Biological invasions: are they dependent on disturbance?

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Abstract: We utilize literature surveys to examine the relationship between establishment of exotic species and human or natural disturbances of ecosystems. Of the 133 papers published in 10 ecological journals between 1993 and 1995, 63 reported on field studies involving 299 and 103 successful, nonredundant plant and animal introductions, respectively. Invasions of terrestrial ecosystems dominated (>97%) the surveyed literature. Disturbance was associated with establishment of exotic species in 56% of these studies, though its importance differed among papers describing plants (68%) and animals (28%). Plants species (86%) were significantly more dependent on disturbance for establishment than were animals (12%). However, animals and plants that were dependent on disturbance for establishment were almost equally dependent (58 versus 68%) on it for range expansion. In a second survey, 402 plant and 103 animal taxa were identified that explicitly linked establishment of exotic species to disturbance. Human activities were attributed with establishment of species in 97 and 57% of these cases, respectively. Common mechanisms associated with establishment of exotic animals included ballast water discharge, intentional releases, and residential development. Establishment of exotic plants was associated with animal activities (e.g., grazing, seed introduction), soil disturbance, forestry, fire, agriculture, and human activities. In contrast to invasions theory, our survey indicates that the association between establishment and spread of exotic species and disturbance ought not be assumed a priori. Some animals repeatedly invade new habitats once geographic barriers are circumvented, indicating that communities may be more receptive to exotic species than previously acknowledged. By contrast, introduced plants established most often in disturbed habitats.

Key words: exotic species, introduced species, biological invasion, disturbance ecology.

Résumé : Les auteurs ont effectué une analyse de la littérature pour examiner l'établissement d'espèces exotiques en relation avec les perturbations naturelles ou anthropiques des écosystèmes. Sur les 133 publications parues dans 10 revues écologiques entre 1993 et 1995, 63 font état d'études sur le terrain impliquant de façon non-redondante, l'introduction réussie de 299 et 103 espèces végétales et animales, respectivement. L'invasion d'écosystèmes terrestres domine (>97%) la littérature examinée. Des perturbation sont associées avec l'établissement d'espèces exotiques dans 56% de ces études, bien que leur importance diffère selon les publications décrivant les plantes (68%) et les animaux (28%). Les espèces végétales (86%) dépendent significativement plus de perturbations pour leur établissement que les animaux (12%). Cependant, les animaux et les plantes qui dépendent de perturbations pour s'établir sont presqu'également dépendants (58 contre 68%) pour l'expansion de leur aire. Dans une deuxième analyse, les auteurs ont identifié 402 et 103 taxons de plantes et d'animaux respectivement, dont l'établissement d'espèces exotiques est explicitement lié aux perturbations. Les activités humaines sont tenues responsables de l'établissement de 97 et 57% de ces cas, respectivement. Les mécanismes communs associées à l'établissement d'animaux exotiques font intervenir le déversement d'eau de lestage, les relâchements intentionnels et les développements résidentiels. L'établissement de plantes exotiques est associé aux activités animales (p. ex., broutage, introduction de semences), aux perturbations du sol, à la foresterie, au feu, à l'agriculture et aux activités humaines. Contrairement à la théorie des invasions, l'étude des auteurs indique qu'on ne devrait pas associer a priori l'établissement et la dispersion des espèces exotiques avec une perturbation. Certains animaux envahissent de nouveaux habitats de façon répétée, une fois que les barrières géographiques sont contournées, ce qui indique que les communautés pourraient être plus receptives aux espèces exotiques qu'on ne le pensait jusqu'ici. Au contraire, les plantes s'établissent plus souvent dans des habitats perturbés.

Mots clés : espèces exotiques, espèces introduites, invasion biologique, perturbation écologique.
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Introduction

Ecological theory developed earlier this century centered on an equilibrium concept of community organization. This view held that species densities and species diversity of communities remained relatively constant over time. A variety of mechanisms have been invoked to explain equilibrium models, most prominently interspecific competition, predation, and island biogeographic principles of immigration and extinction. Communities were often characterized as assemblages of species that had coadapted through niche diversification to minimize strong interspecific competition (Hardin 1960). As such, communities were deemed saturated and relatively immune to invasion (MacArthur 1972; Cody and Diamond 1975; Case 1991; Vermeij 1991).

Juxtaposed against equilibrium theory has been increasing recognition by ecologists of natural, long-term expansion and contraction of species' ranges, and of human-mediated introductions of species into ecosystems to which they are non-native (Lodge 1993). While human-mediated species introductions have occurred for centuries, the rate at which new introductions have been reported has increased dramatically during this century. Species introductions are rapidly changing the composition of terrestrial, freshwater, and marine habitats worldwide (see Simberloff 1986; Carlton 1989; Carlton and Geller 1993; Mills et al. 1993).

Although Bazzaz (1986) distinguished between species that invade unoccupied and occupied habitats, and those that have strong and negligible effects on resident populations, we make no such distinctions. Rather, in this review we focus on the colonization and establishment processes. Specifically, we refer to species that have been introduced to, and successfully established in, habitats to which they are non-native as exotic species. We equate exotic species with other commonly used terms such as introduced species, biological invaders, and non-indigenous or non-native species. For the purpose of this review, we consider exotic species to be those that have established self-sustaining populations subsequent to the colonization event (i.e., invasion). Not all species introduced to new habitats successfully establish self-sustaining populations, however; Williamson and Fitter (1996) reported that only ~10% of species that invade new habitats establish successfully. Of these species, a further 10% eventually achieve pest status (Williamson and Fitter 1996). Pest status is usually conferred on species that have strong ecological or economical effects and that experience considerable range expansion following establishment in a novel habitat.

Examination of species introductions has yielded important insights into how biodiversity of communities is assembled, structured, and maintained (Simberloff 1981; Herbold and Moyle 1986; Drake 1991). Limits to species' geographic distributions are initially determined by the interaction between species-specific dispersal capabilities and the presence of geographic barriers like mountains, deserts, and oceans (MacArthur 1972). A species' natural distribution may be considerably smaller than its theoretical, dispersal-based distribution depending on the presence and strength of physical, chemical, or even biological constraints (see Fig. 1). For example, zooplankton taxa with widespread distributions may be locally rare or absent depending on physical (e.g., temperature) or chemical (e.g., pH) characteristics of individual lakes or on their food web structure (e.g., dominance by vertebrate or invertebrate predators).

