Review

Extinction debt: a challenge for biodiversity conservation

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Local extinction of species can occur with a substantial delay following habitat loss or degradation. Accumulating evidence suggests that such extinction debts pose a significant but often unrecognized challenge for biodiversity conservation across a wide range of taxa and ecosystems. Species with long generation times and populations near their extinction threshold are most likely to have an extinction debt. However, as long as a species that is predicted to become extinct still persists, there is time for conservation measures such as habitat restoration and landscape management. Standardized long-term monitoring, more high-quality empirical studies on different taxa and ecosystems and further development of analytical methods will help to better quantify extinction debt and protect biodiversity.

Extinction debt and its importance for conservation biology

Habitat loss, climate change and invasive species are the main global threats to biodiversity [1–3], constituting key single and synergistic drivers of extinctions [4–6]. The effects of these components of global change can be almost immediate in some cases, but often it takes a considerable amount of time for declining populations to disappear following environmental perturbations. In recent years there has been a notable increase in awareness of delayed extinctions, also called extinction debt, as an important factor to consider in biodiversity conservation.

Extinction debt is a phenomenon that can easily remain unnoticed but that should be taken into account in conservation planning. If the extinction debt is large, the number of effectively endangered species tends to be underestimated [7] and hence the consequences of habitat loss and other effects of global environmental changes on biodiversity might be underestimated. Because a large proportion of natural habitats worldwide have been lost or deteriorated in recent decades, extinction debt might be common in many remaining natural communities. However, as long as the species predicted to eventually become extinct still persist, there is time left to implement countermeasures such as habitat restoration [8]. We review the conceptual and ecological basis of extinction debt, summarize the empirical evidence available and evaluate the limitations of different methodological approaches to studying extinction debt. Finally, we provide a synthesis for conservation and research perspectives. We show that extinction debt is a highly relevant but so far neglected aspect of the impact of global change on biodiversity.

Glossary

Equilibrium state: Also known as stable state. Situation in an ecological community when the number of species is not changing because the rate of local extinctions equals the rate of local colonizations.
Extinction: The disappearance of a species. Extinction might occur locally (at the level of a habitat patch), regionally (at a landscape level) or on larger spatial scales (at country, continent or global levels).
Extinction debt: In ecological communities, the number or proportion of extant specialist species of the focal habitat expected to eventually become extinct as the community reaches a new equilibrium after environmental disturbance such as habitat destruction, climate change or invasion of exotic species. In single species, the number or proportion of populations expected to eventually become extinct after habitat change.
Extinction threshold: The minimum amount of habitat area, connectivity and quality required for a species to persist.
Focal habitat: The habitat type that is currently under observation. Focal patch is the particular habitat patch under observation.
Habitat connectivity: The amount of focal habitat in the landscape surrounding the focal habitat patch (opposite to isolation). Ideally measures of connectivity take into account both the area and distance of the surrounding patches.
Habitat loss: Decrease in area of the focal habitat, used here as a surrogate for habitat area loss and habitat fragmentation, i.e., covering a decrease in both area and connectivity of habitat patches.
Metapopulation: A set of local populations that occupy a network of habitat patches and are linked by dispersal.
Relaxation time: Also known as time lag to extinction, extinction lag, time delay to extinction, time to extinction. The time taken for a community of species to reach a new equilibrium after an environmental disturbance. Extinction debt is gradually paid during the relaxation time as the expected extinctions are realized.

