., Phillimore A. B., Etienne R. S. 2015. Equilibrium and non-equilibrium dynamics simultaneously operate in the Galápagos Islands. *Ecology Letters* 18:844–852.

van Nieukerken E. J., Doorenweerd C., Hoare R., Davis D. R. 2016. Revised classification and catalogue of global Nepticulidae and Opostegidae (Lepidoptera, Nepticuloidea). *ZooKeys* 628:65–246.

Viale E., Martinez-Sanudo I., Brown J. M., Simonato M., Girolami V., Squartini A., Bressan A., Faccoli M., Mazzon L. 2015. Pattern of association between endemic Hawaiian fruit flies (Diptera, Tephritidae) and their symbiotic bacteria: evidence of cospeciation events and proposal of “*Candidatus* Stammerula Trupaneae”. *Molecular Phylogenetics and Evolution* 90:67–79.

Wagner W. L., Funk V. A. 1995. *Hawaiian Biogeography: Evolution on a Hot Spot Archipelago*. Washington (DC): Smithsonian Institution Press.

Wagner W. L., Herbst D. R., Sohmer S. H. 1999. *Manual of the Flowering Plants of Hawai‘i*, Volumes 1 and 2. Revised Edition. Honolulu (Hawai‘i): University of Hawai‘i Press.

Wahlberg N., Rubinoff D. 2011. Vagility across *Vanessa* (Lepidoptera: Nymphalidae): mobility in butterfly species does not inhibit the formation and persistence of isolated sister taxa. *Systematic Entomology* 36:362–370.

Warren B. H., Simberloff D., Ricklefs R. E., et al. 2015. Islands as model systems in ecology and evolution: prospects fifty years after MacArthur-Wilson. *Ecology Letters* 18:200–217.

Wessel A., Hoch H., Asche M., von Rintelen T., Stelbrink B., Heck V., Stone F. D., Howarth F. G. 2013.

Founder effects initiated rapid species radiation in Hawaiian cave planthoppers. *Proceedings of the National Academy of Sciences of the United States of America* 110:9391–9396.

Whittaker R. J., Triantis K. A., Ladle R. J. 2008. A general dynamic theory of oceanic island biogeography. *Journal of Biogeography* 35:977–994.

Wiens J. J., Lapoint R. T., Whiteman N. K. 2015. Herbivory increases diversification across insect clades. *Nature Communications* 6:8370.

Will K. W., Liebherr J. K., Maddison D. R., Galián J. 2005. Absence asymmetry: the evolution of monorchid beetles (Insecta: Coleoptera: Carabidae). *Journal of Morphology* 264:75–93.

Wilson E. O. 1959. Adaptive shift and dispersal in a tropical ant fauna. *Evolution* 13:122–144.

Wilson E. O. 1961. The nature of the taxon cycle in the Melanesian ant fauna. *American Naturalist* 95:169–193.

Yassin A. 2013. Phylogenetic classification of the Drosophilidae Rondani (Diptera): the role of morphology in the postgenomic era. *Systematic Entomology* 38: 349–364.

Yoshimoto C. M., Gressitt J. L. 1959. Trapping of air-borne insects on ships on the Pacific (Part II). *Proceedings of the Hawaiian Entomological Society* 17:150–155.

Yoshimoto C. M., Gressitt J. L. 1960. Trapping of airborne insects on ships on the Pacific (Part 3). *Pacific Insects* 2:239–243.

Yoshimoto C. M., Gressitt J. L. 1961. Trapping of airborne insects on ships on the Pacific (Part 4). *Pacific Insects* 3:556–558.

Yoshimoto C. M., Gressitt J. L. 1963. Trapping of airborne insects in the Pacific-Antarctic area, 2. *Pacific Insects* 5:873–883.

Zimmerman E. C. 1948a. *Insects of Hawaii, Volume 1: Introduction*. Honolulu (Hawai‘i): University of Hawai‘i Press.

Zimmerman E. C. 1948b. *Insects of Hawaii, Volume 3: Heteroptera*. Honolulu (Hawai‘i): University of Hawai‘i Press.

Zimmerman E. C. 1948c. *Insects of Hawaii, Volume 4: Homoptera: Auchenorrhyncha*. Honolulu (Hawai‘i): University of Hawai‘i Press.

Zimmerman E. C. 1942. Distribution and origin of some eastern Oceanic insects. *American Naturalist* 76:280–307.

Associate Editor: Kaustuv Roy
Handling Editor: John J. Wiens

The Quarterly Review of Biology
Complimentary Offer and Page Charge Form

Authors of articles, commentaries, and lead reviews are entitled to 10 complimentary copies of the journal issue or a year's subscription (or renewal) free of charge.

Author(s):
Article title:
Page length of article:

Complimentary Offer

Please check one:
( ) 10 free copies of the journal issue
or
( ) one free year's subscription or renewal

Page Charges

Authors who attribute support to funding agencies will be expected to meet charges of $40 per journal page for each of the first 20 journal pages, and $80 for each journal page in excess of 20. Authors not supported by funding agencies and authors of invited articles are eligible for 20 free journal pages (about 50 double-spaced typewritten manuscript pages or their equivalent in bibliographic or illustrative matter). When such articles are longer than 20 journal pages, authors will be charged $80 for each page above the allotment of 20 free journal pages. These charges will be used for direct support of the issue in which the article appears. For online-only material, authors are eligible for 6 free double-spaced manuscript pages, but authors with funding will be charged $20 for every 3 manuscript pages in excess of 6.

In order to determine the length of your article, please count the number of paged galleys. The cost of author alterations is chargeable to the author and will be invoiced after the article is published, along with the cost of page charges.

Ship To:	**Bill To: (for page charges)**

Email:	
Telephone:	Fax:

Please return this form to *The Quarterly Review of Biology*, 111 Nassau Hall, Stony Brook University, Stony Brook, NY 11794-5004; qrb@stonybrook.edu; Telephone: 631 632 6977. Thank you.