Elton's influence

Charles Elton's (1958) volume *The Ecology of Invasions by Animals and Plants* has had a profound influence on the direction of species invasions research for almost 40 years. In his book, Elton described how biota in each of Wallace's six realms evolved in geographic isolation, and he proposed the existence of a seventh realm. More importantly, Elton's review illustrated the extent to which human activities have intentionally or unwittingly served to circumvent geographic barriers to dispersal by transporting plants, animals, and microorganisms around the world. Species transported to new habitats must contend with the same physical, chemical, and biological limitations to colonization and establishment that may limit natural range expansion, though circumvention of geographic distribution 'filters' by humans can effect tremendous expansion of species' realized ranges. For example, in only 1 decade the zebra mussel has achieved widespread distribution in lakes and rivers throughout eastern North America after being introduced from its native Europe (Ram and McMahon 1996). Dispersal of zebra mussels in Europe and North America has occurred by both passive and active transport (Ram and McMahon 1996).

Ecologists have long sought generalizations regarding features of species that render them good invaders, and attributes of habitats that render them invasible (see reviews in Drake et al. 1989). Ehrlich (1989), for example, suggested that successful invaders tend to have large native ranges, broad diets, short generation times, and high genetic variability, among other features. It also has been suggested that ecosystems vulnerable to invasion share common attributes. These features include climatic match between host and source habitats, early successional state, absence of predators, and low diversity of native species (see Lodge 1993). Lodge stressed that exceptions to these generalizations exist and that statistical analyses have yet to be conducted to verify these patterns. Despite this limitation, many ecologists have conducted studies to test nascent hypotheses regarding species invasions. For example, in contrast to Elton's prediction, Robinson et al. (1995) reported greater invasibility of species-rich grassland plots relative to those with lower diversity of native species.

One of the most frequently cited features of communities thought vulnerable to invasion is that they tend to be disturbed (Elton 1958; Moyle 1986; Orians 1986; Hobbs 1989; Mack 1989; Rejmánek 1989). Elton (1958) reported that invasions "most often come to cultivated land, or to land much modified by human practice." He expanded this view with the concept of biological resistance, wherein resistance by established species against exotic species was greater in intact communities than in those disrupted or disturbed by human activities.

Elton reserved much of his discussion regarding the importance of disturbance and biological resistance to invasion by terrestrial plants and insects, though the concepts have been adopted and studied by many other ecologists (e.g., Joenje 1987; Case 1991; Burns and Sauer 1992; Hill et al. 1995). Disturbance is widely regarded as a mechanism that permits exotic species to avoid or reduce the intensity of biological resistance in the invaded community, which is usually manifested through interspecific competition or predation.

In a variant of the resistance concept, some ecologists have argued that exotic species fill vacant niches or empty spaces (Elton 1958; Nilsson 1985; Tilman 1997), and that they have little effect on native taxa (Simberloff 1981). Herbold and Moyle (1986) contested this point based on alterations of native fish communities following introductions by exotic fishes. Pimm (1991) argued that the concept of vacant niches as applied to exotic species was unlikely to prove helpful in predicting community effects, though he believed that introductions could precipitate large-scale community changes including species extinctions.

Difficulty in objectively defining and quantifying disturbance has limited the utility of Elton's view that disturbance facilitates invasions. In the absence of clear definitions and measurements of disturbance, and identification of mechanisms by which it facilitates establishment of exotic species, arguments as to its importance to invasion success are speculative. Tests of the disturbance hypothesis are very difficult to conduct, since very few communities on earth have not been disturbed or modified to some degree by human activities, and thus most invasions potentially could be ascribed to disturbance. Simberloff (1989) proposed alternative reasons for the seemingly high rate of invasion in disturbed habitats. First, because many of these habitats are agricultural and important to humans, they are well studied and exotic species are likely to be discovered. Second, opportunities for human-mediated introduction of species may be higher in these habitats because of the extent to which humans use and modify them. Thus, it is not clear whether disturbance facilitates invasions.

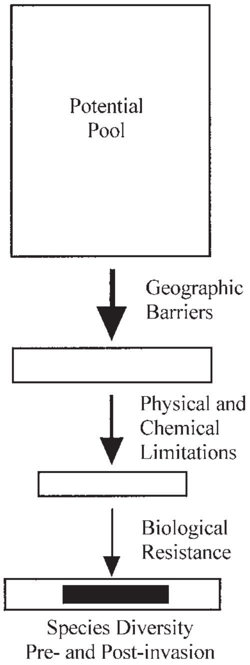
If disturbance is an important determinant of biological invasions, the event must modify species interactions or the nature of the environment in a manner that favours establishment of exotic species. This view is consistent with White and Pickett's (1985) definition of disturbance as "any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment." However, because definitions of disturbance vary among workers, in this review we utilize individual researchers' views of disturbance and its importance to their systems.

How important is disturbance to invasions?

In an effort to determine the degree to which exotic species depend on disturbance for establishment and (or) range expansion, we conducted two separate literature reviews using compact-disk-based BIOSIS software (BIOSIS 1996). This computer program searches titles and abstracts of articles published in biological journals for the presence of requested key words. The objective of the first search was to determine the prevalence of disturbance as a factor associated with exotic species without biasing the search by using disturbance as a search key word. In the second search, we sought to identify disturbance mechanisms by explicitly linking disturbance and exotic species in searched key words. Our key word protocol utilized three criteria to identify articles: use of synonyms for exotic species, words limiting the search to environmental science, and limits to the years used in the search.

The purpose of the first search was to use synonyms of exotic species to identify field-based studies published between January 1993 and December 1995 in five pure ecological journals and five primary applied journals. We then reviewed identified papers to determine whether establishment of exotic species was associated with disturbances of any type. Key words used in the search included exotic, invas*, invad*, alien, and introduced, where the asterisk refers to truncated words (e.g., invasive, invasion).

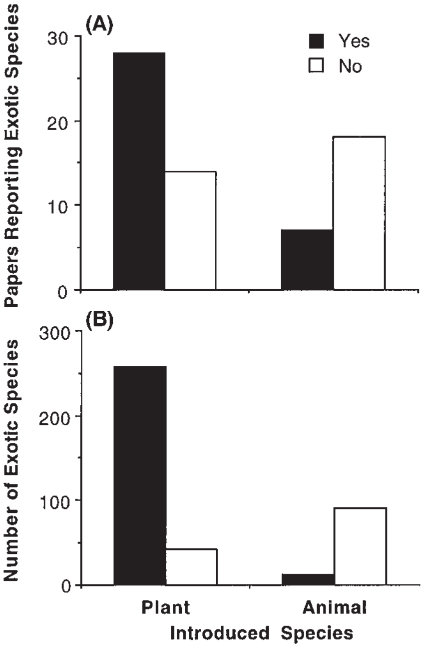
Fig. 1. Representation of factors that affect biodiversity of communities. Species diversity is proportional to the rectangular area. Species diversity is generally higher in the presence (outer, open box) of exotic species than in their absence (inner, solid box).