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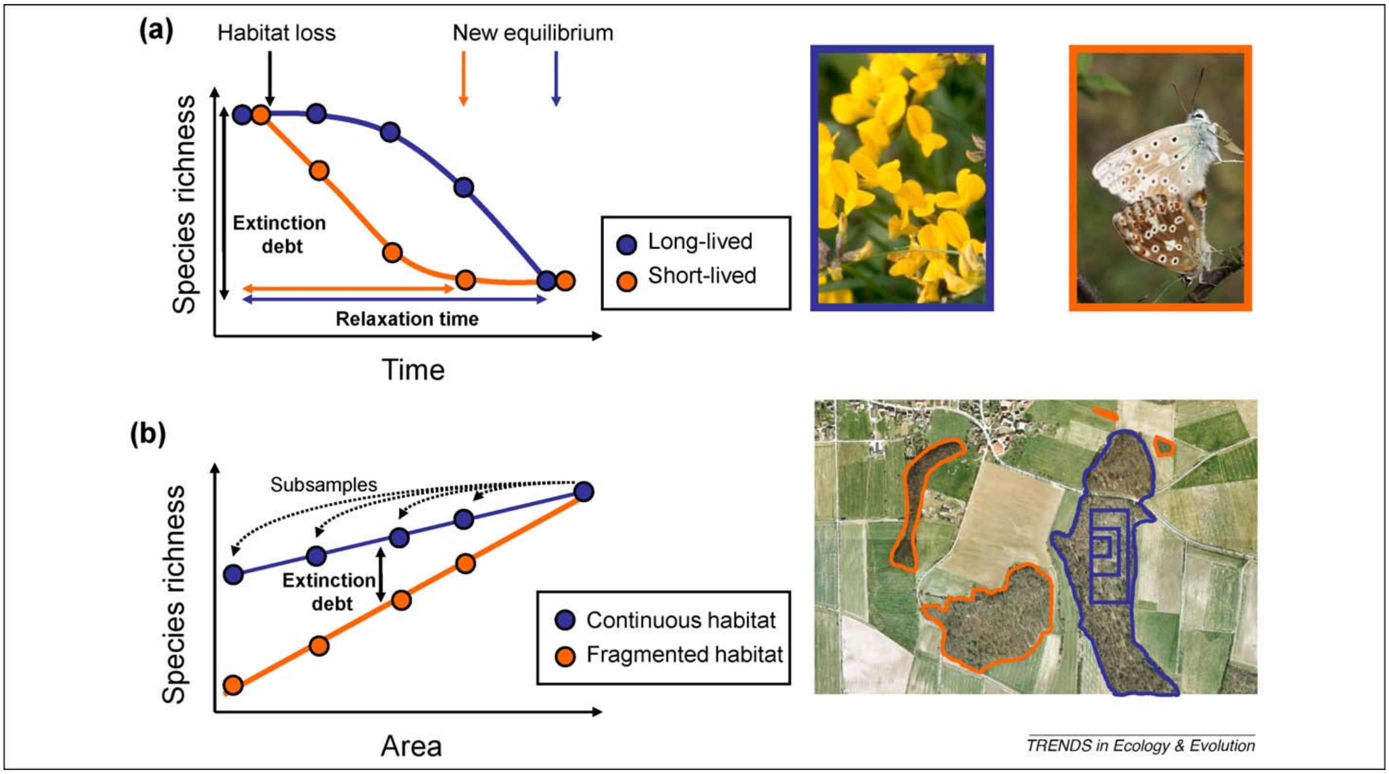

Figure 1. Conceptual model of extinction debt. (a) At equilibrium, species richness in a habitat patch is high. After an environmental perturbation, habitat is lost but this does not necessarily cause immediate extinction of all species to reach a new equilibrium. The difference between the number of species remaining after habitat loss and a new theoretical equilibrium represents a possible extinction debt. Relaxation time is the time elapsed since the habitat was lost until the new equilibrium is attained. Short-lived species (orange dots) are likely to show faster relaxation to a new equilibrium than long-lived species (blue dots). The photographs on the right-hand side are examples of a long-lived perennial herb (*Hippocrepis comosa*) and a short-lived butterfly species (*Polyommatus coridon*). (b) In a continuous habitat, subsamples of different areas show a shallower species–area relationship (blue dots) than those in a fragmented habitat (orange dots). The difference in species numbers between large and small subsamples provides an estimate of the deterministic species loss in the initial phase of habitat loss. In fragmented habitats, several of the initially surviving species will not be able to persist in the long term and thus there is an extinction debt. In a later equilibrium stage, such isolated fragments show steeper species–area relationships (orange dots) than non-fragmented areas of the same size (blue dots). Immediately after perturbation, extinction debt is proportionally higher in small patches (as shown in the figure). Since patch-level extinctions tend to occur faster in small patches, after some time the remaining extinction debt can be higher in large patches. The aerial photograph on the right-hand side illustrates the sampling of different sized areas in a continuous forest (blue patches) versus sampling in smaller and larger isolated forest fragments (orange patches). Both axes are on a log scale.

