

Comparison of insect invasions in North America, Japan and their Islands

Takehiko Yamanaka · Nobuo Morimoto · Gordon M. Nishida ·
Keizi Kiritani · Seiichi Moriya · Andrew M. Liebhold

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Abstract Among the various animal taxa that are have established outside their native ranges, invasions by insect species are the most numerous worldwide. In order to better understand the characteristics of insect species that make them more invasion prone, the characteristics of habitats that make them more susceptible to invasions and to understand the pathways that facilitate invasions, we compared the compositions of the native and non-native insect communities among five Pacific regions: North America, the Hawaiian Islands, mainland Japan, Ogasawara and Okinawa Islands. These regions comprise both island and mainland habitats and have historically been subjected to varying activities affecting insect

movement. Among the five regions, the oceanic islands, Hawaii and Ogasawara, appear to be the most prone to invasions. Specific insect orders such as the Blattodea, Siphonaptera, Thysanoptera and Hemiptera are disproportionately represented in the non-native insect fauna compared to the native fauna in all regions. A large fraction of the non-native insect species in North America (9.4 %) and Hawaii (13.2 %) were introduced intentionally, as part of biological control programs, which were historically pursued more vigorously in those regions than in Japan. Dominance by individual insect orders within invaded communities can be explained by the historical importance of invasion pathways, some of which were likely similar among regions (e.g., movement on live plants), while other pathways appear more region specific. Translocation of insect species among world regions appears to be affected by climatic similarity,

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T. Yamanaka (✉)
Natural Resources Inventory Center, National Institute for
Agro-Environmental Sciences, 3-1-3 Kannondai,
Tsukuba, Ibaraki 305-8604, Japan
e-mail: apple@affrc.go.jp

N. Morimoto
Nasu Research Station, NARO Institute of Livestock and
Grassland Science, 768 Senbonmatsu, Tochigi 329-2793,
Japan

G. M. Nishida
University of California, Berkeley, 1170 Valley Life
Sciences Building, Berkeley, CA 94720-4780, USA

K. Kiritani
1020-292 Futo, Itou, Shizuoka 413-0231, Japan

S. Moriya
National Agricultural Research Center, Tsukuba,
Ibaraki 305-8666, Japan

A. M. Liebhold
USDA Forest Service, Northern Research Station, 180
Canfield St., Morgantown, WV 26505, USA

host plant similarity and propagule pressure, though these effects are often confounded.

Keywords Biological invasion · Invasibility · Invasion pathway · Community composition · Non-native insects · Climatic similarities

Introduction

The Insecta comprise the majority of the world's animal species and thus it comes as no surprise that this class also comprises the majority of non-native animal species recorded in various parts of the world (Cox 1999; Roques et al. 2009). Examples of the large numbers of non-native insect species established among world regions include 1306 species reported in the European Union (Roques et al. 2009), 1385 species in the USA (Sailer 1978), 1585 species in New Zealand (MacFarlane et al. 2010) and 239 species in Japan (Morimoto and Kiritani 1995).

Clearly, the general problem of insect invasions is shared worldwide, but the extent to which the phenomenon is unique in each region is less clear. A simple hypothesis is that pathways driving insect invasions in each part of the world are essentially the same and there is a single pool of species, originating from the same areas, that is the source of most insect invasions worldwide. Alternatively, it is possible that insect invasions in each world region are unique with species arriving via a unique set of pathways from a unique set of geographic origins.

Analysis of the taxonomic composition and of origins invasive communities provides insight into the species characteristics that facilitate invasions as well as clues to the identity of pathways by which species arrive (e.g., Simberloff 1986). While previous region-specific analyses of invasive insect communities have been very informative, there have been no previous attempts to comprehensively compare these communities among different world regions. Here, we perform a detailed comparison of the non-native insect fauna among five regions: North America, the Hawaiian Islands, mainland Japan, the Ogasawara and Okinawa Islands, with the objective of using the taxonomic composition and world origin of these communities to draw inferences about the similarity of invasion history. By examining similarities and

differences in the non-native insect community composition among these five regions, we relate these patterns to regional habitat characteristics and historical trade practices specific to each region. The Hawaii, Ogasawara and Okinawa islands were selected for inclusion both because they are sociologically linked with North America and Japan, but as islands they may be particularly susceptible to invasions (Reaser et al. 2007).

Though several terminologies have been used to represent the character of non-nativity, e.g., invasive, alien, non-indigenous, exotic, introduced, etc., we specifically use here the term non-native because we include in our analysis damaging non-native pests, benign (non-damaging) non-native insect species, as well as intentionally introduced species.

Methods

Data preparation

We compiled comprehensive lists of non-native insect species in North America, the Hawaiian Islands, mainland Japan, Ogasawara and Okinawa Islands. The list was finally updated on 1st. June 2015 (Appendix A—see Electronic supplementary material). Our analysis of non-native insects in North America was limited to the USA and Canada due to a lack of comprehensive information about species in Mexico. The Hawaiian Islands include the Northwestern Hawaiian Islands, reaching from Nihoa to Kure. Below, we refer to the Hawaiian Islands as “Hawaii” and the islands of Okinawa (Nansei Islands) and Ogasawara (Bonin Islands) as “Okinawa” and “Ogasawara”, respectively.

