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Morphological and ecological traits promoting aphid colonization of the Hawaiian Islands

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Abstract Species introductions into novel habitats, especially island ecosystems, can have devastating effects on ecosystem function and stability. Though none are native, at least 96 aphid species can now be found on one or more of the Hawaiian Islands. As aphids cause direct feeding damage and transmit plant viruses, it is important to identify the traits that have enabled these particular species to successfully colonize the archipelago. To address this question, nine morphological and ecological traits that may contribute to successful colonization were assessed for aphids present in Hawaii. As a comparative null model, we assessed the same traits for heterospecific congeners which are not present in the archipelago, but are present elsewhere in the world. Here we report that traits with higher frequencies among colonizing aphid species are: small apterae size, broad host range, anholocycly (i.e., permanent parthenogenesis), and presence in continental USA. Small aphids arriving from the mainland US and capable of feeding on numerous plant species may be intercepted less often by plant protection agents. It is also likely that asexually reproducing species are well suited to the Hawaiian subtropical climate, thereby eliminating the need for sexual phases and egg-laying for overwintering. By understanding the traits that enable aphids to successfully colonize remote islands, it is our hope that plant protection efforts may be enhanced, thereby reducing damage to native ecosystems.

Keywords Aphid · Aphididae · Congener · Hawaii · Homoptera · Introduced species · Invasive species · Life history · Non-indigenous species

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Introduction

The introduction of, or colonization by, species into regions that they did not previously occupy is increasingly recognized as a key threat to biodiversity (Mack et al. 2000; Clavero and Garcia-Berthou 2005). Free from natural enemies, fundamental life history variables such as population growth rate and survivorship are often enhanced, resulting in dynamics unlike those observed in the species' native ranges (Jeffries and Lawton 1984; Torchin et al. 2003; Stastny et al. 2005). As a result, organisms intentionally or unintentionally transferred from one area to another may become invasive, thereby causing large-scale economic and (or) ecological damage (Elton 1958; Simberloff 1996; Vitousek et al. 1996).

The negative effects of species invasions are even more pronounced in small and isolated regions, such as island habitats (Loope et al. 1988; Nafus 1993; Gillespie and Roderick 2002). In these dispersal-limited systems, the population growth of invading species can result in high levels of abundance and, hence, increased damage. On the Hawaiian Islands, for example, species introductions have devastated the native fauna and flora (Vitousek et al. 1987; Sax et al. 2002). It is estimated that these introductions have caused the extinction of 10% of the native flora (Vitousek et al. 1987) and half of the native bird species (Banko et al. 2001; Scott et al. 2001). Over 3,000 arthropod species are believed to have been introduced into Hawaii (Howarth and Ramsay 1991; Miller and Eldredge 1996). Approximately 20 arthropods species are introduced into the Islands each year, with about half becoming invasive (Beardsley 1979).

Plant-feeding Homoptera, such as aphids, can be highly problematic when introduced into island habitats (Pike et al. 2000; Teulon and Stufkens 2002). Even though not a single aphid species is indigenous to Hawaii (Zimmerman 1948), at least 96 species can now be found on one or more of the Islands (Messing, unpubl). Several of these introduced species have become invasive, feeding on agricultural plants (e.g., *Patchiella reaumuri*), horticultural plants (e.g., *Pentalonia nigronervosa*), native plants (e.g., *Aphis spiraecola*), or all three types (e.g., *Aphis gossypii*) (Zimmerman 1948; Messing and Klungness 2001). Aphids cause direct feeding damage, but more importantly, they may also transmit both persistent and non-persistent plant viruses (Ng and Perry 2004). Aphids vector many viral diseases in Hawaii, such as banana bunchy top virus, cucumber mosaic virus, watermelon mosaic virus, zucchini yellow mosaic virus, and papaya ring spot virus (Cho et al. 1991; Ullman et al. 1991). This latter virus, for example, decreased papaya production in Hawaii by ca. 40% between 1993 and 1997 (Messing and Klungness 2001). The degree to which viruses impact native Hawaiian plant populations, however, is unknown.

Here, we attempt to identify the traits that have enabled aphids to successfully colonize the Hawaiian Islands. That is, are there common traits among this diverse group of aphids that have enabled them to successfully colonize the archipelago? In this case, it is not possible to compare the differences and similarities between native and introduced species (e.g., Williamson and Fitter 1996), as there are no native aphids in the Islands (Zimmerman 1948). It can also be difficult to objectively determine which species are invasive versus non-invasive introduced species (e.g., Kolar and Lodge 2001), as this can differ both spatially and temporally. One powerful comparative approach, however, is to directly contrast trait values for introduced species with trait values of non-colonizing congeners (National Research Council 2002). By contrasting introduced species trait values to those of a ''congeneric baseline'', it is possible to determine specific characteristics which may enhance the ability of particular species to colonize novel habitats (National Research Council 2002).

