Chapter 6

Taxonomic Selectivity in Surviving Introduced Insects in the United States

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1. INTRODUCTION

Although ecologists have understood the importance of invasions since the publication of Elton’s book (1958), the factors important to the survival and impact of introduced species are still poorly understood. Several factors can determine whether a species arrives and thrives in a new location. Firstly, the opportunity for colonisation is important. Obviously, a species may have all the traits that would predispose it to prosper in a particular location, but, if it cannot get there, no invasion will occur. Clearly, some species will be introduced more often than others will. For example, the fact that there has been historically more traffic between Europe and North America than between Africa and North America gave European species more opportunities for spread to North America (Sailer 1983).

Secondly, the abiotic and biotic characteristics of the colonised habitat may be important. A tropical species might be ill suited to colonise high latitude areas with colder climates. On the other hand, less extreme habitat differences would probably make a relationship between habitat characteristics and the probability of survival less clear-cut. Biotic interactions between the invader and the native biota might determine whether the invader would thrive — e.g., the biotic resistance hypothesis (Simberloff 1986). As another example, a host-specific insect cannot survive long if its host is not already present. Lonsdale (1999) recently has shown that habitat characteristics (number of native species, whether the site was on the mainland or an island, and whether or not it was a nature reserve) explained much of the variation in the number of invasive plant species in 184 sites around the world. To our knowledge, no similar analysis has been conducted for insects, probably because the necessary data still have to be gathered.

Thirdly, the biological traits of invaders may also be important in determining their success. Historically, many researchers have attempted generalisations concerning the characteristics of invaders. For example, Baker (1965) hypothesized the “ideal weed” to be a species able to germinate in a wide range of conditions, grow quickly, flower early, self-fertilize, produce many seeds that disperse widely, reproduce vegetatively, and compete well. However, Baker’s hypothesis is not supported by existing data. For example, Williamson and Fitter (1996) tested these and other life history characteristics with the Ecological Flora Database, finding weakly significant differences between good and poor invaders for only three of fourteen life history and reproductive characteristics (age at first flowering, type of pollen vector, and decline). Lawton and Brown (1986) reached a similar conclusion in analyzing the characteristics of insect invaders: only a combination of the population’s intrinsic rate of increase (r), carrying capacity (K), and body size seemed to have any relationship with the probability of establishment of insect invaders. However, because this relationship was not very strong, and the analysis was done at the ordinal level, Lawton and Brown concluded that it lacks predictive value.

Below, we analyse data on insect invasions in the United States. We ask: (i) Are introduced species non-randomly distributed among families? (ii) If the answer to question (i) is yes, which families have more introduced species than would be expected by chance alone? (iii) Is this pattern real and not just a statistical artefact?; (iv) If the answer to questions (ii) and (iii) is yes, what generates this pattern? Based on the results of this analysis, we argue that the opportunity for colonisation is a crucial factor determining which introduced insects arrive and survive.

2. MATERIALS AND METHODS

2.1 The Database

We compiled data on the numbers of non-indigenous insect species in each family from Kim and Wheeler (1991). Kim and Wheeler list all known non-indigenous insect species for the United States until the date of publication of their report. They consider a species to be non-indigenous if it is resident or probably resident in the U.S. and was not native to the U.S. prior to European exploration and settlement.

We then calculated the source pool of species available to colonise the U.S. — the total number of species in each family that were not originally native to the U.S. and were thus originally available for invasion — as

$$n_i = w_i - (us_i - x_i) \qquad \text{(EQUATION 2.1.1)}$$

where n_i is the number of source species in family i, w_i is the total number of species in family i in the world, us_i is the total number of species in the US in family i (including non-indigenous species), and x_i is the number of exotic species of family i in the US. The quantity $us_i - x_i$ is the number of native species in family i in the US; we subtracted this quantity from the total number of species in each family because these species are obviously not available to invade the US. We obtained most of our w_i values from Parker (1982), all our us_i values from Arnett (1985), and all our x_i values from Kim and Wheeler (1991).

2.2 Statistical methods

To test whether there is overall selectivity in our data (i.e., whether the non-indigenous species are non-randomly distributed among families) we used a log-likelihood ratio test (*G*-test). Usually, one can compare the *G*-statistic calculated in the test with the χ^2 critical value obtained from tables. However, in order to do this it is necessary that the smallest expected value in the contingency table be no lower than 5 (Sokal and Rohlf 1995). In our case, because we have to fill 949 cells (families) with 1863 invasive species, surely *most* of our expected values will be lower than 5. To circumvent this problem it is possible to use randomizations to generate an expected distribution of the *G*-statistic (Manly 1997). Thus, we first distribute species uniform-randomly among families; for that randomly generated contingency table, we calculate the *G*-statistic; we repeat this procedure 10,000 times. We then compare the *G*-statistic calculated for the real data with the distribution of the simulated *G*-statistics. If the *G*-statistic calculated for our data is an extreme value of the distribution of the simulated *G*-statistics, we can reject the null hypothesis of random distribution of species among families in our data.

Having answered the question of whether there was overall selectivity in our data, we asked which families have more introduced species than would be expected by chance. To answer this question we used a one-tailed binomial test. The binomial test calculates the binomial probability $P(x)$ that a random sample of size n drawn from a binomial population will contain x elements in one of the categories (each element with probability p) and $n – x$ elements in the other category (each with probability $q = 1 – p$) (Zar 1996):

$$P(x) = \binom{n}{x} p^{x} q^{n-x} \qquad \text{(EQUATION 2.2.1).}$$

Thus, for a family i, we calculated the probability $P_i(x_i)$ that x_i species would be introduced out of a total n_i source species (i.e. the number of species that were "available" to invade the US in the world pool; see equation 17.1). Finally, we calculated p as the total number of non-indigenous insects in the U.S. divided by the total insect source species in the world, i.e.,

$$p = \sum_{i=1} x_i \Big/ \sum_{i=1} n_i = 1{,}863/788{,}681 = 0.0024 \qquad \text{(EQUATION 2.2.2).}$$

