

## LETTER

# Predicting and Assessing Progress in the Restoration of Ecosystems

A.R.E. Sinclair<sup>1</sup>, Roger P. Pech<sup>2</sup>, John M. Fryxell<sup>3</sup>, Kevin McCann<sup>3</sup>, Andrea E. Byrom<sup>2</sup>, C. John Savory<sup>4</sup>, Justin Brashares<sup>5</sup>, Anthony D. Arthur<sup>6</sup>, Peter C. Catling<sup>7</sup>, Maggie D. Triska<sup>8</sup>, Michael D. Craig<sup>9,10</sup>, Tim J.E. Sinclair<sup>11</sup>, Jennie R. McLaren<sup>12</sup>, Roy Turkington<sup>1,13</sup>, Rene L. Beyers<sup>1</sup>, & William L. Harrower<sup>1,13,14</sup>

<sup>1</sup> Beaty Biodiversity Research Centre, University of British Columbia, 6270 University Boulevard, Vancouver, BC, V6T 1Z4, Canada

<sup>2</sup> Landcare Research, P.O. Box 69040, Lincoln, 7640, New Zealand

<sup>3</sup> Department of Integrative Biology, University of Guelph, N1G 2W1, Ontario, Canada

<sup>4</sup> Netherham, Station Road, West Linton, Peeblesshire, EH46 7EL, Scotland

<sup>5</sup> Department of Environmental Science, Policy & Management, University of California, Berkeley, CA, USA

<sup>6</sup> Australian Bureau of Agricultural and Resource Economics and Sciences, Department of Agriculture and Water Resources, 18 Marcus Clarke Street, Canberra, ACT 2601, Australia

<sup>7</sup> 33 Gellibrand St., Campbell ACT 2612, Australia

<sup>8</sup> School of Plant Biology, The University of Western Australia, Crawley, Western Australia 6009, Australia

<sup>9</sup> Centre of Excellence for Environmental Decisions, School of Plant Biology, The University of Western Australia, Crawley, Western Australia 6009, Australia

<sup>10</sup> School of Veterinary and Life Sciences, Murdoch University, Murdoch, Western Australia, 6150, Australia

<sup>11</sup> Tonkin & Taylor Ltd., Consulting Engineers, Auckland, New Zealand

<sup>12</sup> Department of Biological Sciences, University of Texas at El Paso, El Paso, TX 79902, USA

<sup>13</sup> Department of Botany, University of British Columbia, Vancouver, BC, V6T 1Z4, Canada

<sup>14</sup> Department of Forest and Conservation Sciences, University of British Columbia, Vancouver, BC V6T 1Z4, Canada

## Keywords

Restoration index; endpoints; resilience; ecosystem restoration; trophic structure.

## Correspondence

William L. Harrower, Department of Forest and Conservation Sciences, Forest Sciences Centre, 3041 - 2424 Main Mall, Vancouver, BC Canada V6T 1Z4. Tel: 604-822-2507; Fax: 604-822-9133. E-mail: harrower@biodiversity.ubc.ca

## Received

16 February 2017

## Accepted

20 June 2017

## Editor

Matt Hayward

Statement of Authorship

A.R.E.S., R.P.P., A.E.B., W.L.H., and R.B. designed the study, performed the research, provided methods and materials, and wrote the original manuscript.

J.M.F. and K.M. provided methods, helped develop the theoretical perspective, and provided revisions to the final manuscript.

C.J.S., J.B., A.D.A., P.C.C., M.D.T, M.D.C., T.J.E.S., J.R.M., and R.T. provided data, helped develop ideas, and each author contributed substantially to the revisions.

