

# Balancing biodiversity in a changing environment: extinction debt, immigration credit and species turnover

Stephen T. Jackson<sup>1</sup> and Dov F. Sax<sup>2</sup>

<sup>1</sup> Department of Botany and Program in Ecology, University of Wyoming, Laramie, WY 82071, USA

<sup>2</sup> Department of Ecology and Evolutionary Biology, Brown University, Providence, RI 02912, USA

**Here, we outline a conceptual framework for biodiversity dynamics following environmental change. The model incorporates lags in extinction and immigration, which lead to extinction debt and immigration credit, respectively. Collectively, these concepts enable a balanced consideration of changes in biodiversity following climate change, habitat fragmentation and other forcing events. They also reveal transient phenomena, such as biodiversity surpluses and deficits, which have important ramifications for biological conservation and the preservation of ecosystem services. Predicting such transient dynamics poses a serious conservation challenge in a time of rapid environmental change.**

## Missing Concepts in Biodiversity Dynamics

Species immigration and extinction are the dominant forces underlying changes in species diversity on timescales of decades to millennia and spatial scales from local to regional [1,2]. Climate change, habitat fragmentation, resource exploitation and transcontinental species introductions are driving immigrations and extinctions [3–9]. Although most ecologists and biogeographers recognize that both transience and determinism in these processes fundamentally influence changes in biodiversity [2,7–9], a surprising gap exists in their current ability to communicate these ideas among researchers and to the general public. This is attributable, in part, to the absence of a simple conceptual framework and unified vocabulary encompassing these elementary aspects of biodiversity change.

Consider a simple example of biodiversity change: Plant diversity has increased on mountain summits in the Alps during the past century [10] because species formerly restricted to lower elevations have moved upslope, whereas incumbent populations have persisted. Is this increase in diversity permanent or transient? Should one expect some of these species, adventive or incumbent, to go extinct? Taken at face value, the message for the general public and policymakers could be that global warming will increase alpine biodiversity. If this is incorrect, how do researchers communicate the alternatives? The term ‘extinction debt’ [11] is a good start, but other

terms are needed. For instance, climate change and direct disturbance create opportunities for immigration of new species, native and non-native. These immigrations might not be immediate, but they are expected nonetheless. What should one call this expectation? How should one discuss the transient versus deterministic aspects of such processes, and their net impact on biodiversity? Currently, there is no immigration counterpart to extinction debt; neither is there a clear concept to account for a transient excess of species (as in the alpine example if incumbents represent an unpaid extinction debt). Here, we argue that these and other concepts are needed, to both facilitate communication and to support research aimed at identifying and reducing uncertainties and surprises arising from delayed extinction and immigration.

## Glossary

**Biodiversity accrual:** a net increase in the number of species following a forcing event.

**Biodiversity balance:** the net difference between immigration credit and extinction debt once equilibrium is achieved.

**Biodiversity loss:** a net decrease in the number of species following a forcing event.

**Biodiversity deficit:** a transient decrease in the number of species following a forcing event.

**Biodiversity surplus:** a transient increase in the number of species following a forcing event.

**Compositional turnover:** community change, particularly species replacements, that occurs following a forcing event.

**Delayed extinction:** the general phenomenon in which one or more extinctions that are caused by a specific event do not coincide precisely with that event, but instead follow it by some significant amount of time, which can range from a single generation (e.g. delayed mortality of a long-lived incumbent that fails to either reproduce or recruit successfully) to multiple generations (whereby populations persist for multiple generations, usually in diminishing numbers).

**Delayed immigration:** the general phenomenon in which one or more immigrations that are caused by a specific event do not coincide precisely with that event, but instead follow it by some significant amount of time.

**Equilibrium biodiversity:** the number of species in a system once it has attained equilibrium.

**Extinction debt:** the number of species committed to eventual extinction following a forcing event.

**Extinction lag:** the time elapsed between an extinction-committing forcing event and the final disappearance of a species.

**Forcing event:** any event that causes the extinction or immigration of one or more populations or species, whether immediate or delayed.

**Immigration credit:** the number of species committed to eventual immigration following a forcing event.

**Immigration lag:** the time elapsed between an immigration-committing forcing event and the establishment of an immigrating species.

Corresponding authors: Jackson, S.T. (Jackson@uwyo.edu); Sax, D.F. (dov.sax@gmail.com)

Our aim here is to provide an elementary vocabulary and conceptual framework that enables both transient and ultimate changes in biodiversity to be discussed and studied. In so doing, we draw on terms and ideas from the often disparate disciplines of ecology, biogeography and paleoecology, all fields that aim to understand changes in biodiversity. As the pace of global change and anthropogenic disturbance accelerate, one can expect large fluxes in biodiversity to become more common; therefore, developing an integrated view of these changes is crucial for scientific study, conservation practice and the formulation of scientifically informed policy.

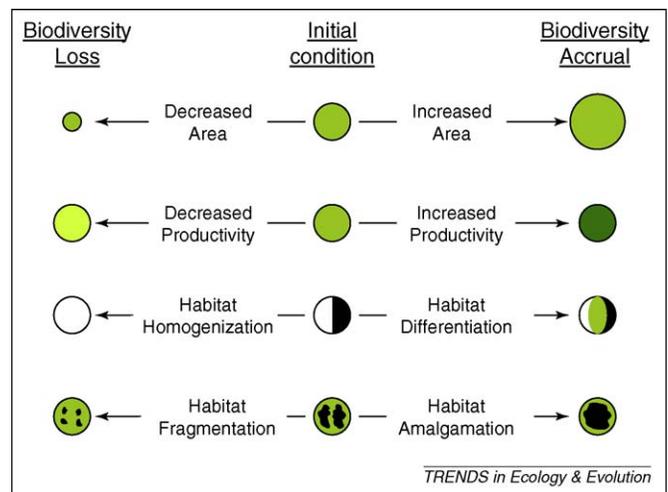
### The biodiversity budget and forcing events

