The role of opportunity in the unintentional introduction of nonnative ants

Andrew V. Suarez[*,†], **David A. Holway**[‡], **and Philip S. Ward**[§]

[*]Departments of Entomology and Animal Biology, University of Illinois at Urbana–Champaign, 320 Morrill Hall, 505 South Goodwin Avenue, Urbana, IL 61801; [‡]Section of Ecology, Behavior, and Evolution, Division of Biological Sciences, University of California at San Diego, 9500 Gilman Drive, La Jolla, CA 92093; and [§]Department of Entomology and Center for Population Biology, University of California, One Shields Avenue, Davis, CA 95616

Edited by May R. Berenbaum, University of Illinois at Urbana–Champaign, Urbana, IL, and approved October 10, 2005 (received for review July 19, 2005)

A longstanding goal in the study of biological invasions is to predict why some species are successful invaders, whereas others are not. To understand this process, detailed information is required concerning the pool of species that have the opportunity to become established. Here we develop an extensive database of ant species unintentionally transported to the continental United States and use these data to test how opportunity and species-level ecological attributes affect the probability of establishment. This database includes an amount of information on failed introductions that may be unparalleled for any group of unintentionally introduced insects. We found a high diversity of species (232 species from 394 records), 12% of which have become established in the continental United States. The probability of establishment increased with the number of times a species was transported (propagule pressure) but was also influenced by nesting habit. Ground nesting species were more likely to become established compared with arboreal species. These results highlight the value of developing similar databases for additional groups of organisms transported by humans to obtain quantitative data on the first stages of the invasion process: opportunity and transport.

biological invasions | introduced species | invasive ants | propagule pressure

An outstanding challenge in ecology lies in identifying the factors that determine whether introduced species establish successfully in new environments (1, 2). To isolate such factors, it is necessary to know not only why certain introductions succeed but also why others do not. Ignoring failed introductions can seriously bias an understanding of invasion success (3). Unfortunately, the scarcity of appropriate data on unsuccessful introductions impedes progress in this area of research.

For studies that focus on the establishment phase of animal introductions, the most complete surveys deal with intentional introductions: insects released for biological control (4) and bivalves (5) or vertebrates (6–9) purposefully introduced for food or aesthetic reasons. Such studies have been instrumental in identifying factors, such as propagule supply, that influence establishment success because they include quantitative data on failed introductions (10). Despite the unquestioned value of such studies, intentional introductions may not be representative of invasions in general. First, humans unintentionally introduce many species into new environments (11), and these accidental events represent a sizeable fraction of the most prominent invasive species (12). Second, deliberate introductions involve species selected by humans with respect to specific characteristics. The species pool for intentional introductions in most cases will thus differ from that for unintentional introductions. Lastly, intentional introductions bypass the first stage of invasion, opportunity or transport. It is this dispersal stage of the invasion process for which appropriate data remain scarce for most organisms (1, 13).

Here, we develop an extensive database of ant species unintentionally transported into the continental United States and use these data to test how opportunity and species-level ecological attributes affect the probability of establishment. Introduced ants are an appropriate group for this approach because they include many ecologically destructive invasive species (14), five of which are considered among the world's top 100 invaders (12). In addition to their significant economic and agricultural impacts, invasive ants attack and displace native ant species, negatively affect vertebrate populations, and disrupt ant–plant mutualisms (reviewed in ref. 14). Although hundreds of ant species have become established outside of their native ranges worldwide (including >60 in the continental United States) (15), we know little about human-mediated transport of this important group of insects.

Materials and Methods

Our database was developed by using ants that were intercepted in commerce inspected by United States Department of Agriculture customs officials between 1927 and 1985. These port-of-entry (POE) samples have been stored at the National Museum of Natural History (formerly the United States National Museum) since acquisition. Each sample includes information on the port of origin, the POE into the United States, and (usually) the type of commerce involved. We only included records for which the port of origin was known or inferred to be within the native range of the species in the sample. By comparing species in our database with detailed regional surveys and museum collections from different parts of the United States (15–18), we were able to ascertain whether or not species in the POE database have established populations in this region. Our data thus provide an amount of information on failed introductions that may be unequalled for any group of unintentionally introduced insects. The lack of data on failed introductions is a recognized constraint in surveys of nonnative insects (19–21).

We assume that this database represents a random sample of the species pool of ants with the opportunity to become established by means of human transport. First, the samples were originally collected without knowledge of species identity and before many introduced ants were known to have been established in the United States. Second, the species in our sample are similar to ants as a whole with respect to taxonomic composition and biogeographic provenance (see *Results and Discussion*). Finally, the material we used to assemble this data set comes from unsorted material stored in bulk lots (in alcohol) at the National Museum of Natural History.