## Abstract

Restoration of degraded landscapes has become necessary to reverse the pervasive threats from human exploitation. Restoration requires first the monitoring of progress toward any chosen goals to determine their resilience and persistence, and second to conduct in a comparable adjacent area but with less human impact the restoration of trophic structures and ecosystem processes to act as reference systems (controls) with which we compare the viability of the chosen goal. We present here the rationale and a method for predicting the trajectory of restoration and assessing its progress toward a predetermined state, the endpoint, using a *restoration index*. This assessment of restoration requires that we know when a predetermined endpoint has been achieved and whether the envisioned community of species and their interactions can be restored. The restoration index can use species' presence or density, and the rate of change of ecosystem processes. The index applies to trophic levels, functional groups, successional stages, alternative states, and novel ecosystems. Also, our method allows measurement of the resilience of ecosystems to disturbance, a desired property for conservation and management. We provide global examples to illustrate these points.

doi: 10.1111/conl.12390

## Introduction

Human impacts are now changing all of Earth's natural ecosystems. Restoration of human-dominated and degraded landscapes has become necessary to reverse the pervasive threats from overexploitation, agricultural expansion, urban development, invasive species, and disease (Herrick *et al.* 2006; Zedler *et al.* 2012; Maxwell *et al.* 2016). Future human-dominated landscapes will inevitably change from predisturbed states to ones with new species complexes (Marris 2011), involving the loss of some species, the arrival of outside species and different ecosystem processes of nutrient cycling, hydrology, and energy flow. Changes in resilience and new ecosystem states are considered likely (Choi 2007; Martínez & López-Barrera 2008; Kareiva & Fuller 2016). In addition, society expresses a range of values, policies, and desired outcomes for future ecosystems and communities (Baker & Eckerberg 2016). The challenge is in determining whether resultant ecosystem states arising from these values and policies are resilient, robust, and supportive of human activity, whether they are degrading to an unsustainable condition, and whether it is possible in some areas to restore a full complement of species and ecological processes that predated substantial human impacts. To determine these outcomes, two actions are necessary. First is to monitor restoration progress toward any chosen goal and observe whether such ecosystems return to a previous state or settle into a new one; and second to conduct in a comparable adjacent area but with less human impact the restoration of trophic structures and ecosystem processes to act as reference systems (controls) with which we compare the viability of the chosen future combination of species in the human-dominated areas (Herrick *et al.* 2006; Svenning *et al.* 2015). There is growing evidence that distortion of trophic structure has been the primary cause of ecosystem instability and shifts to alternative, undesirable states (Terborgh & Estes 2010; Estes *et al.* 2011; Fraser *et al.* 2015; Lorimer *et al.* 2015; Jepson 2016; Malhi *et al.* 2016). This is not to advocate a return to some predetermined pristine condition of such reference areas, but rather to restore some areas in every biome with reduced human impact (Jepson 2016).

Fundamental to a policy of restoration of ecosystems is that an endpoint (baseline or reference condition) should be specified that describes the set of conditions that is expected to be achieved (Svenning *et al.* 2015; Jepson 2016). Choice of endpoint is the subject of much current debate (Choi 2007; Baker & Eckerberg 2016; Kareiva & Fuller 2016; Malhi *et al.* 2016): for example, should we aim to return to the Pleistocene, Holocene, or aim for some future conditions involving either the exclusion or presence of human activity? Multiple endpoints are pos-

sible (known as alternative states) and predicting and assessing which endpoint is most likely valuable for natural resource managers. In this article, we show how the endpoint can be predicted, and progress assessed toward achieving it, in a way that can inform preferred societal values and policies.