Equation 17.2 gives the probability that exactly x elements will be in one of the categories. However, we are interested in the probability of a particular case or more extreme cases, i.e., the tail probabilities; whether we take the upper tail, lower tail or two-tail probabilities will depend on our null hypothesis (H_0). Since we want to test whether the occurrence of x elements in one of the categories with probability p in a random sample of size n is too high to be considered random, we clearly want an upper, one-tailed test. The binomial upper-tail probability for family i is given by

$$p_i(x_i) = \sum_{k=x_i}^{n_i} \left[\binom{n_i}{k} p^{k} q^{n_i-k} \right] \qquad \text{(EQUATION 2.2.3).}$$

There is always some probability that we can get a significant result (a binomial tail probability lower than the critical value) by chance alone, and, as we are performing multiple tests, we may expect some such artifactual results. One possibility for dealing with this problem is to correct the critical value against which each binomial probability is compared; we used one such test, the sequential Bonferroni correction (Rice 1989). This correction works as follows: we order the binomial probabilities from highest (least significant) to lowest (most significant); we then divide the critical value (e.g., $\alpha = 0.05$) by its rank. For example, since in our test we were interested only in which families have "too many" non-indigenous species, we included only those families with at least one non-indigenous species — a total of 170. Thus, the critical value corresponding to our lowest (most significant) tail probability was divided by 170, the second lowest by 169, and so forth.

Table 1. Insect families with binomial probabilities lower than their corresponding critical value. Families are ordered by their corresponding binomial probability. n_i is the number of world source species in family i; x_i is the number of invasive species in the U.S. in the family; $P_i(x_i)$ is the binomial probability for the family; the critical value is calculated as 0.05 divided by the count for the family (see text for a more detailed explanation).

Order	Family	n_i	x_i	$P_i(x_i)$	Count	Critical value
Coleoptera	Staphylinidae	27041	228	0.0000000000	170	0.0002941176
Diptera	Cecidomyiidae	2975	34	0.0000000000	169	0.0002958580
Diptera	Oestridae	31	7	0.0000000000	168	0.0002976190
Hymenoptera	Aphelinidae	4044	61	0.0000000000	167	0.0002994012
Hymenoptera	Encyrtidae	2391	62	0.0000000000	166	0.0003012048
Hymenoptera	Eulophidae	2537	44	0.0000000000	165	0.0003030303
Hymenoptera	Pteromalidae	2446	41	0.0000000000	164	0.0003048780
Hymenoptera	Tenthredinidae	2307	38	0.0000000000	163	0.0003067485
Lepidoptera	Tortricidae	3025	78	0.0000000000	162	0.0003086420
Thysanoptera	Thripidae	1279	43	0.0000000000	161	0.0003105590
Hymenoptera	Tetracampidae	35	6	0.0000000003	160	0.0003125000
Hymenoptera	Eurytomidae	871	15	0.0000000063	159	0.0003144654
Hymenoptera	Diprionidae	65	6	0.0000000140	158	0.0003164557
Coleoptera	Anobiidae	158	7	0.0000001424	157	0.0003184713
Hymenoptera	Aphidiidae	698	12	0.0000002040	156	0.0003205128
Orthoptera	Gryllotalpidae	63	5	0.0000004984	155	0.0003225806
Homoptera	Aphididae	2169	20	0.0000006071	154	0.0003246753
Coleoptera	Dermestidae	732	11	0.0000023576	153	0.0003267974
Siphonaptera	Pulicidae	163	6	0.0000032863	152	0.0003289474
Coleoptera	Coccinellidae	4126	25	0.0000392087	151	0.0003311258
Homoptera	Adelgidae	31	3	0.0000590869	150	0.0003333333
Diptera	Tephritidae	3743	23	0.0000634001	149	0.0003355705
Thysanoptera	Aeolothripidae	178	5	0.0000793799	148	0.0003378378
Coleoptera	Bruchidae	1479	13	0.0000847723	147	0.0003401361
Heteroptera	Anthocoridae	422	7	0.0000867729	146	0.0003424658
Hymenoptera	Cynipidae	572	8	0.0000901753	145	0.0003448276

The sequential Bonferroni correction is designed to account for the possibility of finding some binomial tests significant by chance alone. To test how well this correction was working, we used a simulation. For this simulation, we uniform-randomly selected 1863 “invasive” species from the 788,681 source species, recording the families of the selected species. We then calculated the binomial probabilities for each of the 949 families, and ordered them from lowest to highest. We repeated this procedure 100 times.

We then calculated the mean for each category (the mean of the lowest binomial probabilities in each of the 100 iterations, the mean of the second lowest probabilities, and so on). We compared these means with the rank-ordered binomial probabilities we obtained for the real data. Thus, were the Bonferroni correction working properly, none of our simulated binomial probabilities should be lower than its corresponding critical value, and they should be higher than the significant binomial probabilities calculated from the real data.

The statistical tests described above were performed using computer programs written in C. The programs and the data are available from the first author upon request.

3. IS THERE TAXONOMIC SELECTIVITY IN OUR DATA?

By looking at the list of non-indigenous species in each family (Appendix), we find that all the non-indigenous species in the U.S. occur in just 170 of the 949 families. This fact suggests that the non-indigenous species may not be randomly distributed among families. In the log-likelihood ratio test, the G-value for our data is $G = 1705.04$. This value exceeds all 10,000 simulated G-values (which range between 458.68 and 709.11, with mean 563.81) (Fig. 1). Thus, we can reject at $p < 0.0001$ the null hypothesis of random distribution of introduced species among families. This is, of course, far from surprising. We know that species are not equal and that phylogeny matters (Faith 1992). Why would we then expect non-indigenous species to be randomly distributed among families? — such a result would have been surprising.

