($R^2 = 0.00$, $P = 0.985$) and *Cirsium* ($R^2 = 0.00$, $P = 0.977$), and only a very weak correlation for *Plantago* ($R^2 = 0.02$, $P = 0.033$). These results, along with the more downstream position of the diverse and invaded tussocks, suggest that propagule supply may be one important factor behind the positive correlations between diversity and invasion in this system. Additionally, the difference between these results and those in Fig. 2 may reflect other covariates that were decoupled from diversity in the experiment (e.g., species composition, physical conditions).

Although diversity tends to enhance community resistance at neighborhood scales, other factors covarying with diversity (e.g., propagule pressure in this study) may be more important in driving community-level patterns of diversity and invasion (*6, 19*). That the correlations between native diversity and the success of exotic species are mostly positive is reasonable, because the factors known to promote or limit native diversity are known to similarly influence invasions (*6*). This conclusion raises two concerns that at first may have seemed contradictory. First, the most diverse assemblages might be at the greatest risk of invasion, an important point for managing invasive species (*19*). Second, however, losses of species, if they affect neighborhood-scale diversity, may erode invasion resistance.

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26. The analysis included 256 tussocks of similar size (400 cm^2) and plant cover (90%).
27. Because of a limited choice of riffles after the 1998 El Niño high water, the riffle at which I conducted the experiment was among the highest riffles in the system. Thus, in 1999—a year with little spring rain—the tussocks at this site were much drier than the majority of tussocks, most of which were saturated. I minimized these differences by giving the tussocks in the experiment 1 liter of water daily. Water availability differences between the natural and experimental tussocks were not significant ($t_{1,\ 239} = 3.47$, $P = 0.13$).
28. The pool of transplants included *Conocephalum conicum*, *Epipactis gigantea*, *Equisetum arvense*, *Juncus covillei*, *Marchantia polymorpha*, *Mimulus cardinalis*, *M. guttatus*, *M. moshatus*, and *Panicum pacificum*. Tussocks in the one-, three-, and nine-species treatments received 9 total transplants. For treatments of five species (10 transplants) and seven species (7 transplants), I adjusted transplant size to maintain constant cover and biomass. Throughout 1998 and 1999, I carefully removed species that were not purposely planted. These species were weeded when small to prevent the weeds, or their removal, from affecting invasibility. In spring 1999, Shannon diversity, a measure incorporating both the richness and relative abundance of species, was highly correlated with planted richness ($R^2 = 0.92$, $P = 0.001$). No natural recruits were found in 10 tussocks not sown with seeds, which suggested that natural recruitment did not significantly contribute to variability in the experiment.
29. I added 200 seeds to obtain accurate per capita demographic rates. To prevent seedlings from interfering with one another, I thinned them on the 12 July 1999 and 1 August 1999 sampling dates. I thus calculated the proportion of successful seeds as (proportion that germinated and survived to 12 July) × (proportion of the 12 July unthinned surviving to 1 August) × (proportion of the 1 August unthinned surviving to 3 October).
30. Total cover, the sum of each species' cover, can exceed 100% because species' canopies overlap.
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36. I added seeds of *Agrostis* and *Plantago* to 190 tussocks using the same selection criteria as for the pattern tussocks. I added *Cirsium* to a subset (50) of these tussocks, and fewer seeds per tussock, because I had fewer seeds of this species. Seedlings were followed using the same procedures as in the diversity manipulation experiment. Seedling size yielded similar results to the proportion of successful propagules.

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Homogenization of Fish Faunas Across the United States

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Fish faunas across the continental United States have become more similar through time because of widespread introductions of a group of cosmopolitan species intended to enhance food and sport fisheries. On average, pairs of states have 15.4 more species in common now than before European settlement of North America. The 89 pairs of states that formerly had no species in common now share an average of 25.2 species. Introductions have played a larger role than extirpations in homogenizing fish faunas. Western and New England states have received the most introductions, which is a reflection of the small number of native fishes in these areas considered desirable gamefish by settlers.

Establishment of exotic species and loss of native species reduces regional differences among faunas and floras, a process referred to as biotic homogenization (*1, 2*). Homogenization of Earth's biota is accelerating and is an underappreciated aspect of global environmental change (*3*). Although many biologists have expressed concern about biotic homogenization, there are few quantitative assessments of the increased similarity among biota from different regions. Furthermore, the loss of regional distinctiveness can occur because of the introduction of widespread, cosmopolitan species or the extirpation of localized, endemic species. The relative importance of these two processes in homogenizing biotic communities is poorly known.