BIOSIS data sets organize articles by the major concepts that they describe, thereby permitting searches to be limited to specific disciplines. Our searches identified papers pertaining to, for example, invasive species, while ignoring those describing unrelated biological topics (e.g., invasive cardiology). Our concept codes limited papers to those describing general ecological methods, plants, and animals. Our initial survey was limited to five pure (*American Naturalist*, *Ecology*, *Ecological Monographs*, *Oecologia*, *Oikos*) and five applied (*Biodiversity and Conservation*, *Biological Conservation*, *Conservation Biology*, *Ecological Applications*, *Journal of Applied Ecology*) journals. We selected these journals to eliminate biases that might result from the use of taxon-specific journals. This selection appeared to have had little effect on results, however, as terrestrial plants accounted for most (>74%) invasions in both this survey and the one described below that surveyed all BIOSIS journals. After articles were obtained, we determined whether invasion(s) had taken place and whether disturbance was implicated by the authors as facilitating initial establishment or subsequent range expansion of exotic species.

We constructed a 2 × 2 contingency table to determine whether plant and animal invasions differed with respect to importance of disturbance to initial establishment in recipient communities. This association was tested using Fisher's exact test. Separate tests were conducted on the number of papers in which plant and animal introductions were addressed, and on the actual number of species introduced to new habitats. A number of papers reported establishment of multiple species

Fig. 2. Number of papers (A) and number of species (B) that described establishment of exotic species in relation to disturbance. Species that required disturbance for establishment are indicated by solid bars and those that did not require this disturbance are indicated by open bars.



in which the importance of disturbance to establishment or range expansion varied among species. Although we have no reason to question results from studies involving multiple invasions, the statistical importance of these studies was diminished by testing the number of papers rather than the number of species invasions.

We conducted a second search of the BIOSIS data base in which the key word disturbance was explicitly linked with one of the key words for exotic species (exotic, invas*, invad*, alien, introduced). Our purpose was to identify and classify the types of disturbance mechanisms associated with establishment of exotic plants and animals. This search used more exact key words to identify papers than the previous one; therefore, the scope of the search was expanded to include papers published between 1985 and 1995 inclusive of all journals covered by BIOSIS. Because the objective of this search was to determine the relationship between disturbance and establishment of exotic species, disturbance types were classified into the following categories: agricultural (e.g., tilling, irrigation, mowing, sowing), environmental (e.g., wind), feral or domesticated animal (e.g., goats, pigs, cattle) effects, exotic animals, fire, soil disruption, forestry (e.g., logging, brush clearing, skidding), flooding, development (roads, pathways, waste generation, pipeline corridors), or other forms of human activities. Effects of domesticated and feral animals included grazing and introduction of seeds in dung. Human activities include off-road vehicles, skiing, hiking, and other nonspecified forms of disturbance. Remaining forms of disturbance that were not explicitly described in the original articles were classified as undefined. We also tabulated invasions resulting from ballast water discharge or intentional release, both of which we argue constitute biotic disturbances (Petraitis et al. 1989). Disturbance classes were selected based on their prevalence in reviewed literature. In cases where multiple disturbance mechanisms (e.g., forestry and soil disruption) were implicated in establishment of a single exotic species, each mechanism was considered and tabulated separately. We tested the association of successful species invasions with human disturbances for plant and animal taxa using Fisher's exact test.

We also explored whether plant and animal invasions tended to occur in similar types of ecosystems by classifying the habitats in which exotic species were reported to establish.

Our literature reviews have a number of limitations. First, both searches identified only those papers that used specific key words in either the title or abstract. Other papers that addressed species introductions but which lacked our key words were not identified. Second, our searches are limited by the time intervals covered and the limitations of BIOSIS itself. BIOSIS on CD incorporates information from ~6000 journals (BIOSIS 1996). It is possible that the importance of disturbance to invasion success could vary temporally, particularly if early invasions filled empty niches and did not require disturbance (Elton 1958). Third, because our first survey was limited to 10 journals, we have likely detected only a fraction of the literature published on exotic species during this period that could be relevant to this study. For example, insects have been widely introduced globally (Simberloff 1986), yet they accounted for a relatively low proportion of animal invasions documented in our surveys. Fourth, our surveys included only a relatively small number of studies written primarily in english journals. The first survey was dominated by studies of invasions of oceanic islands (Australia, Hawaii, New Zealand, and others; 54%) and North America (24.9%). Asia (9.7%), Europe (6%), South America (4.2%), and especially Africa (1.2%) had much lower representation in the first survey. We have assumed that our results are not biased by this geographic and linguistic limitation. Fifth, our surveys rely on information provided in original studies that detail the direct relationship between invasion success and disturbance. It is possible that some successful secondary invasions may have occurred that were independent of disturbance, but dependent on the presence of other species that utilized disturbance for establishment. Because the authors of such studies may not have linked secondary invasions with disturbance, the importance of disturbance could be underestimated. Finally, because the literature is dominated by reports of successful invasions, our review focused almost exclusively on introductions in which establishment occurred. Though it is beyond the scope of this review, it would be instructive to establish the relationship between colonization success and disturbance history of invaded communities.

Disturbance and establishment of exotic species

Thirty-five of sixty-three papers (56%) that addressed field studies identified disturbance as essential to establishment of exotic species (Fig. 2). The importance of disturbance differed significantly between papers that surveyed plant and animal taxa (Fisher's exact test, $P = 0.003$). Papers describing plants were more than twice as likely to report disturbance as being associated with successful invasions than were those describing animals (67 versus 28%; Fig. 2). Thus, the plant literature was far more likely to report disturbance as important to successful establishment of biological invaders (Table 1).

Table 1. Summary data for exotic species from the literature review conducted using synonymns of biological invasion.