Current knowledge on the extent and time scale of delayed extinctions is, however, clearly limited by the lack of well-designed empirical studies and long-term monitoring for major taxa and ecosystems.

What is extinction debt?

The idea that species can initially survive habitat change but later become extinct without any further habitat modification has a long history. It was first conceptualized in island biogeography [9] and further elaborated by Diamond [10], who introduced the term relaxation time as the delay of expected extinctions after habitat loss. According to theoretical predictions and supporting empirical data, the relaxation time increases with increasing patch area and with decreasing isolation [10–12].

A second root stems from metapopulation modeling. Tilman *et al.* [13] introduced the term extinction debt and considered the order of extinctions in relation to competitive dominance (for further examination of their model see Refs [14–19]). The concept of extinction debt is related to relaxation time but specifies the number or proportion of extant species predicted to become extinct as the species community reaches a new equilibrium after an environmental perturbation [7] (Figure 1a). The concept can also be applied to single-species metapopulations by estimating the number or proportion of local populations that are predicted to become extinct following a perturbation and by estimating the relaxation time [20,21]. The extent of the environmental perturbation generally influences the number of predicted extinctions, with a larger amount of habitat loss leading to more extinctions [22,23]. The probability that the extinction debt has been paid increases with time since the landscape perturbation occurred [8,24]. Extinction debts are therefore most likely to exist in landscapes where large-scale habitat destruction occurred recently [7].

Species extinctions can be deterministic or stochastic [25]. Immediate deterministic extinctions occur during habitat loss due to a clumped distribution of species within a habitat. Partial destruction of habitat thus leads to immediate extinction of some populations, as illustrated by the relationship between species number and sample area in large continuous habitats (Figure 1b). Local extinctions can also be stochastic due to demographic, genetic or environmental variability. Although a large proportion of deterministic extinctions typically occur almost immediately after habitat loss, both stochastic and deterministic processes can cause extinctions after a considerable delay, thus contributing to extinction debt for many years or generations [26]. This can be particularly important in small habitat remnants, where both abiotic and biotic edge effects can cause gradual deterioration of habitat quality [27,28].

An important basis of all community-level approaches to extinction debt is a clear focus on habitat specialist species that are expected to be more sensitive to habitat changes. When the species specialized on the focal habitat can be separated from habitat generalists and from species inhabiting the surrounding habitats or habitat edges, extinction debt can be measured as the percentage of specialist species predicted to become locally extinct following an environmental perturbation. This measure, together with the time since the environmental perturbation, enables meaningful comparison of estimated extinction debts between studies with varying numbers of focal species [29].

When is extinction debt likely to occur?

The probability and magnitude of extinction debt depends on the life history traits of a particular species, the spatiotemporal configuration of habitat patches, the time since the habitat was altered and the nature of the alteration. Theoretically, the following factors affect the time to extinction after a metapopulation falls below an extinction threshold [23,30]: (1) the strength of the environmental perturbation; (2) the characteristic turnover rate of the species, which is correlated with the generation time of the organism; and (3) the availability of stable large patches within the patch network. The delay to extinction is expected to be particularly long for species living just below their extinction threshold, e.g. when there is only slightly too little habitat available to ensure long-term persistence.

Although information is scarce on the influence of species traits on extinction debt, empirical evidence suggests that delayed extinctions are more likely to occur in species with low compared to those with high turnover rates (e.g. perennial vs. annual plants or mammals vs. insects) [31,32]. Microhabitat specificity and the dispersal probability of the species can also affect extinction debt. When historic and present woodland extent was related to current lichen diversity in Scotland, an indication of extinction debt was found for highly specialized, dispersal-limited microlichens, but not for less specialized macrolichens [33].

