

Range Expansion of the Small Carpenter Bee *Ceratina smaragdula* across the Hawaiian Archipelago with Potential Ecological Implications for Native Pollinator Systems

Author(s): Wyatt A. Shell and Sandra M. Rehan Source: Pacific Science, 71(1):1-15. Published By: University of Hawai'i Press DOI: <u>http://dx.doi.org/10.2984/71.1.1</u> URL: <u>http://www.bioone.org/doi/full/10.2984/71.1.1</u>

BioOne (<u>www.bioone.org</u>) is a nonprofit, online aggregation of core research in the biological, ecological, and environmental sciences. BioOne provides a sustainable online platform for over 170 journals and books published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Web site, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at <u>www.bioone.org/page/</u><u>terms_of_use</u>.

Usage of BioOne content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Range Expansion of the Small Carpenter Bee *Ceratina smaragdula* across the Hawaiian Archipelago with Potential Ecological Implications for Native Pollinator Systems¹

Wyatt A. Shell² and Sandra M. Rehan^{2,3}

Abstract: Invasive bee species may have a widely detrimental impact on their novel host ecosystem. Introduced bees can rapidly disrupt native plantpollinator mutualisms through competition with indigenous pollinator fauna and facilitation of invasive flora reproduction. Island ecosystems, which are inherently limited in physical range, resource availability, and trophic diversity, tend to be particularly sensitive to ecological impacts of invasive species. The small green carpenter bee Ceratina (Pithitis) smaragdula occurs throughout Southeast Asia and across the Hawaiian archipelago. Historical records indicate that C. smaragdula is nonnative to the Hawaiian archipelago and is recently introduced. Here we present a comprehensive synthesis of C. smaragdula's known biological and ecological history, as well as a population genetic analysis of C. smaragdula from Maui, and from locations across its native range, at the cytochrome oxidase I (COI) locus. We update C. smaragdula's known distribution and occurrence elevation in Hawai'i and reveal a lack of genetic structure between Hawaiian and native range populations. We discuss points of origin, means of introduction, and potential ecological impact of this nonnative pollinator.

REPRESENTED BY more than 20,000 species worldwide, bees are among the most diverse and ubiquitous of the pollinating taxa (Kearns et al. 1998, Michener 2007). Bees enable the reproduction of angiosperm species, providing an indispensable service to their host ecosystem (Engel 2000, Michener 2007) and directly facilitating more than a third of all global crop production (Klein et al. 2007, Gallai et al. 2009). Though most bee species will pollinate multiple angiosperm species (Waser et al. 1996), many bees demonstrate some preference for particular flora (e.g., Minckley et al. 1994, Larsson 2005). This selectivity can lead to a highly specialized relationship between pollinator and host, with each relying largely on the other for its reproductive success. Such specialist plants and pollinators often occupy a relatively narrow ecological niche and may thus allow for greater overall ecosystem productivity and biodiversity (Bascompte and Jordano 2007, Rogers et al. 2014). Generalist pollinators, by contrast, are not limited by their host plant species and may ultimately outcompete specialist fauna for resources and habitat use (Huryn 1997, Traveset and Richardson 2006, Hanna et al. 2014). Though relationships between angiosperm and pollinator groups often comprise numerous taxa (Kearns et al. 1998), such plant-pollinator mutualisms remain sensitive systems, directly affected by climatic, trophic, and anthropogenic factors [such as pollution and poor land use practices (Larsen et al. 2005, Müller et al. 2006, Winfree 2010, Roulston and Goodell 2011; Groom, Stevens, et al. 2014)]. Global climate

¹ The University of New Hampshire, New Hampshire Agricultural Experiment Station, and the Tuttle Foundation provided support for this research. Manuscript accepted 18 July 2016.

² Department of Biological Sciences, University of New Hampshire, 46 College Road, Durham, New Hampshire 03824.

³ Corresponding author (e-mail: sandra.rehan@unh .edu).

Pacific Science (2017), vol. 71, no. 1:1–15 doi:10.2984/71.1.1 (Includes online supplements) © 2017 by University of Hawai'i Press All rights reserved

change alone is predicted to cause a loss of up to 27% of European bee species by the year 2050 (Winfree 2010). Plant-pollinator systems may also be damaged by the transmission of disease among bee species (Durrer and Schmid-Hempel 1994), as has been inferred in the collapse of some North American bumblebee populations (Cameron et al. 2011).

The introduction of invasive species into novel ecosystems is a complex and often biologically costly event (Lodge 1993, Reaser et al. 2007, Ricciardi et al. 2013, Vinson 2013, Lee et al. 2015). Once introduced, invasive species may engender a wide range of ecosystem impacts (Kenis et al. 2009, Vinson 2013) and often come into direct competition with residents over shared resources (Snyder and Evans 2006, Hanna et al. 2014, Miller et al. 2015). Introduced pollinator species may thus disrupt or even eliminate ecologically critical native pollinator-plant reproductive systems (Kato et al. 1999, Traveset and Richardson 2006, Inoue et al. 2008; Groom, Ngo, et al. 2014). The initial establishment and ensuing impact of invasive pollinators depends largely on the extant composition of the resident ecosystem (see Sax et al. 2007, Ward and Johnson 2013). Those that are limited in area, resources, or biological diversity are generally more likely to be strongly affected by a competent invader (Stachowicz and Tilman 2005). Island ecosystems are particularly fragile in this regard and thus tend to be of particular conservation concern when invasive species are introduced (Loope and Mueller-Dombois 1989, Kato et al. 1999, Olesen et al. 2002, Reaser et al. 2007, Kenis et al. 2009; Groom, Ngo, et al. 2014).

Owing to their remote location, wide elevation variation, and considerable rainfall gradients, the Hawaiian Islands have come to host a multitude of rich and diverse ecosystems (Simon 1987). As such, the Hawaiian archipelago has long been prized as a model bioregion for studies of speciation (Price and Wagner 2004, Cowie and Holland 2008), trophic interaction (Gruner 2004), and island biogeography (Whittaker et al. 2008). However, despite their geographic isolation (the nearest continental landmass, North America, is over 3,900 km away), the Hawaiian Islands have come to play host to an exhaustive list of invasive taxa (Howarth 1985, Loope and Mueller-Dombois 1989, Snelling 2003, Stohlgren et al. 2006, Chau et al. 2015). The collective impact of invasive species on Hawai'i is daunting (Pejchar and Mooney 2009) and widely relevant to the threatened or endangered status of 375 species endemic to the archipelago (Magnacca and King 2013), with 39 plant and 10 animal species recently elevated to endangered status (see www.gpo .gov/fdsys/pkg/FR-2016-09-30/pdf/2016 -23112.pdf).