The distribution of many fish species has increased throughout the world as a result of intentional introductions for aquaculture and angling (*4*). The distribution of other species has expanded because of ballast water transfers, aquarium releases, and illegal stockings (*5–7*). In some cases, introduced fishes have eliminated native species and reduced regional biodiversity (*8, 9*). The addition of cosmopolitan species and the loss of endemic species is homogenizing the world's fish faunas, but the extent of this process is poorly documented.

Here, I describe the homogenization of freshwater fish faunas across the continental United States and evaluate geographical patterns and the relative importance of introductions versus extirpations in altering fish faunas. I assembled fish faunal lists for each of the 48 coterminous United States from regional textbooks, journal articles, and state

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databases (*10*) and placed species into one of three categories: extant native species, extirpated native species, and introduced species that had established reproducing populations. I did not include species that had been introduced but that had not established reproducing populations. The introduced established species for a state could include species native to other states as well as species whose native range is outside the coterminous United States. The historical fish fauna for each state consisted of native extant and native extirpated species. The current fish fauna for each state consisted of native extant and introduced established species.

Faunal homogenization was quantified in two ways. First, the change in the number of shared species for all 1128 pairwise combinations of the 48 states was determined by subtracting the historical number of shared species from the current number of shared species for each pair of states. Homogenization should increase the number of species in common between pairs of states. The second method was to determine the change in similarity between historical and current fish faunas for each pair of states. Similarity was based on Jaccard's coefficient of similarity (*11*), which ranges from 0% (states have no species in common) to 100% (states have identical fish faunas). The change in similarity was calculated by subtracting the historical similarity of the fish faunas from the current similarity of the fish faunas for each pair of states. Homogenization should increase the similarity of fish faunas among states.

There was a pronounced increase in the number of species in common between pairs of states (Fig. 1). On average, pairs of states have 15.4 more species in common now than before European settlement of North America. In fact, 89 pairs of states that formerly had no species in common now share an average of 25.2 species. For example, Arizona and Montana historically had no fish species in common but they now share 33 species.

The similarity of fish faunas as judged by Jaccard's coefficient also has increased across the United States (Fig. 2A). Most (89.9%) of the changes in similarity among pairs of states were positive, indicating that fish faunas have become more similar with time. The mean increase in similarity was 7.2%. The 89 pairs of states that historically had zero similarity (no species in common) now have an average similarity of 12.2%. Again as an example, Arizona and Montana went from a historical similarity of 0% to a current similarity of 26.8%.

To determine the relative contribution of extirpations versus introductions in homogenizing fish faunas, I recalculated the change in similarity that would have occurred if (i) only extirpations had taken place and (ii) only introductions had taken place. Similarity again was measured with Jaccard's coefficient. Extirpations caused virtually no change in the similarity among state fish faunas, whereas introductions caused increases in similarity that mirrored those due to the combined effects of both processes (Fig. 2, B and C). Thus, homogenization of fish faunas among states was mainly due to the effects of introductions rather than extirpations.

There are two reasons why introductions had a greater effect than extirpations in homogenizing fish faunas. First, introduction events ($n = 901$) were much more common than extirpation events ($n = 196$) across the 48 states (*12*). Second, a group of primarily food and gamefish species has been widely introduced and thus is shared by most states (Fig. 3 and Table 1). These cosmopolitan species contribute greatly to the homogenization of state fish faunas and include popular gamefish such as brown trout, rainbow trout, and smallmouth bass. By contrast, extirpated species generally have been lost from only one or a few states (Fig. 3). In fact, the species lost from the largest number of states is the extinct harelip sucker (*Lagochila lacera*), which was known to occur in only eight states (*13*).

Based on the percent of the fish fauna composed of nonnative species that have become established, the most altered fish faunas occur in the southwestern United States (Fig. 4). More than half the fish species currently found in Nevada, Utah, and Arizona are not native to those states. The other western states and a group of New England states also have highly altered fish faunas; 25 to 49% of the fish species in these states are introduced.

