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Perspectives

Extinction debt of Hungarian reserves: A historical perspective

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Summary

We compiled species lists of the birds, reptiles and amphibians found in Hungarian reserves, and then used these to estimate the level of historical species richness using species–area relationships. The situation in the 18th century, before large-scale land transformation, such as river regulations and drainages, could be approximately reconstructed. The species–area relationship was significant for all three classes. We estimated that 1 amphibian species, 4 reptile species, and 230 species of birds have become extinct in Hungary during the last two centuries. The latter seems unrealistic, so we evaluated extinctions in raptors (Falconiformes) which was the best known taxon. According to our estimation, there should be 23 extinct species of raptors in Hungary. However, we found only 14 potential species, even when considering unlikely species. Therefore, we conclude that the present species richness pattern in the reserves may have not reached equilibrium for several taxa (like birds), but probably has done so for others (amphibians and reptiles). Although, it would be desirable to extend the analysis to other taxa, this result indicates the existence of time-delayed species extinctions after habitat destruction, that is, an extinction debt. Currently, few studies have reported a time-delay effect from Europe. However, the results of this study suggest that an extinction debt may be important and should be considered when developing conservation strategies.
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Zusammenfassung

Wir erstellten Artenlisten der Vögel, Reptilien und Amphibien, die in ungarischen Schutzgebieten gefunden werden und nutzten diese dann dazu, das Ausmaß des historischen Artenreichtums abzuschätzen, indem wir Arten-Areal-Beziehungen verwendeten. Die Situation des 18. Jahrhunderts, bevor großräumige Landschafts-

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veränderungen wie Flussregulierungen und Drainagen stattfanden, konnte näherungsweise rekonstruiert werden. Die Arten-Areal-Beziehung war für alle drei Gruppen signifikant. Wir schätzten ab, dass eine Amphibienart, 4 Reptilienarten und 230 Vogelarten in den letzten zwei Jahrhunderten in Ungarn ausstarben. Das letzte scheint sehr unwahrscheinlich. Deshalb bewerteten wir das Aussterben von Greifvögeln (Falconiformes), welche die bestbekannte Gruppe darstellt. Nach unserer Einschätzung sollte es 23 Greifvogelarten geben, die in Ungarn ausstarben. Wir fanden jedoch nur 14 potenzielle Arten, auch wenn wir unwahrscheinliche Arten mit berücksichtigten. Daraus schlossen wir, dass das derzeitige Muster des Artenreichtums für einige Taxa (wie Vögel) noch keinen Gleichgewichtszustand erreicht hat, während es für andere (Amphibien und Reptilien) diesen bereits erreicht hat. Auch wenn es wünschenswert wäre, die Analyse auf andere Taxa auszudehnen, weist dieses Ergebnis bereits auf die Existenz eines zeitverzögerten Aussterbens der Arten nach der Zerstörung des Habitats hin, also auf eine Aussterbeschuld. Derzeit haben nur wenige Untersuchungen von einem Zeitverzögerungseffekt berichtet. Die Ergebnisse dieser Untersuchung weisen jedoch darauf hin, dass die Aussterbeschuld wichtig sein kann und berücksichtigt werden sollte, wenn Erhaltungsstrategien entwickelt werden.
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Introduction

Human domination of the Earth's ecosystems has resulted in a continuing impoverishment of the biota. The extinction of species is the most serious challenge to nature conservation (e.g. Frankel & Soulé, 1981). This is because globally extinct species are lost forever, and the re-establishment of populations of locally extinct species requires considerable resources. Extinction is an ongoing process, and its rate is predicted to increase due to increasing rate of habitat conversion and other global scale changes (Totten, Pandya, & Janson-Smith, 2003; Wilson, 1988), and to the extinction debt (Loehle & Li, 1996; Tilman, May, Lehman, & Nowak, 1994); the latter is the future ecological cost of current habitat destruction, where the loss of natural habitats causes time-delayed but deterministic extinctions.