To identify the traits that have enabled some aphid species to colonize the Hawaiian Islands, we compiled a list of nine morphological and ecological traits which could be reasonably expected to contribute to the successful introductions. These quantitative and qualitative traits were assessed for species present on one or more of the Hawaiian Islands, and for congeners which have not invaded the archipelago, but are present elsewhere in the world (see Materials and methods for details regarding the congener selection procedure). By contrasting trait values of introduced aphid species against trait values of aphids distributed throughout the world (i.e., a null model), it is possible to identify the particular traits leading to colonization success. Once traits enhancing colonization have been identified, they may help to focus existing control efforts, as well as provide insights into fundamental aspects of invasion biology.

Materials and methods

Our database consisted of 174 aphid species; 96 introduced species and 78 congeners which are not present on the Islands (data set available as Appendix, Table 1). In this paper, we define an ''introduced'' species as one that is regularly

present on one or more of the Hawaiian Islands. Heterospecific congeners were selected for the analysis by randomly choosing (random generation; JMP IN 5.1, SAS Institute 2005), from generic pools, similar numbers of species occurring elsewhere in the world for which detailed information was available. Introduced species were not paired with congeners from their native regions, due to the lack of available data. Even when using a worldwide distribution, data for an equal number of introduced and non-introduced species were not always possible to obtain because: (1) some species present in Hawaii are of monospecific genera (e.g., *Hysteroneura setariae*, *P. reaumuri*, *Rhodobium porosum*), and (2) the biology of many aphid species, apart from those species of economic importance, is little known (Blackman and Eastop 2000).

For our analysis, we used information from the extensive compilations of Blackman and Eastop (1994, 2000). Information was assembled for the following morphological variables:

(1) Average apterae (i.e., unwinged) body size [0.40–5.40 mm]. Body size has previously been shown to be important for arthropod colonization of novel environments (Lawton and Brown 1986). For example, ant species with smaller body sizes are more likely to be successful colonists (Passera 1994; Lester 2005), possibly because they can occupy uninhabited ecological niches (Farji-Brener et al. 2004). It is also feasible that smaller sized individuals more frequently escape detection at points of entry into the Islands.
(2) Average alatae (i.e., winged) body size [1.35–3.30 mm]. Increased dispersal ability has frequently been noted to improve the chances of successful colonization (Moyle 1986; O'Connor 1986). For aphids, larger dispersal morphs may be able to disperse further distances to find suitable host plants.
(3) Average chromosome number [6–26].
(4) Number of karyotypes, $2n$[1–6]. It has been suggested that there may be a relationship between chromosome number and colonization success; such as has been commonly observed in plants (i.e., polyploidy and hybridization) (Ellstrand and Schierenbeck 2000; Lee 2002; Verlaque et al. 2002). The importance of polyploidy and hybridization for the success of animal populations is just starting to be explored (Delmotte et al. 2003; Comai 2005). By assessing both chromosome number and the number of karyotypes in different aphid populations, it is possible to make a preliminary assessment of the importance of this variable.

Information was also compiled for the following ecological variables:

(5) Host range [0–5; one species, multiple species, one genus, multiple genera, one family, and multiple families]. It is plausible that aphids with wider host ranges could more easily colonize novel environments (Teulon and Stufkens 2002). With wider host ranges, newly arriving species would have an increased chance of finding suitable host plants on which to feed.
(6) Feeding site [0–1; below versus above ground]. Aphids may be more likely to enter the islands if undetected, for example, when feeding on inconspicuous plant parts such as roots. Thus, there may be a larger number of root-feeding aphids in Hawaii.
(7) Anholocycly/holocycly (i.e., degree of parthenogenesis) [0–2; strictly anholocyclic (i.e., permanently parthenogenetic), anholocyclic and holocyclic populations known, strictly holocyclic (i.e., an obligate sexual phase)]. Sexually reproducing organisms may be more successful in colonizing novel environments, as genetic recombination can produce at least some adaptive genotypes/phenotypes (Sakai et al. 2001). Thus, aphids with a holocycle (i.e., sexually reproducing species) may be more likely to adapt to novel environments.
(8) Monoecy/heteroecy (i.e., degree of host alternation) [0–2; strictly monoecious (i.e., no host alternation), monoecious and heteroecious populations known, strictly heteroecious (i.e., obligate host alternation]. Monoecious (i.e., non-host alternating) aphid species may be better able to survive in new environments than are heteroecious

(i.e., host alternating) species. Heteroecious aphids must find two suitable host plants, often of different plant families, to complete their lifecycle while monoecious aphids can complete their lifecycle on just one plant species (Dixon 1998).

(9) Present in continental USA [0–1; no versus yes]. The Hawaiian Islands receives more shipments of agricultural and horticultural products from the continental United States than any other country; ca. 75% of the annual shipping tonnage (State of Hawaii 2005). Accordingly, we assessed whether species present in the continental US are more likely to be present on the archipelago, compared to aphids not present on the mainland.