The ecological processes of extinction and immigration can be set in motion by a forcing event that drives changes in the quality, size, density and connectivity of suitable habitat patches. Forcing events can be rapid (e.g. industrial deforestation or abrupt climate change) or gradual (e.g. suburban encroachment, sea-level rise or secular temperature change), and singular (e.g. permanent deforestation, creation of islands in a reservoir or transition to a new climate regime) or sequential (e.g. forest to cropland to forest to suburb or a severe drought followed by a persistent wet period). Although extinctions and immigrations often result from complex causal chains and contingencies, perhaps better described as causal thickets [12], we start here by assuming simple, single-step forcing events that set all subsequent immigration and extinction events in motion.

Once initiated, patterns and rates of immigration and extinction will determine changes in biodiversity for any given locale or region. In considering these changes, we borrow concepts and terms from accounting (e.g. Refs [11,13]), emphasizing both sides of the biodiversity ledger. Equilibrium biodiversity represents the overall number of species in a system at equilibrium (see [Glossary](#)). The biodiversity balance is the difference between pre- and post-forcing equilibrium biodiversity, and could be higher (biodiversity accrual), lower (biodiversity loss), or the same as before the forcing event. The biodiversity balance represents the net community-level or regional aggregate of many individual species extinctions and immigrations once equilibrium is reached. Simple, singular forcing events are likely to lead to predictable accrual or loss of biodiversity ([Figure 1](#)). These predictions and those of more complex, multi-factor and/or sequential forcing events can be based on several alternative theoretical approaches. These include single-time-step equilibrium models that account for changes in area and isolation [14,15], patch-based resource models [16,17], empirical niche-envelope models [4,5,18] and patch-based, landscape-integrated community-dynamics models [19,20], as well as dynamic models that incorporate ongoing changes in the physical environment (e.g. island size or topographic complexity) [21].

### Delays in budget balancing

Equilibrium is rarely achieved quickly in biodiversity dynamics, owing to both delayed immigration and delayed extinction [7,15,22]. Immigration of new species and



**Figure 1.** Expected loss and accrual of biodiversity in response to forcing events, based on classic ecological and biogeographical theory, and empirical observations of responses to changes in area [14,15], productivity [70,71], habitat diversity [35,72] and habitat fragmentation [73]. Outcomes of some of these events might be scale dependent, and might differ among ecosystems. For example, lake eutrophication might increase productivity while decreasing algal biodiversity owing to strong dominance.

extinction of doomed species could be delayed for several reasons, creating several potential transient conditions before biodiversity attains equilibrium.

Delayed immigration is well documented in the literature of both non-native species invasions [23] and natural, climate-driven immigrations [24–26]. Colonization of a suitable site requires sequential successes in the dispersal of propagules, establishment of individuals, survival to reproductive maturity, and growth and persistence of populations via continued reproduction; failure or delay in any of these steps leads to delayed immigration. Propagule dispersal is determined by propagule flux density, which is influenced by the density, proximity and productivity of source populations, and by dispersal mechanisms, particularly those influencing long-distance dispersal [23]. Establishment and survival of propagules is often contingent on suitable microsite conditions and reduced competition from incumbents [27]. Establishment might require disturbances to create suitable microsites [28,29], remove incumbents and liberate resources [30], and could also require specific conditions that do not occur every year [31]. Development of sustainable populations might require several generations of population growth under favorable conditions. Population persistence and growth might be impaired by Allee effects if colonizing populations are small [23]. Finally, stochastic factors of dispersal and establishment reduce the likelihood that small, isolated populations will persist or give rise to additional colonizing populations. The challenges of immigration are illustrated by repeated colonization failures of many invading non-native species before their ultimate establishment [27].

Delayed extinction, similar to delayed immigration, also results from demographic and stochastic processes. In the simplest case, a population in which mortality slightly exceeds natality will ultimately undergo extinction, but many generations might be required to get there. Furthermore, long-lived plants can survive despite diminished

reproductive success [31], populations can retreat or retract to the most favorable local habitats [32], and processes of competitive displacement and demographic decay might take many generations to play out to extinction [15,22]. Transient events (e.g. climate extremes) can induce mortality among remaining populations, but they can also lead to recruitment pulses that facilitate persistence [31,33]. Spatially explicit metapopulation models indicate that environmental change and/or habitat loss might shift the frequency distribution of species toward a higher proportion of rare (and hence extinction-vulnerable) species, with stochastic factors ultimately driving many species over their extinction thresholds [34].

Immigration and extinction processes can interact to accelerate or delay each other. If persistence of incumbents slows down establishment of potential competitors, then a negative feedback ensues whereby both extinction and immigration are slowed down. The dynamic reverses, however, if successful immigrants exert competitive pressure on incumbents, leading to acceleration of extinction and immigration. These feedback processes are poorly understood, and deserve formal analysis and experiment. Delays and accelerations in species turnover can also arise when colonization or extinction is contingent on the colonization or extinction of another species (e.g. mutualists or inhibitors).