We used multiple logistic regression to test the influence of propagule supply (the number of records for each species in the database), nesting behavior, and their interaction on the success or failure of ant introductions for a subset of the data for which nesting habit was available (156 of 232 species). Propagule supply

---

Conflict of interest statement: No conflicts declared.

This paper was submitted directly (Track II) to the PNAS office.

Abbreviation: POE, port of entry.

[†]To whom correspondence should be addressed. E-mail: avsuarez@life.uiuc.edu.

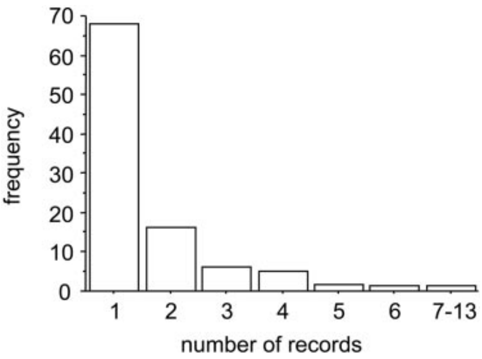

Fig. 1. Distribution of the number of records for each species (represented as the percentage of singletons, doubletons, . . . seven or more records) in our database.

was a continuous variable, and nesting behavior was a dichotomous variable (strictly arboreal versus primarily ground nesting).

Results and Discussion

From a set of 394 samples, we identified 232 species of ants from 58 genera and 12 subfamilies (Table 5, which is published as supporting information on the PNAS web site). The high level of diversity within this limited sample ($>58\%$ of the records represented different species) illustrates the remarkable number of ant species that were moved around by humans throughout the 20th century (Fig. 1). Species in the POE database did not differ from ants generally with respect to taxonomic composition at the level of the subfamily or with respect to biogeographic origin (Table 1). These similarities also held when we compared POE species with introduced ant species that are currently established in the United States (Tables 1 and 2). In addition, we observed similarity in taxonomic composition at the subfamily level between POE species and ants as a whole when the analysis was restricted to species originating from the Neotropics (the most commonly represented region of geographic origin) (Table 3). The patterns summarized in Tables 1–3 strengthen our assumption that the species composition of our database is unbiased and thus represents an approximately random sample of ants unintentionally transported in human commerce. Interestingly, ants in our database differed from insects generally with respect to biogeographic origin (Table 2) (22).

Table 1. The distribution of ant species by subfamily for ants in the POE database, ants established in the United States, and all ants

Subfamily	All POE (%)	Established POE	Established U.S.	All ants (%)
Cerapachyinae	1 (<1)	0	0	198 (2)
Dolichoderinae	26 (11)	5	4	554 (6)
Ecitoninae	3 (1)	0	0	146 (2)
Formicinae	50 (22)	4	14	2,458 (27)
Myrmicinae	108 (47)	16	34	4,377 (47)
Poneromorphs*	24 (11)	3	12	1,299 (14)
Pseudomyrmecinae	16 (7)	1	1	197 (2)

Compared with all known ant species established in the United States, all POE ants and established POE ants do not differ with respect to the distribution of species across major subfamilies [all POE ants (data from ref. 29) versus all established ants in the United States (data from refs. 15–18): $G = 1.796$, $P = 0.62$, df = 3; established POE ants versus all established ants in the United States: $G = 4.69$, $P = 0.20$, df = 3].

*Includes ants from the recently separated subfamilies Ponerinae and Ectatomminae (30).

Table 2. Species as a function of geographical origin for ants in the POE database, ants established in the United States, and all insects established in the United States

Geographical region	All POE	Established POE	Established ants U.S.	Established insects U.S.
Neotropics	128	10	33	170
Palearctic	24	4	4	941
Africa	15	2	6	62
Oriental/Australian	49	9	12	225

Compared with all known ant species established in the United States, all POE ants (POE specimens intercepted by United States Department of Agriculture officials at customs stations) and established POE ants do not differ with respect to their geographical origins [all POE ants versus all established ants in the United States: $G = 1.254$, $P = 0.74$, df = 3; established POE ants versus ants known to have established populations in the United States (data from ref. 15–18): $G = 4.352$, $P = 0.36$, df = 3]. However, compared with known insect species established in the United States (data from ref. 22), established POE ants come from different geographical regions ($G = 86.441$, $P < 0.001$, df = 3). Introduced insects in the United States originate mostly from the western Palearctic, whereas ants come mostly from the Neotropics.