It is important to note that while climate has been shown to be important for the success of many introductions (Blackburn and Duncan 2001; Kolar and Lodge 2002; Forsyth et al. 2004), we did not take climate directly into account in our analysis. With regard to temperature, there is very little fluctuation from season to season in Hawaii (Zimmerman 1948). Thus, aphids would not be exposed to extreme heat or cold upon being introduced, and it is therefore unlikely to have a large effect on aphid introduction success (Zimmerman 1948). Precipitation, while increasing during the winter months, is highly variable both among and within islands (Roy and Balling 2004); ranging from near desert conditions to wet, swamp-like areas.

Statistical analyses

Complete information for all variables, for all species ($n = 174$), was not available. Consequently, we initially ran univariate analyses for each of the nine variables. Morphological variables were: average apterae body size ($n = 145$), average alatae body size ($n = 81$), average chromosome number ($n = 129$), and number of karyotypes ($n = 129$). As these were all continuous variables and the dependent variable was dichotomous (aphid species present in Hawaii [0–1; no versus yes]), logistic regression analyses were conducted, using JMP IN 5.1 (SAS Institute 2005). Ecological variables were: host range ($n = 166$), feeding site ($n = 136$), anholocycly/holocycly ($n = 148$), monoecy/heteroecy ($n = 145$), and presence in continental USA ($n = 166$). As these were all discrete variables and the dependent variable was also discrete, and dichotomous (aphid species present in Hawaii [no versus yes]), Chi-square analyses were performed (SAS Institute 2005).

Variables found to be significant in the univariate analyses were combined into a single multivariate model. Mixed model, stepwise logistic regression was conducted to determine the best fitting model; thereby permitting any significant correlations between the different variables to be simultaneously assessed (Zar 1984). The final multivariate logistic regression model included the variables: average apterae body size, host range, anholocycly/holocycly, and presence in continental USA (complete model, $n = 131$). As in the univariate analyses, the dependent variable was: aphid species present in Hawaii (no versus yes). By incorporating the congeneric baseline directly into the analysis (i.e., as the dependent variable level ''no''), it is possible to objectively identify traits, of greater frequency, shared by species present in Hawaii.

Results

In general, morphological variables were not good predictors of successfully colonizing species. The only important morphological variable was average apterae body size ($x_1^2 = 4.62$, $P = 0.032$). Introduced species were of smaller size, on average, than species not present in the Islands (Fig. 1). Winged (dispersal) morphs, however, were similar in size among introduced and non-introduced species ($x_1^2 = 0.13$, $P = 0.72$). Similarly, neither average chromosome number ($x_1^2 = 1.05$, $P = 0.31$) nor number of karyotypes ($x_1^2 = 0.48$, $P = 0.49$) were good predictors of colonizing species.

Introduced aphid species, however, had many ecological traits in common. For instance, aphids with broader feeding ranges were more likely to be present on the archipelago, than those which feed on a limited number of species ($x_5^2 = 34.01$, $P < 0.0001$; Fig. 2). Degree of anholocycly/holocycly ($x_2^2 = 37.15$, $P < 0.0001$) and monoecy/

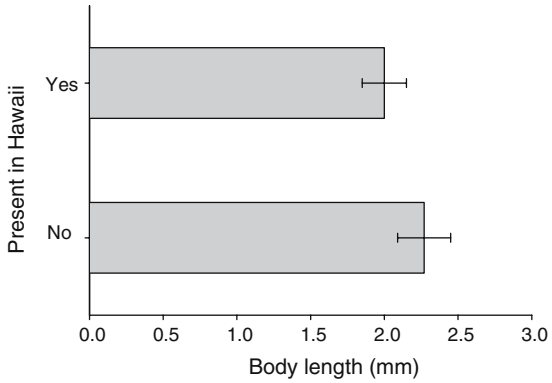

Fig. 1 Average size of apterous, adult female aphid species present in the Hawaiian Islands, as compared to heterospecific congeners ($n = 70$ and 75, respectively). Bars indicate 95% confidence intervals

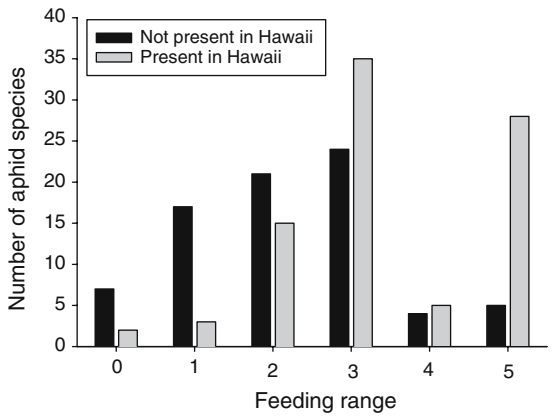

Fig. 2 Feeding ranges exhibited by colonizing and non-colonizing aphid species ($n = 78$ and 88, respectively). Feeding ranges represent: 0—one species, 1—multiple species, 2—one genus, 3—multiple genera, 4—one family, and 5—multiple families