Delayed extinction and immigration combine to delay attainment of biodiversity equilibrium following a forcing event, resulting in two important outcomes. First, extinction debt (the number of species committed to eventual extinction by the forcing) represents the ‘accounts payable’ component of the biodiversity budget (Box 1; Figure 2a). These are species ultimately ‘owed’ by the community, and represent a negative draw on biodiversity. Second, immigration credit (the number of species that are committed to eventual immigration because of suitable environment and opportunity) represents the ‘accounts receivable’ term and a positive input to biodiversity (Figure 2a). Both extinction debt and immigration credit can be measured or estimated. Once all extinction debts and immigration credits are paid, the community is at equilibrium and biodiversity is finally balanced. If extinction debts exceed immigration credits, the community will undergo a net loss of biodiversity (Figure 2b). If immigration credits exceed extinction debts, then it will have a net accrual (Figure 2c).

Compositional turnover can be treated as a temporal analog of beta-diversity [35–37] and can be estimated using beta-diversity indices or, alternatively, by multivariate distance metrics [38,39]. Although we define compositional turnover in terms of the equilibrium state, turnover en route to equilibrium might be of interest, and temporal beta-diversity can be calculated during the course of events between forcing and equilibrium.

### Consequences of differential rates: biodiversity deficit and surplus

Even if extinction debt and immigration credit balance each other, communities can experience transient periods of excess or deficient biodiversity if extinction and immigration rates or peaks are offset. If, for example, extinction debt is paid off faster than is immigration credit, then

#### Box 1. Extinction debt and immigration credit

Our conception of extinction debt and immigration credit builds on the work of many previous investigators. These terms have not always been applied consistently and definitions often drift within individual papers. Both concepts are consistent with delays expected before equilibrium is reached in island biogeography theory; for instance, MacArthur and Wilson [14] recognized that colonization to Krakatau following its defaunation was not instantaneous. Many ecologists and biogeographers have considered the timescales at which species should be lost following forcing events, such as loss of habitat area (e.g. Refs [15,22]).

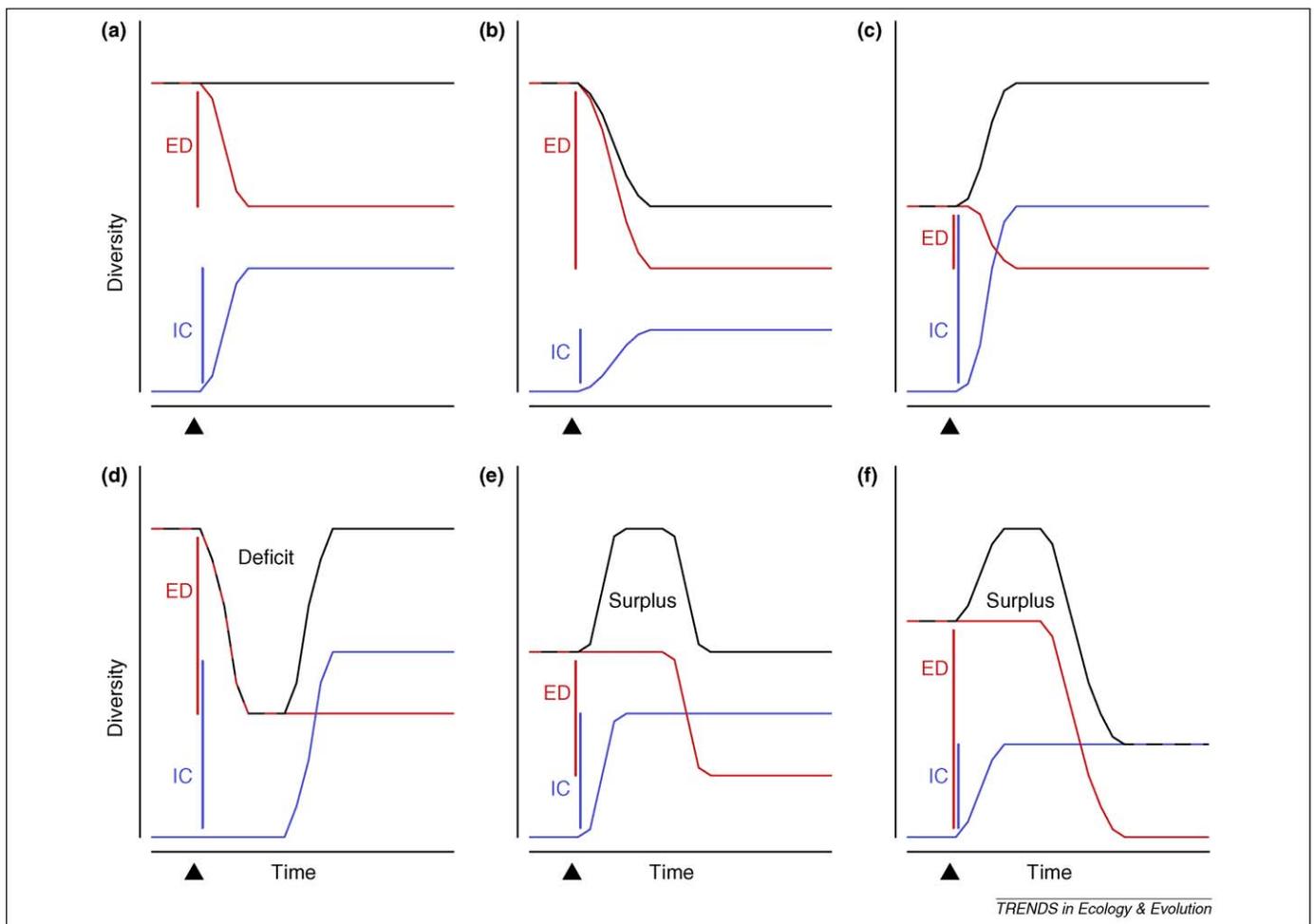
The term ‘extinction debt’ was coined by Tilman *et al.* [11] to describe the deterministic loss of species, in order of their competitive ability, following habitat loss and fragmentation. In subsequent literature, extinction debt has been generalized as delayed loss of species attributable to metapopulation dynamics following fragmentation [7,34,74–76]. We retain this definition, but expand it to incorporate any species that is fated for eventual extinction following a forcing event. Thus, a species population that is unsustainable after a change in climate (e.g. owing to reduced reproductive or competitive success under the new conditions) would contribute to extinction debt.