In this paper we use species lists of amphibians, reptiles, and birds in Hungarian reserves to construct species–area curves. These relationships in their logarithmic form predict a linear relationship between species number and area, and seem to be fairly robust across taxa (Rosenzweig, 1995, Storch & Gaston, 2004). Therefore, it is widely used to predict species richness, e.g. in relation to the projected losses of natural habitat (Brashares, Arcese, & Sam, 2001; Lawton & May, 1995; Pimm & Askins, 1995; Pimm & Raven, 2000; Ulrich & Buszko, 2004; Whitmore & Sayer, 1992).

Species–area curves are useful not only to predict species numbers after habitat loss, but also to estimate historical species numbers, when natural habitats were more extensive (Wiersma & Nudds, 2001). The estimated past species number (PastSN) can be compared by the potential historical species numbers (PotSN) calculated from historical data and from extrapolations of recent species ranges and trends, which can reveal the long-term trend of present species richness. The slope of the species–area relationship curve indicates difference between the estimated PastSN and the PotSN (Fig. 1). Underestimation reflects a

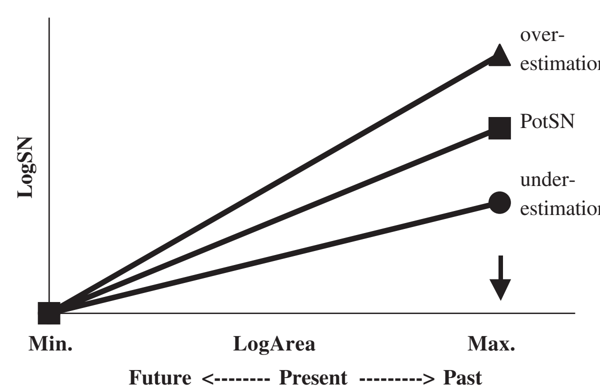

Figure 1. A hypothetical species–area relationship. Area of natural habitats changes with time due to human habitat conversion: area will decrease from the present to the future. If going back in time, area of natural habitats is increasing, with a maximum value equal to the total available land area (indicated by an arrow). The species–area relationship can be calculated using existing reserves, because these are remnants of natural habitats. Then, this relationship can be used for extrapolation in time. However, past species numbers can be over or underestimated, compared to the potential historical species number (PotSN), which is based on historical data and distribution maps.

relative decrease in species number in large reserves. However, this is unlikely, because extinction rates are slower in larger areas (MacArthur & Wilson, 1967). Overestimation indicates unexpectedly high species numbers in large reserves. If an extinction debt is present in the reserves, we expect overestimation rather than underestimation, because the time delay of extinction is longer in larger areas (Newmark, 1987), resulting in more species in large areas than expected under equilibrium. As the species number declines more slowly in the large reserves, the slope also decreases (Gonzalez, 2000).

The presumption of this analysis is that the natural status and environmental conditions of present reserves are similar to those found before the large-scale transformation in both status and conditions. As in most countries in Europe, recent "natural" habitats in Hungary are the result of long-term co-existence of humans and nature. The maintenance of this low intensity traditional management, e.g. grazing in grasslands by ancient cattle, is a prerequisite to preserve biodiversity. Both intensification and abandonment result in a loss of diversity (Kleijn & Báldi, 2005). The main aim of grassland conservation is to maintain and restore extensive traditional management (Kelemen, 1997). Therefore, we argue that it is a reasonable assumption that the status and condition of reserves reflect historical conditions. The other areas where transformation has occurred are agricultural regions, urbanized areas or those under other forms of intensive management. Our questions were: what was the species richness of Hungary in the late 18th Century, before the large scale land transformation began? Are there taxon-specific differences? Does the use of species–area relationship provide reliable estimates of historical species richness?