As the introduced species are not randomly distributed among families, we can go further and ask which families have more non-indigenous representatives than would be expected by chance. Using the upper-tail binomial test we see that 26 families have binomial probabilities lower than their corresponding critical values (Table 1).

4. IS THE PATTERN REAL?

Although our corrected binomial test tells us that 26 families have more non-indigenous species than we would expect, we want to be sure that this pattern is not a statistical artifact — in other words, that the Bonferroni correction adequately accounts for the fact that we performed multiple tests. For this test we used the simulations described above to calculate the binomial probabilities for randomly generated data. We find that none of the binomial probabilities calculated in our simulations is lower than any of the significant binomial probabilities calculated for the real data (Fig. 2). This means that the pattern we found is not a statistical artifact.

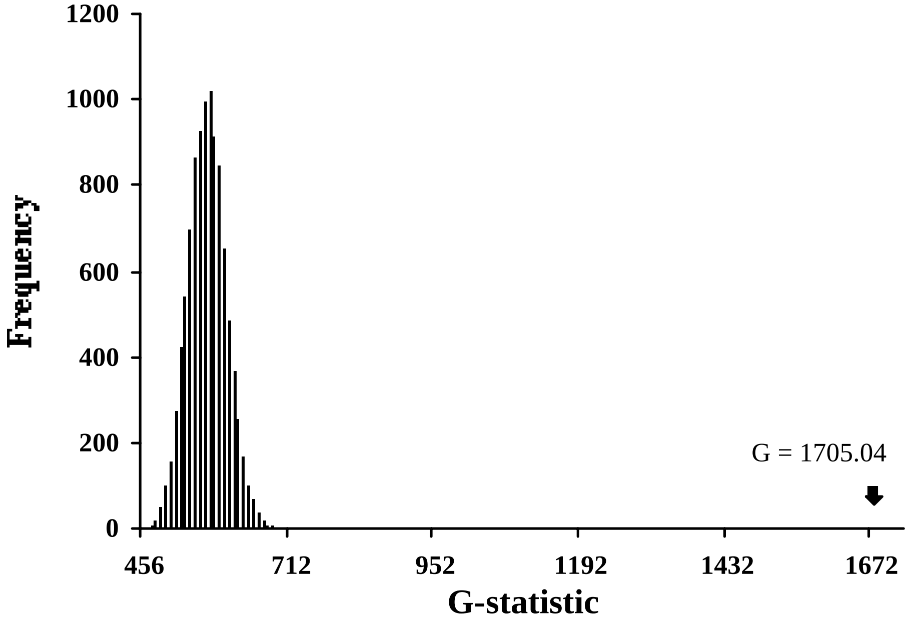

Figure 1. Distribution of the randomly generated *G*-statistics. The arrow shows, for comparison, the value of the *G*-statistic calculated for the real data.

5. WHAT IS PRODUCING THE PATTERN?

As the pattern is real, we can ask a more interesting question: what generates it? We must look at the particular families at the top of our list — those that show much higher numbers of non-indigenous species than expected (Table 1).

As we discussed in the introduction, several factors can determine which species will establish in a new location: the opportunity for colonisation, the characteristics (both biotic and abiotic) of the colonised habitat, and the biological characteristics of invaders. Below we analyze the only one of these factors that can be studied with the available data: the opportunity for colonisation. In particular, we ask whether the way species are transported can explain the pattern we observed in our data. Several families in our list are used in biological control, either as parasitoids (most Hymenoptera) or predators (Coccinellidae and Anthocoridae). Those families whose life history is linked to soil form a second group, and these may have arrived in soil brought from other continents, mainly from Europe and South America until the late nineteenth century. A third group comprises species that live on plants, mainly crops and other plants of economic importance. Several families fall in none of these groups; some are ectoparasites of vertebrates, scavengers, or predators of insects.

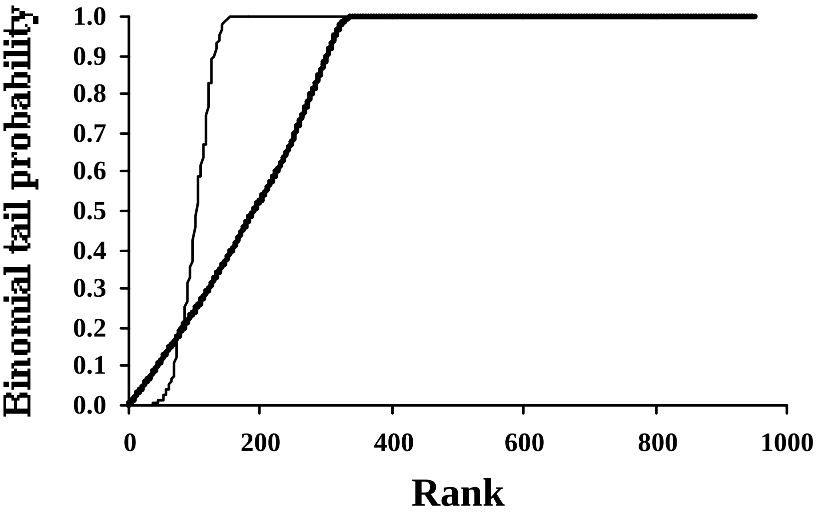

Figure 2. Rank-ordered binomial probabilities. Thick line: mean binomial probabilities calculated for the simulated data; thin line: binomial probabilities calculated for the real data (see the text for a more detailed explanation).

5.1 Biocontrol agents

Of the families listed in Table 1, only two were introduced to the U.S. as predators: the Coccinellidae and the Anthocoridae. Coccinellids are one of the first groups of insects used for biological control (Caltagirone and Doutt 1989), and they are the main biological agents introduced for the control of several homopteran plant pests, such as whiteflies (Aleyrodidae), scale insects (Coccidae), aphids (Aphididae), psyllids (Psyllidae), and several mites (Acari) (Obrycki and Kring 1998). Besides the coccinellids, a few species the Anthocoridae (Heteroptera) were also introduced as biocontrol agents of plant pests, such as the pear psylla (Clausen 1978). Of seven introductions of anthocorids into America north of Mexico, only two appear to have established (Lattin 1999). Most non-indigenous species in this last family were, however, apparently accidentally introduced (six of the seven species listed by Kim and Wheeler [1991]). To our knowledge, no predaceous insect families other than Coccinellidae and Anthocoridae have been introduced for biological control.