Immigration credit has not, to our knowledge, been applied previously in ecological literature. This concept differs from ‘species credit’ [13], which refers to otherwise-doomed species that are likely to benefit from mitigation or restoration of a fragmented or disturbed habitat. Our term refers instead to new species that are likely to immigrate to a region following a forcing event, such as a change in environmental conditions. The size of an immigration credit can be reduced by species migration, but also by the evolution of new species *in situ*. The latter will typically be important over longer timescales or in situations in which rapid speciation occurs.

biodiversity values will fall below the equilibrium level until immigration catches up (Figure 2d). This constitutes a biodiversity deficit, in which the community is temporarily impoverished in terms of species number. The opposite situation, a biodiversity surplus, will occur if immigration rates exceed extinction rates (Figure 2e). This could be the case in the alpine-plant example discussed above [10].

Metapopulation models will be useful in identifying the range of circumstances under which deficits and surpluses might arise. However, these outcomes will often depend on situation-specific circumstances, such as proximity of propagule sources and effectiveness of immigrant dispersal, magnitude and rate of incumbent mortality following the forcing event, and the influence of spatial and temporal environmental variability on the rates at which extinction debt is paid off.

Empirical assessment of biodiversity deficits and surpluses, as well as extinction debt and immigration credit, is rendered difficult because of the long time required for immigration and extinction processes to run their course, the difficulty of attributing specific immigrations and extinctions to previous forcing events, and the probable prevalence of complex causal chains and thickets in most realistic settings. Nevertheless, there are several approaches that can be used to measure or estimate these outcomes. First, systematic, long-term observational data sets with accompanying environmental monitoring, modeling and experimentation are ideally suited. Unfortunately, such studies are few (but increasing) in number. They can be applied to ongoing or future climate change as well as to major disturbance or isolation events [40–46].



**Figure 2.** Biodiversity scenarios following a forcing event. The black trace represents the total biodiversity trajectory. The red trace represents the number of incumbent species (i.e. species occurring before forcing). The blue trace represents the number of immigrant species (i.e. species that did not occur before forcing). The arrow on the x-axis denotes onset of forcing. **(a)** Equilibrium biodiversity does not change after forcing, but extinctions and immigrations are set in motion and delays create extinction debt (ED) and immigration credit (IC). In this scenario, each extinction is balanced immediately by an immigration, so total biodiversity remains constant. **(b)** Biodiversity declines after forcing. **(c)** Biodiversity increases after forcing. **(d)** Long-term biodiversity is unchanged by the forcing event. However, rapid extinction and delayed immigration create a transient biodiversity deficit. **(e)** As in (d), except extinction is delayed and immigration is rapid, leading to transient biodiversity surplus. **(f)** Biodiversity is ultimately reduced by the forcing event, despite a transient biodiversity surplus.

Consider, for example, the simple case of a mountain-top plant community under a warming climate. Extinction debt could be estimated by identifying species undergoing population decline. Immigration credit could be estimated by modeling or measuring climatic tolerances of species occupying sites at lower altitudes. Biodiversity surpluses or deficits could be estimated by contrasting estimates of the time lags in mountain-top species extinctions with the rate of altitudinal expansion of lower-elevation species. The confidence and range of all these estimates could be calibrated with results from other long-term studies of population trajectories following comparable forcing events. These estimates would involve integration of several approaches (e.g. population biology, ecophysiology, biogeography and dispersal ecology).

Second, biodiversity outcomes could be estimated using space-for-time substitutions, following the tradition of island biogeography and other community studies [7]. Biodiversity balance could be estimated, for example, by contrasting species number between habitat fragments that underwent a recent size reduction with comparable habitat

fragments isolated long ago. The pitfalls of this approach are well known and can be minimized in many settings. Finally, the fossil record is rich in time-series and before–after comparisons [47]. These can provide several unplanned experiments of various kinds, involving both human-driven and natural forcings in terrestrial, lacustrine, estuarine, and marine estuarine systems (Box 2). No one of these methods is ideal, and all are prone to error, but testing and refining such approaches should be a research priority.

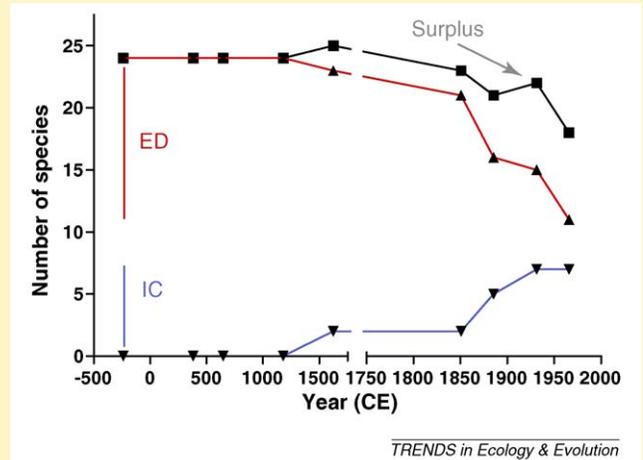
### Biodiversity forcing by environmental change and habitat fragmentation

Climate change is a powerful force in driving both immigration and extinction, as indicated by the numerous local–regional extinctions and immigrations documented from post-glacial paleoecological studies throughout the world [2,31,38,47,48]. Recent climate change has also triggered immigration and extinction processes across the globe [6,49], and current climate forecasts indicate that more ecological change will occur over the coming decades [50–52].