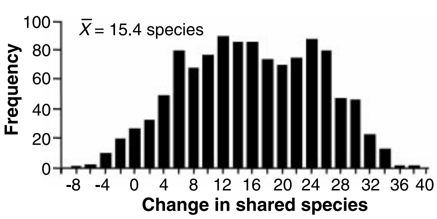

Fig. 1. Changes in number of shared species among 1128 pairwise combinations of the 48 coterminous United States. Change was measured as current number of shared species minus historical number of shared species. On average, states share 15.4 more species now than before European settlement of North America.

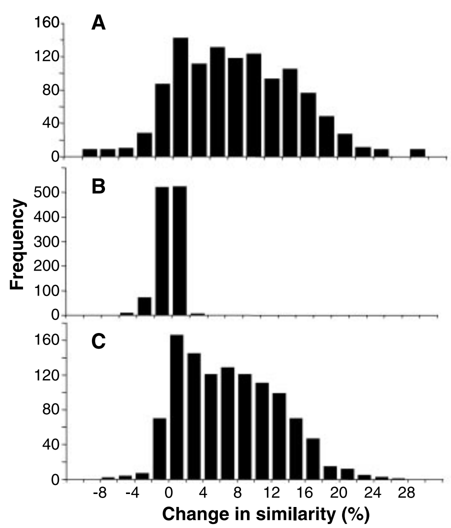

Fig. 2. Changes in similarity of fish faunas among 1128 pairwise combinations of the 48 coterminous United States. Change was measured as current similarity minus historical similarity with Jaccard's coefficient of similarity. (**A**) Change in similarity based on combined effects of species extirpations and introductions. Distribution is skewed toward positive values, which indicate that fish faunas have become more similar with time by an average of 7.2%. (**B**) Change in similarity based on species extirpations only. Extirpations have caused a negligible change in the similarity among state fish faunas. (**C**) Change in similarity based on introductions only. Distribution resembles that in (A), which indicates that most of the increased similarity in fish faunas is due to introduction of a group of cosmopolitan species.

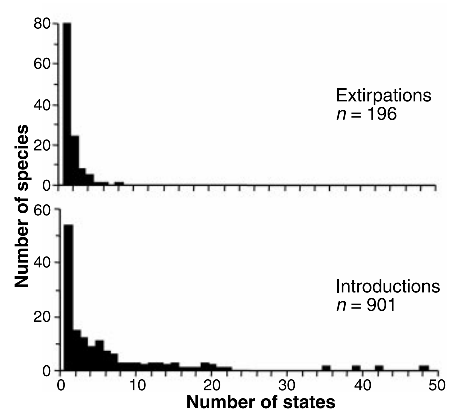

Fig. 3. Number of species extirpated from (top) or introduced and established in (bottom) a given number of states. Most extirpations involve species lost from just a few states, whereas introductions involved many species introduced into a large number of states. These widely introduced cosmopolitan species have contributed greatly to homogenization of fish faunas across the United States.

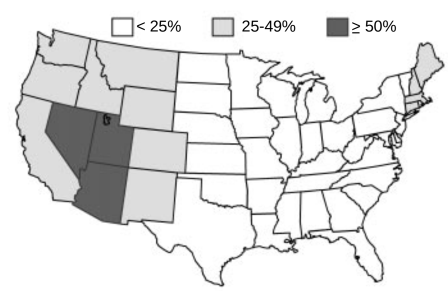

Fig. 4. Geographic distribution of species introductions across the continental United States. Degrees of shading represent percent of a state's current fish fauna composed of introduced species that have established reproducing populations. Western states and several New England states have the largest proportion of introduced established species.

Table 1. Most commonly introduced fish species in the coterminus United States. Only introduced species that had established a reproducing population in the state are included. For native range designations, western and eastern North America refer to drainages located west or east of the Rocky Mountain continental divide.

