Extinction Rates of North American Freshwater Fauna

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Abstract: *Since 1900, 123 freshwater animal species have been recorded as extinct in North America. Hundreds of additional species of fishes, mollusks, crayfishes, and amphibians are considered imperiled. Using an exponential decay model, we derived recent and future extinction rates for North American freshwater fauna that are five times higher than those for terrestrial fauna. Assuming that imperiled freshwater species will not survive throughout the next century, our model projects a future extinction rate of 4% per decade, which suggests that North America's temperate freshwater ecosystems are being depleted of species as rapidly as tropical forests.*

Tasas de Extinción de Fauna de Agua Dulce en Norteamérica

Resumen: *Desde 1900, 123 especies animales de agua dulce han sido reportadas como extintas en Norteamérica. Cientos de especies adicionales de peces, moluscos, langostinos y anfibios están considerados como amenazados. Utilizando un modelo exponential de disminución, derivamos tasas de extinciones recientes y futuras para la fauna de agua dulce de Norteamérica, mismas que son cinco veces mayores que aquellas para la fauna terrestre. Asumiendo que las especies de agua dulce en peligro no sobrevivirán a lo largo del próximo siglo, nuestro modelo proyecta una tasa de extinción futura de 4% por décda, lo cual sugiere una disminución de especies en los ecosistemas templados de agua dulce de Norteamérica tan rápida como la que ocurre en bosques tropicales.*

Introduction

Commonly cited warnings of an impending mass extinction have focused on declining species in terrestrial habitats, particularly tropical forests (e.g., Myers 1988; Wilson 1992; Mace 1994; Pimm et al. 1995; Brooks et al. 1997; Reid 1997). By contrast, relatively little media attention has been given to species loss in freshwater ecosystems, presumably because their terrestrial counterparts are perceived to be in greater peril. This view persists despite several recent studies that demonstrate a growing number of freshwater extinctions (Miller et al. 1989; Williams et al. 1993; Taylor et al. 1996; Neves et al. 1997), including a survey by the Nature Conservancy which first drew attention to the disproportionate imperilment of North American fishes, mussels, crayfishes, and amphibians (Master 1990). Direct comparisons of rates of species loss in freshwater and terrestrial ecosystems would shed stronger light on this issue and help set conservation priorities. Such analyses are hampered by the lack of extinction-rate estimates for freshwater fauna.

Exponential Decay Model

Extinction intensities for taxa or biomes of differing diversities can be compared by means of rates that are standardized according to the size of the species pool (Jablonski 1994). For each of several common North American faunal groups, we have modeled the proportional species loss per decade, r, as an exponential decay process expressed by the equation $r = 1 - P^{1/n}$, where P is the proportion of extant native fauna and n is the number of decades over which the extinctions have occurred. Our use of an exponential decay model as-

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sumes only that the proportion of species going extinct is constant over a given time interval.

We calculated recent rates for aquatic and terrestrial fauna based on extinctions recorded from at least the beginning of this century ($n \geq 10$), and we projected future rates by assuming that all species currently imperiled (i.e., endangered or threatened, as determined from known or inferred population abundances and range sizes) will not survive throughout the next century. We obtained the conservation status of each species from published "red lists" (Miller et al. 1989; Williams et al. 1989, 1993; Taylor et al. 1996; Neves et al. 1997; Turgeon et al. 1998) and the Natural Heritage Central Databases (NHCD) of the Nature Conservancy internet website (http://www.consci.tnc.org). For example, given that 35 out of 297 species of freshwater mussels have become extinct since 1900 (Turgeon et al. 1998), we calculated a recent extinction rate of 1.2% per decade ($r = 1 - (0.882)^{0.1}$). Barring effective conservation action, we project that at least 127 imperiled mussel species (Bogan 1996; Turgeon et al. 1998) will disappear within the next 100 years, inferring a future extinction rate of 6.4% per decade ($r = 1 - (0.515)^{0.1}$). This estimate is conservative because it does not consider a growing number of extirpations caused by competition with the invading Eurasian zebra mussel (*Dreissena polymorpha*) (Ricciardi et al. 1998).