Methods and analysis

Species lists of amphibians, reptiles, and birds in Hungarian reserves (national parks, nature conservation areas, landscape protection areas) were compiled from the literature and from personal interviews of experts of a taxon, or locality. Bird species were included on the list if the species bred there at least once in the last 30 years. Some of the reserves were composed of more then one site, but we used the whole reserve as a sampling unit because the subsites were close (<5 km) to each other, which did not seem to be a barrier to movement between sites for birds. In contrast, for the amphibians and reptiles a few kilometers of inhospitable habitat means isolation, because of their much lower (usually <2000 m) dispersal distances (Madsen, 1984; Nöllert & Nöllert, 1992; Ùjvári & Korsós, 1997). Therefore, all reserves and subsites were included in the analysis separately, which contributed to the large number of reserves for amphibians and reptiles. The range of reserve areas was from a few hectares to 63,635 ha, with a mean area of ca. 5500 ha for amphibians and reptiles, and 6900 ha for birds (where subsites were not separated).

We generated the species–area curves for amphibians, reptiles and birds using base 10 logarithmically transformed species numbers and area. Then, we substituted the total area of Hungary (9,350,000 ha) to the species–area equation to estimate the species number in Hungary, if it were covered by semi-natural habitats, as in the protected areas.

The reliability of PastSN was tested using raptors (Falconiformes), where both the historical occurrence data and the recent distributions are well known (Haraszthy, 1998; Snow & Perrins, 1998). The five smallest reserves, where no raptors were detected, were excluded from the analysis due to their small size (<50 ha). Therefore, PotSN was estimated using both well-documented historical data and less reliable records, and recent ranges; if a species' breeding habitat is present in Hungary, and/or the species range limit is within 1–2000 km, we included it as a potential historical breeding species.

Results

We listed 14 amphibians, 15 reptiles and 205 breeding bird species in various reserves across Hungary. The reserves cover ca. 350,000 ha. The species–area relationship was highly significant for all the three classes, explaining roughly half of the variation in species numbers (Fig 2, Table 1). The slope was very low in amphibians (0.08), higher in reptiles (0.16) and highest in birds (0.20). The estimated number of species (PastSN) in Hungary was higher by 1 species of amphibian, 4 species of reptile, and almost 230 bird species than the recent species numbers (Table 1).

The number of breeding raptors in the reserves is 19 currently, but 23 more species were estimated to be present few centuries before (Table 1). This is unreliable, because only 14 species can be added to the recent list, even if unlikely breeders are included. There are five species which were recorded to breed in Hungary previously (Griffon Vulture *Gyps fulvus,* Golden Eagle *Aquila chrysaetos,* Spotted Eagle *Aquila clanga,* Lesser Kestrel *Falco naumanni,* Red Kite *Milvus milvus*). However these have not bred in Hungary recently; therefore they were not included in the analysis. Four other species (Black Vulture *Aegypius monachus,* Egyptian Vulture *Neophron percnopterus,* Osprey *Pandion haliaetus,* Levant Sparrowhawk *Accipiter brevipes*) are likely to have bred in Hungary previously, although there are no reliable historical records. By including species which possibly bred in Hungary, only five more species can be added (Bearded Vulture *Gypaetus barbatus,* Steppe Eagle *Aquila nipalensis,* Bonelli's Eagle *Hieraaetus fasciatus,* Pallid Harrier *Circus macrouros,* Lanner Falcon *Falco biarmicus*). These are considered unlikely because either their breeding range is thousands of kilometers away from Hungary (Steppe Eagle, Pallid Harrier, Lanner Falcon), or their preferred breeding habitat is missing from Hungary (higher mountains; Bearded Vulture, Bonelli's Eagle).