The probability that extinction debt will occur can be high in landscapes where large habitat patches [12,34] and high connectivity remain [11] even after severe habitat loss or deterioration. The delay can, however, be long and difficult to detect in such landscapes because of a slow response of populations that are just below their extinction threshold. Alternatively, there might be no extinction debt if populations of all species are able to persist above their extinction threshold in the remaining large and only slightly fragmented habitats. At the other extreme, extinction debt might not exist just because species become extinct immediately after a very severe habitat loss.

The time elapsed since landscape perturbation is crucial because of the possibility that extinction debt has already been paid via realized extinctions [8]. In Belgium, forest plants still showed an extinction debt after habitat fragmentation during the last 200 years, whereas such debt was considered unlikely in similar landscapes in England where fragmentation occurred approximately 1000 years ago [31]. In addition, there is a strong link between spatial and temporal scales. Extinction debt will be paid off faster in landscapes with small and isolated patches (Figure 1). Cousins [29] reviewed grassland fragmentation studies on plants and reported that extinction debt has been found in landscapes with more than 10% of the original grassland area remaining, but not in landscapes with less than 10% original area left. A potential explanation is that most extinctions would already have occurred in the highly fragmented landscapes where the habitat loss started 70–200 years ago [29]. The magnitude of landscape perturbation can thus also affect the length of the relaxation time.

Empirical evidence of extinction debt

Despite a considerable number of conceptual papers, no theoretically based summary or guidelines on how extinction debt should be studied empirically are currently available. The large number of approaches applied to study extinction debt empirically can be categorized into five groups, based mainly on the type of data available: (1) past and present habitat information; (2) comparison of stable versus unstable landscapes; (3) past and present information on species and habitats; (4) time series data on species and habitats; and (5) empirically based spatially explicit modeling for single species (see Box 1 and Table 1 for further details). The first three approaches aim to detect existing extinction debt from relationships between species richness and habitat variables, for example species–area relationships (SAR). An important assumption is that species richness was in equilibrium before the environmental perturbation. The fourth approach has been used to quantify relaxation times and extinction debts from regular monitoring of species occurrences or richness after the habitat change. The fifth approach combines empirical data and population modeling to evaluate extinction debts for individual species. In general, more comprehensive data on past and current biodiversity patterns and landscape structure facilitate more reliable evaluation of the occurrence of extinction debt. However, all empirical approaches have clear limitations, especially in quantifying the magnitude of extinction debt and the respective relaxation times for entire communities (see the section on limitations of empirical studies).

Despite increasing awareness that different environmental changes can cause extinction debts [4–6], empirical studies have hitherto largely examined delayed extinctions following habitat loss and fragmentation (Table 1). We found 42 empirical studies that specifically examined potential extinction debt, of which 38 found evidence. There has been a strong focus on vascular plants and wood-inhabiting cryptogams, whereas animals other than birds have rarely been examined. An important exception is the study by Cowlishaw [35], who estimated that extinction debt in African forest primates was >30% of all the species still present approximately 50 years after the start of large-scale forest fragmentation (Box 1).

Box 1. Evaluating extinction debts

Unless adequate long-term data on either species occurrences or richness and on habitat extent are available, evaluation of extinction debts is fraught with uncertainty. Many approaches are based on the premise of positive species–area relationships and assume that species richness was in equilibrium before habitat loss. Here we distinguish five main approaches to empirically evaluate extinction debts and illustrate each with a recently published example. The approaches are ordered by increasing data requirement and potential accuracy. In all approaches, habitat quality and connectivity can also be considered instead of habitat area. For the first two approaches no information on species distributions in the past is required. It should be noted that although extinction debts were originally addressed in the context of habitat loss, the concept can be applied to a wide range of environmental drivers that decrease the amount or quality of available habitat, e.g. climate and land use change, and invasive species.