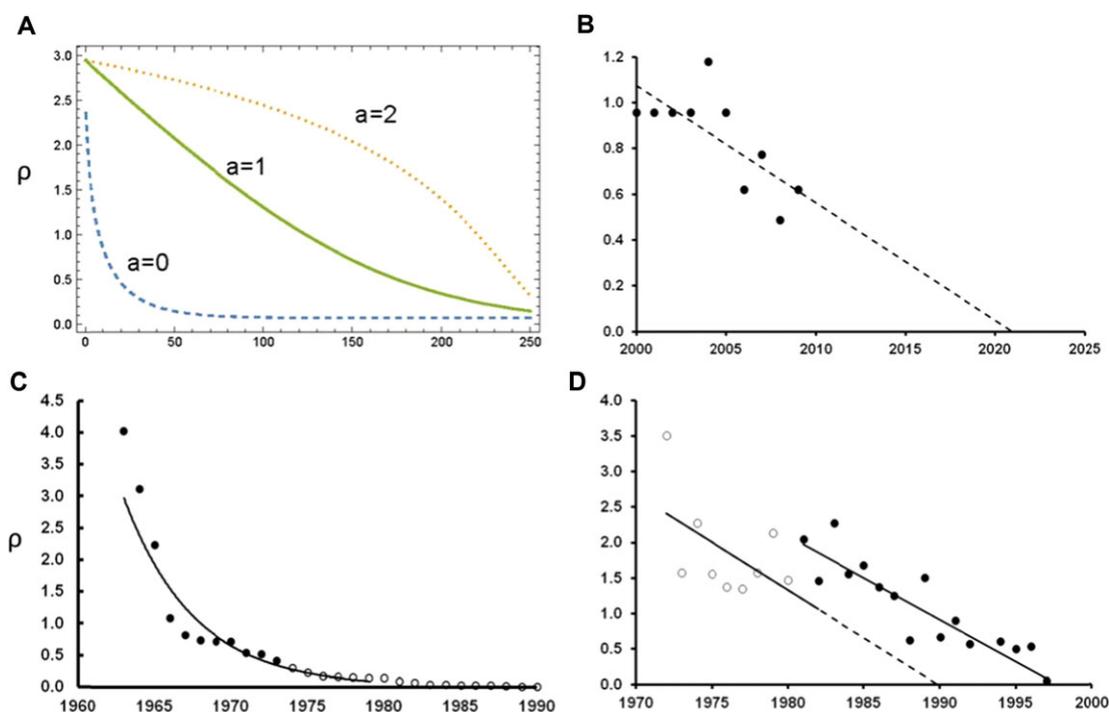
## The endpoint

The endpoint or baseline can be chosen from what is present in areas that are undisturbed, from estimates of what was present in past times, or even set out hypothetically as an estimate of what a conservation manager believes should be present now or what might occur in the future. Whether these endpoints are valid and achievable will be determined by assessment of progress toward them. The parameters used in measuring the endpoint are determined both by what managers need and what is available to them. Importantly, an endpoint can be measured in terms of a list of species, or by the densities of those species, or by ecosystem process measures such as nutrient concentrations in soil or water pollution. If original species frequencies or densities are available, then those data can be used to determine the endpoint. More often, however, species presence/absence records are all that are available; managers can decide whether to accept, as a measure of progress, the first case of arrival of a species or its sustained presence for a predetermined length of time. Specification of the endpoint requires decisions about species that are not indigenous. This allows managers to accept foreign species that have arrived over time and are now regarded as part of the ecological community. Foreign species that have a negative impact on the endpoint community (e.g., exotic predators and competitors on islands, invasive plants) need to be removed because they will prevent achieving the endpoint.

We address two questions: first, how can we quantitatively determine the rate of restoration to a specified endpoint; and second, because some environments may have changed since the original community was disturbed, how can we detect whether the ecosystem is tracking toward the desired community or is heading toward a new state? We outline a method of measuring the rate of restoration based on a theoretical model of community assembly dynamics. This theory allows us to predict different *restoration trajectories* from the types of species interactions that occur.