Five species of tephritid flies of the genus *Urophora* are listed in the North American Non-Indigenous Arthropod Database (NANIAD; Kim 1991) as having been introduced for the biological control of the knapweeds *Centaurea maculosa* and *C. diffusa*. Yet many other introduced tephritid flies are important pests of cultivated plants.

Two species of cecidomyiid flies were introduced for biological control of plants. But, again, the rest of the non-indigenous species in this family were accidentally introduced, probably with soil or introduced plants of economic importance (see below).

Of the ten Hymenoptera families listed in Table 1, seven are used as biological control agents in the United States. However, not all of the introduced species in those families are used for that purpose: the proportion of observed species mentioned by Clausen (1978; regrettably, the only comprehensive compendium of biological control agents introduced into the U.S. and world-wide) as having been purposefully introduced for biological control ranges between 0.25 and 0.67 (Table 2). Although Clausen's report is obviously outdated, it is likely that several of the species introduced in those families were actually accidental introductions. For example, Sailer (1983) mentions that, of the 232 *beneficial* Hymenoptera introduced in 1982, 35% arrived accidentally. So the numbers given by Clausen are probably not so far from reality. Frank et al. (1997) give two examples of parasitoids that arrived in Florida accompanying their hosts, which were also accidentally introduced: *Trichospilus distraeae* (Eulophidae), a wasp that parasitizes the introduced geometrid moth *Epimecis detexta*, and *Arrhenophagus albitibiae* (Encyrtidae), a parasite of scale insects. Although only the latter species has also been purposefully introduced for biological control (Kim 1991), these examples demonstrate the possibility of accidental introduction of parasitoids. On the other hand, while some diprionid parasitoids are used as biological control agents, others feed on plants and are considered pests (see below). Finally, Howarth (1991) argues that many of the apparently accidental introductions of biocontrol agents in Hawaii were actually unreported purposeful introductions. If Howarth's claim is true and typical beyond Hawaii, it might well be possible that some of Sailer's 35% accidental introductions of biological control agents were indeed purposeful unreported introductions.

If biological control were important in determining which families will be "selected" to be introduced (i.e., which will be at the top of our list), we would expect those families to have proportionally more species introduced for biological control than those towards the bottom of the list. If we take the binomial tail probabilities of section 17.3 as a selectivity index (lower binomial probability would mean higher selectivity), then we would expect a negative correlation between this index and the proportion of species in a family introduced for biocontrol (we used the proportion and not the actual number because this number will of course depend on family size). Since many hymenopteran families are used as biological control agents, we can use the Hymenoptera as a model group to test our hypothesis. In Fig. 3 we have plotted the proportion of species that is known to have been introduced for biological control vs. the binomial tail probabilities. Far from a nice negative correlation, our r^2 is 0.0449, and the relationship is obviously non-linear. However, if we look at Fig. 3, we do see that for very low values of binomial probabilities (i.e., those that are statistically significant) the proportion of species introduced for biological control seems to increase. If we use a statistical test to compare those families that have a statistically significant binomial probability with those that do not, we see that the two groups have significant differences in the proportion of species introduced for biological control (non-parametric two-sample Wilcoxon test, $p = 0.0064$).

5.2 Species associated with soil

Many, probably most, of the early insect introductions to the United States were of species associated with soil brought as ship ballast (Lindroth 1957). Early ship traffic came mainly from European ports — which explains the predominance of European species in early invasions (Sailer 1983). Later, in the late nineteenth century, with the increased commerce with South American countries, many new introductions came from that continent.

Mole crickets (Orthoptera, Gryllotalpidae) were introduced from South America, most likely in soil brought as ship ballast (Sailer 1983). Staphylinid beetles live under dead trees and are usually associated with soils (Borror et al. 1989), which makes them also candidates to have been introduced with ship ballast.

Finally, several cecidomyiid flies feed on grasses imported to the U.S. It is possible that these species came in soil brought with those grasses (Kim 1991).

5.3 Crop pests and other herbivores

Many herbivorous insect species have been introduced with their host plants. The Tenthredinidae are leaf-mining sawflies that feed on tree species such as the birch and hazelnut (Clausen 1978). All introductions in this family were accidental. Four tenthredinid sawflies are considered major pests: *Caliroa cerasi*, *Heterarthrus nemoratus*, *Hoplocampa brevis*, and *Pristiphora erichsonii*; 16 are considered minor pests and the remaining 18 have no apparent economic impact (Kim 1991).

The Thripidae and Aelothripidae (Thysanoptera) are, in many cases, associated with economically important plant species. For example, the onion thrips (*Thrips tabaci*) is a pest of many cultivated plant species (Clausen 1978). Most introduced thrips found in Florida (probably the most important port of entry for thrips) are associated with cultivated plants (Frank et al. 1997).

Eurytomidae (Hymenoptera) present a wide variety of biologies. Most species are either endophytic phytophages or parasitoids of phytophagous insects (Gauld and Bolton 1988, Whitfield 1998). Most non-indigenous eurytomids were probably accidentally introduced. Of the 15 species listed by Kim and Wheeler (1991) as having been introduced into the U.S., none seems to have been purposefully introduced (Kim 1991); yet the ROBO Database (B.C.D.C. 1999) lists four eurytomids introduced for biocontrol between 1981-1983, although those introductions probably failed.