### Box 2. Biodiversity dynamics in a disturbed wetland

The coastal complex of concentric beach ridges and swales in the Miller Woods tract of the Indiana Dunes National Lakeshore is a classic setting for ecological studies of aquatic and terrestrial communities [76]. Wetlands of the swale complex underwent fragmentation and hydrological alteration during the mid-late 19th century with the construction of a series of railroad corridors transecting the area [77]. Pollen and plant macrofossil data from sediments of one of the largest remnant wetlands show little change in wetland vegetation composition from wetland inception 1250 BCE until the mid-19th century CE [77]. By contrast, the past 150 years have been marked by multiple immigrations and extinctions.

We apply the biodiversity budget to the Miller Woods record, assuming a primary forcing event starting ca. 1850 CE with construction of the first railroad corridor in the wetland. (Subsequent disruption and fragmentation might have further influenced immigration and extinction.) Of some 24 wetland species consistently present before the forcing, 13 became extinct by the mid-1960s, and 11 persisted (although many in apparently reduced numbers). Seven species new to the pond invaded during this period. By the 1960s, these changes represent a biodiversity loss of six species; although immigration had apparently stabilized by this time, additional work will be needed to determine if extinctions are ongoing. The species that went extinct decades after the original disturbance represent the extinction debt. Owing to the different rates of immigration and extinction, the wetland underwent a modest biodiversity surplus in the early-mid 20th century (Figure 1). An ecologist examining the wetland at that time might have concluded, erroneously, that disturbance effects on biodiversity were neutral or even positive.



**Figure 1.** Time series showing the number of incumbent (red line), immigrant (blue line) and total (black line) species recorded in a sediment core at Miller Woods Pond 51 [77]. The data, available at <http://www.ncdc.noaa.gov/paleo/plantmacros.html>, were filtered to include only local wetland species. Also, range-through corrections were made, such that species were assumed to occur at all points between first and last identified occurrences. To minimize bias from a range-through approach, the first two and last time steps were removed. The penultimate time-step from the original data (1966 CE) was retained to illustrate the downward trajectory of both incumbent and total plant diversity. ED and IC refer respectively to inferred extinction debt and immigration credit.

Human-driven habitat reduction and fragmentation have been underway for decades to millennia, leading to reduced local biodiversity and local extinctions in many areas [7,11,34]. Indeed, the speed and predictability of these losses can often be characterized for individual taxonomic groups [22]. By contrast, habitat fragmentation and reduction are not always accompanied by widespread species loss on regional or biogeographic scales. For instance, in the heavily transformed landscapes of Hawaii and New Zealand, species extinctions are concentrated in certain taxonomic groups. Birds and other animals directly preyed upon by humans and human-introduced mammals have undergone massive extinctions, whereas plants and other groups have persisted [1,8,53]. Similarly, few regional or universal extinctions have occurred in extensively fragmented continental settings [54].

The dearth of widespread plant extinctions in highly fragmented landscapes might indicate that habitat fragmentation is a relatively weak force in driving extinction. Perhaps species are more able to persist in remnant or modified habitats than is suggested by island biogeography and metapopulation models. However, extinction debt suggests a sobering alternative: that insufficient time has elapsed to drive all doomed species to extinction [55]. These and other regions might be in a transient surplus phase, with immigration of non-native species occurring rapidly and extinctions more slowly [8].

Climate change, particularly when rapid or abrupt, might interact with habitat fragmentation in unexpected ways. Climate change will force many species to colonize new regions [2,6,31,48,49]. On the one hand, fragmentation might delay immigration by creating dispersal barriers and reducing the density and size of suitable patches. Climate change itself will alter the area, density, connec-

tivity and suitability of individual habitat patches; past climate changes have led to fragmentation and coalescence of suitable habitats [2,38,56,57]. Delayed immigration owing to fragmentation and other factors is motivating discussion of ‘managed relocation’ or ‘assisted migration’ of species to keep pace with climate change [58,59]. On the other hand, fragmentation might create opportunities for many migrating species by providing disturbed and seral sites that are suitable for colonization. Similarly, inadvertent human activities, particularly motorized transportation, might facilitate dispersal of native species in the same ways that they have spread exotic species.

### Surprises and uncertainties in a world of global change

The biodiversity ledger spotlights three risks to biodiversity stemming from differential response times of immigration and extinction to forcing events. First, biodiversity deficits could become commonplace, particularly on broad geographic scales. Although many species are adjusting their elevational and/or latitudinal ranges in response to warming climate (e.g. Ref. [6]), many might lack the capacity to colonize new territory fast enough to match extirpation at their retreating margins. For example, the equatorward range margin of the quiver tree *Aloe dichotoma* in southern Africa is being eroded by climate warming, but its poleward margin is stationary [60]. If rates of climate change accelerate over the coming century [51,52], then many species could experience rapid extirpation at retreating margins and slow expansion at advancing margins. Slow expansion at the leading edge might be expected even for some highly vagile species, as recently demonstrated in the UK for two butterfly species, which are not keeping pace with the northward expansion of suitable climate [26]. Thus, although equilibrium diversity might

be unchanged, and even though biodiversity deficits could be transient, the deficit period might span decades or centuries [25]. Key ecosystem services could be compromised during the interim and deficits might become permanent: individual species that undergo extinction because they are trapped between rapid retreat and slow advance cannot contribute to paying off immigration credit.