Seven of the 10 animal species now listed as endangered by the U.S. Fish and Wildlife Service are members of Hawai'i's native yellow-faced bees [genus Hylaeus (Magnacca and King 2013)]. Hawai'i's 63 endemic species of *Hylaeus* appear to be largely specialist pollinators of native flora (Daly and Coville 1982, Magnacca 2007*a*, Wilson et al. 2010, Koch and Sahli 2013). Though historically ubiquitous across the archipelago, many of Hawai'i's Hylaeus are now considered rare, threatened, or endangered (Magnacca 2007*a*, Magnacca and King 2013); and invasive Hymenoptera have been named as chief contributors to this extensive and ongoing decline (Wilson and Holway 2010, Hanna et al. 2014, Miller et al. 2015). There are currently at least 19 species of introduced bees across the Hawaiian archipelago, many of which were first recorded in the past 65 yr (Snelling 2003), and four within the last 5 yr (Magnacca et al. 2013). Some of these invasive pollinators, such as the European honey bee, Apis mellifera (Kato et al. 1999, Miller et al. 2015), are generalists: known to compete with native Hylaeus for resources while simultaneously promoting the reproduction of noxious, invasive angiosperm species (Richardson et al. 2000). It is thus of some ecological concern that a generalist small green carpenter bee, Ceratina (Pithitis) smaragdula (Fabricius, 1787), has been steadily establishing itself across the Hawaiian archipelago (Arakaki et al. 2001, Magnacca 2007b).

The small carpenter bees, genus *Ceratina*, occur globally and comprise approximately 200 described species (Michener 2007, Rehan and Schwarz 2015, Shell and Rehan 2016).



FIGURE 1. Female (*left*) and male (*right*) Ceratina (Pithitis) smaragdula: face, a, b; dorsal view, c, d; lateral view, e, f. Body length is between 6 and 8 mm on average. Note relatively prominent facial maculation and black abdominal patches of the male.

Ceratina smaragdula is a small, vividly metallic-green carpenter bee (Figure 1) native to Southeast Asia (Hirashima 1969), where it ranges widely from western India, east throughout China and the Ryukyu Islands, and south into Indonesia and Malaysia (van der Vecht 1952, Shiokawa and Sakagami 1969). *Ceratina smaragdula* is a highly efficient generalist pollinator (van der Vecht 1952, Batra 1976) and, like some members of Hawai'i's native genus *Hylaeus*, makes its nest within the narrow passages of pithy stems (Batra 1978, Maeta et al. 2010). *Ceratina smaragdula* has undergone documented global anthropogenic transport and was brought to Californian alfalfa farms in the early 1970s in an effort to promote crop production (Daly et al. 1971, Batra 1976). Though the species Ceratina smaragdula was first observed in Hawai'i in 1984 and was found only on the island of O'ahu at the time (Arakaki et al. 2001, Snelling 2003). Ceratina smaragdula is known to have since spread south to the island of Hawai'i, but little has been done to directly assess the species' invasive impact. Here, we present a detailed synthesis of C. smaragdula's known biological and dispersal history, along with a population genetic analysis of C. smaragdula within its native and introduced ranges, to initiate comprehensive research and management of this invasive generalist.

MATERIALS AND METHODS

Sample Collection Locations

Southeast Asian samples were collected in 2008 from 21 locations across India, Thailand, Vietnam, and Malaysia (Figure 2a). Samples were collected via Malaise traps, nest sampling, and sweep-netting methods. Hawaiian samples were collected on the island of Maui in 2013 using pan-trap deployments (Leong and Thorp 1999). During both collection periods, samples were secured from coastal and inland locales, ranging from low (0-150 m above sea level) to high altitude [1,200 to over 2,000 m above sea level (Supplemental Table S1)]. Taken together, collections were made from sites separated by over 13,000 km (between the island of Maui in the Hawaiian archipelago and Lonavala, India).

Authors' Note: Supplemental materials available on BioOne (http://www.bioone.org/) and Project MUSE (http://muse.jhu.edu/ journals/pacific_science).

DNA Extraction Amplification and Sequencing

All specimens, collected in Hawai'i (HA) and across Southeast Asia [India (IN), Thailand (TH), Vietnam (VI), and Malaysia (MA)], were confirmed as *Ceratina smaragdula* using a key to *Ceratina* (*Pithitis*) of the world (Hirashima 1969). We removed three legs from the left side of each individual and extracted DNA from these tissues via a modified phenol-chloroform isolation (Kirby 1956). Isolated genetic material was amplified at the COI region following the methods of Hebert et al. (2003), employing a slightly modified Lep1 (F + R) primer pair (Lep1F, 5'-ATTCAACCAATCATAAAGATATT-GG-3'; Lep1R, 5'-TAAACTTCTGGATG-TCCAAAAAATCA-3'). PCR reactions were assembled as follows: 7.2 µl double distilled H₂O, 2.0 µl 10× buffer, 2.0 µl MgCl₂ [25 mM], 1.0 μl Lep1-F [10 μM], 1.0 μl Lep1-R [10 µM], 0.4 µl dNTPs [10 mM], 2 units Taq, 6.0 µl DNA for a 20 µl reaction volume. Reactions were executed in an Eppendorf Mastercycler gradient thermocycler following cycling settings from Hebert et al. (2004): 94°C for 1 min; followed by six cycles of 94°C for 1 min, 45°C for 90 sec, and 72°C for 75 sec; followed by 36 cycles of 94°C for 1 min, 51°C for 90 sec, and 72°C for 75 sec; followed by a final extension period of 72°C for 5 min. Amplification of the target locus was confirmed via electrophoresis (3 µl sample load, 1% agarose gel, 87V run, 10-45 min GelRed bath stain). Successful reactions were loaded into 96-well plates, and 17 µl of PCR product for each sample was sent to Eurofins Genomics (Louisville, Kentucky) for PCR cleanup and Sanger sequencing on an ABI 3730xl (Applied Biosystems).

Sequence Quality and Alignment

Sequences were visually inspected and manually edited for base call accuracy using BioEdit software (Hall 1999). Sequences (GenBank accession numbers KU664397– KU664499) were then aligned via ClustalW using default settings (Thompson et al. 1994) and trimmed to a consensus region of 593 unambiguous, gap-free base pairs (bp). We then screened the entire data set for *Wolbachia* contamination via BLASTn database search.