## The rate of restoration

Restoration focuses on a measurable parameter as it returns to a chosen endpoint. We recognize this endpoint



**Figure 1** A) Restoration index trajectories ( $\rho$ ) for three different cases of the colonization acceleration coefficient ( $a$ ). The  $a = 0$  case corresponds to a slowing colonization. When the non-linear colonisation co-efficient  $C_2 > 0$ , increasing  $a$  accelerates the rate of colonization with species diversity. This acceleration first linearizes the restoration trajectory ( $a = 1$ ), before producing a restoration trajectory that is convex ( $a = 2$ ). Parameters for curves are:  $\{a = 0, C_1 = 0.05, C_2 = 0.02, e = 0.001; a = 1, C_1 = 0.000005, C_2 = 0.1, e = 0.001; a = 2, C_1 = 0.000005, C_2 = 0.1, e = 0.001\}$ . B) The rate of return of biota using the restoration index ( $\rho$ ) can predict when the original community (endpoint) will be achieved as shown by the return of forbs to the boreal forest following the cessation of a ten-year fertilization experiment in 2000 (J. McLaren and R. Turkington unpublished data). C) Restoration also exhibits different trajectories, being concave in the recolonization by fish species to the River Thames in England (Cloern 2001); the curve estimated from the first ten years (black circles) predicts the observations from the subsequent 16 years (open circles). D) Reversals in restoration can be seen in the return of marsupial folivores to eucalypt woodlands of Nadgee Reserve in New South Wales after fires in 1972 and 1980. The estimated original endpoint of 1990 (open circles) was delayed until 1997 as a result of the second fire (black circles) (Data from Arthur *et al.* 2012).

is a dynamic equilibrium that will fluctuate, but for practical purposes we use a stated set of species or processes as an approximation. The *restoration value* ( $RV$ ) is the proportion of this predetermined species pool or process (the endpoint  $S_{Loc}^*$ ) that is present locally at time  $t$  ( $S_{Loc}(t)$ ) during recolonization. Hence,  $RV = S_{Loc}(t) / S_{Loc}^*$ . The associated *restoration index* ( $\rho$ ) at time  $t$  is given by  $\rho(t) = \ln(S_{Loc}^* / S_{Loc}(t))$ . The advantage of using this restoration index is that when the predetermined set of parameters is achieved the index is at zero, so that we can measure the rate and shape of approach to zero. The theoretical derivation of the restoration index is given in Box 1, and the change in  $\rho$  with time is shown in Figure 1(A).

#### Box 1: Restoration and the Theory of Island Biogeography (TIB)

Following the theory of island biogeography (MacArthur & Wilson 1967), we assume that a locally fragmented community that is restored at any

time  $t$ , to be a random sample of species drawn from a nearby regional pool of species ( $S_{REG}$ ). The theory of island biogeography assumes that every species has the same probability of being a member of the local restoration pool at any time  $t$  ( $S_{Loc}(t)$ ) and that this time-dependent probability is mediated entirely by successful colonization and extinction. Given these simple assumptions, the patch-occupancy model (Gyllenberg & Hanski 1992; Holt 1996) from TIB can be expressed as:

$$dp/dt = c(1 - p) - ep \quad (1)$$

where  $p(t)$  is the probability any one species is in the local habitat,  $c$  is the colonization rate from the regional pool, and  $e$  is the extinction rate of the local pool. Colonization can be via natural processes or aided through human intervention. The key point is that both extinction and colonization are essentially probabilistic, with success being the stochastic process in human-aided restoration.

Over time  $p(t)$  is expected to approach an equilibrium  $p^* = c/(c+e)$  at which the probability of new colonization is balanced by species losses from the local community. The restoration diversity  $S_{Loc}(t)$  is then calculated in the following manner:

$$S_{Loc}(t) = p(t)S_{Reg} \quad (2)$$

Given the equilibrium, the reswilling “endpoint” is given by

$$S_{Loc}^* = p^*S_{Reg} = S_{Reg} c/(c+e) \quad (3)$$

As a quantitative metric of the degree of restoration value ( $RV$ ), we define it as

$$RV = S_{Loc}(t)/S_{Loc}^* = p(t)S_{Reg}/p^*S_{Reg} = p(t)/p^* \quad (4)$$

with an associated restoration index  $\rho$  at time  $t$  given by

$$\rho(t) = \ln(p^*/p(t)). \quad (5)$$

The dynamical equation for community richness (eq. (1)) can be solved for any combination of initial community values,  $p(0)$  to calculate  $p(t)$ :

$$p(t) = p^* + e^{-(c+e)t}(p(0) - p^*) \quad (6)$$

Given an initial condition,  $p(0)$ , the rate of approach of the restoration state to the endpoint (i.e., the rate of return resilience of the system) is entirely governed by  $\lambda$ , where  $\lambda = -(c+e)$ . In Eq. (6), this is evident from the fact that the decaying exponential (in the 2<sup>nd</sup> term) acts to minimize the distance between the initial value and the end state,  $p^*$ .