Second, biodiversity surpluses are likely to occur on many local scales. Extirpation of incumbent populations (particularly of long-lived plant species) could lag behind immigration of new species, leading to transient biodiversity surplus. The increase in alpine plant diversity of the Alps over the past century [10] might represent such a case. In such instances, biodiversity will ultimately decline as extinction debt is paid off (e.g. Box 2). Transient increases in diversity, masking eventual decline (Figure 2f), could lead to misguided complacency. In cases where the species being added are non-natives, local increases in diversity might be transient, with native species eventually going extinct [8].

Third, the course and outcome of biodiversity dynamics could be idiosyncratic for particular locales and regions. This unpredictability arises because of the large number of interacting and often conflicting factors, and the accumulation and lingering impacts of historical contingencies. Climate variability on interannual to multidecadal scales, as well as abrupt shifts in climate regimes, will influence the actual sequence of extinction and immigration events [31], as will changes in human land-use and resource exploitation [61]. Consequently, a priori determination of which areas face short-term biodiversity surplus and deficit, and long-term biodiversity loss and accrual, might remain uncertain.

## Conclusions

Understanding, predicting and mitigating global-change impacts on biodiversity pose crucial challenges for ecologists, conservation biologists and resource managers. The biodiversity-balance framework provides a starting point for identifying what is known and what needs to be learned to address these challenges. To date, there has been little integration of extinction processes and extinction debt with invasion processes and delayed immigration, despite considerable volumes of literature on both topics. Clearly, both are needed to understand biodiversity dynamics. Can indicators of biodiversity surplus or deficit in existing ecosystems be developed? Can early-warning signs be identified for imminent biodiversity decline owing to extinction-debt payoff? How precisely can immigration credit and immigration rates be estimated? What risks and benefits accrue if managers attempt to intervene to, for example, foster immigration via managed relocation [59,62] or to prevent local extinction by taking extraordinary measures, such as modifying the physical environment to maintain previous conditions [63,64]?

Articulation of contrasting approaches is also needed in studies of extinction and immigration dynamics. Biogeographers concerned with global-change effects have utilized either Grinnellian realized-niche modeling or species-area relationships to estimate species loss and displacement. Comparison or integration of these

approaches could yield complementary insights and independent assessment of predictions. Only rarely (e.g. Ref. [65]) have either of these approaches been applied in tandem with the more-mechanistic approaches routinely used by population ecologists. Empirical and modeling studies of extinction and immigration need to be linked with each other and with biogeographical studies to develop a comprehensive understanding of their underlying mechanisms and probable rates following environmental change. This understanding can, in turn, be augmented by incorporating the potential role of species interactions in driving positive and negative feedbacks on compositional turnover.

A further challenge is imposed by the timescales required for extinction and immigration processes to run their course, ranging from years to centuries or more. Long-term data sets, including paleoecological time-series, are needed to understand the processes and test the mechanisms. Targeted studies applying such data sets to specific forcing events can provide estimates of the magnitudes and order of biodiversity surplus and deficit, and the rates at which immigration credits and extinction debts are settled. The 20 000 years that have elapsed since the last glacial maximum offer several rapid climatic changes of various kinds for potential study, from the rapid warming of the Bölling-Alleröd [66] and the rapid cooling and warming of the Younger Dryas Interval [67] to lower-magnitude events (transient droughts and transitions) of the Holocene [68]. Paleoecological records can also be applied to examine biodiversity dynamics following human disturbances of the past several centuries (e.g. Box 2). Long-term data sets also provide opportunities for study, particularly when severe disturbances have occurred in the course of the study [69]. Long-term monitoring studies could incorporate experimentally induced disturbances.

Meeting the research and management challenges of global change will require unprecedented levels of research effort, integrating multiple disciplines as well as multiple approaches, including analytical theory, targeted experiments and empirical observations spanning a range of spatial and temporal scales. Outcomes of biodiversity dynamics could ultimately reside in the fundamental biology of specific suites of species in specific contexts. To achieve even partial success in addressing biodiversity risks under global change, a comprehensive research enterprise must get underway quickly. The rate of climate change already entrained [52] threatens to outpace the current scientific capacity to understand and predict its consequences, let alone develop effective adaptation and mitigation strategies [64]. The best hope of maintaining biodiversity and its essential services lies in simultaneously slowing the rate of global change and accelerating the scientific effort to understand and mitigate its effects.

## Acknowledgments

This paper was supported by the National Science Foundation. Mark Vellend, Simon Brewer, Tom Minckley and three anonymous reviewers provided valuable comments and discussion.

## References

- 1 Sax, D.F. and Gaines, S.D. (2003) Species diversity: from global decreases to local increases. *Trends Ecol. Evol.* 18, 561–566