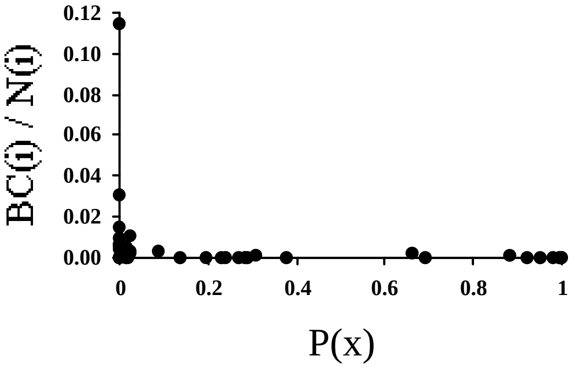

Figure 3. Proportion of species in each family of Hymenoptera known to have been introduced for biological control vs. the binomial tail probabilities (see section 17.3). Only families with at least one invasive species are included in the graph.

Most tortricid moths (if not all) are, once more, associated with introduced plants, mostly cultivated, such as apple, several berries, plum, currant, etc. (Kim 1991). For example, the omnivorous leaf-tier (*Cnephasia longana*) attacks many different species of crops, weeds, and native plants (Clausen 1978). Yet some species are associated with highly noxious non-indigenous plant species, such as Scotch broom.

Most non-indigenous aphids were introduced to the U.S. with their host plants. Virtually all these species are either major or minor pests of cultivated plants (Kim 1991).

Fruit flies (Tephritidae) are an important group of fruit and vegetable pests. Twenty three species are listed by Kim and Wheeler (1991) as introduced into the U.S., of which around 15 are pests. Interestingly enough, several species in the same family (*Urophora*) were introduced for biological control of weeds.

Of the six non-indigenous diprionid sawflies (Hymenoptera), four are plant feeders and pests of trees, such as most species of spruce (*Picea*) and pine (Clausen 1978). We have no information on how these species arrived in the U.S., although they probably came to North America in European trees imported in the 1920s to Ottawa, where they were first recorded (Clausen 1978). The other two non-indigenous diprionids were purposefully introduced for biological control (see above).

Most introduced bruchid beetles are pests, feeding mainly on seeds, such as beans, peas and other leguminous crops (Clausen 1978). They are believed to have entered the U.S. in their host seeds. Some species feed on invasive plants such as *Cytisus scoparius* (Scotch broom) (Kim 1991).

Although, as we mentioned above, two cecidomyiid flies were introduced for biological control, most species were accidentally introduced with plants or soil. And, again, one species is listed by Kim (1991) as feeding on brooms of the genus *Cytisus* (most likely Scotch broom).

Aphids of the family Adelgidae were accidentally introduced from Europe (Clausen 1978), probably as hosts of imported European plant species. The three species listed by Kim and Wheeler (1991) are listed as major pests by Kim (1991).

Finally, the Cynipidae (Hymenoptera) are gall-forming wasps that were most likely accidentally introduced with cultivated plants.

5.4 Other families

The Oestridae (Diptera) are internal parasites of mammals, especially of livestock. Four species in the genus *Gasterophylus* are intestinal parasites of horses; two species of *Hypoderma* are parasites of cattle and caribou; and one species of *Oestrus* is a parasite of sheep (Borror et al. 1989). All seven species are believed to have been introduced with their hosts (Frank et al. 1997).

The fleas (Siphonaptera, Pulicidae) are ectoparasites of birds and mammals and, again, are believed to have arrived with their hosts (Borror et al. 1989). These introduced pulicid fleas are cosmopolitan, having also been introduced by human transport to all continents except Antarctica (Lewis 1995).

Table 2. Species with significantly higher numbers of invasive species than the random expectation. Letters between brackets indicate orders: C, Coleoptera; D, Diptera; H, Hymenoptera; He, Heteroptera; Ho, Homoptera; L, Lepidoptera; O, Orthoptera; S, Siphonaptera; T, Thysanoptera. Numbers between brackets in the biological control column indicate numbers of species intentionally introduced for biocontrol over the total of introduced species in the family, according to Clausen (1978).

Biological control	Soils	Introduced with cultivated plants — crop pests	Other
Cecidomyiidae (D) (2/23)	Staphylinidae (C)	Bruchidae (C)	Oestridae (D) (endoparasites of mammals)
Tephritidae (D) (5/23)	Cecidomyiidae (D)	Cecidomyiidae (D)	Pulicidae (S) (ectoparasites of mammals)
Aphidiidae (H) (3/12)	Gryllotalpidae (O)	Tephritidae (D)	Anobiidae (C) (mainly stored food feeders)
Aphelinidae (H) (37/61)		Aphididae (Ho)	Dermestidae (C) (scavengers; dead animal tissue feeders)
Diprionidae (H) (2/6)		Adelgidae (Ho)	
Encyrtidae (H) (35/62)		Cynipidae (H)	
Eulopidae (H) (14/44)		Diprionidae (H)	
Pteromalidae (H) (16/41)		Eurytomidae (H)	
Tetracampidae (H) (4/6)		Tenthredinidae (H)	
Anthocoridae (He) (1/7)		Tortricidae (L)	
Coccinellidae (C) (12/25)		Thripidae (T)	
		Aeolothripidae (T)	

The dermestid beetles are mainly scavengers, feeding primarily on materials rich in protein. Most introduced species are pests of stored materials such as wool, silk and dry food. Some species, notably *Athrenus museorum*, feed on dead animal tissues and are a serious threat to museum collections. All non-indigenous dermestids probably arrived in the U.S. in their food sources.

All introduced anobiid beetles are considered pests, feeding on stored products, mainly food. Probably the best-known species is the drugstore beetle, *Stegobium paniceum,* which is known for eating “almost everything”, from food to books (Borror et al. 1989).

6. DISCUSSION

Perhaps the most obvious result of our analysis is that there is a highly non-random distribution of invasive species among insect families. This result has important implications for the theme developed in this book: by favoring the spread of only species clustered in certain families we are contributing to the homogenization of the world’s biota — the production of a “planet of weeds” (Quammen 1998).