Restoration index trajectories can be reasonably approximated as linear for small  $c$  and  $e$  values over large ranges in the restoration trajectory. However, there is increasing departure from linearity towards a negative concave curve as  $p(t)$  approaches equilibrium. In contrast there can be accelerating arrival of species. To see this, one can modify the classical TIB model to represent a range of colonization assumptions encompassing both the classic TIB as well as nonlinear increases in colonization rates (i.e., acceleration),  $FC(p)$ , as follows:

$$\frac{dp}{dt} = FC(p)(1-p) - ep \quad (7)$$

where  $FC(p)$  is a function of  $p$ . A simple model representation that allows a combination of linear and nonlinear colonization rates is:

$$\frac{dp}{dt} = (C_1 + C_2 p^a)(1-p) - ep \quad (8)$$

where  $C_1$  and  $C_2$  are the linear and nonlinear colonization coefficients and  $a$  is the colonization acceleration coefficient. The impact of such a positive feedback on colonization, as discussed above, is

to either further linearize the restoration trajectory (Fig. 1; with a colonization acceleration coefficient of  $a = 1$ ) or produce accelerated trajectories of the restoration index with negative convex trajectories (Fig. 1; with a colonization acceleration coefficient of  $a = 2$ ). Further, this type of nonlinearity can readily produce multiple equilibria or alternative states.

Theory on the assembly and connectance of species in food webs predicts the shape of a restoration trajectory. A concave trajectory occurs when there is good linkage among species (Figure 1A with  $a = 0$ ). For food webs with lower connectance, the lack of species at lower trophic levels slows the entry of species at higher trophic levels (e.g., predators require the presence of prey) which produces a more linear trajectory (Figure 1A with  $a = 1$ ) as colonization rates accelerate. Arrival of some species may accelerate the arrival of other species so that the restoration trajectory can develop a negative convex trajectory (Figure 1A with  $a = 2$ ). These theoretical trajectories can be reversed and altered if foreign competitors and predators, environmental disturbances, or distorted processes are not mitigated beforehand.

Our first question concerns how to predict when restoration has achieved a desired ecosystem state. We demonstrate this using the rate of restoration of herbaceous plants in the boreal forests of northern Canada (Figure 1B) as part of the experimental perturbation of trophic cascades (Turkington *et al.* 2002, and J. McLaren and R. Turkington, unpublished data). The disturbance involved fertilizing herbaceous species for 10 years (1990-1999). Fertilization treatments ended after 10 years but annual monitoring of the recovery of herbaceous species continued, with the endpoint known from simultaneous adjacent controls. Assuming for this example a linear progression, the restoration index predicts that all species will have returned to the plots by 2021. Here we use for convenience species presence only, but cover measures could also be used.

The second question concerns the shape of the restoration trajectory. Restoration indices for fish species of the River Thames in England (Cloern 2001) demonstrate a concave recolonization trajectory, which is predicted if species are added at a constant number per unit time (Figure 1C). The endpoint was determined by prior knowledge. This concave trajectory was predicted from the first 10 years of Thames River fish data, and matches the subsequent 16 years of observations.