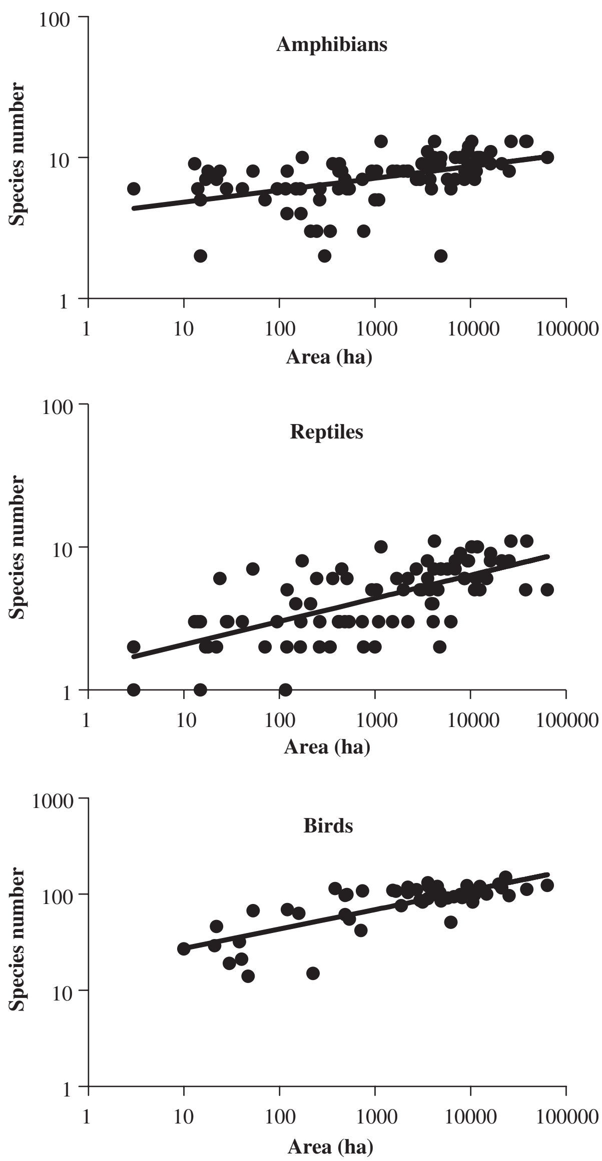

Figure 2. Species–area relationship of three vertebrate taxa in Hungarian reserves.

Discussion

We have estimated the number of bird, reptile and amphibian species that would occur in Hungary if large-scale habitat modifications had not happened in the last 2–3 centuries. The estimate are conservative because the habitat composition of reserves and the country is different: protected areas contain more low-productivity lands (e.g. alkaline and sandy soils), whereas more highly productive lands (e.g. loess, floodplains) are used for intensive agriculture (see also Margules & Pressey, 2000). Therefore, several productive land types are under-represented in the samples, resulting in a flattened slope, i.e. in a conservative estimation of historical species number based on the reserves. An additional issue is the degree to which the species richness of reserves is manipulated; i.e. if a reserve is managed for biodiversity, it may have higher species richness than it would under natural circumstances. However, resources of nature conservation in Hungary are too limited to consider it as increasing species richness at the national level.

Table 1. Data on the studied taxa, their species–area equation, the estimated past species number (PastSN) and the increase in the number of species

Taxon	Species number	Number of areas	Equation	R^2	P	PastSN	Increase
Amphibians	14	86	$\log S = 0.085 \log A + 0.599$	0.474	<0.001	15.4	1
Reptiles	15	87	$\log S = 0.162 \log A + 0.155$	0.454	<0.001	19.2	4
Bird species	205	50	$\log S = 0.201 \log A + 1.236$	0.589	<0.001	433.9	228
Raptors	19	45	$\log S = 0.249 \log A - 0.108$	0.537	<0.001	42.4	23

We used the log–log model of the species number–reserve area relationship to estimate the species number in the absence of large–scale land conversions (PastSN). This estimate is rather sensitive to the model and data, since there is a large gap between the area of studied reserves (350,000 ha) and the country (9,350,000 ha) (see also Ulrich & Buszko, 2004). However, our aim is not to prove that the log–log model is the best-fit model, or that extinction debt is the only possible explanation for the steep slope, but to show that there is a good chance that an extinction debt is present. Below, we will describe a possible way to test the presence of an extinction debt in Europe.