Haplotype Diversity and Population Genetic Analyses

We assembled a minimum spanning tree in Haploview (Salzburger et al. 2011) partitioning individuals by collection location (i.e.,



FIGURE 2. (*a*) Global range of locations sampled, including India (green), Thailand (dark blue), Vietnam (light blue), Malaysia (purple), and Hawai'i (orange). Insert details Hawaiian archipelago with previous records (orange) or new records (red) of *C. smaragdula*: O'ahu (Arakaki et al. 2001), Hawai'i (Magnacca 2007*b*), and Maui (Howarth and Preston 2007; this study). (*b*) *Ceratina smaragdula* 2013 collection locales from the island of Maui, Hawai'i. Open black diamond indicates site of first collection and detection in 2006 (one male and one female). Gray circles indicate 2013 collection sites and sample counts (small, 1–2 bees; medium, 3–8; large, 9+); approximate elevation gradient and scale are portraved; N indicates north.

HA, IN, VI, TH, or MA). We ran all analyses of population genetic structure in Arlequin v 3.5.1.2 (Excoffier and Lischer 2010). We performed an analysis of molecular variance (AMOVA) to compare genetic variation within and among regional populations, and ran Tajima's D and Fu's F_s tests of neutrality (based on 1,000 simulations) to assess

1.262

(0.213)

Overall Population Structure of Ceratina smaragdula by Region versus Hawaiian Population						
Region	Hawaiʻi	Malaysia	India	Thailand	Vietnam	SE Asia
Hawaiʻi	0.240	0.328	0.461	1.271	0.378	0.769
	(0.040)	(0.055)	(0.078)	(0.214)	(0.064)	(0.130)
Malaysia	0.117	0.355	0.533	1.343	0.450	· · · ·
	$(P \ 0.051)$	(0.06)	(0.090)	(0.226)	(0.075)	
India	0.118	0.067	0.667	1.476	0.583	
	(P 0.160)	(P 0.26)	(0.112)	(0.249)	(0.098)	
Thailand	0.056	0.004	0.031	2.196	1.389	
	(P 0.002)	(P 0.10)	(P 0.479)	(0.370)	(0.234)	
Vietnam	0.033	0.039	0.0186	0.019	0.500	
	$(P \ 0.055)$	(P 0.18)	(P 0.454)	(P 0.245)	(0.084)	

TABLE 1

Note: Diagonal indicates average pairwise differences within regions, and value in parentheses indicates representative percentage sequence divergence; above diagonal are average pairwise differences between regions, and parentheses indicate percentage sequence divergence <u>between</u> those regions; below diagonal are pairwise F_{ST} values. Significance values (P < .05) indicated in **bold**. Fixation index over all loci $F_{ST} = 0.033 \ (P = .108)$.

intraregional population dynamics. Wright's F statistics were calculated and an exact test of sample differentiation was performed to determine F_{ST} and comprehensive pairwise differences between each regional population. We also calculated similar population structure parameters within our Hawaiian population sample (N = 39), subdividing the population by longitude (at 156.2947° W, West Maui N = 20; East Maui N = 19).

0.014

(P 0.133)

RESULTS

New Records in Hawai'i

Here we present an additional 39 records of C. smaragdula in Maui, Hawai'i, and an additional 64 records of this species from across its native range. Elevation of individual collection sites ranged from 1 to 2,176 m, with a collection altitude average of 210 m above sea level. In Hawai'i, collection sites were mainly coastal, gathered from an average altitude of 41 m, with only a handful collected from the central portion of Maui and at high elevation (819 and 2,176 m) (Figure 2*b*).

Population Structure Analysis

A total of 103 C. smaragdula sequences was generated for population genetic analysis (Supplemental Table S2). Regional populations of C. smaragdula did not vary significantly from each other, as indicated by very few pairwise differences between or within populations and a nonsignificant overall F_{ST} of 0.033 (P = .108) (Table 1). The one exception was a significant genetic difference between Hawaiian and Thai populations with a very low F_{ST} of 0.056 (P = .002) and an average of 1.271 bp (0.2%) pairwise base pair differences (P = .035). AMOVA of the Hawaiian population against the combined Southeast Asian cohort (i.e., India, Thailand, Vietnam, and Malaysia) revealed no significant population structuring, also with a very low F_{ST} of 0.014 (P = .133) and few (0.8 bp; 0.13%) pairwise differences (P = .135).

Minimum spanning tree construction revealed 11 distinct haplotypes, with the most common haplotype present in both most Hawaiian and most Southeast Asian samples (N = 87, 84% sequence identity) (Figure 3). There was no significant genetic structuring detected between eastern and western Maui populations despite the presence of three distinct haplotypes (Supplemental Table S3) $(F_{\rm ST} < 0.001, P = .387)$. The majority of Hawaiian individuals (N = 36, 92%) shared the "Haw01" haplotype, and individuals representative of the two other Hawaiian haplo-

SE Asia



FIGURE 3. Minimum spanning tree (MST) displaying haplotype variation among *Ceratina smaragdula* populations in Thailand (TH), Vietnam (VI), India (IN), Malaysia (MA), and Hawai'i (HA). Each circle represents a unique haplotype; the number at the center of each circle represents the total number of individuals who share that haplotype.

types were found mixed among these populations (Supplemental Table S1).

Tajima's *D* scores were negative for all populations except Malaysia (Supplemental Table S4), with significant scores for Thailand (D = -1.605, P = .032), Vietnam (D = -1.974, P = .004), and the Southeast Asian cohort (D = -2.315, P < .001). The more sensitive Fu's $F_{\rm S}$ resulted in significantly negative values for only the Southeast Asian cohort as a whole ($F_{\rm S} = -5.882$, P = .009).

DISCUSSION

This work extends *C. smaragdula*'s known range across the island of Maui and provides new genetic and geographic records of the species. Our analyses demonstrate no significant genetic variation between native and introduced populations. Though individuals collected from *C. smaradula*'s native range collectively represented the majority of observed haplotype variation, low and nonsignificant fixation indices (ranging between 0.004 and 0.118) are evidence of little genetic structuring across populations. Our significantly negative Tajima's D and Fu's F_S values for the Southeast Asian cohort as a whole support a recent or ongoing population expansion, with greatest population mobility reflected in the Thailand and Vietnam groups. Though nonsignificant, the negative Tajima's D and Fu's F_S values for our Maui population similarly suggest the possibility that this group may have recently undergone an expansion event.