We limited our compilation to include only species that are considered established in the respective regions (i.e., we did not include species that were transiently detected and for which there is no evidence of continuously reproducing populations; species that have been successfully eradicated were not included).

Information on the native range of each species was also compiled in addition to their taxonomic status. The native region was classified using Wallace's ecozone system but the Palearctic was further divided into Asia and Europe if the species' distribution was restricted to one or the other (Fig. 1). Consequently we recognized eight ecozones of origin: European



Fig. 1 Geographical ranges of the world's ecozones. These areas are slightly modified from Wallace's classification, i.e., Taiwan is classified in Indomalaya and Mexico is in Neotropic

Palaearctic, Asian Palaearctic, Indomalaya, Afrotropic, Australasia, Oceania, Nearctic and Neotropic. Some species are native to multiple ecozones. It also should be noted that Taiwan is considered part of Indomalaya and Mexico is designated Neotropic rather than North America because of a technical issue related to discrimination difficulties.

Intentionally introduced species, such as those imported as biological control agents (e.g., hymenopteran parasitoids), were included in lists though each species was classified as either intentionally or accidentally introduced using available information.

Our list of non-native insects established in North America represents an unprecedented compilation that is vastly more comprehensive than previous attempts (Sailer 1978; Kim and Wheeler 1991). It was initially based on The North American Non-Indigenous Arthropod Database (NANIAD) developed by Kim and Wheeler (1991). However, the original NANIAD database was not regularly updated, it contained many omissions, numerous errors and many species names in the list were synonyms. Therefore, we systematically checked each NANIAD entry and revised the list using several resources (Appendix A—see Electronic supplementary material). We also attempted to identify all species that were intentionally introduced. Though we were able to identify hundreds of species that were intentionally introduced to North America (e.g., as biological control agents), we believe that a large number of other species were intentionally introduced but a record of their introduction could not be found.

The list of non-native insect species established in the Hawaiian Islands is almost entirely from Nishida

(2002). We confirmed or corrected taxonomic information using several internet resources (Appendix A—see Electronic supplementary material). Species origins were checked using the resources of the Hawaiian Entomological Society.

The list of the non-native species in Japan is based on Morimoto and Kiritani (1995). Their list discriminated species established in Ogasawara and Okinawa from the other parts of Japan. The list was thus used to compile sublists of species established in mainland Japan as well as species established in Ogasawara and Okinawa. We also updated these lists using other information sources (Appendix A—see Electronic supplementary material).

Community analysis

In addition to the direct comparison of the number of non-native species with numbers of native species in each insect order, Nonmetric Multidimensional Scaling (NMDS) was employed to characterize differences among the seven communities: native and non-native communities in North America, Hawaii, mainland Japan, Ogasawara and Okinawa as well as the non-native community of all (Kenkel and Orlóci 1986). The fractional composition of each insect order was first square-root transformed to stabilize the scale effect. Following multidimensional scaling, the position of the seven communities in the space defined by two axes provided a map of the taxonomic similarity among communities and each insect order was plotted in the same two-dimensional space. The NMDS ordination was computed using the R-library vegan

in the statistical software R (Version 2.14.0, <http://www.r-project.org>).

Results and discussion

Overview

Considering that the islands comprise relatively small land areas (16638, 104 and 4648 km² for Hawaii, Ogasawara and Okinawa, respectively), their numbers of non-native insect species are remarkably high (Table 1). In fact, Hawaii and Okinawa had fairly large numbers of non-native species slightly less than those in corresponding mainland regions. Expressed as numbers of species per unit land area, Hawaii, Ogasawara and Okinawa are much more invaded, with 0.16, 1.6 and 0.080 species/km² respectively, compared with 0.00018 species/km² in North America and 0.0012 species/km² in mainland Japan.

Numbers of total non-native species among the regions (Table 1) are proportionally similar to those of native species (Table 2). Similarly, expression of numbers of native species per unit land area indicates that the densities of native species in the islands (Hawaii: 0.32 species/km², Ogasawara: 10.6 species/km², Okinawa: 1.6 species/km²) are similarly higher than in their mainland (North America: 0.0044 species/km², mainland Japan: 0.066 species/km²). The major islands in Hawaii, Ogasawara and Okinawa have climates ranging from tropical to subtropical, and this likely explains higher density of species in the islands than North America and mainland Japan, which mostly range from temperate to subarctic. Also indicative of the propensity for island invasions, the ratio of non-native to native species is highest for Hawaii (0.50), followed by Ogasawara (0.15) and lowest for the mainland Japan (0.019). The ratio in Okinawa (0.046) was similar to North America (0.044).