- 2 Jackson, S.T. and Overpeck, J.T. (2000) Responses of plant populations and communities to environmental changes of the Late Quaternary. *Paleobiology* 26 (Suppl.), 194–220
- 3 Fahrig, L. (2003) Effects of habitat fragmentation on biodiversity. *Annu. Rev. Ecol. Evol. Syst.* 34, 487–515
- 4 Thomas, C.D. *et al.* (2004) Extinction risk from climate change. *Nature* 427, 145–148
- 5 Thuiller, W. *et al.* (2005) Climate change threats to plant diversity in Europe. *Proc. Natl. Acad. Sci. U. S. A.* 102, 8245–8250
- 6 Parmesan, C. (2006) Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol. Evol. Syst.* 37, 637–669
- 7 Vellend, M. *et al.* (2006) Extinction debt of forest plants persists for more than a century following habitat fragmentation. *Ecology* 87, 542–548
- 8 Sax, D.F. and Gaines, S.D. (2008) Species invasions and extinction: the future of native biodiversity on islands. *Proc. Natl. Acad. Sci. U. S. A.* 105, 11490–11497
- 9 Scheller, R.M. and Mladenoff, D.J. (2008) Simulated effects of climate change, fragmentation, and inter-specific competition on tree species migration in northern Wisconsin, USA. *Climate Res.* 36, 191–202
- 10 Walther, G.R. *et al.* (2005) Trends in the upward shift of alpine plants. *J. Veg. Sci.* 16, 541–548
- 11 Tilman, D. *et al.* (1994) Habitat destruction and the extinction debt. *Nature* 371, 65–66
- 12 Wimsatt, W.C. (2007) *Re-Engineering Philosophy for Limited Beings: Piecewise Approximations to Reality*, Harvard University Press
- 13 Hanski, I. (2000) Extinction debt and species credit in boreal forests: modeling the consequences of different approaches to biodiversity conservation. *Ann. Zool. Fenn.* 37, 271–280
- 14 MacArthur, R.H. and Wilson, E.O. (1967) *The Theory of Island Biogeography*, Princeton University Press
- 15 Diamond, J.M. (1972) Biogeographic kinetics: estimation of relaxation times for avifauna of southwest Pacific Islands. *Proc. Natl. Acad. Sci. U. S. A.* 69, 3199–3203
- 16 Levins, R. (1969) Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bull. Entomol. Soc. Am.* 15, 237–240
- 17 Hanski, I.A. and Gaggiotti, O.E., eds (2004) *Ecology, Genetics and Evolution of Metapopulations*, Academic Press
- 18 Keith, D.A. *et al.* (2008) Predicting extinction risks under climate change: coupling stochastic population models with dynamic bioclimatic habitat models. *Biol. Lett.* 4, 560–563
- 19 Mladenoff, D.J. (2004) LANDIS and forest landscape models. *Ecol. Model.* 180, 7–19
- 20 Purves, D.W. *et al.* (2008) Predicting and understanding forest dynamics using a simple tractable model. *Proc. Natl. Acad. Sci. U. S. A.* 105, 17018–17022
- 21 Whittaker, R.J. *et al.* (2008) A general dynamic theory of oceanic island biogeography. *J. Biogeogr.* 35, 977–994
- 22 Brooks, T.M. *et al.* (1999) Time lag between deforestation and bird extinction in tropical forest fragments. *Conserv. Biol.* 13, 1140–1150
- 23 Kinlan, B.P. and Hastings, A. (2005) Rates of population spread and geographic range expansion. In *Species Invasions: Insights into Ecology, Evolution and Biogeography* (Sax, D.F. *et al.*, eds), pp. 381–419, Sinauer
- 24 Gavin, D.G. and Hu, F.S. (2006) Spatial variation of climatic and non-climatic controls on species distribution: the range limit of *Tsuga heterophylla*. *J. Biogeogr.* 33, 1384–1396
- 25 Menendez, R. *et al.* (2006) Species richness changes lag behind climate change. *Proc. R. Soc. B* 273, 1465–1470
- 26 Willis, S.G. *et al.* (2009) Assisted colonization in a changing climate: a test-study using two U.K. butterflies. *Conserv. Lett.* 2, 45–51
- 27 Sax, D.F. and Brown, J.H. (2000) The paradox of invasion. *Global Ecol. Biogeogr.* 9, 363–371
- 28 Beckage, B. and Clark, J.S. (2003) Seedling survival and growth of three forest tree species: the role of spatial heterogeneity. *Ecology* 84, 1849–1861
- 29 Romme, W.H. *et al.* (2005) Establishment, persistence, and growth of aspen (*Populus tremuloides*) seedlings in Yellowstone National Park. *Ecology* 86, 404–418
- 30 Davis, M.A. *et al.* (2000) Fluctuating resources in plant communities: a general theory of invasibility. *J. Ecol.* 88, 528–534
- 31 Jackson, S.T. *et al.* (2009) Ecology and the ratchet of events: climate variability, niche dimensions, and species distributions. *Proc. Natl. Acad. Sci. U. S. A.* 106, 19685–19692
- 32 Channell, R. and Lomolino, M.V. (2000) Dynamic biogeography and conservation of endangered species. *Nature* 403, 84–86
- 33 Levine, J.M. and Rees, M. (2004) Effects of temporal variability on rare plant persistence in annual systems. *Am. Nat.* 164, 350–363
- 34 Hanski, I. and Ovaskainen, O. (2002) Extinction debt at extinction threshold. *Conserv. Biol.* 16, 666–673
- 35 Whittaker, R.H. (1972) Evolution and measurement of species diversity. *Taxon* 21, 213–251
- 36 Legendre, P. *et al.* (2005) Analysing beta diversity: partitioning the spatial variation of community composition data. *Ecol. Monogr.* 75, 435–450
- 37 Jost, L. (2007) Partitioning diversity into independent alpha and beta components. *Ecology* 88, 2427–2493
- 38 Williams, J.W. *et al.* (2004) Late-Quaternary vegetation dynamics in North America: scaling from taxa to biomes. *Ecol. Monogr.* 74, 309–344
- 39 Chao, A. *et al.* (2005) A new statistical approach for assessing similarity of species composition with incidence and abundance data. *Ecol. Lett.* 8, 148–159
- 40 Terborgh, J. *et al.* (2001) Ecological meltdowns in predator-free forest fragments. *Science* 294, 1923–1926
- 41 Laurance, W.F. *et al.* (2002) Ecosystem decay of Amazonian forest fragments: a 22-year investigation. *Conserv. Biol.* 16, 605–618
- 42 Ferraz, G. *et al.* (2003) Rates of species loss from Amazonian forest fragments. *Proc. Natl. Acad. Sci. U. S. A.* 100, 14069–14073
- 43 Laurance, W.F. *et al.* (2006) Rapid decay of tree-community composition in Amazonian forest fragments. *Proc. Natl. Acad. Sci. U. S. A.* 103, 19010–19014
- 44 van Mantgem, P.J. *et al.* (2009) Widespread increase of tree mortality rates in the western United States. *Science* 323, 521–524
- 45 Ernest, S.K.M. *et al.* (2009) Long-term monitoring and experimental manipulation of a Chihuahuan Desert ecosystem near Portal, Arizona. *USA. Ecology* 90, 1708
- 46 Tingley, M.W. *et al.* (2009) Birds track their Grinnellian niche through a century of climate change. *Proc. Natl. Acad. Sci. U. S. A.* 106, 19637–19643
- 47 National Research Council (2005) *The Geologic Record of Ecological Dynamics*, National Academies Press
- 48 Betancourt, J.L. (2004) Arid lands paleobiogeography: the rodent midden record in the Americas. In *Frontiers of Biogeography* (Lomolino, M.V. and Heaney, L.R., eds), pp. 27–46, Sinauer
- 49 Root, T.L. *et al.* (2003) Fingerprints of global warming on wild animals and plants. *Nature* 421, 57–60
- 50 Williams, J.W. *et al.* (2007) Projected distributions of novel and disappearing climates by 2100 AD. *Proc. Natl. Acad. Sci. U. S. A.* 104, 5738–5742
- 51 IPCC (2007) *Climate Change 2007: The Physical Science Basis*, Cambridge University Press
- 52 Solomon, S. *et al.* (2009) Irreversible climate change due to carbon dioxide emissions. *Proc. Natl. Acad. Sci. U. S. A.* 106, 1704–1709
- 53 Sax, D.F. *et al.* (2002) Species invasions exceed extinctions on islands worldwide: a comparative study of plants and birds. *Am. Nat.* 160, 766–783
- 54 Budiansky, S. (1994) *Nature* 370, 105
- 55 Pimm, S.L. and Raven, P. (2000) Extinction by numbers. *Nature* 403, 843–845
- 56 Lyford, M.E. *et al.* (2003) Influence of landscape structure and climate variability on a late Holocene plant migration. *Ecol. Monogr.* 73, 567–583
- 57 Hu, F.S. *et al.* (2009) Paleoecology meets genetics: deciphering past vegetational dynamics. *Front. Ecol. Environ.* 7, 371–379
- 58 McLachlan, J.S. *et al.* (2007) A framework for debate of assisted migration in an era of climate change. *Conserv. Biol.* 21, 297–302
- 59 Richardson, D.M. *et al.* (2009) Multidimensional evaluation of managed relocation. *Proc. Natl. Acad. Sci. U. S. A.* 106, 9721–9724
- 60 Foden, W. *et al.* (2007) A changing climate is eroding the geographical range of the Namib Desert tree *Aloe* through population declines and dispersal lags. *Div. Distrib.* 13, 645–653
- 61 Hobbs, R.J. *et al.* (2009) Which way to the future? Novel ecosystems and their implications for conservation and restoration. *Trends Ecol. Evol.* 24, 599–605