A second important result of our analysis is that, for those families that have more introduced species than would be expected by chance, human transport seems to be an important “selectivity factor”. All the families at the top of our list (Table 1) had substantial numbers of species introduced either purposefully for biological control or accidentally as hosts of introduced plants, soils, animals or food products. Others have suggested the role of human transport as an important factor determining the introduction of propagules of invasive species. For example, Chown et al. (1998) have found a strong relationship between the number of human occupants and the number of species introduced in islands of the southern ocean; they found this to be the case for plants, insects, and mammals, but not for land birds. Lockwood (1999) also found human transport to be the most important factor determining the introduction of non-indigenous birds at a global scale. Finally, Williamson (1996) argues that human introductions are a crucial factor determining propagule pressure, which ultimately determines the establishment of introduced species. Thus, human transport would increase the likelihood of establishment of an invasive species by increasing propagule pressure. The role of propagule pressure as a determinant of the establishment of invasive species has been formally analysed by Hooper and Roush (1993). They found that, for parasitoids introduced for biological control of lepidopteran pests, the proportion of parasitoid populations that established increased with the number of parasitoids per release, the total number released, and the number collected.

It could be argued that the role of human transport might also be important for those families that show no selectivity (i.e., that the number of human-introduced species per family does not differ from the random expectation). Because of the difficulty of gathering information on transport for all 170 families with at least one introduced species, we tested this hypothesis only for the Hymenoptera. Within this order, the proportion of species in a family that is used for biological control seems to be related to the overall selectivity operating on that particular family. It could be argued that biological control agents are not “true invasives,” because they are purposefully introduced to control particular target pest species, and therefore they do not have an important impact on the native biota. However, biological control agents do indeed colonise native, non-target hosts. Hawkins and Marino (1997) found that 16% of parasitoids introduced into North America have colonised native hosts. Furthermore, owing to the characteristics of the available database, they judged this figure to be an underestimate.

It is noteworthy that many (most) non-biological control insects were introduced accidentally on their hosts. In most cases, those hosts are economically important plants, vertebrates or food products, although there are some examples in which the host itself was accidentally introduced (e.g., three species that feed on Scotch broom). We know that introduced host species also show taxonomic selectivity, at least in the case of plants (Daehler 1998, Pysek 1998); we hypothesise that the taxonomic selectivity observed in our insect database could be driven, at least in part, by the taxonomic selectivity operating on their hosts.

We must consider another alternative explanation for our finding: it is possible that the patterns we found, even though they are statistically robust, simply reflect which data are gathered. In particular, species important to humans either as pests or as useful tools for biocontrol are noticed more than species that do not have such direct importance. Although we believe that this is scenario is quite possible, again, because of the state of the available database, this hypothesis is untestable.

An important drawback in our data (as well as in most available data on species introductions) is that they are adequate only for those species that arrived and survived, not those that arrived but disappeared. For insects, only for biological control are there substantial data on failed introductions. Furthermore, we have no systematic data to quantify the impact of the different survivors on the native ecosystems, although absence of standardized impact data plagues all research on non-indigenous species (Parker et al. 1999).

Another possibility that we did not analyze is whether the biology of the invaders determines their success. Leston (1957) suggested that high level taxa have inherent properties that predispose some of them to be better colonists than others. Daehler (1998) found that some traits were indeed common among plant families that are over-represented in terms of the number of invasive species they contain. He found that over-represented families include: (i) species belonging to freshwater aquatic plant families, which are more likely to be both weedy and natural area invaders than species from other plant families; (ii) other weedy species that posses several of the life history characteristics of "ideal weeds" proposed by Baker (1965), such as flowering at an early age, high seed production, facultative self-pollination, and rapid vegetative growth; (iii) other natural area invaders that are grasses, nitrogen fixers, climbers, and clonal trees. Regrettably, as we mentioned in the introduction, other attempts to find those biological characteristics have been unsuccessful.

Nevertheless, we believe that the biological characteristics of insect invaders are potentially important determinants of their success after their introduction; however, the current development of the database precludes any generalisation. Furthermore, the very fact that we are working at higher taxonomic levels makes any attempt at finding such generalisations likely to fail. However, where the search for biological characteristics is done at lower taxonomic levels, and particularly when comparing closely related species within a taxonomic group, more useful generalisations may arise. Rejmánek's (1996) analysis of several reproductive morphological traits in closely related *Pinus* species is a good example. We believe that this approach — the detailed study of particular, closely related groups — is more promising than the approach taken by us and by several other authors in the present volume.

Ten years ago, Simberloff (1989) concluded that "it is depressing to be unable to draw striking generalisations about introduced insects but it would serve no worthwhile purpose to generalize prematurely". We believe that, in these respects, our degree of knowledge about insect invasions — and of invasions in general — has not changed significantly. The only possible generalisation, if any, is that human transport is an important factor in promoting the biotic homogenization of our changing world. We view this conclusion as neither new nor striking. However, until there are more comprehensive data on introductions, including those that fail, useful analysis of the roles of the biotic and abiotic nature of the location of introductions and the biology of introduced species are impossible.

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Appendix. Insect families with at least one species introduced in the United States (according to Kim and Wheeler 1991).