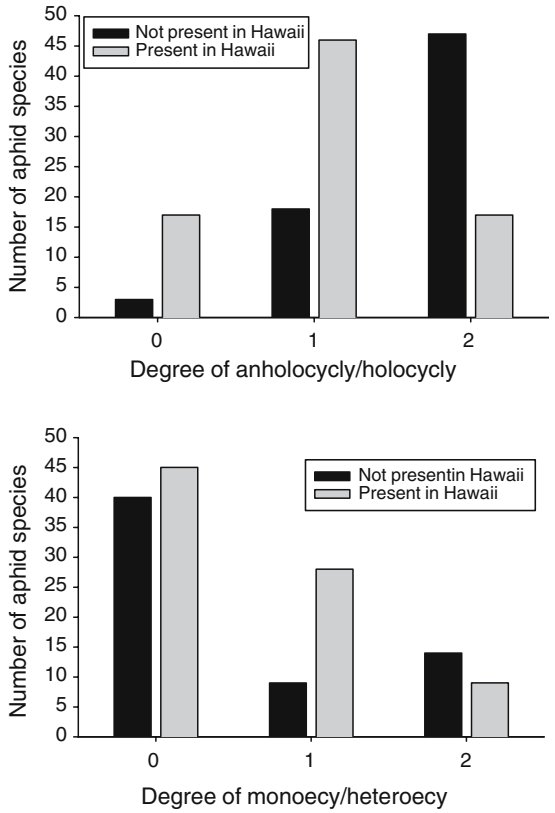

Fig. 3 Aphid presence as a factor of: (**a**) anholocycly/holocycly (levels represent: 0—strictly anholocyclic [i.e., permanently parthenogenetic], 1—holocyclic with anholocyclic populations known, and 2—strictly holocyclic [i.e., an obligate sexual phase]; $n = 68$ colonizing, 80 non-colonizing), and (**b**) monoecy/heteroecy (levels represent: 0—strictly monoecious [i.e., no host alternation], 1—heteroecious with monoecious populations known, 2—strictly heteroecious [i.e., obligate host alternation]; $n = 63$ colonizing, 82 non-colonizing)

heteroecy ($x_2^2 = 9.13$, $P = 0.010$) were also found to be significant. Aphids colonizing the Islands were more likely to be either strictly or facultatively parthenogenetic, rather than having a sexual phase (Fig. 3a). Similarly, aphids known to complete their lifecycle on just one plant species (i.e., monoecious aphid species) are more likely to be present on the Islands compared to heteroecious aphid species (Fig. 3b). A strong relationship between aphid presence on the mainland and aphid presence in Hawaii was also found to exist. Aphids present in the continental US are more likely to have been introduced into Hawaii, than species absent from the mainland ($x_1^2 = 33.01$, $P < 0.0001$; Fig. 4). Feeding site was the only non-significant ecological variable ($x_2^2 = 1.80$ $P = 0.41$). Root-feeding species are uncommon among both introduced and non-introduced species.

When all significant variables were simultaneously entered in a multivariate model, four of the five variables remained significant. Traits promoting aphid colonization of the Hawaiian Islands were: small average apterae size ($x_1^2 = 3.81$, $P = 0.051$), wide host feeding range ($x_5^2 = 12.24$, $P = 0.032$), anholocycly ($x_2^2 = 18.86$, $P < 0.0001$), and presence on mainland USA ($x_1^2 = 11.57$, $P = 0.0007$); (overall model:

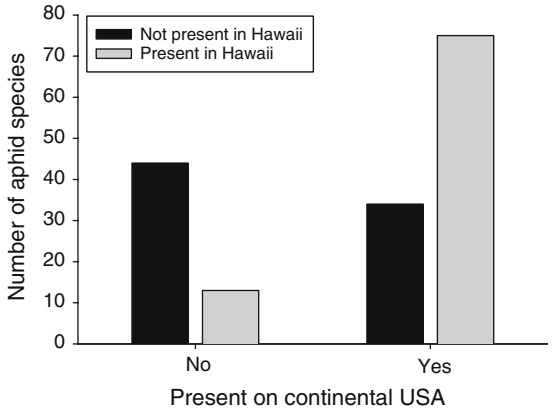

Fig. 4 Numbers of aphids present versus not present in the Hawaiian Islands, according to species presence in the continental United States (n = 78 and 88, respectively)

$x_9^2 = 75.05$, $P < 0.0001$; $r^2 = 0.41$). Only monoecy/heteroecy became non-significant in the stepwise selection procedure. As there was low correlation between significant traits (0.03–0.40), characteristics common to aphid species in Hawaii do not simply reflect traits exhibited by species in the continental US (i.e., the results are not due to a proximity effect).

Discussion

Biological homogenization, through both purposeful and accidental introductions of exotic species, is a threat to virtually every known ecosystem (Mack et al. 2000; Clavero and Garcia-Berthou 2005). Identifying the traits common to successfully colonizing species is a useful endeavor as it may: (1) focus existing control efforts, when resources for such projects are limited, (2) increase our predictive ability for identifying which species may next invade particular habitats (Sakai et al. 2001), and (3) offer insights into invasibility as a general phenomenon. Here we were able to identify four traits of greater frequency among aphid species colonizing the Hawaiian Islands, than in species present elsewhere in the world. These traits are: small apterae size, broad host range, anholocycly (i.e., the ability to persist as permanently parthenogenetic populations), and presence in continental USA.