- 62 Sax, D.F. *et al.* (2009) Managed relocation: a nuanced evaluation is needed. *Trends Ecol. Evol.* 24, 472–473
- 63 Hobbs, R.J. and Cramer, V.A. (2008) Restoration ecology: interventionist approaches for restoring and maintaining ecosystem function in the face of rapid environmental change. *Annu. Rev. Environ. Resour.* 33, 39–61
- 64 Jackson, S.T. and Hobbs, R.J. (2009) Ecological restoration in the light of ecological history. *Science* 325, 567–569
- 65 Anderson, B.J. *et al.* (2009) Dynamics of range margins for metapopulations under climate change. *Proc. R. Soc. B* 276, 1415–1420
- 66 Liu, Z. *et al.* (2009) Transient simulation of last deglaciation with a new mechanism for Bølling-Allerød warming. *Science* 325, 310–314
- 67 Hu, F.S. *et al.* (2002) Response of tundra ecosystem in southwestern Alaska to Younger-Dryas climatic oscillation. *Global Change Biol.* 8, 1156–1163
- 68 Shuman, B.N. *et al.* (2009) Abrupt climate change as a catalyst of ecological change in the Northeast U.S. throughout the past 15,000 years. *Quat. Sci. Rev.* 28, 1693–1709
- 69 Woods, K.D. (2004) Intermediate disturbance in a late-successional hemlock-northern hardwood forest. *J. Ecol.* 92, 464–476
- 70 Wright, D.H. (1983) Species-energy theory – an extension of species-area theory. *Oikos* 41, 496–506
- 71 Wylie, J.L. and Currie, D.J. (1993) Species-energy theory and patterns of species richness: I. Patterns of bird, angiosperm, and mammal species richness on islands. *Biol. Conserv.* 63, 137–144
- 72 Whittaker, R.H. (1960) Vegetation of the Siskiyou Mountains. *Oregon and California. Ecol. Mon.* 30, 279–338
- 73 Saunders, D.A. *et al.* (1991) Biological consequences of ecosystem fragmentation – a review. *Conserv. Biol.* 5, 18–32
- 74 Hanski, I. and Ovaskainen, O. (2003) Metapopulation theory for fragmented landscapes. *Theor. Pop. Biol.* 64, 119–127
- 75 Loehle, C. and Li, B-L. (1996) Habitat destruction and the extinction debt revisited. *Ecol. Appl.* 6, 784–789
- 76 Shelford, V.E. (1913) *Animal Communities in Temperate America as Illustrated in the Chicago Region*, University of Chicago Press
- 77 Jackson, S.T. *et al.* (1988) A paleoecological test of a classical hydrosere in the Lake Michigan Dunes. *Ecology* 69, 928–936