Table 1 Taxonomic composition (order level) of non-native insect species established in North America, Hawaii, mainland Japan, Ogasawara and Okinawa

Locality	North America	Hawaii	Mainland Japan	Ogasawara	Okinawa
Total	3540	2651	471	168	349
Coleoptera	26.8 %	21.5 %	35.5 %	28.0 %	31.8 %
Hymenoptera	22.5 %	25.5 %	11.0 %	13.7 %	12.0 %
Hemiptera	27.3 %	16.4 %	22.5 %	26.8 %	22.6 %
Diptera	8.1 %	16.3 %	8.3 %	6.5 %	5.7 %
Lepidoptera	8.2 %	7.9 %	9.6 %	7.1 %	15.8 %
Thysanoptera	2.5 %	4.3 %	4.2 %	5.4 %	4.0 %
Psocodea	1.7 %	3.4 %	2.3 %	1.2 %	0.6 %
Blattodea	1.0 %	0.8 %	1.5 %	3.6 %	2.3 %
Orthoptera	0.6 %	1.1 %	1.7 %	1.8 %	1.7 %
Siphonaptera	0.3 %	0.3 %	1.1 %	3.0 %	1.4 %
Dermaptera	0.3 %	0.5 %	—	—	—
Isoptera	0.1 %	0.3 %	1.3 %	1.8 %	0.9 %
Odonata	0.2 %	0.4 %	—	—	—
Thysanura	—	0.2 %	0.4 %	0.6 %	0.6 %
Mantodea	0.1 %	0.2 %	—	0.6 %	0.3 %
Neuroptera	0.1 %	0.3 %	0.2 %	—	—
Embiopoda	0.1 %	0.1 %	—	—	—
Strepsiptera	0.0 %	0.1 %	0.4 %	—	—
Trichoptera	—	0.1 %	—	—	—
Ephemeroptera	0.1 %	0.0 %	—	—	—
Microcoryphia	0.1 %	—	—	—	—
Phasmida	—	0.0 %	—	—	0.3 %

Table 2 Taxonomic composition (order level) of insect species native to North America, Hawaii, mainland Japan, Ogasawara and Okinawa

Locality	World total ^a	N America ^a	Hawaii ^b	Mainland Japan ^c	Ogasawara ^c	Okinawa ^c
Total	744,133	86,459	5354	24,970	1106	7519
Coleoptera	39.0 %	27.4 %	26.7 %	30.8 %	25.9 %	38.4 %
Hymenoptera	13.8 %	20.6 %	12.2 %	16.0 %	9.5 %	10.8 %
Hemiptera	11.0 %	11.5 %	8.9 %	9.2 %	14.9 %	8.7 %
Diptera	13.2 %	19.6 %	20.0 %	19.0 %	15.7 %	12.2 %
Lepidoptera	15.1 %	13.1 %	17.9 %	18.6 %	23.8 %	23.3 %
Thysanoptera	0.5 %	0.8 %	0.5 %	0.5 %	1.0 %	0.6 %
Psocodea	1.0 %	1.5 %	1.7 %	0.9 %	1.0 %	0.4 %
Blattodea	0.5 %	0.1 %	–	0.1 %	0.3 %	0.5 %
Orthoptera	1.7 %	1.2 %	4.9 %	0.7 %	3.5 %	–
Siphonaptera	0.3 %	0.4 %	0.0 %	0.3 %	–	–
Dermaptera	0.1 %	0.0 %	0.2 %	0.1 %	0.5 %	0.2 %
Isoptera	0.3 %	0.1 %	0.0 %	0.0 %	0.3 %	0.1 %
Odonata	0.7 %	0.5 %	0.6 %	0.6 %	1.6 %	1.4 %
Thysanura	0.0 %	0.0 %	–	0.0 %	0.2 %	0.0 %
Mantodea	0.2 %	0.0 %	–	0.0 %	0.2 %	0.1 %
Neuroptera	0.6 %	0.4 %	–	0.5 %	1.3 %	0.8 %
Embiopoda	0.0 %	0.0 %	–	0.0 %	–	0.0 %
Strepsiptera	0.1 %	0.1 %	–	0.1 %	0.2 %	0.1 %
Trichoptera	0.9 %	1.5 %	–	1.4 %	–	0.1 %
Ephemeroptera	0.3 %	0.7 %	0.0 %	0.4 %	–	0.1 %
Microcoryphia	0.0 %	0.0 %	0.1 %	0.0 %	0.1 %	0.0 %
Phasmida	0.3 %	0.0 %	–	0.0 %	–	0.1 %
Grylloblattodea	0.0 %	0.0 %	–	0.0 %	–	–
Zoraptera	0.0 %	0.0 %	0.0 %	–	–	–

^a Data from Arnett (2000) Some non-native species also included in the list

^b Data from Nishida (2002)

^c Data from <http://konchudb.agr.agr.kyushu-u.ac.jp/mokuroku/> and identified insects' distributions using additional resources (Azuma et al. 2002; Ohbayashi et al. 2004)