Species colonizing the Islands were found to be of smaller (apterae) size. It has been suggested that smaller insects can more easily occupy uninhabited ecological niches (Farji-Brener et al. 2004). It is also possible, however, that this trait is correlated with other traits contributing to invasive success, such as high intrinsic rates of increase and rapid maturity (Crawley 1986). Conversely, smaller sized individuals may simply be intercepted less often by plant protection agents. Many, if not all, of these traits may act in concert to promote aphid success (Lawton and Brown 1986). Interestingly, winged (alatae) morphs did not show a similar trend, even though good dispersal ability is frequently cited as a key trait of invasive species (Moyle 1986; O'Connor 1986). It is likely that the importance of dispersal may depend on the scale, and temporal sequence, at which the colonization event is being viewed (Davis and Thompson 2000). Dispersal ability may be very important for species colonizing novel environments though ''natural'' dispersal mechanisms (Levine 2000). Dispersal may not be as important a trait, as say escaping detection, for organisms being introduced by humans into novel habitats. Once the species enter the archipelago, however, dispersal may be of greater importance depending on habitat characteristics (e.g., plant distribution; Smith et al. 1999).

In Hawaii, there are a disproportionate number of aphid species that feed on multiple plant families. Successful colonization would be anticipated with increased feeding range, as it would be easier to find suitable host plant species in the novel environment (Blackman and Eastop 2000; Teulon and Stufkens 2002). As well as feeding on a wide range of plants, aphids present on the archipelago transmit more plant viruses, on average, than those not present. The ''average'' aphid in Hawaii transmits 12 ± 3 viruses (range 0–100), while those not present only transmit 2 ± 1 viruses (range 0–12). While we are making progress in assessing the problems associated with virus transmission in agricultural plant species (e.g., papaya, banana, etc.), the effect of plant viruses in native plant populations is unknown (Teulon and Stufkens 2002). Aphids are known to feed on at least 60 native Hawaiian plant species

(Messing, unpubl.), though degrees of feeding damage and virus transmission in these taxa are currently unknown.

Most surprisingly, anholocyclism was more prevalent among introduced species than was holocyclism. While sexually reproducing species do require mates, they generally have a key advantage when colonizing novel environments, as natural selection is dependent on the degree of genetic variation in a population (Fisher 1930). A common trait among introduced and especially invasive plants, however, is the ability to propagate asexually (Baker 1965, 1974; Reichard and Hamilton 1997; Daehler 1998). Thus, perhaps invasive species analyses should not be viewed as an invasive animal versus invasive plant dichotomy, but rather, as asexual versus sexual organisms. A wealth of information could be obtained through a better understanding of how organisms with asexual, as opposed to sexual, reproduction cope with selective pressures in novel environments. For example, it could be predicted that clonal organisms would more rapidly colonize areas with little environmental heterogeneity. Meanwhile, if conditions change radically from year to year, asexual organisms would be selected against, due to their inability to produce new, adaptive genotypes/phenotypes (Lee 2002).

One key trait of many successfully colonizing species is propagule pressure. The chances of successful colonization increases as individuals are repeatedly introduced into a novel environment (Duncan 1997), as multiple introductions mitigate the stochastic effects that frequently cause invasions to fail. For sexually reproducing species, numerous introductions introduce additional genetic variation (Sakai et al. 2001), which increases the chances of adaptive genotypes/phenotypes being produced through genetic recombination. As asexually reproducing organisms do not undergo recombination, assessing the degree of genetic diversity within and between populations (Lee 2002) may provide important information as to the frequency of species introductions (Sakai et al. 2001).

A strong relationship exists between the presence of aphids in the continental United States and their presence in the Hawaiian Islands. Improved control efforts are desperately required, at different regional scales, to reduce the rate at which species are being introduced into the Islands (Daehler et al. 2004). Plant and produce shipments entering the islands are regularly inspected, but it is impossible for plant protection agents to inspect all cargo (Hawaii DOA 2002). Furthermore, if aphids are detected, it may be difficult for ''frontline'' personnel to identify the pest organism to species, especially for immature morphs (Hawaii DOA 2002). Without knowing the spatial and temporal distribution of aphid introductions into the Islands, it can only be assumed that, like other species, the rate of colonization is dependent on the introduction rate (Barrett and Husband 1990). Clearly, improved and more focused screening procedures, at multiple levels, are required if species introductions are to be mitigated (Daehler et al. 2004).

Here, we identified the traits shared by aphid species colonizing the Hawaiian Islands, in contrast to a congeneric baseline, i.e., traits common to species distributed elsewhere in the world. It is important to note, however, that Hawaii is not one continuous landmass, but a series of individual islands. Distinctly different habitats can be found both within and between islands. Future research should attempt to determine whether any traits, or trait deviations, may be more prevalent on certain islands or in particular habitat types. It is not possible to accurately assess this question at the current time, as species' detections on individual islands may be biased due to differences in collection efforts.