The restoration of marsupial folivores in the Nadgee Reserve of southern New South Wales, Australia, following two severe fires, was monitored using data on indices of abundance from track counts from 1972 to

1996 (Arthur *et al.* 2012; Figure 1D). This area is temperate eucalypt woodland; it was severely burnt in 1972 and again in 1980. Restoration indices following a linear trajectory commenced after a more complex structure of trees and shrubs had regenerated following the 1972 fire, but this return was reversed with the 1980 fire. Following this second fire, the restoration trajectory proceeded linearly to the endpoint in 1997, known from simultaneous data on control areas. This case also illustrates how repeat disturbances can be monitored and any delays in achieving the endpoint predicted. Following the 1972 fire, the trajectory of the folivore index predicted an endpoint in 1990 but the 1980 fire set this back to 1997.

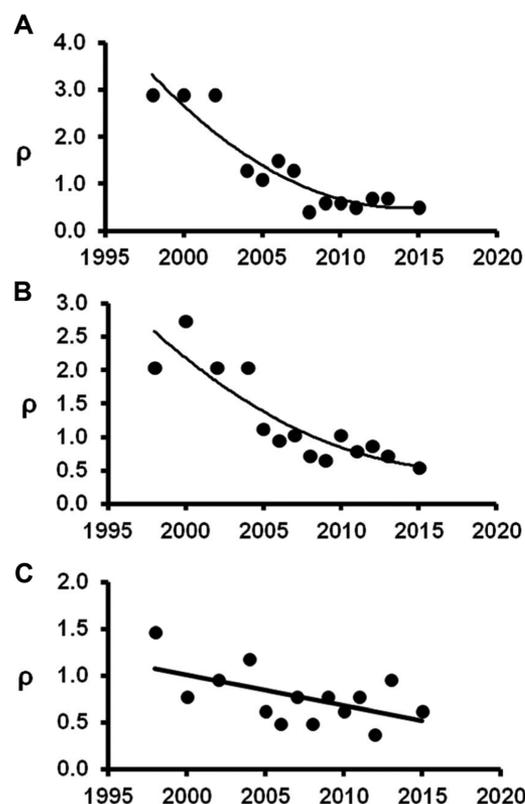
### Restoring trophic structure

One objective of restoration is to restore trophic structure and complexity to ecosystems (Svenning *et al.* 2015), hence we need to measure its progress at each trophic level independently. Because higher trophic levels are more prone to disturbance, we should expect that greater proportions of species are lost at higher trophic levels (Estes *et al.* 2011). Hence, we predict that during restoration higher trophic levels will take longer to recover than lower levels.

The Carrifran Wildwood Project aims to replant the Carrifran valley in the Moffat hills of southern Scotland with woodland vegetation that existed there about 6,000 years ago. Planting began in 2000 and, in most years since, the bird community has been recorded in the regenerating woodland (Savory 2016). With an endpoint estimated from expert knowledge of 62 species, restoration indices for each year from 1998 to 2015 show a negative concave trajectory for granivores (Figure 2A) and insectivores (Figure 2B), while there is a linear trajectory for carnivores (Figure 2C). Hence, predators show the slowest rate of return as predicted.

### Accelerated restoration: unraveling and reconstitution of ecosystems

One of the major concerns in conservation is that, as species are lost from a community the ecosystem becomes less suitable for the remaining species, resulting in an accelerated decline or unraveling of the ecosystem (Walker 1995; Ehrlich & Walker 1998) as seen in the local extinction of large mammals from six protected areas in Ghana from 1968 to 1992 (Brashares *et al.* 2004, J. Brashares pers. comm.). Relative abundances of ungulates, primates, and carnivores, recorded by park rangers, showed when each species disappeared. Using the 64 species that were lost as the baseline, the restoration in-