Taxon						
Phylum or division	Species	Habitat	Country	Establishment?	Range expansion?	Ref.
			Kingdom: Animalia			
Arthropoda	*Orconectes rusticus*	Lakes	Wisconsin, U.S.A.	No	No	Garvey et al. 1994
	Orconectes propinquus	Lakes	Wisconsin, U.S.A.	No	No	Garvey et al. 1994
	Solenopsis invicta	Coastal bend	U.S.A.	No	No	Allen et al. 1995
	Arthropods (34 spp.)	Crops	Japan	No	No	Andow and Imura 1994
	Phyllonorycter leucographella	Bushes	British Isles	No	No	Nash et al. 1995
	Sigara nigrolineata	Small rock pools	Finland	No	No	Pajunen and Pajunen 1993
	Biosteres arisanus	Guava orchard	Hawaii, U.S.A.	No	No	Stark et al. 1994
	Biosteres vandenboschi	Guava orchard	Hawaii, U.S.A.	No	No	Stark et al. 1994
	Diachasmimorpha longicaudata	Guava orchard	Hawaii, U.S.A.	No	No	Stark et al. 1994
	Pysttalia incisi	Guava orchard	Hawaii, U.S.A.	No	No	Stark et al. 1994
	Andricus quercuscalicis	Oak forest	Europe	No	No	Schonrögge et al. 1995
	Trechisibus antarcticus	Coastal habitat	South Georgia Island	No	No	Ernsting et al. 1995
	Bactrocera dorsalis	Guava orchard	Hawaii, U.S.A.	Yes	Yes	Stark et al. 1994
	Corophium curvispinum	Rhine River	Netherlands	Yes	Yes	Van Den Brink et al. 1993
	Iridomyrmex humilis	Mountain fynbos	South Africa	Yes	Yes	McDonald and Cowling 1995
Mollusca	*Mytilus californianus*	Intertidal zone	U.S.A.	Yes	Yes	Menge et al. 1994
Chordata	*Phasianus colchicus*	Shrubland	Hawaii, U.S.A.	No	No	Cole et al. 1995
	Alectoris chukar	Shrubland	Hawaii, U.S.A.	No	No	Cole et al. 1995
	Salmo trutta	Stream community	New Zealand	No	No	Flecker and Townsend 1994
	Molothrus ater	Temperate forest	U.S.A.	No	No	Hahn and Haffield 1995
	Tilapia zillii	Lake Victoria	Tanzania	No	No	Lowe-McConnell 1993
	Oreochromis leucostictus	Lake Victoria	Tanzania	No	No	Lowe-McConnell 1993
	Oreochromis niloticus	Lake Victoria	Tanzania	No	No	Lowe-McConnell 1993
	Dama dama	Beech forest	New Zealand	No	No	Nugent and Frampton 1994
	Aphelocoma coerulescens	Oak woodlands	U.S.A.	No	No	Peterson 1993
	Passeriform birds (25)	Multiple habitats	Saint Helena	No	No	Brooke et al. 1995
	Mus musculus	Subantarctic islands	France	No	No	Chapuis et al. 1994
	Rattus rattus	Subantarctic islands	France	No	No	Chapuis et al. 1994
	Rattus norvegicus	Subantarctic islands	France	No	No	Chapuis et al. 1994
	Felis catus	Subantarctic islands	France	No	No	Chapuis et al. 1994
	Oryctolagus cuniculus	Subantarctic islands	France	No	No	Chapuis et al. 1994
	Bos taurus	Subantarctic islands	France	No	No	Chapuis et al. 1994
	Rangifer tarandus	Subantarctic islands	France	No	No	Chapuis et al. 1994
	Ovis aries	Subantarctic islands	France	No	No	Chapuis et al. 1994
	Ovis ammon musimon	Subantarctic islands	France	No	No	Chapuis et al. 1994
	Mus musculus	Shrub steppe	U.S.A.	No	Yes	Brandt and Rickard 1994
	Rattus norvegicus	Shrub steppe	U.S.A.	No	Yes	Brandt and Rickard 1994
	Hemidactylus frenatus	Tropical forests	Pacific Islands	No	Yes	Case et al. 1994
	Passeriform birds (5)	Multiple habitats	Saint Helena	Yes	No	Brooke et al. 1995
	Sturnus vulgaris	Shrub steppe	U.S.A.	Yes	Yes	Brandt and Rickard 1994
	Columba livia	Shrub steppe	U.S.A.	Yes	Yes	Brandt and Rickard 1994
	Hippocastanaceae sp.	Desert	U.S.A.	Yes	Yes	Burkett and Thompson 1994

Table 1 (*continued*).

Taxon						
Phylum or division	Species	Habitat	Country	Establishment?	Range expansion?	Ref.
		Kingdom: Plantae				
Spermaphyta	*Rumex acetosella*	Subantarctic forest	Argentina	No	No	De Pietri 1995
	Elaeagnus angustifolia	Water courses	U.S.A.	No	No	Shaforth et al. 1995
	Hyparrhenia rufa	Neotropic savannas	Venezuela	No	No	Baruch and Fernandez 1993
	Ailanthus altissima	Hardwood forest	U.S.A.	No	No	Fraver 1994
	Allium vineale	Hardwood forest	U.S.A.	No	No	Fraver 1994
	Broussonetia papyrifera	Hardwood forest	U.S.A.	No	No	Fraver 1994
	Chenopodium album	Hardwood forest	U.S.A.	No	No	Fraver 1994
	Commelina communis	Hardwood forest	U.S.A.	No	No	Fraver 1994
	Duchesnea indica	Hardwood forest	U.S.A.	No	No	Fraver 1994
	Hypericum perforatum	Hardwood forest	U.S.A.	No	No	Fraver 1994
	Lespedeza bicolor	Hardwood forest	U.S.A.	No	No	Fraver 1994
	Ligustrum sinense	Hardwood forest	U.S.A.	No	No	Fraver 1994
	Lonicera japonica	Hardwood forest	U.S.A.	No	No	Fraver 1994
	Stellaria media	Hardwood forest	U.S.A.	No	No	Fraver 1994
	Microstegium vimineum	Hardwood forest	U.S.A.	No	No	Fraver 1994
	Tsuga canadensis	Mesic forest	U.S.A.	No	No	Frelich et al. 1993
	Pinus taeda	Large old field	U.S.A.	No	No	Golley et al. 1994
	Acer rubrum	Right-of-way	U.S.A.	No	No	Hill et al. 1995
	Fraxinus americana	Right-of-way	U.S.A.	No	No	Hill et al. 1995
	Acacia karro	Grasslands	U.S.A.	No	No	O'Connor 1995
	Impatiens glandulifera	Riparian habitats	Europe	No	No	Pysek and Prach 1 995
	Pennisetum setaceum	Low arid regions	Hawaii, U.S.A.	No	No	Williams and Black 1994
	Carya tomentosa	Old field	U.S.A.	No	No	Myster and Pickett 1993
	Juniperus virginiana	Old field	U.S.A.	No	No	Myster and Pickett 1993
	Cornus florida	Old field	U.S.A.	No	No	Myster and Pickett 1993
	Solidago sp.	Old field	U.S.A.	No	No	Myster and Pickett 1993
	Ouercus sp.	Old field	U.S.A.	No	No	Myster and Pickett 1993
	Pinus radiata	*Eucalyptus* forest	Australia	No	No	Burdon and Chilvers 1994
	Forest fruiting plants (l3 spp.)	Mediterranean vegetation	Chile	No	No	Debussche and Isenmann 1994
	Andropogon scoparius	Tallgrass prairie	U.S.A.	No	Yes	Gibson et al. 1993
	Hyparrhenia rufa	Savanna	Brazil	Yes	No	Klink 1994
	Melinis minutiflora	Savanna	Brazil	Yes	No	Klink 1994
	Hyptis suaveolens	Tropical	Australia	Yes	No	Lonsdale and Lane 1994
	Sida acuta	Tropical	Australia	Yes	No	Lonsdale and Lane 1994
	Cynodon dactylon	Tropical	Australia	Yes	No	Lonsdale and Lane 1994
	Datura ferox	Tropical	Australia	Yes	No	Lonsdale and Lane 1994
	Senecio jacobaea	Pastures	U.S.A.	Yes	No	McEvoy and Rudd 1993
	Aira caryophyllea	Roadside habitat	Australia	Yes	No	Milberg and Lamont 1995
	Trifolium stellatum	Roadside habitat	Australia	Yes	No	Milberg and Lamont 1995
	Wahlenbergia capensis	Roadside habitat	Australia	Yes	No	Milberg and Lamont 1995
	Erodium botrys	Roadside habitat	Australia	Yes	No	Milberg and Lamont 1995