Current estimates suggest that 20 exotic arthropod species are introduced into the Hawaiian Islands each year (Beardsley 1979). While the massive ecological destruction caused by some introduced species is obvious (e.g. pigs, goats, fowl; Scott et al. 2001), invertebrate introductions may be less visible but no less important. A better understanding of the traits that make species successful colonists on remote island chains may be useful for helping to focus plant protection efforts in key areas, to help halt the destruction of island ecosystems.

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Appendix

Table 1 Aphid data set used for the statistical analyses. For explanations of trait values, please see "Materials and methods" section

Genus	Species	Average apterae size	Average alate size	Average chromosome number	Number of karyotypes 2n	Host range	Feeding site	Anholocycly/ Holocycly	Monoecy/ Heteroecy	Present in continental USA	Present in Hawaii
Acyrthosiphon	gossypii	3.15	2.80	6	1	4		1	1	0	0
Acyrthosiphon	ilka	2.25				5				0	0
Acyrthosiphon	lactucae	2.30	2.35	17	2	1	2	2	0	1	0
Acyrthosiphon	kondoi	2.50	2.15	10	1	3	2	1	0	1	1
Acyrthosiphon	malvae	2.10	2.25	10	1	2	2	2	0	0	1
Acyrthosiphon	pisum	3.45	3.30	8	1	3	2	1	0	1	1
Aphis	farinosa	2.05		6	1	2	2	2	0	1	0
Aphis	forbesi	1.40	1.55	8	1	2	1	2	0	1	0
Aphis	grossulariae	1.85	2.00			3	2	2	1	0	0
Aphis	idaei	1.50	1.50	8	1	1	2	2	0	0	0
Aphis	ilicis	2.30		8	1	0	2	2	0	0	0
Aphis	illinoiensis	1.85	1.65			1	2	1	1	1	0
Aphis	maidiradicis			8.5	2	3	0	2	0	1	0
Aphis	neogilletei	1.20		8	1	0	2	2	0	1	0
Aphis	pomi	1.75	1.80	8	1	3	2	2	0	1	0
Aphis	ruborum	1.65	1.60	8	1	2	2	2	0	0	0
Aphis	schneideri	1.70	1.90			1	2	2	0	0	0
Aphis	coreopsidis	1.65				5	2	1	1	1	1
Aphis	craccivora	1.80	1.75	8	1	5	2	1	1	1	1
Aphis	fabae	2.30	1.95	8	1	5	2	2	2	1	1
Aphis	gossypii	1.35	1.45	8	1	5	2	1	1	1	1
Aphis	middletonii										1
Aphis	nasturtii	1.65	1.60	8	1	5	2	1	1	1	1
Aphis	nerii	2.05	2.05	8	1	5	2	0	0	0	1
Aphis	oenotherae			8	1	3	2	2	1	1	1
Aphis	oestlundi	1.90				0	2	2	0	1	1
Aphis	sedi										1
Aphis	spiraecola	1.70	1.70	8	1	5	2	1	1	1	1
Aulacorthum	linderae	2.25				0	2	2	0	0	0
Aulacorthum	magnoliae	2.75		12	1	5	2	1	1	0	0
Aulacorthum	circumflexum	1.90	2.00	8	1	5		0	0	1	1
Aulacorthum	solani	2.40	2.40	10	1	5	1	1	0	1	1
Brachycaudus	cardui	2.25	1.95	11	2	3	2	2	2	1	0
Brachycaudus	helichrysi	1.45	1.65	12	1	5	2	1	1	1	1
Brevicoryne	brassicae	2.10	2.20	16	1	4	2	1	1	1	1
Capitophorus	carduinus	1.90		16	1	1		2	0	0	0
Capitophorus	horni	2.05		16	1	1		2	0	0	0