Order	Family	w_i	us_i	n_i	x_i	$P_i(x_i)$
Ephemeroptera	Baetidae	520	147	374	1	0.593
Orthoptera	Tettigoniidae	375	243	134	2	0.042
Orthoptera	Gryllidae	800	96	705	1	0.816
Orthoptera	Gryllotalpidae	65	7	63	5	5×10^{-7}
Mantodea	Mantidae	1500	14	1490	4	0.480
Blattodea	Blattidae	525	8	522	5	0.009
Blattodea	Blattellidae	1740	15	1728	3	0.783
Blattodea	Blaberidae	1020	9	1015	4	0.229
Dermaptera	Forficulidae	30	4	28	2	0.002
Dermaptera	Anisolabididae	300	9	294	3	0.035
Dermaptera	Labiidae	384	9	377	2	0.229
Isoptera	Kalotermitidae	293	18	276	1	0.485
Isoptera	Rhinotermitidae	159	9	151	1	0.304
Coleoptera	Anobiidae	450	299	158	7	1×10^{-7}
Coleoptera	Anthribidae	2600	79	2523	2	0.984
Coleoptera	Bostrichidae	700	64	643	7	0.001
Coleoptera	Brentidae	2300	5	2296	1	0.996
Coleoptera	Bruchidae	1500	34	1479	13	8×10^{-5}
Coleoptera	Buprestidae	15000	675	14333	8	1.000
Coleoptera	Byrrhidae	300	72	229	1	0.423
Coleoptera	Cantharidae	5000	468	4534	2	1.000
Coleoptera	Carabidae	30000	2271	27778	49	0.990
Coleoptera	Cerambycidae	35000	956	34051	7	1.000
Coleoptera	Chrysomelidae	35000	1481	33575	56	0.998
Coleoptera	Cleridae	4000	266	3737	3	0.994
Coleoptera	Coccinellidae	4500	399	4126	25	4×10^{-5}
Coleoptera	Colydiidae	1300	87	1214	1	0.946
Coleoptera	Curculionidae	50000	2614	47539	153	0.188
Coleoptera	Dermestidae	850	129	732	11	2×10^{-6}
Coleoptera	Derodontidae	19	7	13	1	0.031
Coleoptera	Elateridae	9000	885	8123	8	0.999
Coleoptera	Eucnemidae	1200	71	1130	1	0.934

Order	Family	w_i	us_i	n_i	x_i	$P_i(x_i)$
Coleoptera	Histeridae	3000	499	2503	2	0.983
Coleoptera	Hydrophilidae	2000	284	1721	5	0.397
Coleoptera	Lampyridae	2000	124	1881	5	0.471
Coleoptera	Lathridiidae	500	120	382	2	0.234
Coleoptera	Merylidae	5000	520	4481	1	1.000
Coleoptera	Nitidulidae	3000	183	2823	6	0.670
Coleoptera	Oedemeridae	1000	86	917	3	0.378
Coleoptera	Pselaphidae	5000	654	4349	3	0.998
Coleoptera	Scarabaeidae	25000	1395	23641	36	0.999
Coleoptera	Silphidae	175	42	134	1	0.275
Coleoptera	Staphylinidae	30000	3187	27041	228	0.000
Coleoptera	Tenebrionidae	18000	1008	16995	3	1.000
Coleoptera	Trogossitidae	600	64	538	2	0.370
Siphonaptera	Ceratophyllidae	760	125	639	4	0.070
Siphonaptera	Pulicidae	190	33	163	6	3×10^{-6}
Diptera	Agromyzidae	1800	188	1614	2	0.899
Diptera	Anthomyidae	1000	148	861	9	3×10^{-4}
Diptera	Braulidae	4	1	4	1	0.010
Diptera	Calliphoridae	3000	78	2928	6	0.703
Diptera	Cecidomyiidae	4000	1059	2975	34	0.000
Diptera	Ceratopogonidae	1200	463	739	2	0.530
Diptera	Chamaemyiidae	100	36	66	2	0.011
Diptera	Chloropidae	1000	273	728	1	0.826
Diptera	Cryptochetidae	20	1	20	1	0.047
Diptera	Culicidae	3000	150	2853	3	0.967
Diptera	Drosophilidae	1500	117	1384	1	0.964
Diptera	Ephydridae	1000	426	575	1	0.749
Diptera	Hippoboscidae	330	28	305	3	0.038
Diptera	Lauxaniidae	1200	135	1066	1	0.923
Diptera	Lonchaeidae	500	38	463	1	0.671
Diptera	Muscidae	3000	622	2388	10	0.066
Diptera	Oestridae	65	41	31	7	0.000
Diptera	Opomyzidae	50	13	38	1	0.087
Diptera	Otitidae	400	127	275	2	0.142
Diptera	Platystomatidae	1000	41	960	1	0.900
Diptera	Psilidae	200	34	167	1	0.331
Diptera	Rhagionidae	300	104	200	4	0.001
Diptera	Rhinophoridae	85	4	82	1	0.179
Diptera	Sepsidae	240	34	209	3	0.014
Diptera	Stratiomyidae	1400	254	1149	3	0.521
Diptera	Syrphidae	5000	874	4135	9	0.659
Diptera	Tachinidae	6000	1277	4743	20	0.013