Of the 232 species in the POE database, only 28 species from 17 genera now occur as established nonnative species in the continental United States, and three species can be considered invasive (*Linepithema humile*, *Technomyrmex albipes*, and *Wasmannia auropunctata*) (15–18). By compiling empirical data from a variety of different organisms Williams and Fitter (23) suggested that ≈10% of species in any given taxonomic group would be successful at each of the four stages of the introduction process (opportunity, escape, establishment, and spread) resulting in ≈0.1% of species becoming widespread invaders from any given species pool. The percentages of established species and invasive species in our data set (12% and 1%, respectively) are approximately an order of magnitude higher than those predicted by the "tens rule" pattern ($\chi^2 = 327.96$, df = 1, $P < 0.001$) (23). As with recent surveys on intentionally introduced vertebrates (9), our results suggest that even unintentionally introduced insects are more likely to become established than the "tens rule" would predict. Using this rule for predictive purposes therefore seems unwarranted. Compared with solitary insects, eusocial insects, such as ants, could have a relatively high probability of establishment because their colonies may be able to better withstand environmental stresses that occur during the process of introduction.

Intercepted ants occurred predominantly on plants or plant material. Of the 363 records for which the type of commerce was listed on the POE label, 94% involved cases where ants were found on plants. Predominant categories included orchids and

Table 3. Ant species as a function of subfamily for Neotropical ants (the most represented source region for POE ants)

Subfamily	POE (%)	Neotropical ants (%)
Cerapachyinae	0 (0)	25 (1)
Dolichoderinae	17 (11)	209 (9)
Ecitoninae	3 (2)	129 (5)
Formicinae	34 (22)	422 (18)
Myrmicinae	67 (43)	1,109 (47)
Poneromorphs*	21 (14)	348 (15)
Pseudomyrmecinae	13 (8)	115 (5)

Compared with all neotropical ants, all POE ants (data from ref. 29) that originated in the neotropics do not differ with respect to the distribution of species across major subfamilies ($G = 5.16$, $P = 0.2713$, df = 4).

*Includes ants from the recently separated subfamilies Ponerinae and Ectatomminae (30).

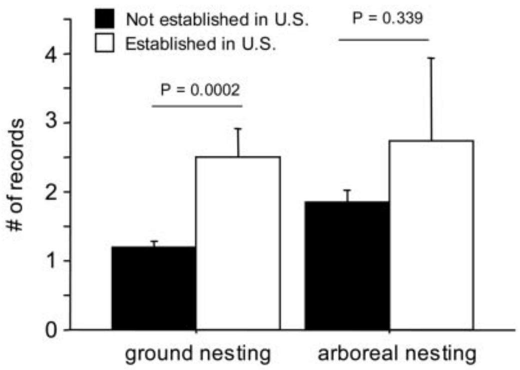

Fig. 2. Interaction between propagule pressure (number of records in the database), nesting habitat, and establishment success in the United States.

bromeliads (49%), fruits (14%), other ornamental plants (11%), and trees in the genus *Acacia* (4%). Less important categories included cactus, sugar cane, ferns, moss, and nonplant material, such as soil, pallets, and military cargo. Not surprisingly, arboreal ants occurred often in our samples. Of the 156 species for which definitive data on nest site preferences exist, strictly arboreal ants made up 52% of the species and 57% of the records. Despite the prevalence of arboreal ants, their nesting habit reduced the likelihood of establishment; strictly arboreal ants made up only 14% of those species in our samples with established populations in the United States ($\chi^2 = 19.664$, df = 1, $P < 0.0001$). Presumably, the low rate of establishment for arboreal ants results from the lack of suitable nest sites in new environments; arboreal ants often exhibit preferences for particular types of trees. Moreover, of the four arboreal ants in our data set that have become established in new (nonnative) locations in the United States (*Camponotus planatus*, *Plagiolepis alluaudi*, *Monomorium floricola*, and *Pseudomyrmex gracilis*), all exhibit considerable flexibility in their choice of nesting sites and will persist in a wide variety of tree species.