The phenomenon of exceptionally large numbers of biological invasion on islands has received considerable attention (e.g., Kiritani 2001; Sax 2001). Our result also showed that the numbers of non-native insects per area on islands are much larger than those on the mainland. The causes of excessive island invasions have been debated, but theoretical studies indicate establishment of invading species occurs more freely as a result of the typically low diversity of native island species (Herben 2005). This low diversity may result in diminished pressure from competitors, predators and other types of species, thereby

facilitating establishment (Mooney and Cleland 2001). However, as discussed above, native insect diversity in Hawaii, Ogasawara and Okinawa is also greater than in their mainland and thus this hypothesis does not explain the propensity for invasions there. In fact mainland Japan also consists of many islands but the ratio of non-native to native species was the lowest though the area of the major Japanese islands are far greater than the area of Okinawa and Ogasawara Islands. Small islands typically receive more cargo from the mainland than they export. This excess amount of inflow may facilitate the elevated richness

of their non-native insect communities. In addition, the oceanic islands, Hawaii and Ogasawara, may be more prone to invasion than the continent of North America or the continental islands of mainland Japan and Okinawa because of their geographical isolation.

Intentional versus accidental

Though most of the non-native species in each region have arrived as a result of accidental transport, many were introduced via intentional release and the vast majority of these were released for the purpose of classical biological control (Clausen 1978) (Table 3).

North America and Hawaii each have more than 10 times the number of intentional introductions than those in mainland Japan and Okinawa (Table 3). Historically, there has been considerable effort put into biological control in the USA, Canada and Hawaii (Clausen 1956, 1978; Beirne 1975; Funasaki et al. 1988). Early enthusiasm about importing biological control agents followed the dramatic success of releasing the predaceous vedalia beetle, *Rodolia cardinalis* (Mulsant), in California in 1889, saving citrus groves there from the damaging cottony cushion scale, *Icerya purchasi* (Maskell) (Caltagirone and Douth 1989). The US Department of Agriculture, as well as scientists at various universities, played central roles importing, breeding and releasing a wide variety of insect predators, parasitoids and herbivores from around the world (Clausen 1956). A large number of successes have been recorded in the USA (Vail et al. 2001). The propensity for classical biological control in North America and Hawaii may be at least partially attributed to the dominance of non-native pest species there. According to Sailer (1978), more than 50 % of US crop losses are attributed to non-native pests.

Classical biological control almost always targets non-native pests (Caltagirone 1981) so it is quite natural that many non-native natural enemies have been introduced to North America and Hawaii to control their plethora of non-native insect pests.

In contrast, classical biological control has not been widely practiced in Japan. The dominance of native agricultural pests (over non-native species) in Japan may have resulted in less motivation for the introduction of non-native biological control agents there. In addition, pest management in Japan shifted toward chemical control after the World War II.

In all regions, 50 % or more of the intentionally introduced species were Hymenoptera (Table 3). Almost all of these are parasitoid species (Appendix E—see Electronic supplementary material) introduced for biological control of pest insects as were tachinid parasitoids belonging to Diptera (Appendix D—see Electronic supplementary material). These parasitoids were mostly released for control of agricultural pests in North America and in Hawaii. Though several parasitoids have been introduced as biological pesticides in Japanese greenhouses, there are only a few successful introductions of parasitoids in open fields of Japan (e.g., Moriya 2009; Mochizuki 2008).

The Coleoptera is second only to the Hymenoptera in the number of intentionally released species (Table 3). Many are insect predators in the family Coccinellidae, introduced as biological control agents (Appendix B—see Electronic supplementary material). Hawaii has had eight intentional introductions of carabid predator species while many other coleopteran species, including dung beetles, were introduced to control the horn fly, *Haematobia irritans*, (Linnaeus), because they can quickly decompose cattle manure thereby destroying horn fly habitats (Funasaki et al. 1988).

Table 3 Numbers of intentionally introduced non-native insect species established in North America, Hawaii, mainland Japan, Ogasawara and Okinawa

Locality	North America	Hawaii	Mainland Japan	Ogasawara	Okinawa
Total	332	351	28	2	17
Coleoptera	78	110	2	1	5
Hymenoptera	199	168	20	1	10
Hemiptera	4	12	2	—	—
Diptera	42	32	1	—	—
Lepidoptera	8	26	2	—	1
Thysanoptera	1	1	—	—	1
Neuroptera	—	2	1	—	—

Several insect species were released for the purpose of biological control targeting non-native weeds (Spencer and Coulson 1976; Appendix B—see Electronic supplementary material). Releases of phytophagous Coleoptera have been particularly common, as have releases of Diptera (Vail et al. 2001; Appendix E—see Electronic supplementary material) and a few Lepidoptera (Spencer and Coulson 1976; Appendix C—see Electronic supplementary material) in North America. In contrast, biological agents of non-native weeds have never been released in Japan. A cultural aversion to introducing non-native herbivores may have contributed to the avoidance of this practice in Japan.