Order	Family	w_i	us_i	n_i	x_i	$P_i(x_i)$
Diptera	Tephritidae	4000	280	3743	23	6×10^{-5}
Diptera	Tipulidae	13000	1517	11484	1	1.000
Heteroptera	Alydidae	250	29	223	2	0.101
Heteroptera	Anthocoridae	500	85	422	7	9×10^{-5}
Heteroptera	Cimicidae	75	14	63	2	0.010
Heteroptera	Coreidae	1800	120	1683	3	0.768
Heteroptera	Cynidae	300	7	296	3	0.035
Heteroptera	Lygaeidae	3000	288	2718	6	0.635
Heteroptera	Miridae	10000	1777	8259	36	0.001
Heteroptera	Nabidae	300	48	253	1	0.456
Heteroptera	Pentatomidae	5000	247	4760	7	0.937
Heteroptera	Reduviidae	5000	106	4895	1	1.000
Heteroptera	Rhopalidae	142	36	108	2	0.028
Heteroptera	Tingidae	1800	157	1649	6	0.208
Homoptera	Adelgidae	50	22	31	3	6×10^{-5}
Homoptera	Aleyrodidae	1156	99	1059	2	0.722
Homoptera	Aphididae	3500	1351	2169	20	6×10^{-7}
Homoptera	Cicadellidae	20000	2507	17553	60	0.005
Homoptera	Delphacidae	1300	145	1156	1	0.938
Homoptera	Diaspididae	1500	194	1314	8	0.015
Homoptera	Phylloxeridae	60	29	32	1	0.074
Homoptera	Pseudococcidae	1100	280	823	3	0.317
Hymenoptera	Andrenidae	4000	1199	2802	1	0.999
Hymenoptera	Anthophoridae	4000	920	3082	2	0.995
Hymenoptera	Aphelinidae	4000	17	4044	61	0.000
Hymenoptera	Aphidiidae	800	114	698	12	2×10^{-7}
Hymenoptera	Apidae	1000	57	944	1	0.897
Hymenoptera	Argidae	500	59	442	1	0.654
Hymenoptera	Bethylidae	1000	196	805	1	0.855
Hymenoptera	Braconidae	40000	1937	38170	107	0.062
Hymenoptera	Cephidae	102	12	92	2	0.021
Hymenoptera	Ceraphronidae	150	48	103	1	0.219
Hymenoptera	Chalcididae	1400	102	1303	5	0.206
Hymenoptera	Chrysididae	3120	227	2897	4	0.916
Hymenoptera	Cimbicidae	140	12	129	1	0.267
Hymenoptera	Colletidae	3000	153	2848	1	0.999
Hymenoptera	Cynipidae	1200	636	572	8	9×10^{-5}
Hymenoptera	Diprionidae	100	41	65	6	1×10^{-8}
Hymenoptera	Encyrtidae	2800	471	2391	62	0.000
Hymenoptera	Eucoilidae	700	80	624	4	0.065
Hymenoptera	Eulophidae	3000	507	2537	44	0.000

Order	Family	w_i	us_i	n_i	x_i	$P_i(x_i)$
Hymenoptera	Eupelmidae	700	95	610	5	0.017
Hymenoptera	Eurytomidae	1100	244	871	15	6×10^{-9}
Hymenoptera	Evaniidae	500	11	491	2	0.330
Hymenoptera	Figitidae	250	60	193	3	0.012
Hymenoptera	Formicidae	14000	696	13353	49	0.003
Hymenoptera	Ichneumonidae	15000	3322	11726	48	4×10^{-4}
Hymenoptera	Megachilidae	3000	682	2326	8	0.201
Hymenoptera	Mymaridae	1200	120	1088	8	0.005
Hymenoptera	Pamphiliidae	170	72	99	1	0.212
Hymenoptera	Platygastridae	1100	192	915	7	0.007
Hymenoptera	Pteromalidae	2800	395	2446	41	0.000
Hymenoptera	Scelionidae	3000	275	2727	2	0.989
Hymenoptera	Signiphoridae	75	21	55	1	0.124
Hymenoptera	Siricidae	90	19	74	3	0.001
Hymenoptera	Sphecidae	7700	1139	6571	10	0.952
Hymenoptera	Tenthredinidae	3000	731	2307	38	0.000
Hymenoptera	Tetracampidae	35	6	35	6	3×10^{-10}
Hymenoptera	Tiphiidae	1500	225	1278	3	0.592
Hymenoptera	Torymidae	1000	175	831	6	0.016
Hymenoptera	Trichogrammatidae	440	43	401	4	0.017
Hymenoptera	Vespidae	800	415	391	6	0.000
Hymenoptera	Xiphydriidae	90	9	82	1	0.179
Trichoptera	Hydropsychidae	900	130	771	1	0.843
Trichoptera	Hydroptilidae	600	201	400	1	0.618
Lepidoptera	Agonoxenidae	4	1	4	1	0.010
Lepidoptera	Arctiidae	2000	264	1737	1	0.985
Lepidoptera	Argyresthiidae	100	52	49	1	0.111
Lepidoptera	Bombycidae	100	1	100	1	0.214
Lepidoptera	Choreutidae	400	29	372	1	0.591
Lepidoptera	Coleophoridae	500	169	334	3	0.047
Lepidoptera	Cossidae	1000	45	956	1	0.899
Lepidoptera	Gelechiidae	4000	630	3381	11	0.195
Lepidoptera	Geometridae	20000	1404	18604	8	1.000
Lepidoptera	Gracillariidae	1000	275	728	3	0.255
Lepidoptera	Hesperiidae	3000	290	2711	1	0.999
Lepidoptera	Lycaenidae	3000	136	2865	1	0.999
Lepidoptera	Lymantriidae	2500	35	2468	3	0.935
Lepidoptera	Lyonetiidae	300	122	179	1	0.350
Lepidoptera	Nepticulidae	400	82	319	1	0.535
Lepidoptera	Noctuidae	25000	2925	22085	10	1.000
Lepidoptera	Ochsenheimeriidae	23	1	23	1	0.054
Lepidoptera	Oecophoridae	4000	225	3788	13	0.131

Order	Family	w_i	us_i	n_i	x_i	$P_i(x_i)$
Lepidoptera	Phaloniidae	500	110	391	1	0.609
Lepidoptera	Pieridae	2000	225	1776	1	0.986
Lepidoptera	Psychidae	6000	26	5976	2	1.000
Lepidoptera	Pyralidae	20000	1374	18649	23	1.000
Lepidoptera	Saturniidae	1000	69	932	1	0.893
Lepidoptera	Sesiidae	1000	115	888	3	0.359
Lepidoptera	Sphiingidae	850	124	727	1	0.826
Lepidoptera	Tineidae	3000	175	2828	3	0.965
Lepidoptera	Tortricidae	4000	1053	3025	78	0.000
Lepidoptera	Yponomeutidae	1000	32	977	9	0.001
Thysanoptera	Aeolothripidae	230	57	178	5	0.000
Thysanoptera	Phlaeothripidae	3000	348	2667	15	0.003
Thysanoptera	Thripidae	1500	264	1279	43	0.000

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