Table 1 (*continued*).

Taxon						
Phylum or division	Species	Habitat	Country	Establishment?	Range expansion?	Ref.
	Trifolium sp.	Roadside habitat	Australia	Yes	No	Milberg and Lamont 1995
	Arctotheca calendula	Roadside habitat	Australia	Yes	No	Milberg and Lamont 1995
	Vellereophyton dealbatum	Roadside habitat	Australia	Yes	No	Milberg and Lamont 1995
	Lactuca serriola	Roadside habitat	Australia	Yes	No	Milberg and Lamont 1995
	Vulpia membranacea	Roadside habitat	Australia	Yes	No	Milberg and Lamont 1995
	Acacia saligna	Fynbos	South Africa	Yes	No	Musil 1993
	Gentiana pneumonanthe	Heathland	Netherlands	Yes	No	Oostermeijer et al. 1994
	Ouercus robus	Heathland	England	Yes	No	Rose and Webb 1994
	Rubus futicosus	Heathland	England	Yes	No	Rose and Webb 1994
	Chamaenerion angustifolium	Heathland	England	Yes	No	Rose and Webb 1994
	Poa annua	Heathland	England	Yes	No	Rose and Webb 1994
	Betula pendula	Heathland	England	Yes	No	Rose and Webb 1994
	Holcus lanatus	Heathland	England	Yes	No	Rose and Webb 1994
	Juncus bulbosus	Heathland	England	Yes	No	Rose and Webb 1994
	Juncus effusus	Heathland	England	Yes	No	Rose and Webb 1994
	Pedicularis sylvatica	Heathland	England	Yes	No	Rose and Webb 1994
	Rubus futicosus	Heathland	England	Yes	No	Rose and Webb 1994
	Syzygium jambos	Forest	Pitcairn Islands	Yes	No	Waldren et al. 1995
	Carduus nutans	Pastures	New Zealand	Yes	No	Wardle et al. 1995
	Bromus tectorum	Shrub steppe	U.S.A.	Yes	No	Brandt and Rickard 1994
	Chorispora tenella	Shrub steppe	U.S.A.	Yes	No	Brandt and Rickard 1994
	Draba verna	Shrub steppe	U.S.A.	Yes	No	Brandt and Rickard 1994
	Erodium cicutarum	Shrub steppe	U.S.A.	Yes	No	Brandt and Rickard 1994
	Holosteum umbellatum	Shrub steppe	U.S.A.	Yes	No	Brandt and Rickard 1994
	Lactuca serriola	Shrub steppe	U.S.A.	Yes	No	Brandt and Rickard 1994
	Salsola kali	Shrub steppe	U.S.A.	Yes	No	Brandt and Rickard 1994
	Sisymbrium altissimum	Shrub steppe	U.S.A.	Yes	No	Brandt and Rickard 1994
	Tragopogon dubius	Shrub steppe	U.S.A.	Yes	No	Brandt and Rickard 1994
	Tamarix ramosissima	Riparian areas	U.S.A.	Yes	No	Busch and Smith 1995
	Cytisus scoparius	Coastal dunes	U.S.A.	Yes	No	Bossard and Rejmánek 1994
	Forbs (42 spp.)	Goldenrod cultures	U.S.A.	Yes	No	Brown 1994
	Senecio vulgaris	Ryegrass swards	Britain	Yes	Yes	Bergelson et al. 1993
	Acer saccharum	Right-of-way	U.S.A.	Yes	Yes	Berkowitz et al. 1995
	Betula populifolia	Right-of-way	U.S.A.	Yes	Yes	Berkowitz et al. 1995
	Betula pendula	Heathland mosaics	Britain	Yes	Yes	Bullock and Webb 1995
	Carpobrotus edulis	Maritime chaparral	U.S.A.	Yes	Yes	D'Antonio et al. 1993
	Lonicera japonica	Coastal plain	U.S.A.	Yes	Yes	Dillenburg et al. 1993
	Andropogn bladhii	Tallgrass prairie	U.S.A.	Yes	Yes	Gibson et al. 1993
	Annual grasses (4 spp.)	Basalt paddocks	Australia	Yes	Yes	Gilfedder and Kirkpatrick 1993
	Annual herbs (8 spp.)	Basalt paddocks	Australia	Yes	Yes	Gilfedder and Kirkpatrick 1993
	Perennial grasses (5 spp.)	Basalt paddocks	Australia	Yes	Yes	Gilfedder and Kirkpatrick 1993
	Perennial herbs (8 spp.)	Basalt paddocks	Australia	Yes	Yes	Gilfedder and Kirkpatrick 1993

Table 1 (*concluded*).