Taxonomic composition

Numbers of non-native species in each order are plotted against numbers of native species in Fig. 2 and the result of NMDS ordination is shown in Fig. 3. All the native communities were located in the right side of the diagram (Fig. 3a). The relative frequencies of species in each order are particularly similar among the native communities in Ogasawara and Okinawa; these regions are characterized by high numbers of Lepidopteran species and low numbers of Hymenoptera. The composition of the native communities in North America, Hawaii and mainland Japan were also quite similar (Fig. 3a and Table 2). The primary NMDS axis clearly separated the composition of the native versus non-native communities. This axis is characterized by high frequencies of Diptera, Lepidoptera and Orthoptera in the native region of the space, and abundance of Blattodea, Siphonaptera, Thysanoptera and Hemiptera at the non-native portion of the space. Numbers of non-native species in these orders were always above expected levels (based upon assumption of a constant fraction non-native across all orders) in five regions while those of Diptera and Lepidoptera were abundant but fell slightly below the line of expected frequency (Fig. 2). The cockroaches (Blattodea) and fleas (Siphonaptera) are mostly cosmopolitan pests with life histories closely linked to human life. Cockroaches expanded their distributions together with migrant humans beginning in the 15th and 16th centuries (Sailer 1983). There were no Blattodea species in Hawaii until the end of nineteenth century but now 21 species are present (Table 1). The thrips (Thysanoptera) and Hemiptera, including scale

insects (Diaspididae, Pseudococcidae and Coccidae) aphids (Aphididae), leafhoppers (Cicadellidae) and whiteflies (Aleyrodidae), are common invaders in all regions (Fig. 2, Appendix F—see Electronic supplementary material). They are generally small and cryptic; consequently they may elude detection by quarantine inspectors when live plants are imported, thus contributing to their increased propagule pressure and more frequent establishment (Kiritani and Yamamura 2003; Liebhold et al. 2012).

Non-native communities from Hawaii and North America are most similar to each other as are non-native communities in mainland Japan, Ogasawara and Okinawa (Fig. 3a). Differences between the North America/Hawaii and the mainland Japan/Ogasawara/Okinawa communities can largely be attributed to differences along the secondary NMDS axis. This axis is characterized by high abundance of Blattodea in mainland Japan/Ogasawara/Okinawa area and high abundance of Hymenoptera and Psocodea in the North America/Hawaii space. Though numbers of non-native Blattodea and Siphonoptera in mainland Japan and Okinawa/Ogasawara are not greatly different from those in North America and Hawaii, their fractional representations among all non-native species in mainland Japan, Ogasawara Okinawa are greater than those in North America and Hawaii (Table 2).

North America and Hawaii tend to have greater numbers of Hymenopteran species because historical biological control efforts have been more extensive in these regions, as described in the previous section. Excluding the intentionally introduced species, the Formicidae (ants) are the largest family of non-native Hymenoptera in all regions (Appendix E—see Electronic supplementary material). Many ant species are successful at exploiting various types of disturbed environments. Ants also have highly developed social behaviors and consequently are very tolerant of severe conditions and also are strong competitors against other terrestrial vertebrates and invertebrates (McGlynn 1999). In fact, five ant species were included in the World's 100 Worst Alien Invasive Species (ISSG 2014). Hawaii lacks any native ant species but currently 53 non-native ant species are established there (Appendix E—see Electronic supplementary material).

Though it is not clear in the ordination diagram, the proportion of non-native Coleoptera in mainland Japan, Ogasawara and Okinawa are slightly higher