Although numerous studies argue for a prominent role for propagule pressure in the establishment of introduced species (10, 11, 24), we found that the extent to which this variable influenced establishment success in ants depended on the nesting habits of the species involved. Using multiple logistic regression, we found that propagule pressure (defined as the number of records in our database), nesting behavior, and their interaction were all significantly associated with the success or failure of ant introductions (overall model: $\chi^2 = 36.46$, df = 3, $P < 0.0001$; propagule supply: Wald $\chi^2 = 9.32$, df = 1, $P = 0.0023$; nesting behavior: Wald $\chi^2 = 14.65$, df = 1, $P < 0.0001$; interaction: Wald $\chi^2 = 4.46$, df = 1, $P = 0.0347$). For primarily ground-nesting ants, species with established populations in the United States had more records in our database compared with species that never established ($P = 0.0002$, Mann–Whitney *U* test) (Fig. 2). For strictly arboreal ants, in contrast, the number of records was not significantly different for species that established versus species that failed ($P = 0.399$, Mann–Whitney *U* test) (Fig. 2). The higher probability of establishment for ground-dwelling ants illustrates how a key ecological attribute can interact with propagule pressure to affect the probability of establishment. In general, interactions between propagule pressure and species-level characteristics may influence invasion success in a number of taxa (10, 24). Unfortunately, efforts to include other ecological variables in our analyses are limited by the scarcity of information concerning the biology of the majority of the ant species in our sample. Traits, such as general dietary requirements, large colony size, polygyny, and unicoloniality, have been implicated in the success of invasive ants (14, 25). How these traits may interact with propagule pressure to influence establishment success remains unresolved and provides a strong justification for the continued study of the basic natural history of ants (e.g., 26).

Table 4. The number of records in our data set for the 16 most common genera separated by whether they represent established or nonestablished species

Genus	No. of records Established	 Nonestablished	Ratio of established to nonestablished species
Azteca	0	9	0.0
Dolichoderus	0	13	0.0
Crematogaster	0	15	0.0
Temnothorax	0	18	0.0
Solenopsis	0	9	0.0
Pseudomyrmex	3	32	0.09
Linepithema	1	10	0.09
Pheidole	2	18	0.10
Pachycondyla	1	7	0.13
Camponotus	11	52	0.18
Paratrechina	2	9	0.18
Tapinoma	4	11	0.27
Monomorium	12	9	0.57
Technomyrmex	4	3	0.57
Tetramorium	15	2	0.88
Cardiocondyla	8	0	1.0

For 11 genera, nonestablished species were overrepresented relative to established species. The exceptions (*Cardiocondyla, Monomorium, Technomyrmex,* and *Tetramorium*) are genera with many known tramp species (15).

Our data suggest that opportunity alone may not be sufficient to promote establishment. For seven of the 11 most common genera in our database with known introduced species, established species were underrepresented relative to species that have not successfully established populations in the United States (Table 4). Of the most widespread invasive ants in North America, for example, the red imported fire ant (*Solenopsis invicta*) and the black imported fire ant (*Solenopsis richteri*) were absent from our samples, and the Argentine ant (*L. humile*) was represented only by a single record. In contrast, four genera in our sample (*Cardiocondyla*, *Monomorium*, *Technomyrmex*, and *Tetramorium*) were dominated by records of species known to have established populations in the United States (Table 4). These genera are predominantly old-world in origin and have relatively few or no species native to the new world. The differences in success among genera suggest that with a larger data set we may able to determine how factors, such as competition from taxonomically similar species, specific ecological characteristics, and propagule pressure, may interact to promote invasion success.

Concerns that our data set does not represent a random sample stem from a number of limitations inherent in our approach. First, there may have been biases concerning differential detectability of taxa in quarantine or uneven retention of particular groups. Evidence that these biases are not large comes from the data summarized in Tables 1–3, which demonstrate that, on a coarse level, the species composition of the POE sample resembles that of both ants as a whole and ants successfully established in the United States. Any differences in the detectability of ground-nesting ants versus arboreal ants would be unlikely to alter our major conclusions about nesting habit or propagule pressure because we obtained qualitatively similar results when we analyzed the entire data set or when we split the data set according to nesting habit. Second, it is possible that select taxa were removed from museum stores after the deposition of specimens. As noted above, the unsorted nature of this material greatly diminishes the feasibility of selective removal of specific species or genera. Moreover, any bias toward the omission of common species would make it harder for us to have detected a significant effect of propagule pressure. Efforts to increase the size of this data set and to include records from a wider variety of sources will help to reduce these potential biases.

This study illustrates how museum collections can contribute invaluably to the study of invasions (27). Although insects, including ants, represent prominent invasive species (14, 20, 23), unintentional introductions of insect taxa remain woefully understudied with respect to the determinants of establishment success (1, 20). Because an important component of any such study would involve a historical record of species that have the opportunity to establish in new environments, insects intercepted in quarantine represent an invaluable resource to test hypotheses concerning establishment success in new environments. We submit that reinstating this or similar programs (e.g., ref. 28) and initiating efforts to effectively curate intercepted material would be a wise investment of resources in the battle against invasive species.