Common name	Genus and species	Number of states where species is			Reason for introduction	Native range
		Introduced	Native	Present		
Common carp	*Cyprinus carpio*	48	0	48	Aquaculture	Eurasia
Goldfish	*Carassius auratus*	42	0	42	Aquarium release	Eurasia
Brown trout	*Salmo trutta*	39	0	39	Gamefish	Eurasia
Rainbow trout	*Oncorhynchus mykiss*	35	6	41	Gamefish	Western North America
Smallmouth bass	*Micropterus dolomieu*	22	23	45	Gamefish	Eastern North America
Northern pike	*Esox lucius*	21	15	36	Gamefish	Circumpolar
Black crappie	*Pomoxis nigromaculatus*	20	28	48	Gamefish	Eastern North America
Yellow perch	*Perca flavescens*	20	26	46	Gamefish	Eastern North America
Fathead minnow	*Pimephales promelas*	19	25	44	Baitfish	Eastern North America
Walleye	*Stizostedion vitreum*	19	25	44	Gamefish	Eastern North America
Largemouth bass	*Micropterus salmoides*	19	29	48	Gamefish	Eastern North America
White crappie	*Pomoxis annularis*	18	27	45	Gamefish	Eastern North America
Striped bass	*Morone saxatilis*	17	16	33	Gamefish	Eastern North America
Bluegill	*Lepomis macrochirus*	16	31	47	Gamefish	Eastern North America
Mosquitofish	*Gambusia affinis*	15	13	28	Mosquito control	Eastern North America
Brook trout	*Salvelinus fontinalis*	15	23	38	Gamefish	Eastern North America
Green sunfish	*Lepomis cyanellus*	15	30	45	Gamefish	Eastern North America

The exchange of fish species between the eastern and western United States has been asymmetrical. The predominant pattern has been introduction of species native to the eastern United States into western states, primarily in association with angling. Of the 17 most widely introduced species, 12 fit this pattern (Table 1). By contrast, only one western species (rainbow trout) has been widely introduced into eastern states. The asymmetry is clearly illustrated by comparing the number and origin of introduced fish species in Nevada (a western state) and Kentucky (an eastern state). In Nevada, 44 of 85 fish species (51.8%) are introduced and 24 of these are gamefish or associated forage species native to the eastern United States. In Kentucky, 14 of 212 fish species (6.6%) are introduced and only 1 species (rainbow trout) is native to the western United States.

In the case of North American fish faunas, the strong east-to-west bias in introductions reflects the colonization history of North America by European settlers and the fact that western waters lacked what were considered desirable gamefish such as walleye, bass, sunfish, and catfish species. Further accelerating the east-to-west movement of fish was the creation of large impoundments that provided habitats for many eastern species that required warm water lake environments that were naturally uncommon in the American West (*14, 15*).

Introduction of species outside their native range continues to be a major problem in the United States, but the source of introductions has shifted. In particular, government-sanctioned introductions of gamefish or forage species outside their native range have declined in the United States in recent years (*8*). This reduction reflects both a saturation of gamefish species in many water bodies and a heightened awareness by fisheries biologists of the problems of introducing species outside their native range (*16*). However, illegal introductions associated with sportfishing continue to be a problem. Recent examples of illegal introductions include northern pike and walleye throughout the Pacific northwest and widespread introduction of bait minnows far beyond their native ranges (*7, 17*). Also, inadvertent introductions continue to be a problem, as shown by the recent establishment of round goby (*Neogobius melanostomous*) and ruffe (*Gymnocephalus cernuus*) in the Great Lakes through release of ship ballast water (*5*). Finally, release of aquarium fish is a problem, especially in warmer climates (*18*). Although control efforts such as restricting the use of bait fish or limiting the discharge of ballast water may slow the rate of homogenization, fish faunas across North America are likely to continue to be altered by a growing list of cosmopolitan species.

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10. For most states, data came from post-1985 textbooks about the fishes of that state or from compilations in peer-reviewed journals. For states where species lists predated 1985, I contacted state agency biologists or academic ichthyologists for a current fish species list. Although the loss and addition of species to a region's fish fauna is an ongoing process, the species lists I used are a good representation of the status of fish faunas across the United States in the late 20th century. A list of data sources can be found at www.sciencemag.org/feature/data/1047612.shl. Analyses were done by comparing across states rather than drainage basins because data on extirpated, extant, and introduced species that had become established were most reliable and available for a continental-scale comparison through state fishery management agencies or state fish books.
11. Similarity was calculated as follows: percent similarity = $[a/(a + b + c)] \times 100$ where a = number of species present in both states, b = number of species present only in the first state, and c = number of species present only in the second state [C. J. Krebs, *Ecological Methodology* (Harper & Row, New York, 1989)].
12. An introduction event refers to a single species being introduced and establishing a reproducing population in a state. Thus, the total number of introduction events was the sum of introductions across all 48 states. Likewise, the total number of extirpation events was the sum of extirpations across all 48 states.
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