Capitophorus	elaeagni	2.20	1.95	16	1	3	2	2	2	1	1
Capitophorus	hippophaes	1.80		10	1	3		2	2	1	1
Cavariella	konoi	2.40		8	1	3	2	2	2	1	0
Cavariella	aegopodii	1.80	2.05	10	1	4	2	1	1	1	1
Cerataphis	bambusifoliae	2.00				3	2			0	0
Cerataphis	brasiliensis	1.40	1.65	18	1	1	2	2		0	0
Cerataphis	formosana	2.10				2	2			0	0
Cerataphis	fransseni	1.30	1.40			4	2		2	0	1
Cerataphis	lataniae	1.09				3				0	1
Cerataphis	orchidearum	1.30	1.50	17	2	4		0	0	1	1
Cinara	juniperi	2.80		12	1	0	2	1	0	1	0
Cinara	maritimae	3.35		16	1	2	2	1	0	0	0
Cinara	pilicornis	3.40		12	2	2	2	2	0	1	0
Cinara	pinea	4.15		12	3	1	2	2	0	1	0
Cinara	pruinosa	3.70		10	1	2	1	1	0	1	0
Cinara	atlantica	2.75		10	1	2	2	1	0	1	1
Cinara	cupressi	2.85	2.85	12	1	2	2	1	0	1	1
Cinara	fresai	3.20		13	1	3	2	1	0	1	1
Cinara	tujafilina	2.60		12	1	3	1	1	0	1	1
Cinara	watsoni	3.50				2	2	2	0	1	1
Coloradoa	rufomaculata	1.35	1.35	13	2	0	2	1	0	1	1
Dysaphis	devecta	2.10	2.05			2	2	2	0	0	0
Dysaphis	foeniculus	1.95	2.05	12	1	3	1	0	0	1	0
Dysaphis	pyri	2.45	1.90	12	1	3	2	2	2	0	0
Dysaphis	apiifolia	2.00	1.95	12	1	3	1	1	1	1	1
Dysaphis	aucupariae			12	1	1	2	1	1	1	1
Dysaphis	tulipae	2.00	1.90	11.5	2	5	1	0	0	1	1
Ericaphis	gentneri			20	6	3		2	0	1	0
Ericaphis	fimbriata					2				1	1
Eriosoma	lanuginosum	2.35	2.60	10	1	2	1	2	2	0	0
Eriosoma	lanigerum	1.90	2.05	12	1	3	1	0	0	1	1
Eulachnus	pumilae	2.65				1	2	2	0	0	0
Eulachnus	rileyi	2.40		8	1	1	2	1	0	1	1
Greenidea	ficicola	1.85		22	1	2	2	0	0	0	0
Greenidea	formosana	2.25		12.5	4	3	2			0	1
Hayhurstia	atriplicis										1
Hyadaphis	foeniculi	1.80	1.80	13	2	3	2	2	2	1	0
Hyadaphis	coriandri	1.70	1.70	13.5	2	3	2	1	1	1	1
Hyperomyzus	pallidus	2.55	2.50			1	2	2	2	1	0
Hyperomyzus	rhinanthi	2.65	2.35	12	1	1	2	2	2	0	0
Hyperomyzus	carduellinus										1
Hyperomyzus	lactucae	2.35	2.35	12	1	3	2	1	1	1	1
Hysteroneura	setariae	1.80		12	1	5	2	1	1	1	1
Idiopterus	nephrelepidis										1
Illinoia	alni	2.80		10	1	0	2	2	0	1	0

Table 1 continued

Genus	Species	Average apterae size	Average alate size	Average chromosome number	Number of karyotypes 2n	Host range	Feeding site	Anholocycly/ Holocycly	Monoecy/ Heteroecy	Present in continental USA	Present in Hawaii
Illinoia	azaleae	2.05		10	1	3	2	0	0	1	1
Lipaphis	erysimi	1.90	1.80	9	3	3	2	1	0	1	1
Macrosiphoniella	oblonga	4.00		12	1	3	2	2	0	0	0
Macrosiphoniella	sanborni	1.65	2.20	12	1	3	2	0	0	1	1
Macrosiphum	albifrons	3.85		10	1	2	2	1	0	1	0
Macrosiphum	pallidum	3.35		10	1	5		2	2	1	0
Macrosiphum	euphorbiae	2.65	2.55	10	1	5	2	1	1	1	1
Macrosiphum	rosae	2.65	2.80	10	1	5	2	1	1	1	1
Melanaphis	pahanensis	1.95				4	2		2	0	0
Melanaphis	pyraria	1.70		8	1	3	2	2	2	0	0
Melanaphis	bambusae	1.10		9	2	3			1	1	1
Melanaphis	sacchari	1.55	1.55	8	1	3	2	1	0	0	1
Metopolophium	festucae	1.80	2.00	16	1	3	2	1	0	1	0
Metopolophium	dirhodum	2.25	2.45	18	1	3		1	1	1	1
Myzus	cerasi	2.05	1.75	10	1	3	2	2	1	1	0
Myzus	ligustri	1.25		12	1	1	2	2	0	1	0
Myzus	mumecola	2.20		12	1	1	2	2	2	0	0
Myzus	hemerocallis			10	2	2	2			1	1
Myzus	ornatus	1.35	1.65	12	1	5	2	0	0	1	1
Myzus	persicae	1.65	1.65	12	1	5	2	1	1	1	1
Nasonovia	cynosbati			10	1	3		1	0	1	0
Nasonovia	ribisnigri	2.00	2.00	12	1	5	2	2	2	1	1
Neophyllaphis	brimblecombei	1.75		26	1	1		2		0	0
Neophyllaphis	grobleri	1.75		18	1	2		2		0	0
Neophyllaphis	araucariae	1.30		18	1	2	2	1	0	1	1
Neophyllaphis	podocarpi	2.20		25	2	2	2	2	0	1	1
Neotoxoptera	formosana	1.95		12	1	1	1	0	0	1	1
Neotoxoptera	oliveri	1.55		12	1	5	2	0	0	1	1
Neotoxoptera	violae										1
Ovatus	malisuctus	1.35		12	1	1	2	2	0	0	0
Ovatus	crataegarius	1.50	1.80	12	1	5	1	1	1	1	1
Patchiella	reaumuri		2.40			3	1	1	1	0	1
Pemphigus	dorocola		2.10	20	1	1	2		2	0	0
Pemphigus	populitransversus		1.85	20	1	3	1	1	1	1	1
Pentalonia	kalimpongensis	1.70				1		1		0	0
Pentalonia	nigronervosa	1.45	1.45	14	1	5	2	1	0	1	1
Pleotrichophorus	chrysanthemi					2	2	0	0	1	1
Pleotrichophorus	glandulosus					2		2		1	1
Reticulaphis	mirabilis	0.40				2	2			0	0