Invasive Dispersal History

As detailed by Arakaki and colleagues (2001), *C. smaragdula* was first detected in Hawai'i in 1984 on the island of O'ahu (Figure 2). The single specimen was considered anomalous at the time, and no record was announced. Three additional specimens were collected from O'ahu in 1987, 1996, and 1997 (Arakaki et al. 2001). *Ceratina smaragdula* was subsequently considered an established nonnative species on the island of O'ahu, though still rare and limited to a coastal range (Figure 2) (Snelling 2003). Shortly thereafter, in 2003, two female *C. smaragdula* were collected from North Kona on the island of Hawai'i (Magnacca 2007b), where it appears to have spread rapidly along the island's coast (Magnacca and King 2013). Then, in 2006, one male and one female C. smaragdula were collected from the Kahului Airport environs of Maui (Figure 2b) (Howarth and Preston 2007). Our report of C. smaragdula on Maui is based on a collection of samples gathered in 2013 (Figure 2b). Since its first detection on Maui, C. smarag*dula* appears to have spread across the entirety of the island and, notably, may currently occupy a much broader elevational range than has previously been described. Expansion beyond coastal habitats and into high-elevation locations greatly extends the potential invasive impact of C. smaragdula across the Hawaiian archipelago, as has been observed in another Ceratina species (C. dentipes) invasive to the Fijian Islands (da Silva et al. 2016).

Invasive Impact

Though no study has yet been performed to directly assess the impacts of C. smaragdula in Hawai'i, studies on other invasive hymenopteran taxa across the archipelago predict future (Krushelnycky 2015) or current ecological displacement of native bees (Chau et al. 2015, Lee et al. 2015). Recent research has demonstrated dramatic disparities in pollen carriage and plant fidelity between native Hylaeus and the invasive European honey bee, Apis mellifera, affording the latter a considerable competitive advantage (Miller et al. 2015). As a generalist, A. mellifera has little floral preference or limitation and will freely forage on both native and invasive angiosperm species. Like A. mellifera, C. smaragdula is a generalist pollinator (van der Vecht 1952, Batra 1976) and can thus be expected to promote the establishment and spread of invasive angiosperm species across the Hawaiian archipelago (Miller et al. 2015). Unlike honey bees, which have colonies with hundreds and thousands of foraging workers, C. smaragdula's colony size is relatively small (females rear about eight offspring on average) (Maeta et al. 2010, Ali et al. 2016). Regardless of colony size, introduced bees can disturb native pollination services even when representing a relatively minor proportion of the total pollinator community (Kenta et al. 2007). In addition, given *C. smaragdula*'s stem-nesting biology (Batra 1976, Rehan et al. 2009, Ali et al. 2016), it may be in direct competition with members of native *Hylaeus* for habitable resources.

Hylaeus have diversified widely across the Hawaiian archipelago and currently comprise over 63 species (Daly and Magnacca 2003, Magnacca 2011), of which 40 are considered single-island endemics (Magnacca 2007*a*). All Hylaeus are solitary bees that burrow into the earth, occupy hollow stems, or secure other preexisting cavities to establish their nests (Daly and Magnacca 2003). This adaptability has enabled the genus to collectively occur in all habitable terrains across the archipelago (Magnacca 2007*a*, Koch and Sahli 2013). Though relatively little is yet understood regarding the natural history, general biology, and specific nesting habits of Hylaeus species in Hawai'i, the implications of ongoing species losses are dire. As Hawai'i's only native bee genus, Hylaeus are of considerable importance to the reproductive success of endemic angiosperm species (Hopper 2002, Magnacca 2007*a*), many of which may be poorly equipped to compete with introduced flora (Denslow et al. 2006, Gallaher and Merlin 2010).

It is possible that *C. smaragdula* is having a positive impact on native flora, though these data are currently lacking. In other systems, an introduced generalist (*A. mellifera*) was found to be a comparably effective pollinator group with native bee species (Freitas and Paxton 1998, Gross 2001, Dupont et al. 2004). Thus, though *C. smaragdula* may contribute to the competitive exclusion of native *Hylaeus*, it may also help to maintain pollination services historically carried out by that group.

Possible Means of Introduction

Current analysis of the *COI* locus revealed less population structure than expected, both within and between *C. smaragdula*'s native and introduced ranges. This observed genetic homogeneity suggests that these populations have been in geographic isolation for relatively little time. This idea is further supported by historic records, which indicate that C. smaragdula initially arrived on Hawai'i within the last 40 yr (Arakaki et al. 2001, Snelling 2003). It is theorized that terrestrial animals colonize islands primarily via one of three modes: island hopping (e.g., Garb and Gillespie 2006), long-distance dispersal (LDD) (Bellemain and Ricklefs 2008), or through anthropogenic facilitation (Reaser et al. 2007, Däumer et al. 2012). Island hopping, for instance, has been observed in many arthropod species [e.g., bees (Dafni et al. 2010, Chenoweth and Schwarz 2011); tree crickets (Tinghitella et al. 2011); leaf hoppers (Su et al. 2014)] and has been suggested as a means of long-range bee dispersal across the Southwest Pacific (Schwarz et al. 2006).

Many bee groups, including genus Ceratina, are known for their capacity for longdistance dispersal (Rehan et al. 2010, Rehan and Schwarz 2015). Oil-collecting bees (Ctenoplectrini) (Schaefer and Renner 2008), stingless bees (Meliponini) (Rasmussen and Cameron 2010), and some allodapine bees (genus Braunsapis) (Fuller et al. 2005) are all considered to have reached their current distributions via LDD, over both continental and oceanic expanses. Moreover, Hawai'i's native Hylaeus are considered the descendants of a single pre-historic introduction following a chance LDD event out of East Asia (Daly and Magnacca 2003, Magnacca and Danforth 2006). Although it is unlikely that C. smaragdula reached Hawai'i via oceanic LDD, the apparent high mobility of populations in its native range may support LDD as an ongoing means of invasive establishment between the Islands. Historically, the vast majority of Hawai'i's invasive species were introduced via some form of anthropogenic mediation (Howarth 1985), and it is not unreasonable to expect that C. smaragdula arrived by similar means.