Taxon						
Phylum or division	Species	Habitat	Country	Establishment?	Range expansion?	Ref.
	Synedrella nodiflora	Tropical	Australia	Yes	Yes	Lonsdale and Lane 1994
	Tridax procumbens	Tropical	Australia	Yes	Yes	Lonsdale and Lane 1994
	Cenchrus ciliaris	Tropical	Australia	Yes	Yes	Lonsdale and Lane 1994
	Pennisetum pedicellatum	Tropical	Australia	Yes	Yes	Lonsdale and Lane 1994
	Pennisetum polystachion	Tropical	Australia	Yes	Yes	Lonsdale and Lane 1994
	Rhynchelytrum repens	Tropical	Australia	Yes	Yes	Lonsdale and Lane 1994
	Deschampsia flexuosa	Heathlands	England	Yes	Yes	Marrs 1993
	Polygonum capitatum	Cloud forest	Azores	Yes	Yes	Ramos 1995
	Leicesteria formosa	Cloud forest	Azores	Yes	Yes	Ramos 1995
	Clethra arborea	Cloud forest	Azores	Yes	Yes	Ramos 1995
	Pteridium aquilinum	Cloud forest	Azores	Yes	Yes	Ramos 1995
	Paspalum paspalodes	Marshes	France	Yes	Yes	Mesléard et al. 1993
	Bromus madritensis	Desert	U.S.A.	Yes	Yes	Schiffman 1994
	Erodium cicutarium	Desert	U.S.A.	Yes	Yes	Schiffman 1994
	Hordeum murinum	Desert	U.S.A.	Yes	Yes	Schiffman 1994
	Medicago polymorpha	Desert	U.S.A.	Yes	Yes	Schiffman 1994
	Schismus barbatus	Desert	U.S.A.	Yes	Yes	Schiffman 1994
	Ammophila arenaria	Sand dunes	U.S.A.	Yes	Yes	Buell et al. 1995
	Poa pratensis	Ski slopes	Japan	Yes	Yes	Tsuyuzaki 1993
	Agrostis alba	Ski slopes	Japan	Yes	Yes	Tsuyuzaki 1993
	Dactylis glomerata	Ski slopes	Japan	Yes	Yes	Tsuyuzaki 1993
	Trifolium repens	Ski slopes	Japan	Yes	Yes	Tsuyuzaki 1993
	Festuca rubra	Ski slopes	Japan	Yes	Yes	Tsuyuzaki 1993
	New world annuals (49 spp.)	Tropical park	Australia	Yes	Yes	Cowie and Werner 1993
	Old world annuals (34 spp.)	Tropical park	Australia	Yes	Yes	Cowie and Werner 1993
	Class Dicotyledon (26 spp.)	Tuff cone	Hawaii, U.S.A.	Yes	Yes	Wester 1994
	Class Monocotyledon (10 spp.)	Tuff cone	Hawaii, U.S.A.	Yes	Yes	Wester 1994

Note:The heading “Establishment?” refers to whether disturbance was required for successful establishment. “Range Expansion?” refers to whether established exotic species required disturbance for range expansion. The number of exotic species surveyed is indicated in parentheses where individual species names were not provided and in cases involving large numbers of invasions. Twenty studies were eliminated because they reported on redundant species introductions or because they did not specify the number of exotic species.

These patterns also hold for individual species (Fig. 2). A total of 402 different successful biological invasions (= species × habitat) were identified in the first survey, of which plants comprised 74% of the species surveyed. All identified successful plant invasions occurred in terrestrial habitats. Reports of successful animal invasions were only slightly less biased toward terrestrial habitats (91%). The importance of disturbance to establishment of individual exotic species differed significantly for plant (86%) and animal (12%) taxa (Fisher's exact test, $P < 0.0001$; Fig. 2).

Disturbance was important to establishment of animals in 22% of the cases involving aquatic habitats, but only 11% of those occurring in terrestrial habitats. However, only two species (of nine) were reported to require disturbance to invade aquatic environments, including *Mytilus californianus* that established in intertidal habitat (Menge et al. 1994). It is equivocal as to whether this study represents a valid example of establishment by an exotic species considering the study was conducted in the Pacific northwest United States, a region to which this species is native. Thus, it is not clear whether disturbance is any more important to successful invasions of aquatic habitats than to terrestrial ones. This is an important issue since invasions of freshwater habitats have become increasingly common and have garnered considerable attention in recent years. As examples, molluscs (*Dreissena polymorpha*, *Dreissena bugensis*, *Corbicula fluminea*, *Marisa cornuarietis*), water fleas (*Bythotrephes cederstroemi*, *Bosmina coregoni*, *Daphnia lumholtzi*), amphipods (*Corophium curvispinum*), and crayfish (*Orconectes rusticus*) are but a small fraction of the invertebrate fauna that have invaded freshwater ecosystems in North America and Europe (McMahon 1983; Sprules et al. 1990; Hartog et al. 1992; Horne et al. 1992; Havel and Hebert 1993; Demelo and Hebert 1994; Garvey et al. 1994; Ram and McMahon 1996). Marine and estuarine systems have proven equally vulnerable to species introductions (Leidy and Fiedler 1985; Nichols and Thompson 1985; Carlton 1989; Hutchings 1992; Carlton and Geller 1993; Kelly 1993; Cohen et al. 1995).

Exotic species' range expansion

Plants and animals also differ with respect to the importance of recognized disturbance to range expansion following establishment. Overall, 58% of the plants required disturbance for both establishment and range expansion (Fig. 3). Of the 257 plants that required disturbance for establishment, 174 (68%) also required it for range expansion (Fig. 3). Among animals, only 7% required disturbance for both establishment and range expansion, though 58% of those that required disturbance for establishment also required it for range expansion. (Fig. 3). The percentage of animals that required disturbance for neither establishment nor dispersal was far higher than that for plants (85 versus 14%; Table 1).

A small percentage of species that invade communities in the apparent absence of disturbance require it for range expansion from the establishment site. For example, Case et al. (1994) explored ecological effects of introduced lizards (*Hemidactylus frenatus*) in forests of islands in the South Pacific Ocean. These lizards have utilized human transport to travel between and invade islands. Even though the species invades islands in the apparent absence of disturbance, it depends on human disturbance to expand its distribution (T. Case, personal communication). *Hemidactylus frenatus* is competitively dominant to native lizard species on sides of buildings where insect prey accumulate (Petren et al. 1993; Case et al. 1994).