Reticulaphis	distylii	0.70	1.70			3	2	2	2	0	1
Rhodobium	porosum	1.85	1.80	14	1	2	2	1	0	1	1
Rhopalosiphoninus	staphylaeae	1.95	1.95	10	1	5	0	1	1	1	0
Rhopalosiphoninus	latysiphon	1.95	1.95	7	1	3	0	0	0	1	1
Rhopalosiphum	cerasifoliae	2.25		8	1	3	2	1	1	1	0
Rhopalosiphum	insertum	2.00		10	1	3	2	2	2	1	0
Rhopalosiphum	padiformis	1.80		10	1	3	2	2	2	1	0
Rhopalosiphum	rufulum	2.25		8	1	2		2	1	0	0
Rhopalosiphum	maidis	1.65	1.65	9	3	5	2	1	1	1	1
Rhopalosiphum	nymphaeae	2.10		8	1	3	2	2	2	1	1
Rhopalosiphum	padi	1.80	1.80	8	1	5	2	1	1	1	1
Rhopalosiphum	rufiabdominalis	1.70	1.70	8	1	5	1	1	1	1	1
Schizaphis	graminum	1.70	1.70	8	1	3	2	1	0	1	0
Schizaphis	rotundiventris	1.45	1.45			5	2	1	1	1	1
Semiaphis	dauci	1.45				0	2	1	0	0	0
Semiaphis	heraclei			8	1	3	2	2	2	0	1
Sipha	glyceriae	1.95		12	1	5	2	2	0	1	0
Sipha	flava	1.65	1.65			5	2	1	0	1	1
Siphonatrophia	cupressi	1.35				3	2	2	0	1	1
Sitobion	africanum	2.35				3		2		0	0
Sitobion	cornifoliae	2.20				2	2	2	0	0	0
Sitobion	graminis	2.35		18	1	3				0	0
Sitobion	nigrinectarium	2.35		18	1	3				0	0
Sitobion	rosaeiformis	2.70		18	1	2	2	1	0	0	0
Sitobion	fragariae	2.30	2.50	18	1	5	2	2	2	1	1
Sitobion	ibarae	2.60	2.60			2	2	1	0	0	1
Sitobion	luteum	1.70		12	1	3	2	0	0	1	1
Sitobion	miscanthi	2.35	2.50	19	3	3	2	1	0	0	1
Sitobion	phyllanthi	1.80				2	2			0	1
Takecallis	arundicolens		2.30	18	1	3	2	1		1	0
Takecallis	arundinariae		2.05	18	1	3	2	0	0	1	1
Tetraneura	ulmi	2.25	2.10	14	1	4	1	1	1	1	0
Tetraneura	nigriabdominalis	2.00	1.90	16.5	6	3	1	1	1	1	1
Therioaphis	luteola					0		2	0	0	0
Therioaphis	trifolii	1.80	1.80	16	1	3		1	0	1	1
Tinocallis	saltans		1.80	16	1	2		2		1	0
Tinocallis	kahawaluokalani		1.50	6	1	2	2	2	0	1	1
Toxoptera	schlingeri	1.70				2				0	0
Toxoptera	aurantii	1.55	1.55	8	1	5	2	0	0	1	1
Toxoptera	citricidus	1.95	1.95	8	1	5	2	1	0	1	1
Toxoptera	odinae	1.85	1.85	8	1	5	2	0	0	0	1
Tuberolachnus	sclerata	4.70				2	2			0	0
Tuberolachnus	salignus	5.40		20	1	3	2	0	0	1	1
Uroleucon	cichorii	3.35		12	1	3		2	0	0	0

Table 1 continued

Genus	Species	Average apterae size	Average alate size	Average chromosome number	Number of karyotypes 2n	Host range	Feeding site	Anholocycly/ Holocycly	Monoecy/ Heteroecy	Present in continental USA	Present in Hawaii
Uroleucon	compositae	3.00		12	1	4	2	0	0	0	0
Uroleucon	jaceae	3.00		12	1	2	2	1	0	0	0
Uroleucon	rudbeckiae			12	1	2	2	2	0	1	0
Uroleucon	erigeronense										1
Uroleucon	illini					2		2	0	1	1
Uroleucon	pseudambrosiae					3			0	1	1
Uroleucon	sonchi	3.70				3		1	0	1	1
Vesiculaphis	caricis										1
Wahlgreniella	nervata	1.95		12	1	3	2	1	1	1	1

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