1) Detection of extinction debt using past and present habitat characteristics

If current species richness is better described by past than by present landscape variables, the presence of extinction debt can be assumed (Figure Ia). For example, Lindborg and Eriksson [39] found that present-day plant species diversity in Swedish semi-natural grasslands was significantly related to past but not to present habitat connectivity. The magnitude of the extinction debt can, however, not be estimated using this approach.

2) Estimating extinction debt by comparing present-day stable and unstable landscapes

To assess the number and proportion of species committed to extinction, the equilibrium species number in habitats of constant area and connectivity can be used to predict the expected species number for habitats that experienced a reduction in habitat area or connectivity in the past. The difference between the predicted equilibrium species number and the observed species number is the magnitude of the extinction debt (Figure Ib). This approach can be used either by dividing all of the data into equilibrium and non-equilibrium subsets, by choosing a stable reference habitat from other regions, or by using species–area relationships typical for the stable habitat. For example, Helm *et al.* [38] used species–area relationships for a subset of grassland sites that had lost only a small amount of habitat to predict species richness for sites that lost a larger proportion of their original area. They estimated the magnitude of the extinction debt as the difference between observed and predicted species richness.

3) Estimating extinction debt based on past and present species richness and habitat characteristics

With a known relationship between the past habitat area and past richness, it is possible to calculate the predicted number of species for the current area more precisely than in approach 2. In this way, it is possible to estimate past extinctions that occurred immediately after fragmentation as well as the present extinction debt remaining to be paid (Figure Ic). For example, Cowlishaw [35] first estimated the relationship between primate species richness and forest area before forest fragmentation in Africa and then used this relationship to predict species richness in African countries in the current situation after habitat loss. The difference between the predicted and current species richness was used as an estimate of extinction debt.

4) Tracking extinction debt based on time series data

When repeated monitoring data on both the occurrence of species and changes in habitat area are available for a long enough period, relaxation times and past extinctions can be calculated directly (Figure Id), but such data are rarely available. For example, experimental fragmentation of rainforest in Brazil and subsequent long-term monitoring allowed direct calculation of species loss curves in relation to the remaining fragment area [12,54].

5) Evaluating extinction debt for single species using empirical population data and spatially explicit modeling

Future extinctions might also be inferred from empirical data on population growth rates in habitat fragments and reference sites with negative growth rates indicating population decline and long-term extinction. Combining such empirical data and modeling is a potentially powerful method for evaluating extinction debt. For species with detailed population data, empirically parameterized metapopulation models can be used to assess the long-term metapopulation persistence and expected time to extinction in different habitat patch networks. For example, Bulman *et al.* [21] parameterized a metapopulation model for the threatened marsh fritillary butterfly *Euphydryas aurinia* in Britain using data from one landscape and then used the model to simulate the future of six existing metapopulations occupying networks of suitable habitat patches. The simulation results indicated that four metapopulations are expected to become extinct within the next 15–126 years even if the landscape around these metapopulations remains constant [21].