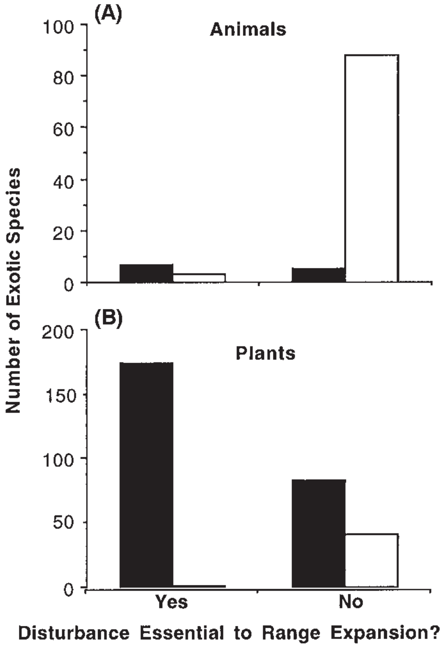


Fig. 3. Range expansion of exotic animal (A) and plant (B) species in relation to whether establishment was affected by (solid bars) or occurred independent of (open bars) disturbance. Note different *y*-axis scales.

Invasion mechanisms

Our second search sought to identify papers that explicitly linked establishment of invading species with disturbance. This survey recorded a total of 505 nonredundant successful species introductions, of which plants were again dominant (80%). Natural disturbance mechanisms were responsible for facilitating establishment of exotic species in only 11% of all species invasions. Human-associated mechanisms were central to establishment of most exotic species that depended on disturbance, though its importance differed significantly between plant (97%) and animal (57%) species (Fisher's exact test, $P < 0.0001$). It is not surprising that both exotic plants and animals were more dependent on disturbance for establishment in this survey than in the preceding one, considering that the search criteria used here were more specific.

Domesticated and feral animals were the most important factor associated with establishment of exotic plants (22%; Fig. 4). Domesticated and feral animals may affect biological, chemical, and physical attributes of the sites that they occupy. For example, grazing may reduce or eliminate aboveground plant biomass, increase nutrient availability via release of wastes, and alter light and temperature regimes at the soil surface. Grazing animals may also deposit seeds to the site and disrupt the soil surface, increasing habitat availability for colonists (Brown and Archer 1987; Aplet et al. 1991).

Other factors of quantitative importance to plant introductions included soil disturbance, activities related to forestry practices (e.g., logging, skidding, shrub removal), human

Fig. 4. Entry mechanisms identified as facilitating establishment of exotic animals and plants. More than one mechanism was attributed with establishment of some exotic species.

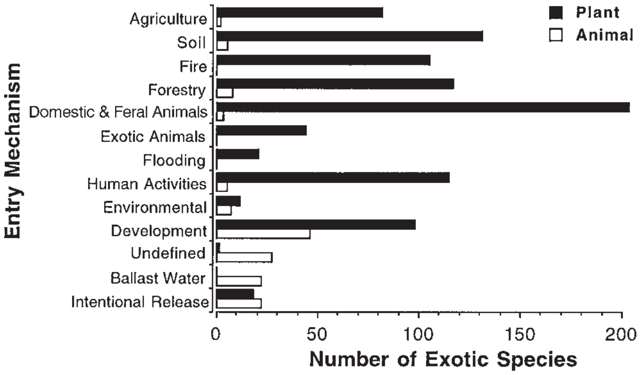
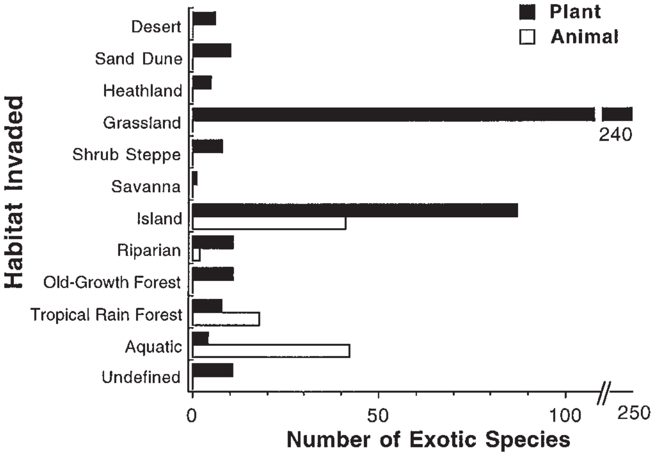


Fig. 5. Habitats in which disturbance facilitated establishment of exotic plants and animals. Old-growth forest refers to those growing in temperate regions.



activities (e.g., hiking, skiing, use of off-road vehicles), fire, development (e.g., roads, paths, residential establishment, pipeline construction), and agriculture (Fig. 4). Many of these factors likely operate interactively in an additive, synergistic, or antagonistic manner. It also seems likely that the importance of these interactions depends on the combination of habitats and exotic species involved.

Mechanisms associated with successful animal invasions differed substantially from those for plants (Fig. 4). Two studies contributed most of the introduced animal species. Nichols and Thompson (1985) reported 22 species of introduced annelids, crustaceans, and molluscs in San Francisco Bay. Most of these species were apparently introduced to the bay since the mid-1800s as boring, fouling, or ballast-dwelling organisms in ships (Nichols and Thompson 1985). These species are complemented by a suite of 22 fish species, primarily from the eastern United States, that have been intentionally released (Leidy and Fiedler 1985).

Other less important mechanisms that permitted animals to invade included unspecified environmental disturbance (seven bird species; Feinsinger et al. 1988), and forestry and associated soil disturbance (five earthworm species; Abbott 1985). Presence of domesticated and feral animals, the most important mechanism facilitating plant invasions, was relatively unimportant to establishment of invading animals (<3%; Fig. 4). Twenty-seven species of ants have established in Florida; mechanisms responsible for these introductions have not been ascertained, though many appear related to international commerce transacted through seaports (Deyrup et al. 1988).

Because such a high percentage (43%) of introduced animals in this survey occurred in a single habitat (San Francisco Bay), we also classified species entry mechanisms for the first survey. Of the 12 successful invasions in that survey, 5 were bird species introduced intentionally to modified habitat on St. Helena Island, and an additional 4 species colonized agricultural lands (Brandt and Rickard 1994; Burkett and Thompson 1994; Stark et al. 1994; Brooke et al. 1995). Domesticated and feral animals were associated with none of the 103 animal invasions that were classified in the first survey. Likewise, soil disturbance was not associated with establishment of any exotic animals in the first survey. Taken together, these findings indicate entry mechanisms for exotic plants and animals differ very substantially.