Ceratina smaragdula was intentionally transported to California in the 1970s for agricultural purposes (Daly et al. 1971), but, unlike *A. mellifera* (Eckert 1951), there are no records of its introduction to Hawai'i. As such, any human transport is likely to have been accidental. As a stem-nesting bee, it is

conceivable that C. smaragdula may have been brought to O'ahu within any number of ornamental and fruit-bearing softwood plants widely imported from Southeast Asia to the Hawaiian Islands (Schmidt and Drake 2011). Numerous shipments of exotic plants could have contained unseen C. smaragdula, unwittingly collected from otherwise disparate native populations. This "introduction by import" could explain the higher than expected haplotype variation of the Hawaiian population. Elsewhere, fruiting bramble (Rubus) species are preferentially occupied by Ceratina, because they represent a reliable pollen resource and ideal pithy plant for nest construction (Kislow 1976, Rehan and Richards 2010, McFrederick and Rehan 2016). Himalayan vellow raspberry (*Rubus ellipticus*) (Starr et al. 2003) was originally introduced to Hawai'i for agricultural experimentation (Degener and Degener 1968) and has rapidly become one of the archipelago's most noxious invasive plants (Starr et al. 2003). Rubus ellipticus shares much of its native range with that of C. sma*ragdula*, and, although it is uncertain to have been the vector for initial introduction, further research could reveal whether the two species are mutually aiding one another's continued establishment across Hawai'i.

CONCLUSIONS

Here we present additional genetic records and document a range expansion of C. smaragdula across Maui. These data reveal an extended distribution of this species to both inland and high-elevation habitats. Molecular analyses demonstrate little genetic distinction between this species' introduced and native populations and indicate a recent introduction to the archipelago, most likely via anthropogenic facilitation. Future molecular analyses could benefit from targeting microsatellite loci or single-nucleotide polymorphisms for fine-scale exploration of native and invasive population structures. Further systematic surveys across each of the Hawaiian Islands are also necessary to better assess C. smaragdula's expanding distribution and ecology. More broadly, additional biofaunistic and genetic studies are critical to understanding the dynamics underlying invasive pollinator dispersal, establishment, and impact.

ACKNOWLEDGMENTS

We thank Sam Droege and Laurence Packer for bee specimens; we also thank Cullen Franchino for imaging specimens.

Literature Cited

- Ali, H., A. S. Alqarni, M. Shebl, and M. S. Engel. 2016. Notes on the nesting biology of the small carpenter bee *Ceratina smaragdula* (Hymenoptera: Apidae) in northwestern Pakistan. Fla. Entomol. 99:89–93.
- Arakaki, K. T., W. D. Perreira, D. J. Preston, and J. W. Beardsley. 2001. *Pithitis smaragdula* (Fabricius), an asiatic bee (Hymenoptera: Apidae) now apparently established on O'ahu. Proc. Hawaii. Entomol. Soc. 35:151.
- Bascompte, J., and P. Jordano. 2007. Plantanimal mutualistic networks: The architecture of biodiversity. Annu. Rev. Ecol. Evol. Syst. 38:567–593.
- Batra, W. T. 1976. Comparative efficiency of alfalfa pollination by Nomia melanderi, Megachile rotundata, Anthidium florentinum, and Pithitis smaragdula (Hymenoptera: Apoidea). J. Kans. Entomol. Soc. 49:18–22.
- ——. 1978. Aggression, territoriality, mating and nest aggregation of some solitary bees (Hymenoptera: Halictidae, Megachilidae, Colletidae, Anthophoridae). J. Kans. Entomol. Soc. 51:547–559.
- Bellemain, E., and R. E. Ricklefs. 2008. Are islands the end of the colonization road? Trends Ecol. Evol. 23:461–468.
- Cameron, S. A., J. D. Lozier, J. P. Strange, J. B. Koch, N. Cordes, L. F. Solter, and T. L. Griswold. 2011. Patterns of widespread decline in North American bumble bees. Proc. Natl. Acad. Sci. U.S.A. 108:662–667.
- Chau, L. M., C. Hanna, L. T. Jenkins, R. E. Kutner, E. A. Burns, C. Kremen, and A. D. Goodisman. 2015. Population genetic structure of the predatory, social wasp *Vespula pensylvanica* in its native and invasive range. Ecol. Evol. 5:5573–5587.

- Chenoweth, L. B., and M. P. Schwarz. 2011. Biogeographical origins and diversification of the exoneurine allodapine bees of Australia (Hymenoptera, Apidae). J. Biogeogr. 38:1471–1483.
- Cowie, R. H., and B. S. Holland. 2008. Molecular biogeography and diversification of the endemic terrestrial fauna of the Hawaiian Islands. Philos. Trans. R. Soc. Lond. B Biol. Soc. 363:3363–3376.
- Dafni, A., P. Kevan, C. L. Gross, and K. Goka. 2010. *Bombus terrestris*, pollinator, invasive and pest: An assessment of problems associated with its widespread introductions for commercial purposes. Appl. Entomol. Zool. 45:101–113.
- Daly, H. V., G. E. Bohart, and R. W. Thorp. 1971. Introduction of small carpenter bees into California for pollination 1. Release of *Pithitis smaragdula*. J. Econ. Entomol. 64:1145.
- Daly, H. V., and R. E. Coville. 1982. Hylaeus pubescens and associated arthropods at Kīlauea, Hawai'i Volcanoes National Park (Hymenoptera: Apoidea and Chalcidoidea; Mesostigmata: Ameroseiidae). Proc. Hawaii. Entomol. Soc. 24:75–81.
- Daly, H. V., and K. N. Magnacca. 2003. Hawaiian Hylaeus (Nesoprosopis) bees (Hymenoptera: Apoidea). Insects of Hawai'i, Vol. 17. University of Hawai'i Press, Honolulu.
- da Silva, C. R. B., S. V. C. Groom, M. I. Stevens, and M. P. Schwarz. 2016. Current status of the introduced allodapine bee *Braunsapis puangensis* (Hymenoptera: Apidae) in Fiji. Aust. Entomol. 55:43– 48.
- Däumer, C., C. Greve, R. Hutterer, B. Misof, and M. Haase. 2012. Phylogeography of an invasive land snail: Natural range expansion versus anthropogenic dispersal in *Theba pisana pisana*. Biol. Invasions 14:1665–1682.
- Degener, O., and I. Degener. 1968. Flora Hawaiiensis: The new illustrated flora of the Hawaiian Islands. Honolulu.
- Denslow, J. S., A. L. Uowolo, and R. F. Hughes. 2006. Limitations to seedling establishment in a mesic Hawaiian forest. Oecologia (Berl.) 148:118–128.