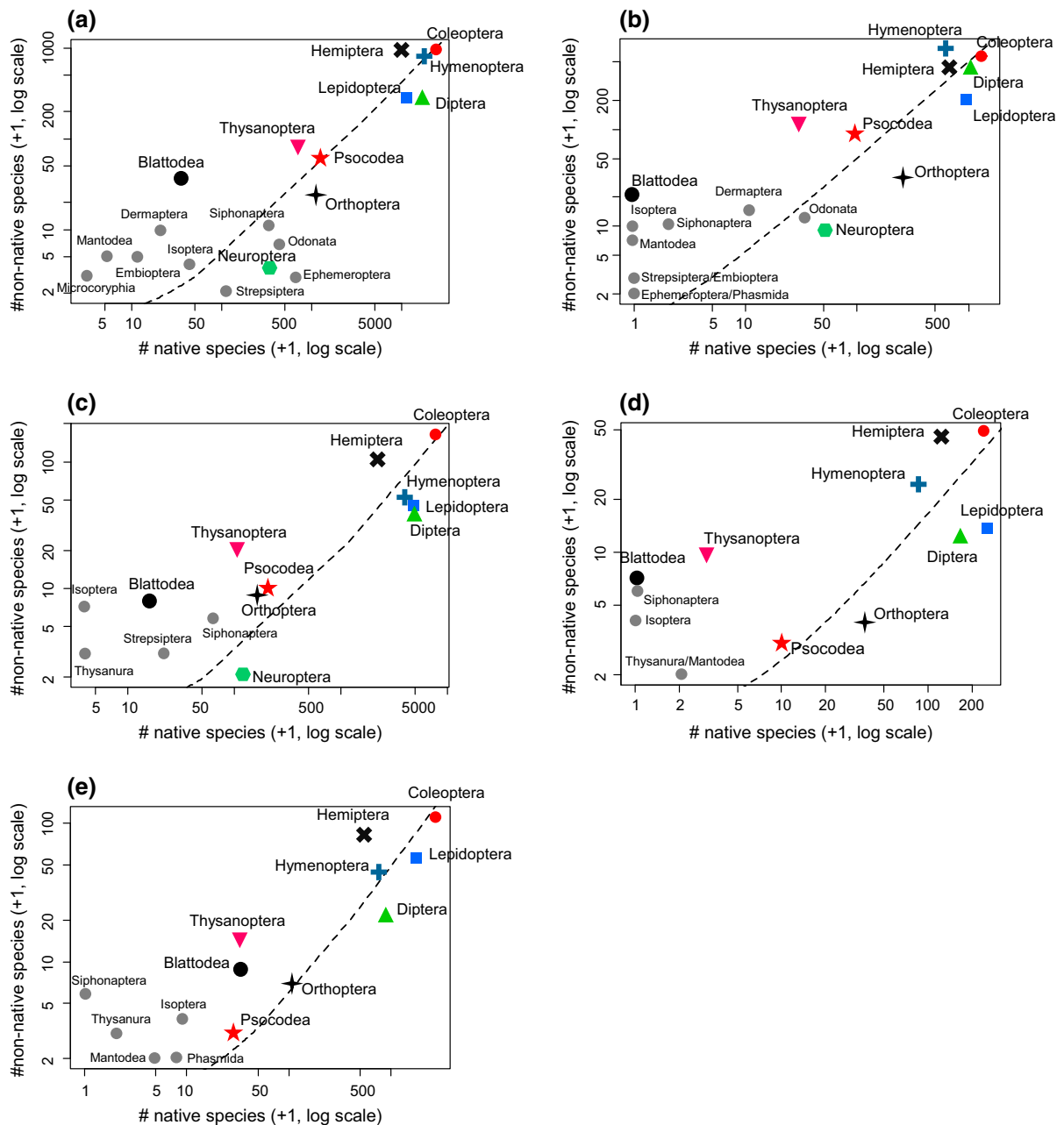


Fig. 2 Numbers of non-native species in each order relative to the number of native species in the same order for North America (a), Hawaii (b), mainland Japan (c), Ogasawara (d) and

Okinawa (e). Dashed lines correspond to the total (all orders) numbers of non-native species as fractions of total numbers of species (native and non-native)

than in North America and Hawaii (Table 1). Mainland Japan has a large number of Dermestid species, as well as other stored product pests in the Tenebrionidae, Lathridiidae, Silvanidae, Bostrichidae, Cleridae and Ptinidae. Kiritani et al. (1963) reported that grain

storage and milling facilities in Japan harbored a large number of non-native stored product pests and facilitated invasions. Directly following the World War II, extensive food shortages in Japan necessitated importation of large volumes of grain, mainly from North

America. The plethora of non-native stored products pests established in mainland Japan, Ogasawara and Okinawa are likely a consequence, in part, of this historical demand for imported grain.

Origins

Origins of non-native species established in each region are summarized in Table 4. The compositional difference of origins among the five regions were

highly significant with the multinomial-probit model using R-library VGAM ($\chi^2 = 2660.8$, $df = 32$, $p < 0.0001$; Yee 2010) although the taxonomic composition of North America/Hawaii, and of mainland Japan/Ogasawara/Okinawa, were nearly identical (Fig. 3a). North America has received the majority of its non-native insects from either the European Palearctic (47.6 %) or the Asian Palearctic (21.4 %). Though North America is the most common (16.3 %) origin of non-native insects in Hawaii, a substantial