Invaded habitats

Plants and animals from the second survey also differed with respect to the types of habitats successfully invaded (Fig. 5). Reports of animal invasions were limited almost exclusively to aquatic, unspecified island, tropical rain forest, and riparian habitats. Most animal introductions (39%) were reported in aquatic habitats adjacent to urbanized areas. This finding is consistent with established patterns of ballast water discharge, species additions from fish release, and habitat destruction or degradation near cities. In contrast to this pattern, exotic plants established in a much wider array of habitats. The habitat most commonly invaded was grassland (Fig. 5), perhaps because of its widespread conversion and degradation by human activities. Virtually all of the disturbance mechanisms identified above for plants were implicated in establishment of exotic species in grasslands, though domesticated and feral animals, fire, soil disruption, and development were most important. Introduced plants were also commonly reported on island, riparian, temperate old-growth forest, and sand dune habitats. The prevalence of successful plant and animal introductions to island areas is consistent with Elton's (1958) prediction, though the pattern is also consistent with the view that colonization opportunities may be higher on islands than on mainlands (Simberloff 1986).

Why do plant and animal invasions differ?

Plants and animals differed with respect to the number of species established in non-native habitats, the types of habitats successfully invaded, the mechanisms responsible for facilitating establishment, and the importance of disturbance to initial establishment and subsequent range expansion. These differences indicate that determinants of invasion success likely differ substantially for these taxa. In particular, the vast majority of animals apparently were dependent on disturbance for neither establishment nor range expansion, whereas plants were highly dependent for both establishment and range expansion (Fig. 3).

One hypothesis that may explain these differences is that plants and motile animals, which dominated successful animal invasions in our survey, differ fundamentally and importantly with respect to their need for spatial resources, specifically colonization substrates. Plants require empty space or suitable sites for access to soil surface, in addition to adequate supplies of resources including water, nutrients, and light (Harper 1977; Rejmánek and Richardson 1996; Tilman 1997). Disturbance may disrupt ecosystem, community, or population structure and thereby alter availability of resources or substrates (White and Pickett 1985). The strong correspondence between establishment of exotic plants and disturbance (Figs. 2 and 3) suggests that many of the surveyed species were not limited by dispersal or propagule production but rather by availability of empty or suitable sites. This view is consistent with the general observation that invasive plant species tend to produce large numbers of small seeds that are capable of dispersing long distances (see Rejmánek and Richardson 1996). It is also consistent with Simberloff's (1986) hypothesis that successful introductions depend on species' habitat requirements and habitat availability, and only secondarily on the intensity of biological resistance. If availability of empty sites is important to invasion success, then establishment rates of exotic species should be higher in habitats with fewer competitors, all things being equal. For example, establishment of exotic plant species introduced as seed into native grassland was negatively related to native species diversity, indicating that invasion was more successful in species-poor than species-rich plots (Tilman 1997). Rejmánek (1989) proposed that open space created by biomass destruction might be the only critical factor responsible for successful species invasions, rather than native species diversity. This view is consistent with findings of Peart and Foin (1985), who observed that invasion of California grasslands was negatively related to resident plant biomass but unrelated to resident species diversity.

Tilman (1997) also argued that dispersal-associated recruitment limitation was a key determinant of plant diversity in grasslands, because total diversity increased linearly in all plots that received seeds of exotic species, irrespective of the initial diversity of native species.

Marine, benthic-invertebrate communities may be the closest animal analogue to terrestrial plant communities. We sought to compare establishment patterns of introduced species in plant communities with those of immobile animal communities (e.g., sessile marine invertebrates), though too few cases were identified to permit this analysis. Recruitment limitation has been recognized as an important factor affecting animal populations, particularly marine invertebrates (Grosberg and Levitan 1992; Roughgarden et al. 1994). Our survey indicated that establishment of most introduced animals was dependent on disturbance for neither establishment nor range expansion. Successful animal invasions were, however, tightly coupled with human-assisted transport and occurred most often in aquatic habitats or on islands. Aquatic habitats are highly vulnerable to species invasions (Mills et al. 1993), as are islands owing to their generally low level of native species diversity and high level of invasion opportunities (Elton 1958; Simberloff 1986, 1989). Taken together, these patterns suggest that animal communities may be relatively receptive or open to exotic species and that recruitment limitation associated with dispersal problems may be a primary factor limiting diversity of these systems. By transporting animals to habitats that they otherwise would never reach, humans have bridged the biological 'filter' imposed by geographic barriers (Simberloff 1989; Williamson 1989).

Even species-rich ecosystems are vulnerable to invasions by and establishment of exotic species. For example, piscivorous Nile perch (*Lates niloticus*) successfully invaded and devastated fish biodiversity of Lake Victoria, which formerly contained one of the world's richest fish faunas (Lowe-McConnell 1993). Zebra mussels (*Dreissena polymorpha*) readily invaded the Mississippi River, which has very high native mollusc biodiversity (Schloesser et al. 1996). The water flea *Bythotrephes cederstroemi* has invaded many lakes in North America adjacent to the Great Lakes, including Harp Lake, Ont., which has among the highest zooplankton biodiversity levels in the region (Yan and Pawson 1997). Finally, the species-rich flora of the South African fynbos has been successfully invaded and modified by a variety of tree and shrub species (Macdonald and Richardson 1986; Musil 1993). These cases call into question the frequently cited view that invasion success is higher in species-poor than in species-rich communities (Elton 1958; see review, Lodge 1993).

Doubtless cases exist in which invasions fail owing to intensive biological resistance (Lake and O'dowd 1991; Burns and Sauer 1992; Hill et al. 1995). However, observations from nature and the patterns reported here suggest that widespread transport of organisms by human activities poses a serious threat to the integrity of communities. Recognition of the severity of this problem may increase as advances in molecular biology permit identification of cryptic, exotic species that were once thought to be native (Geller et al. 1994).

In summary, plants and animals differed markedly with respect to the number of successful invasions reported in surveyed journals in recent years, by their dependence on disturbance for establishment and range extension, the mechanisms that facilitated establishment, and the habitats they invaded. Despite these differences, circumvention of geographic barriers and disturbance of natural habitats by humans will ensure continued spread of species to ecosystems to which they are non-native.

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