The strongly significant species-area relationships found for birds, reptiles and amphibians in the reserves are in accordance with expectations and other species–reserve area studies (e.g. Brashares, Arcese, & Sam, 2001). Similarly, the relationships between the slopes (higher for birds than for amphibians and reptiles) are similar to other studies (Brook, Sodhi, & Ng, 2003; Ricklefs & Lovette, 1999).

The difference between PastSN and PotSN is small in amphibians and reptiles, suggesting that little decline has occurred in the last two centuries in Hungary. It does not contradict the global pattern of amphibian population decline, because Europe is the least affected region in the world (Green, 2003; Houlahan, Findlay, Schmidt, Meyer, & Kuzmin, 2000). The presence of amphibians primarily depends on the existence, and not extent of preferred habitats locally (Hofer, Bersier, & Borcard, 2004). Therefore, the large-scale extent of their habitats may have minor influence. Nevertheless, there is a population decline for several species in Hungary, and some species are on the brink of extinction (Korsós, 1997).

The large difference between PastSN and PotSN in birds, and more specifically in raptors, shows that species number is highly overestimated when extrapolated from the species–area relationship. In other words, recent species number in large reserves is much higher than it should be according to the species–area relationship under equilibrium. The reason for this overestimation is assumed to be the extinction debt.

Time-delayed extinction is a well-known process in island ecology, where it termed faunal relaxation and defined as the loss of species through time from newly isolated islands (Diamond, 1972). The process has been described in both landbridge islands (Downs & Wirminghaus, 1997; Wilcox, 1980), and habitat islands (e.g. Brooks, Pimm, & Oyugi, 1999; Brown, 1971), including nature reserves (Carroll, Noss, Paquet, & Schumaker, 2004; Newmark, 1987). Faunal relaxation may cause species richness decline in reserves, as reaching new equilibrium over time. This is a long process, taking centuries (Brooks, Pimm, & Oyugi, 1999; Rosenzweig, 1995). Therefore, the present status of reserves a priori should be considered as not being in equilibrium as this study has found, at least for birds.

The difference in time of reserve establishments and large scale land conversions across Europe makes it possible to test the extinction debt at the continental scale. We predict that in countries with a long history of drainage, river control and other types of land transformations, the slope of the log–log species–area relationship of raptor species in reserves will be lower. This is because a larger proportion of the debt has already been paid, or, in other words, the fauna is more relaxed and closer to equilibrium than in Hungary. If extinction debt proves to be present in more reserve systems and more taxa in Europe, then it should be clearly considered in conservation management. For example, there is a strong tendency in the EU to manage farmland in an environmentally friendly way using agri-enviromental schemes (Kleijn & Sutherland, 2003). Farmland covers roughly half of the continent, therefore schemes that are designed to support the most threatened species may mitigate extinction debt. It is not a naive expectation, because most endangered species in Europe depend on some form of human land management. It is a consequence of the thousands of years of human land conversion in Europe (Dieterich & Van der Straaten, 2004). Such general guidelines are not new in conservation planning and management. The novel component is the urgency of realizing the actions to stop species loss. The status of reserves in Hungary is similar to that in other Central and Eastern European countries. Therefore, the delayed decline of species richness of many reserves on a continental scale seems to be a serious threat. Extinction debt in European landscapes has only recently been considered (Durell & Clarke, 2004; Hanski, 2000, Hanski, & Ovaskainen, 2002; Lindborg & Eriksson, 2004), therefore, it has not been incorporated into conservation planning. However, this study questions the long-term reliability of most continental and national biodiversity action plans in Europe.

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