We thank Julie Lockwood and two anonymous reviewers for insightful comments on previous versions of the manuscript. We thank the United States Department of Agriculture and the National Museum of Natural History for their foresight in collecting and retaining these POE specimens. Funding was provided by National Science Foundation Grants NSF INT 0305773, NSF DBI 0447379, and NSF EF 0431330.

1. Kolar, C. S. & Lodge, D. M. (2001) *Trends Ecol. Evol.* **16,** 199–204.
2. Shea, K. & Chesson, P. (2002) *Trends Ecol. Evol.* **17,** 170–176.
3. Simons, A. M. (2003) *Ecol. Lett.* **6,** 278–280.
4. Hopper, K. R. & Roush, R. T. (1993) *Ecol. Entomol.* **18,** 321–331.
5. Roy, K. D., Jablonski, D. & Valentine, J. W. (2001) *Ecol. Lett.* **4,** 366–370.
6. Case, T. J. (1996) *Biol. Conserv.* **78,** 69–96.
7. Kolar, C. S. & Lodge, D. M. (2002) *Science* **298,** 1233–1236.
8. Duncan, R. P., Blackburn, T. M. & Sol, D. (2003) *Annu. Rev. Ecol. Syst.* **34,** 71–98.
9. Jeschke, J. M. & Strayer, D. L. (2005) *Proc. Natl. Acad. Sci. USA* **102,** 7198–7202.
10. Lockwood, J. L., Cassey, P. & Blackburn, T. M. (2005) *Trends Ecol. Evol.* **20,** 223–228.
11. Ruiz, G. M., Fofonoff, P. W., Carlton, J. T., Wonham, M. J. & Hines, A. H. (2000) *Annu. Rev. Ecol. Syst.* **31,** 481–531.
12. Lowe, S., Browne, M., Boudjelas, S. & De Poorter, M. (2004) *100 of the World's Worst Invasive Alien Species: A Selection from the Global Invasive Species Database* (Invasive Species Specialist Group, Gland, Switzerland).
13. Puth, L. M. & Post, D. M. (2005) *Ecol. Lett.* **8,** 715–721.
14. Holway, D. A., Lach, L., Suarez, A. V., Tsutsui, N. D. & Case, T. J. (2002) *Annu. Rev. Ecol. Syst.* **33,** 181–233.
15. McGlynn, T. P. (1999) *J. Biogeogr.* **26,** 535–548.
16. Deyrup, M. (2003) *Fla. Entomol.* **86,** 43–48.
17. Deyrup, M., Davis, L. & Cover, S. (2000) *Trans. Am. Entomol. Soc.* **126,** 293–326.
18. Ward, P. S. (2005) *Zootaxa* **936,** 1–68.
19. Simberloff, D. (1986) in *Ecology of Biological Invasions of North America and Hawaii*, eds. Mooney, H. A. & Drake, J. A. (Springer, New York), pp. 3–26.
20. Simberloff, D. (1989) in *Biological Invasions: A Global Perspective*, eds. Drake, J. D., Mooney, H. A., di Castri, F., Groves, R. H., Kruger, F. J., Rejmanek, M. & Williamson, M. (Wiley, New York), pp. 61–72.
21. Vazquez, D. P. & Simberloff, D. (2001) in *Biological Homogenization*, eds. Lockwood, J. L. & McKinney, M. L. (Kluwer, New York), pp. 103–124.
22. Sailer, R. E. (1978) *Bull. Entomol. Soc. Am.* **24,** 3–11.
23. Williams, M. & Fitter, A. (1996) *Ecology* **77,** 1661–1665.
24. Cassey, P., Blackburn, T. M., Duncan, R. P. & Lockwood, J. L. (2005) *J. Anim. Ecol.* **74,** 250–258.
25. Passera, L. (1994) in *Exotic Ants: Impact and Control of Introduced Species*, ed. Williams D. F. (Westview, Boulder, CO), pp. 23–43.
26. Tschinkel, W. R. (1991) *Insectes Sociaux* **38,** 77–82.
27. Suarez, A.V. & Tsutsui, N. D. (2004) *BioScience* **54,** 66–74.
28. Wonham, M. J., Walton, W. C., Ruiz, G. M., Freese, A. M. & Galil, B. S. (2001) *Mar. Ecol. Prog. Ser.* **215,** 1–12.
29. Bolton, B. (1995) *J. Nat. Hist.* **29,** 1037–1056.
30. Bolton, B. (2003) *Mem. Am. Entomol. Inst.* **71,** 1–370.