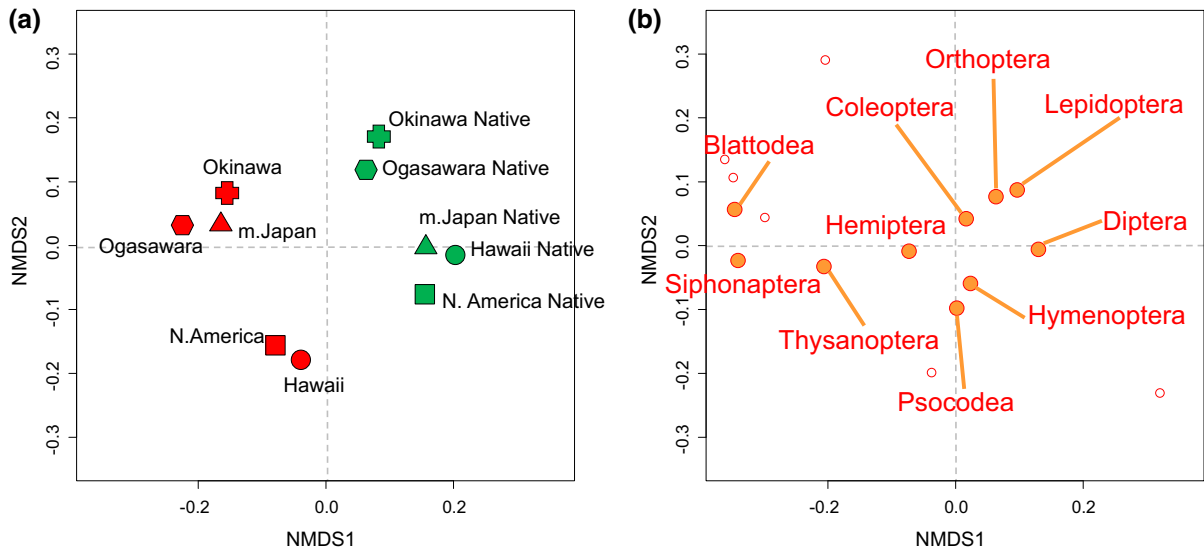


Fig. 3 Ordination diagram of the ten communities: native and non-native communities in North America, Hawaii, mainland Japan, Ogasawara and Okinawa (a) and the taxonomic order (b). Positions of the insect orders in Fig. 3b are centroids of the

numbers of species belonging to the orders in the seven communities. The ten most abundant non-native insects are plotted in orange and the others are represented by hollow points. *m. Japan* mainland Japan, *N. America* North America

Table 4 Origin (classified in Fig. 1) of non-native insect species established in North America, Hawaii, mainland Japan, Ogasawara and Okinawa

Locality	North America (%)	Hawaii (%)	Mainland Japan (%)	Ogasawara (%)	Okinawa (%)
European Palearctic	47.6	9.5	21.7	6.5	8.0
Asian Palearctic	21.4	11.3	29.7	25.0	22.6
Indomalaya	4.7	14.9	20.4	29.2	43.6
Afrotropic	5.8	6.4	7.9	16.1	12.0
Australasia	3.1	6.5	3.2	3.0	3.7
Oceania	0.9	5.6	0.6	3.6	2.9
Nearctic	—	16.3	11.7	6.0	5.2
Neotropic	14.1	12.4	9.1	12.5	10.6
Unknown	15.2	25.4	12.7	6.0	4.6

Many species originate from multiple world regions and are listed in both

number are also from Indomalaya (14.9 %) and the Neotropic region (12.4 %). Moreover, a substantial number of non-native insects in Hawaii are from Oceania (5.6 %). Most of the non-native insects in mainland Japan originate from the Asian Palearctic (29.7 %) and the European Palearctic (21.7 %). The largest sources of non-native insects in Ogasawara and Okinawa are Indomalaya (43.6 and 29.2 %, respectively, including Taiwan) and the second largest were from Asia Palearctic (25.0 and 22.6 %, respectively). Substantial numbers in Ogasawara and Okinawa are also from the Afrotropic and Neotropic regions. These patterns reflect climatic similarity between source and invaded regions. If the climate in a species' native range is similar to that in a non-native region, then that species is more likely to successfully establish in that region. North America and mainland Japan share 187 species that are non-native in both regions; of these species, 53 are from Europe and 42 are from Asia. Similarly, Hawaii and Okinawa share 181 non-native species; of these species, 117 are from tropical or subtropical world regions. These results indicate that the majority of invasive species in each region are coming from a unique set of geographic origins though the regions share substantial numbers of common non-native species. Ogasawara and Okinawa share 138 species and these comprise 82.1 % of the non-native insects in Ogasawara. This similarity likely arises both due to the similarity in climate between Ogasawara and Okinawa but also the similarity of historical events that may have facilitated introductions in both regions. These islands were governed under the U.S. military control following the World War II and insect species have been inadvertently introduced with extensive imports of military and other supplies. Ogasawara and Okinawa also have continuously received considerable cargo from mainland Japan after their return to Japanese control in 1968 and 1972, respectively, and this could have facilitated introduction of Japanese and cosmopolitan insect species.

It should be noted that ecozones specific to the Southern Hemisphere (Afrotropica and Australasia) comprised a relatively small fraction of the origins of non-native species for all regions (Table 4). While climates in portions of the temperate Southern Hemisphere are very similar to those in the Northern Hemisphere, the opposing seasonality could represent a formidable barrier to the successful establishment of a species transported among the opposing temperate

regions, particularly for species with obligate diapause requirements (e.g., Pitt et al. 2007). Also, the insects transported (e.g., on freighters) might experience substantial heat stress when passing through equatorial regions (Kiritani 1983). In addition to transportation barriers, plant phylogeny may also play an important role. Since a large number of invading insects are phytophagous, the biogeographical patterns of plants constrain the ability of herbivorous insect species to establish outside of their native range (Mattson et al. 2007). Most plants in the temperate Northern Hemisphere are in different families from those in the Southern Hemisphere and such phylogenetic dissimilarity represents a serious hurdle to the establishment of many monophagous or oligophagous phytophagous insects.

Even though the effect of climatic similarity is prominent, we can also observe in Table 4 the effect of propagule pressure, i.e., strength of trading connections, a phenomenon that is well known to promote insect establishment (Liebhold and Tobin 2008). Nearly a half of all non-native insects in North America originated from the European Palearctic region (Table 4). While similarities in climate and host plant phylogenies between North America and Europe may contribute to the successful transfer of species, much of this pattern simultaneously reflects historical patterns of trade, military transport and immigration (Lindroth 1957). For example, ground beetles (Staphylinidae and Carabidae) were accidentally introduced from Europe to North America with soil ballast unloaded in North America (Lindroth 1957; Spence and Spence 1988).