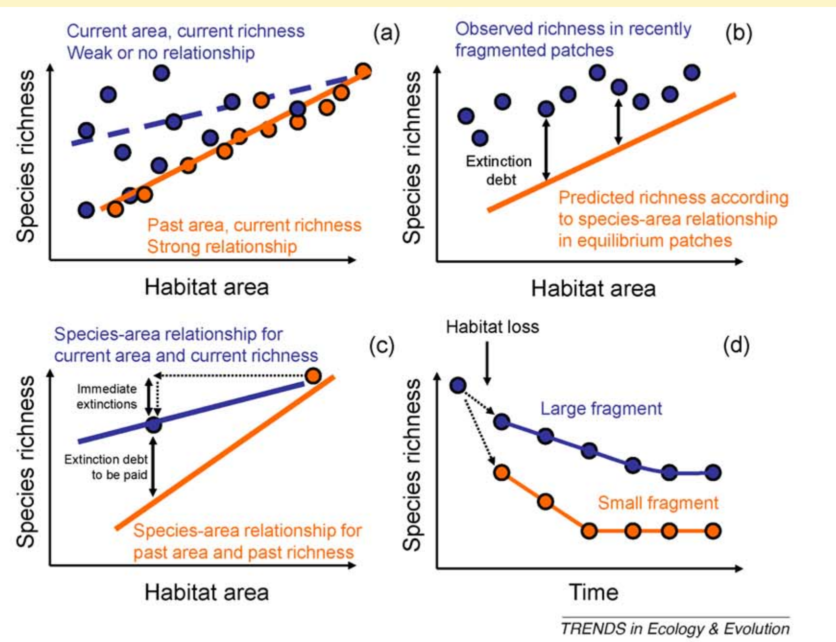

Figure I. Four approaches for evaluating extinction debt. (a) Detection of extinction debt using past and present habitat characteristics. (b) Estimation of extinction debt from species–area relationships in equilibrium patches. (c) Estimation of extinction debt based on past and present species richness and habitat characteristics. (d) Tracking of extinction debt based on time series data.

Table 1. Empirical studies on extinction debt

Approach[a]	Extinction debt	Taxa	Level of analyses	Spatial scale	Refs
1. Past and present habitat information					
	Yes	Meadow plants	Community	Habitat patches	[39,55,56]
	No	Meadow plants	Community	Habitat patches	[40–42]
	No	Meadow plant, *Anthyllis vulneraria*	Single species	Habitat patches	[57]
	Yes	Heathland and forest plants	Community	Landscapes	[58]
	Yes	Epiphytic lichens	Community	Habitat patches	[33]
	Yes	12 Red-List lichen and 9 Red-List fungal spp.	Single species and community	Landscapes	[59]
	Yes	Forest plants and wood-inhabiting fungi	Community	Habitat patches	[48]
	No	Lichens and bryophytes	Community	Habitat patches	[48]
	Yes	4 species of wood-inhabiting fungi	Single species	Habitat patches	[60]
	Yes	Amphibians	Community	Habitat patches	[61]
	Yes	3 species of amphibians	Single species	Habitat patches	[61]
	Yes	Fish and water invertebrates	Community	Streams	[62]
	Yes	Carabid beetle, *Abax parallelepipedus*	Single species	Habitat patches	[63]
	Yes	A range of terrestrial and freshwater taxa	Community	Landscape	[32]
	Yes	Plants	Community	Landscape	[64]
2. Stable vs. unstable landscapes					
	Yes	Epiphytic lichens	Community	Habitat patches	[43]
	No	Wood-inhabiting fungi	Community	Habitat patches	[43]
	Yes	Meadow plants	Community	Habitat patches	[38,65]
	Yes	36 forest plant spp.	Single species	Habitat patches	[31]
	Yes	Birds	Community	Islands	[10]
	Yes	Forest birds	Community	Habitat patches	[11]
	Yes	Birds	Community	Country	[66]
	No	Amphibians and reptiles	Community	Country	[66]
	Yes	Meadow plants	Community	Habitat patches	[67]
	Yes	Wood-living fungi	Single species and community	Habitat patches	[50]
	Yes	6 wood-living fungi and 6 saproxylic beetle spp.	Single species	Habitat patches	[68]
	Yes	Forest beetles	Community	Landscapes	[7]
	Yes	Forest species	Community	Country	[8]
3. Past and present information on species and habitats					
	Yes	Primates	Community	Countries	[35]
	Yes	Forest birds	Community	Habitat patches	[44]
	Yes	Endemic birds	Community	Landscape	[45]
4. Time series data on species and habitats					
	Yes	Microarthropods	Community	Habitat patches	[34,37]
	Yes	Forest birds	Community	Habitat patches	[12,54]
	Yes	Meadow butterflies	Community	Habitat patches	[69]
5. Empirically based spatially explicit modeling for single species					
	Yes	Meadow butterfly, *Melitaea cinxia*	Single species	Habitat patches, landscapes	[20,30]
	Yes	Meadow butterfly, *Euphydryas aurinia*	Single species	Habitat patches, landscapes	[21,36]
	Yes	Meadow plant, *Succisa pratensis*	Single species	Habitat patches	[70]

[a]See Box 1 for a description of the five main study approaches.