Extinction Rate Comparisons

Although crude, our estimates facilitate instructive comparisons between faunal groups or biomes. Imperiled species account for 48.5% of North American freshwater mussels (Bogan 1996; Turgeon et al. 1998), 22.8% of freshwater gastropods (108 of 474 extant spp.; Neves et al. 1997), 32.7% of crayfishes (110 of 336 extant spp.; Taylor et al. 1996), 25.9% of amphibians (63 of 243 extant spp.; NHCD), and 21.3% of freshwater fishes (217 of 1021 extant spp.; Williams et al. 1989). Some imperiled species may survive the next century, but a potentially larger number of taxa not currently at risk will disappear because of future biological invasions (e.g., Ricciardi 1998; Ricciardi & Rasmussen 1998) and the cascading effects of keystone extinctions (Spencer et al. 1991). Furthermore, several species may be functionally extinct already; for example, populations of over 40% of the mussel species in the Tennessee River are not reproducing (Neves et al. 1997). If current trends persist, extinction rates of these common faunal groups will increase severalfold—by more than an order of magnitude for crayfishes and amphibians (Table 1).

It is striking to note that the projected mean future extinction rate for freshwater fauna is about five times greater than the rate for terrestrial fauna and three times the rate for coastal marine mammals. Even more remarkable is that freshwater rates fall within the range of estimates for tropical rainforest communities (1-8% loss per decade; Reid 1997), which are thought to be being depleted faster than any other biome (Myers 1988). This is compelling evidence that North American freshwater biodiversity is diminishing as rapidly as that of some of the most stressed terrestrial ecosystems on the planet. Although larger absolute numbers of species are at risk in the tropics, the elimination of even a few species in temperate habitats can promote further extinctions and disrupt ecosystem functioning (Carpenter et al. 1985; Schindler 1989; Power 1990; Spencer et al. 1991). At least 123 North American freshwater fishes, mollusks, crayfishes, and amphibians have already gone extinct since the beginning of the century (Miller et al. 1989; Taylor et al. 1996; Neves et al. 1997; Turgeon et al. 1998; NHCD). This estimate of biodiversity loss is probably conservative because there have likely been extinctions of species that we did not know existed, as suggested by the fact that several extinct fishes are known from only a few specimens (Miller et al. 1989).

A comparison of our extinction-rate estimates with those from the fossil record provide another illustration of how rapidly freshwater fauna are disappearing. The estimated mean duration of fossil freshwater fish species is 3 million years, which is longer than that of birds and mammals (McKinney 1997). Assuming extinction events to be independent, we can infer a background rate of one extinction

Table 1. Extinction rate estimates (percent loss per decade) for continental North American fauna.*

Freshwater fauna	*Recent*	*Future*	*Terrestrial and marine fauna*	*Recent*	*Future*
Fishes	0.4	2.4	Birds	0.3	0.7
Crayfishes	0.1	3.9	Reptiles	0	0.7
Mussels	1.2	6.4	Land mammals	0	0.7
Gastropods	0.8	2.6	Marine mammals	0.2	1.1
Amphibians	0.2	3.0			
Mean rate	0.5	3.7		0.1	0.8

**Data were obtained from published sources for fishes (Miller et al. 1989; Williams et al. 1989), crayfishes (Taylor et al. 1996), mussels (Williams et al. 1993; Bogan 1996; Turgeon et al. 1998), and gastropods (Neves et al. 1997; Turgeon et al. 1998). Data for amphibians, birds, reptiles, and mammals were obtained from the Natural Heritage Central Databases (The Nature Conservancy and the International Network of Natural Heritage Programs, November 1997).*

every 3 million species-years. Given that 40 of 1061 North American freshwater fish have become extinct in this century, the modern regional rate (in the recent past) is equivalent to one extinction every 2600 species-years, which is 1000 times higher than the background rate.

Widespread Modification of Lakes and Rivers

The alarming trends for freshwater fauna are linked to extensive habitat deterioration caused by sediment loading and organic pollution from land-use activities, toxic contaminants from municipal and industrial sources, stream fragmentation and flow regulation by dams, channelization and dredging projects, and interactions with increasing numbers of exotic species (Benke 1990; Allan & Flecker 1993; Dynesius & Nilsson 1994; Neves et al. 1997; Richter et al. 1997; Ricciardi et al. 1998). Of 5.2 million km of stream habitat in the contiguous United States, <2% (<100,000 km) is of sufficiently pristine quality to be federally protected, and only about 40 rivers >200 km long remain free-flowing (Benke 1990). Such massive habitat deterioration threatens some of the world's richest freshwater faunal assemblages (Bogan 1993; Taylor et al. 1996; Neves et al. 1997). Given that human activities have dramatically modified rivers worldwide (e.g., O'Keefe 1989; Dudgeon 1992; Cole et al. 1993; Dynesius & Nilsson 1994) and thus have caused global declines in mussels and fishes (Moyle & Leidy 1992; Bogan 1993), we suspect that interbiome comparisons on other continents will also reveal freshwater fauna to be disproportionately imperiled.

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