- Dupont, Y. L., D. M. Hansen, A. Valido, and J. M. Olesen. 2004. Impact of introduced honey bees on native pollination interactions of the endemic *Echium wildpretii* (Boraginaceae) on Tenerife, Canary Islands. Biol. Conserv. 118:301–311.
- Durrer, S., and P. Schmid-Hempel. 1994. Shared use of flowers leads to horizontal pathogen transmission. Proc. R. Soc. Lond. B Biol. Sci. 258:299–302.
- Eckert, J. E. 1951. Rehabilitation of the beekeeping industry in Hawai'i. Industrial Research Advisory Council, Honolulu.
- Engel, M. S. 2000. A new interpretation of the oldest fossil bee (Hymenoptera: Apidae). Am. Mus. Novit. 3296:1–11.
- Excoffier, L., and H. E. L. Lischer. 2010. Arlequin suite ver 3.5: A new series of programs to perform population genetics analyses under Linux and Windows. Mol. Ecol. Resour. 10:564–567.
- Fabricius, J. 1787. Mantissa insectorum sistens eorum species nuper detectas adiectis characteribus, genericis, differentiis, specificis, emendationibus, observationibus. Tome I. C. G. Profit.
- Freitas, B. M., and R. J. Paxton. 1998. A comparison of two pollinators: The introduced honey bee *Apis mellifera* and an indigenous bee *Centris tarsata* on cashew *Anacardium* occidentale in its native range of NE Brazil. J. Appl. Ecol. 35:109–121.
- Fuller, S., M. Schwarz, and S. Tierney. 2005. Phylogenetics of the allodapine bee genus *Braunsapis*: Historical biogeography and long-range dispersal over water. J. Biogeogr. 32:2135–2144.
- Gallaher, T., and M. Merlin. 2010. Biology and impacts of Pacific island invasive species. 6. *Prosopis pallida* and *Prosopis juliflora* (Algarroba, Mesquite, *Kiawe*) (Fabaceae). Pac. Sci. 64:489–526.
- Gallai, N., J.-M. Salles, J. Settele, and B. E. Vaissière. 2009. Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. Ecol. Econ. 68:810–821.
- Garb, J. E., and R. G. Gillespie. 2006. Island hopping across the central Pacific: Mitochondrial DNA detects sequential colonization of the Austral Islands by crab spiders

(Araneae: Thomisidae). J. Biogeogr. 33:201–220.

- Groom, S. V. C., H. T. Ngo, S. M. Rehan, P. Skelton, M. I. Stevens, and M. P. Schwarz. 2014. Multiple recent introductions of apid bees into Pacific archipelagos signify potentially large consequences for both agriculture and indigenous ecosystems. Biol. Invasions 16:2293–2302.
- Groom, S. V. C., M. I. Stevens, and M. P. Schwarz. 2014. Parallel responses of bees to Pleistocene climate change in three isolated archipelagos of the southwestern Pacific. Proc. R. Soc. B 281:2013393.
- Gross, C. L. 2001. The effect of introduced honeybees on native bee visitation and fruit-set in *Dillwynia juniperina* (Fabaceae) in a fragmented ecosystem. Biol. Conserv. 102:89–95.
- Gruner, D. S. 2004. Attenuation of top-down and bottom-up forces in a complex terrestrial community. Ecology 85:3010–3022.
- Hall, T. A. 1999. Bioedit: A user-friendly biological sequence alignment editor and alignment program for Windows 95/98 NT. Nucleic Acids Symp. Ser. 41:95–98.
- Hanna, C., D. Foote, and C. Kremen. 2014. Competitive impacts of an invasive nectar thief on plant-pollinator mutualisms. Ecology 95:1622–1632.
- Hebert, P. D. N., A. Cywinska, S. L. Ball, and J. R. deWaard. 2003. Biological identifications through DNA barcodes. Proc. R. Soc. Lond. B Biol. Sci. 270:313–321.
- Hebert, P. D. N., E. H. Penton, J. M. Burns, D. H. Janzen, and W. Hallwachs. 2004. Ten species in one: DNA barcoding reveals cryptic species in the Neotropical skipper butterfly *Astraptes fulgerator*. Proc. Natl. Acad. Sci. U.S.A. 101:14812–14817.
- Hirashima, Y. 1969. Synopsis of the genus *Pithitis* Klug of the world (Hymenoptera: Anthophoridae). Pac. Insects 11:649–669.
- Hopper, D. 2002. The reproductive biology and conservation of the endangered Hawaiian legume, *Sesbania tomentosa*, with emphasis on its pollination system. Ph.D. diss., University of Hawai'i at Mānoa, Honolulu.
- Howarth, F. G. 1985. Impacts of alien land arthropods and mollusks on native plants

and animals in Hawai'i. Pages 149–179 *in* Hawai'i's terrestrial ecosystems: Preservation and management. Cooperative National Park Resources Studies Unit, University of Hawai'i, Honolulu.

- Howarth, F. G., and D. J. Preston. 2007. Monitoring for arthropods (insects and relatives) occurring within the Kahului Airport environs, Maui, Hawai'i, Phase II Final Report. Submitted to Edward K. Noda & Associates, Inc., 615 Pi'ikoi Street, Suite 300, Honolulu, Hawai'i 96814, and the State of Hawai'i, Department of Transportation, Airports Division.
- Huryn, V. M. B. 1997. Ecological impacts of introduced honey bees. Q. Rev. Biol. 72:275–297.
- Inoue, M. N., J. Yokoyama, and I. Washitami. 2008. Displacement of Japanese native bumblebees by the recently introduced *Bombus terrestris* (L.) (Hymenoptera: Apidae). J. Insect Conserv. 12:135–146.
- Kato, M., A. Shibata, T. Yasui, and H. Nagamasu. 1999. Impact of introduced honeybees, *Apis mellifera*, upon native bee communities in the Bonin (Ogasawara) Islands. Res. Popul. Ecol. (Kyoto) 41:217–228.
- Kearns, C. A., D. W. Inouye, and N. M. Waser. 1998. Endangered mutualisms: The conservation of plant-pollinator interactions. Annu. Rev. Ecol. Syst. 29:83–112.
- Kenis, M., M.-A. Auger-Rozenber, A. Roques, L. Timms, C. Péré, M. J. W. Cock, J. Settele, S. Augustin, and C. Lopez-Vaamonde. 2009. Ecological effects of invasive alien insects. Biol. Invasions 11:21–45.
- Kenta, T., N. Inari, T. Nagamitsu, K. Goka, and T. Hiura. 2007. Commercialized European bumblebee can cause pollination disturbance: An experiment on seven native plant species in Japan. Biol. Conserv. 134:298–309.
- Kirby, K. S. 1956. Isolation and characterization of ribosomal ribonucleic acid. Biochem. J. 96:266–269.
- Kislow, C. J. 1976. The comparative biology of two species of small carpenter bees, *Ceratina strenua* F. Smith and *C. calcarata* Robertson (Hymenoptera, Xylocopinae). Ph.D. diss., University of Georgia, Athens.