Studies on short-lived animals are rare. However, butterfly research that combined empirical population data with theoretical modeling has provided some of the most convincing examples of extinction debt and has led to a better understanding of the spatio-temporal scales at which the phenomenon can be relevant [20,21,30,36] (Table 1, Box 1). In an inspiring microcosm fragmentation experiment with artificial micro-arthropod communities, Gonzalez and Chaneton [34,37] demonstrated an extinction debt of 26–40% of species following experimental reduction of 92–99% of the focal moss habitat. They showed that for these short-lived organisms the extinction debt was already paid 6–12 months (many micro-arthropod generations) after fragmentation, and sooner in smaller than in larger fragments. Such controlled experiments are important in demonstrating that extinction debts can occur and are useful for testing predictions of time lags to extinction for species with contrasting life history traits.

Studies focusing on plants included some convincing examples for the existence of extinction debts [31,38,39]. In a Swedish study on the occurrence of plants in patches of semi-natural grassland [39], time lags of 50–100 years were found for the response of species diversity to habitat fragmentation, but the magnitude of the extinction debt could not be estimated because of data limitations and the method used (approach 1, Box 1). An Estonian study estimated that extinction debt was approximately 40% of grassland specialist species 70 years after the onset of habitat loss [38] (Box 1). However, results from other plant studies using similar approaches have shown no evidence of extinction debt [40–42], possibly because of differences in habitat or landscape history [29].

Most studies on extinction debt have examined species occupancy or richness at the level of the habitat patch (Table 1), because this is the spatial scale for which most data are available. The accuracy of data on biodiversity and on the structure of past landscapes typically decreases with increasing spatial scale, increasing uncertainty in evaluations of extinction debt. Moreover, even though some indication of extinction debt has been reported in most empirical studies (Table 1), the results are often uncertain, mainly because of data limitations.

The most conclusive demonstrations of extinction debt are based on comparisons of stable and fragmented landscapes [31,38,43] (approach 2 in Box 1) or time series data [12] (approach 4 in Box 1), whereas examples of the potentially powerful approach using past and current species and landscape data are rare [35,44,45] (approach 3 in Box 1). Taken together, the available studies suggest that time lags for species extinction exist widely in various landscapes and habitat types with severe fragmentation and degradation histories and in populations of species with certain life history traits. In particular, species with relatively stable populations, long generations and apparently low extinction risk seem to face the highest probability of delayed future extinctions.

Limitations of empirical studies

If an empirical study fails to detect extinction debt, it is important to assess whether adequate methods have been used, appropriate data are lacking or there really is no extinction debt. In the following we discuss the main obstacles to detecting extinction debt and provide suggestions on how to avoid them.

First, it is important to target the appropriate species. Extinction debt is only predicted for species that are specialized for the study habitat. If generalist and non-native species are included in measurements of species richness, these might mask an existing extinction debt. For example, grassland specialist species showed an extinction debt in Estonian calcareous grasslands, whereas generalist species did not [38]. However, even different habitat specialist species react individually, because they can differ in the habitat area required and respond to habitat availability at different spatial scales [46,47]. Detailed analysis of each key species can thus help to detect extinction debt.

Second, the choice of habitat parameters and the scale at which these are measured can affect the results. Some frequently used variables such as patch area might show no relationship with species occurrence or richness, whereas others such as connectivity or habitat quality might do so. In Swedish grasslands, current species richness was related to historical connectivity but not to historical habitat area [39]. Even though habitat parameters are often correlated with each other, several alternative habitat parameters should be tested in *a priori* hypotheses to detect extinction debt. In addition, the extinction risk depends on the spatial scale and is more likely to be detected if an appropriate scale or, even better, several spatial scales are used [39,48].