The largest fraction (29.7 %) of all non-native species in mainland Japan originated from the Asian Palearctic region and this likely reflects historical patterns of trade, military and passenger movement with Eastern Asian countries. Even though contemporary trade volumes are vastly greater than what existed 100 or more years ago, trade during these historical periods played an important role in facilitating invasions (Aukema et al. 2010). Despite the much lower volume of trade a century ago, quarantine regulations were minimal and as a consequence relatively low volumes of trade facilitated a multitude of invasions (MacLeod et al. 2010). The largest (16.3 %) origin of non-native species in Hawaii is the Nearctic. This fraction is high considering the climatic and plant phylogeny dissimilarity between most of the

Nearctic with Hawaii, but likely reflects the very high level of historical cargo, military and passenger movement between the USA and the Hawaiian Islands. Before the advent of long-range vessels and aircraft, Hawaii was a frequent stop for trans-pacific crossings. High rates of tourism in Hawaii also have historically driven extensive passenger traffic, both by air and by sea. This may explain the substantial number of invasions in Hawaii from the Indomalaya (14.9 %), Neotropic (12.4 %) and Oceania (5.6 %) regions. Okinawa received a large fraction of non-native species from the Asian Palearctic region (22.6 %) with most of these species originating from mainland Japan, again reflecting historical patterns of cargo and passenger movement (Kiritani 2001). Many non-native species from elsewhere in the Asian Palearctic moved to Okinawa via intermediate establishment in the mainland Japan (Kiritani 2001).

In addition to intercontinental movement, range expansion from adjacent (or near-by) regions is also responsible for the accumulation of certain non-native insects. North America received 14.1 % of species from the Neotropic region, including Mexico (Table 4). For example, Sailer (1983) pointed out that natural range expansions are continuously occurring from Mexico and the Caribbean islands, and several non-native insects established in Okinawa and mainland Japan, originated from Taiwan and countries along the South China Sea via transport on monsoonal winds (Hayashi et al. 1979). Instances of invasion from adjacent areas appear to be minor compared to intercontinental movement via trade pathways (Sailer 1983). However, there are several recent instances of range expansion, apparently facilitated by climate change, and this phenomenon may accelerate in the future (Lawler et al. 2006).

Conclusions

Our results indicate that while distinct similarities exist among non-native communities, insect invasions in each world region are unique, with species arriving via a unique set of pathways from a unique set of geographic origins reflecting the history and geography of each region. The origins of non-native insects vary among the five regions and these patterns reflect the effects of both propagule pressure and habitat similarity (e.g., climatic similarity and phylogenetic

similarity of host plants) on invasions. Unfortunately, variation in propagule pressure and habitat similarity are often confounded and teasing apart their relative impacts on invasion success is difficult (Liebhold et al. 2013). We believe that both propagule pressure and habitat similarity act together to form unique assemblages of non-native species in region.

Though we did not comprehensively explain the taxonomic composition of invaded communities based on geographic variation in invasion pathways, examination of the communities of non-native insect species clearly indicates that some taxa are disproportionately (relative to native fauna) over- or under-represented in some or all of the five regions and these higher rates of species establishment reflect the identity of invasion pathways. For example, solid wood packing material is recognized as the dominant pathway by which several groups of wood-boring insects are transported (Haack et al. 2014). Importation of living plants is another type of cargo that is recognized as an important invasion pathway for a variety of phytophagous insects (Kiritani and Yamamura 2003; Liebhold et al. 2012). Fruit carried by international air passengers is known as a serious pathway by which invading fruit flies move among continents (Kiritani 2001). Considerable progress has been made in identifying these pathways and establishing quarantine measures to minimize their impact on facilitating invasions. For example, unsterilized soil may no longer be imported to Japan, the USA or Canada, and this has greatly reduced the rate of establishment of a variety of ground-dwelling insects and other organisms. International Standards for Phytosanitary Measures No. 15 (ISPM-15) was recently implemented by the International Plant Protection Convention. This international regulation prescribes heat treatment or fumigation of all SWPM (solid wood packing material) used for export and has at least partially lowered propagule pressure of wood-boring insects (Haack et al. 2014). However, these and other pathways are not entirely “closed”; there continues to be a need to further characterize invasion pathways and search for new procedures that reduce species establishments while minimizing adverse economic impacts on trade and travel.

In conducting the analysis reported here, considerable effort went into compiling data on established species in each of the five regions. Unfortunately, these data are not perfect and more work is needed in

compiling and updating species records. Verified records of species establishment are important not only for facilitating analyses such as those reported here, but also for the use of quarantine agencies in establishment of import quarantine policies which may target exclusion of pest species. Progress needs to be made in harmonizing these records among countries. If comparable data were available for a much larger number of world regions, this could yield useful insight beyond what was gleaned from the current study.

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