- Klein, A. M., B. E. Vaissière, J. H. Cane, I. Steffan-Dewenter, S. A. Cunningham, C. Kreme, and T. Tscharntke. 2007. Importance of pollinators in changing landscapes for world crops. Proc. R. Soc. Lond. B Biol. Sci. 274:303–313.
- Koch, J. B., and H. F. Sahli. 2013. Patterns of flower visitation across elevation and successional gradients in Hawai'i. Pac. Sci. 67:253–266.
- Krushelnycky, P. D. 2015. Ecology of some lesser-studied introduced ant species in Hawaiian forests. J. Insect Conserv. 19:659–667.
- Larsen, T. H., N. M. Williams, and C. Kremen. 2005. Extinction order and altered community structure rapidly disrupt ecosystem functioning. Ecol. Lett. 8:538– 547.
- Larsson, M. 2005. Higher pollinator effectiveness by specialist than generalist flower-visitors of unspecialized *Knautia arvensis* (Dipsacaceae). Oecologia (Berl.) 146:394–403.
- Lee, D. J., M. Motoki, C. Vanderwoude, S. T. Nakamoto, and P. Leung. 2015. Taking the sting out of Little Fire Ant in Hawai'i. Ecol. Econ. 111:100–110.
- Leong, J. M., and R. W. Thorp. 1999. Colour-coded sampling: The pan trap colour preferences of oligolectic and nonoligolectic bees associated with a vernal pool plant. Ecol. Entomol. 24:329–335.
- Lodge, D. M. 1993. Biological invasions: Lessons for ecology. Trends Ecol. Evol. 8:133–137.
- Loope, L. L., and D. Mueller-Dombois. 1989. Characteristics of invaded islands, with special reference to Hawai'i. Pages 257–280 *in* J. A. Drake, F. DiCastri, R. H. Groves, F. J. Kruger, M. Rejmanek, and M. Williamson, eds. Biological invasions: A global perspective. Wiley, New York.
- Maeta, Y., S. W. T. Batra, and S. F. Sakagami. 2010. Intra-nest behaviors and artificially induced sociality of the tropical Asian basically solitary bee, *Ceratina (Pithitis) smaragdula* Fabricius, with notes on the nest architecture and other bionomic matters (Hymenoptera, Apidae, Xylocopinae). Chugoku Kontyu 24:23–48.

- Magnacca, K. N. 2007*a*. Conservation status of the endemic bees of Hawai'i, *Hylaeus* (*Nesoprosopis*) (Hymenoptera: Colletidae). Pac. Sci. 61:173–190.
 - ——. 2007b. New records of *Hylaeus* (*Nesoprosopis*) and *Ceratina* bees in Hawai'i. Bishop Mus. Occas. Pap. 96:44–45.
- ——. 2011. Two new species of *Hylaeus* (*Nesoprosopis*) (Hymenoptera: Colletidae) from Oʻahu, Hawaiʻi. Zootaxa 3065:60– 65.
- Magnacca, K. N., and B. N. Danforth. 2006. Evolution and biogeography of native Hawaiian *Hylaeus* (Hymenoptera: Colletidae). Cladistics 22:393–411.
- Magnacca, K. N., J. Gibbs, and S. Droege. 2013. Notes on alien and native bees (Hymenoptera: Apoidea) from Hawaiian Islands. Records of the Hawai'i Biological Survey for 2012. Pages 61–65 *in* N. L. Evenhuis and L. G. Eldredge, eds. Bishop Mus. Occas. Pap. 114.
- Magnacca, K. N., and C. B. A. King. 2013. Assessing the presence and distribution of 23 Hawaiian yellow-faced bee species on lands adjacent to military installations on O'ahu and Hawai'i Islands. The Hawai'i-Pacific Islands Cooperative Ecosystems Studies Unit and Pacific Cooperative Studies Unit (http://scholarspace .manoa.hawaii.edu/bitstream/handle/ 10125/34064/v185.pdf).
- McFrederick, Q. S., and S. M. Rehan. 2016. Characterization of pollen and bacterial community composition in brood provisions of a small carpenter bee. Mol. Ecol. 25:2302–2311.
- Michener, C. D. 2007. The bees of the world. 2nd ed. Johns Hopkins University Press, Baltimore, Maryland.
- Miller, A. E., B. J. Brosi, K. Magnacca, G. C. Daily, and L. Pejchar. 2015. Pollen carried by native and nonnative bees in the large-scale reforestation of pastureland in Hawai'i: Implications for pollination. Pac. Sci. 69:67–79.
- Minckley, R. L., W. T. Wcislo, D. Yanega, and S. L. Buchmann. 1994. Behavior and phenology of a specialist bee (*Dieunomia*) and sunflower (*Helianthus*) pollen availability. Ecology 75:1406–1419.

- Müller, A., S. Diener, C. Sedviy, and S. Dorn. 2006. Quantitative pollen requirements of solitary bees: Implications for bee conservation and the evolution of bee-flower relationships. Biol. Conserv. 130:604–615.
- Olesen, J. M., L. I. Eskildsen, and S. Venkatasamy. 2002. Invasion of pollination networks on oceanic islands: Importance of invader complexes and endemic super generalists. Divers. Distrib. 8:181–192.
- Pejchar, L., and H. A. Mooney. 2009. Invasive species, ecosystem services and human well-being. Trends Ecol. Evol. 24:497–504.
- Price, J. P., and W. L. Wagner. 2004. Speciation in Hawaiian angiosperm lineages: Cause, consequence, and mode. Evolution 58:2185–2200.
- Rasmussen, C., and S. A. Cameron. 2010. Global stingless bee phylogeny supports ancient divergence, vicariance, and long distance dispersal. Biol. J. Linn. Soc. 99:206–232.
- Reaser, J. K., L. A. Meyerson, Q. Cronk, M. D. Poorter, and L. G. Eldredge. 2007. Ecological and socioeconomic impacts of invasive alien species in island ecosystems. Environ. Conserv. 34:98–111.
- Rehan, S. M., T. W. Chapman, A. Craigie, M. H. Richards, S. J. Cooper, and M. P. Schwarz. 2010. Molecular phylogeny of the small carpenter bees (Hymenoptera: Apidae: Ceratinini) indicates early and rapid global dispersal. Molec. Phylogenet. Evol. 55:1042–1054.
- Rehan, S. M., and M. H. Richards. 2010. Nesting and life cycle of *Ceratina calcarata* in southern Ontario (Hymenoptera: Apidae: Xylocopinae). Can. Entomol. 142:65–74.
- Rehan, S. M., M. H. Richards, and M. P. Schwarz. 2009. Evidence of social nesting in the *Ceratina* of Borneo (Hymenoptera: Apidae). J. Kans. Entomol. Soc. 82:194– 209.
- Rehan, S. M., and M. P. Schwarz. 2015. A few steps forward and no steps back: Longdistance dispersal patterns in small carpenter bees suggest major barriers to backdispersal. J. Biogeogr. 42:485–494.
- Ricciardi, A., M. F. Hoopes, M. P. Marchetti, and J. L. Lockwood. 2013. Progress

toward understanding the ecological impacts of nonnative species. Ecol. Monogr. 83:263–282.