Third, most studies on extinction debt rely on assumptions of community equilibrium. For example, the SAR slope is usually shallower for sample areas within continuous habitats than in fragmented habitats [49] (Figure 1b). Assuming similar slopes before and after fragmentation can therefore lead to inaccurate estimates of extinction debt. Similarly, if a reference landscape is used that does not represent a long-term stable situation, it might not reflect equilibrium conditions. It could, for example, be far from a stable state because of earlier environmental perturbations. To overcome such problems, careful consideration of the assumptions for equilibrium [29] and further development of extinction debt theory involving these limitations are needed.

Fourth, and importantly, the general lack of appropriate high-quality historical data is a key limiting factor for studying extinction debt. Monitoring that results in time series of changes in landscape structure and the occurrence of habitat specialist species is needed to more accurately detect and quantify extinction debts in changing landscapes. It is also important to note that our understanding of drivers other than habitat loss, such as climate change and the invasion of alien species likely to affect extinction debts, is currently limited owing to a lack of empirical studies. Further work on the effects of these drivers on extinction debt is urgently needed.

Mitigating the future loss of biodiversity

Despite shortcomings in data, the studies available suggest that time lags for species extinction exist for widely different ecosystems and species communities. The alarming implication is that, even with no further habitat loss, many species are doomed to become locally or regionally extinct. However, the identification of an unpaid extinction debt implies that there still is a chance to counteract future biodiversity loss by targeted habitat restoration and conservation actions. In cases for which substantial extinction debts are recognized, critical appraisal of the conservation plans developed for conservation of the species of concern and their habitat is highly recommended.

An example of extinction debt that has challenged practical nature conservation in northern Europe concerns beetle and fungi species that are threatened in boreal forests [7,50,51]. Although most forest landscapes in Finland are intensively managed, some eastern areas have been subject to severe fragmentation only in the last few decades. It seems that large extinction debts exist in such areas and there are several alternative conservation strategies for mitigating the expected future loss of species in these degraded boreal forest landscapes [51]. Results of simulation studies suggest that it is essential to concentrate conservation efforts in improving habitat quality in areas where the probability of long-term species persistence is highest [8]. Unfortunately, empirical examples of how and where predicted extinctions could be best prevented by focused habitat restoration are still rare, even though there are examples of where carefully planned habitat restoration efforts have rescued declining populations [52,53].

Conclusions

Extinction debt presents a great challenge for the conservation of biodiversity. Although many studies support its

Box 2. Directions for future research

To improve our knowledge on the existence and magnitude of extinction debt, it will be necessary to target further work along the following lines:

- The objective evaluation and quantification of extinction debt should be improved by methodological development. In particular, the magnitude of extinction debt, the shape of the extinction path and the time to reach a new community equilibrium need further research.
- More empirical studies and experiments based on careful designs, appropriate habitat and species data and improved data on land use history should be carried out using replicated landscapes with varying expectations for the occurrence of extinction debt.
- Comparative studies are needed to investigate how the occurrence of extinction debt varies between groups of species varying in traits and potentially results in long time lags in response to environmental perturbation. Evaluation of the performance of the different approaches described in Box 1 for the same study system is required.
- Quantitative meta-analyses of existing studies should be conducted to summarize current knowledge.
- Large-scale monitoring schemes of relevant species groups should be implemented in conservation areas to build a basis for future assessment of temporal biodiversity changes and extinction risks.
- High-resolution monitoring of land use change based on ecologically relevant landscape element categories is needed to complement monitoring of biodiversity and to help select landscapes in which to perform studies on extinction debt.

existence, extinction debt is difficult to detect in natural communities and there is much scope for future studies to improve our understanding of this phenomenon through careful study design, comparative studies and methodological development (Box 2). A broader perception of extinction debt will hopefully support conservation efforts in a wider range of ecosystems currently facing rapid degradation caused by land use and climate changes and by invasions of alien species. As long as the species predicted to become extinct still persist, there is time for conservation measures such as habitat restoration and landscape management.

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