- Richardson, D. M., N. Allsopp, C. M. D'antonio, S. J. Milton, and M. Rejmánek. 2000. Plant invasions: The role of mutualisms. Biol. Rev. 75:65–93.
- Rogers, S. R., D. R. Tarpy, and H. J. Burrack. 2014. Bee species diversity enhances productivity and stability in a perennial crop. PLoS ONE 9:e97307.
- Roulston, T. H., and K. Goodell. 2011. The role of resources and risks in regulating wild bee populations. Annu. Rev. Entomol. 56:293–312.
- Salzburger, W., G. B. Ewing, and A. Von-Haeseler. 2011. The performance of phylogenetic algorithms in estimating haplotype genealogies with migration. Mol. Ecol. 20:1952–1963.
- Sax, D. F., J. J. Stachowicz, J. H. Brown, J. F. Bruno, M. N. Dawson, S. D. Gaines, R. K. Grosberg, A. Hastings, R. D. Holt, M. M. Mayfield, M. I. O'Connor, and W. R. Rice. 2007. Ecological and evolutionary insights from species invasions. Trends Ecol. Evol. 22:465–471.
- Schaefer, H., and S. S. Renner. 2008. A phylogeny of the oil bee tribe Ctenoplectrini (Hymenoptera: Anthophila) based on mitochondrial and nuclear data: Evidence for Early Eocene divergence and repeated outof-Africa dispersal. Mol. Phylogenet. Evol. 47:799–811.
- Schmidt, J. P., and J. M. Drake. 2011. Time since introduction, seed mass, and genome size predict successful invaders among the cultivated vascular plants of Hawai'i. PLoS One 6:e17391.
- Schwarz, M. P., S. Fuller, S. M. Tierney, and S. J. B. Cooper. 2006. Molecular phylogenetics of the exoneurine allodapine bees reveal an ancient and puzzling divergence from Africa to Australia. Syst. Biol. 55:31–45.
- Shell, W. A., and S. M. Rehan. 2016. Recent and rapid diversification of the small carpenter bees in eastern North America. Biol. J. Linn. Soc. 117:633–645.
- Shiokawa, M., and S. F. Sakagami. 1969. Additional notes on the genus *Pithitis* or green

metallic small carpenter bees in the Oriental Region, with descriptions of two species from India. Nat. Life Southeast Asia 6:139–151.

- Simon, C. 1987. Hawaiian evolutionary biology: An introduction. Trends Ecol. Evol. 2:175–178.
- Snelling, R. R. 2003. Bees of the Hawaiian Islands, exclusive of *Hylaeus* (*Nesoprosopis*) (Hymenoptera: Apoidea). J. Kans. Entomol. Soc. 76:342–356.
- Snyder, W. E., and E. W. Evans. 2006. Ecological effects of invasive arthropod generalist predators. Annu. Rev. Ecol. Evol. Syst. 37:95–122.
- Stachowicz, J. J., and D. Tilman. 2005. Species invasions and the relationships between species diversity, community saturation, and ecosystem functioning. Pages 41–64 *in* D. F. Sax, J. J. Stachowicz, and S. D. Gaines, eds. Species invasions: Insights into ecology, evolution, and biogeography. 1st ed. Sinauer Associates, Sunderland, Massachusetts.
- Starr, F., K. Starr, and L. Loope. 2003. Rubus ellipticus Yellow Himalayan raspberry (Rosaceae). U. S. Geological Survey, Biological Resources Division, Haleakalā Field Station, Maui, Hawai'i.
- Stohlgren, T. J., D. Barnett, C. Flather, P. Fuller, B. Peterjohn, J. Kartesz, and L. L. Master. 2006. Species richness and patterns of invasion in plants, birds, and fishes in the United States. Biol. Invasions 8:427–447.
- Su, Y.-C., J.-F. Wang, R. J. T. Villanueva, and O. M. Nuñeza. 2014. Hopping out of Mindanao: Miocene–Pliocene geological processes and cross-island dispersal as major drivers of diversity of Philippine treehoppers. J. Biogeogr. 41:1277–1290.
- Thompson, J. D., D. G. Higgins, and T. J. Gibons. 1994. CLUSTAL W: Improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice. Nucleic Acids Res. 22:4673–4680.
- Tinghitella, R. M., M. Zuk, M. Beveridge, and L. W. Simmons. 2011. Island hopping introduces Polynesian field crickets to

novel environments, genetic bottlenecks and rapid evolution. J. Evol. Biol. 24:1199– 1211.

- Traveset, A., and D. M. Richardson. 2006. Biological invasion as disruptors of plant reproductive mutualisms. Trends Ecol. Evol. 21:208–216.
- van der Vecht, J. 1952. A preliminary revision of the Oriental species of the genus *Ceratina* (Hymenoptera: Apidae). Zool. Verh. (Leiden) 16:1–85.
- Vinson, S. B. 2013. Impact of the invasion of the imported fire ant. Insect. Sci. 20:439– 455.
- Ward, M., and S. D. Johnson. 2013. Generalised pollination systems for three invasive milkweeds in Australia. Plant Biol. (N.Y.) 15:566–572.
- Waser, N. M., L. Chittka, M. V. Price, N. M. Williams, and J. Ollerton. 1996. General-

ization in pollination systems, and why it matters. Ecology 77:1043–1060.

- Whittaker, R. J., K. A. Triantis, and R. J. Ladle. 2008. A general dynamic theory of oceanic island biogeography. J. Biogeogr. 35:977–994.
- Wilson, E. E., and D. A. Holway. 2010. Multiple mechanisms underlie displacement of solitary Hawaiian Hymenoptera by an invasive social wasp. Ecology 91:3294– 3302.
- Wilson, E. E., C. S. Sidhu, K. E. LeVan, and D. A. Holway. 2010. Pollen foraging behaviour of solitary Hawaiian bees revealed through molecular pollen analysis. Mol. Ecol. 19:4823–4829.
- Winfree, R. 2010. The conservation and restoration of wild bees. Ann. N.Y. Acad. Sci. 1195:169–197.