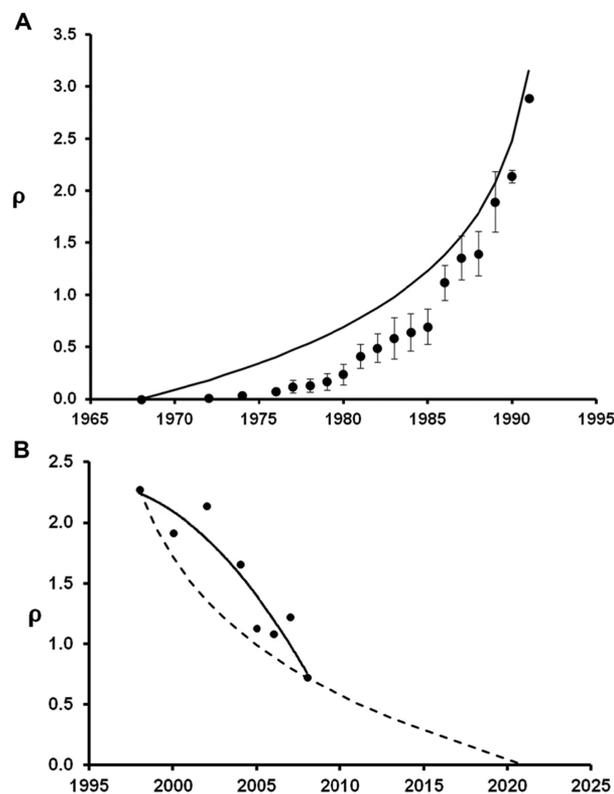
**Figure 2** Restoration trajectories for birds at different trophic levels in the Carrifran valley of the Moffat Hills, Scotland after replanting of native woodland began in 2000: A) granivores, B) insectivores, C) carnivores (Data from Savory 2016). Carnivores take longer to return than lower trophic levels.

dex (points on Figure 3A) showed an initial rate of extinction slower than expected, followed by an accelerating rate faster than expected relative to the expected curve of constant rate of loss.

If ecosystems can unravel as evidenced here, they could also exhibit accelerated restoration indices with a convex curve through early species facilitating later ones (Figure 1A,  $a = 2$ ). Annual data for the total Carrifran woodland birds show such a convex curve for the index in the first 10 years of renewal relative to an expected curve for a constant rate of arrival of species (Figure 3B), probably due to progressive development of the revegetated woodland.

### Alternative states, novel communities, and management policy

There are occasions when an ecosystem cannot be restored to an hypothesized endpoint because: the environment has changed (conditions 6,000 years ago at Carrifran may not be equivalent to the present; MacDougall



**Figure 3** Accelerated rates of loss or gain of species can cause a positive feedback unravelling or reconstitution of the community. A) Accelerated rate of local extinction of large mammals from six protected areas in Ghana (Brashares *et al.* 2004, J. Brashares pers. comm.). Solid line shows the expected rate if the 64 species had been lost at a constant number of species per unit time over the 14 years. The observed rate is slower initially but accelerated at later stages when more species had disappeared. B) The accelerated restoration index for the annual counts of all bird species in the Carrifran woodland over the first ten years (solid line). Accelerated arrival produces a convex curve compared to the expected concave curve (broken line) for a constant arrival per unit time of the same number of species (Savory 2016).

*et al.* 2013); disturbance has irreversibly shifted an ecosystem into an alternative state (Fukami & Nakajima 2011); or arrival of non-native species may prevent a return to chosen biotic communities (Ricciardi *et al.* 2013). Restoration options for managers may also result in “novel ecosystems” different from a previous hypothesized endpoint (Martinez & Lopez-Barrera 2008; Hobbs *et al.* 2013).

In these cases, the trajectory of the restoration index does not reach zero, but instead levels out. For example, densities of Serengeti carnivores have been increasing since removal of the disturbance of rinderpest in 1963 with the exception of wild dog (*Lycaon pictus*), which declined to local extinction in 1992 (Sinclair *et al.* 2007). Using an endpoint where all species were at their maximum

stable densities, the restoration index leveled out above zero due to the absence of wild dogs (concave curve in Figure 4A). A policy of active reintroduction of wild dogs inside the protected area was implemented from 2012 to 2015. The new restoration trajectory predicts the establishment of the pre-rinderpest community in 2025 (Figure 4A). However, success is far from certain because the conditions leading to the original extinction are still present.

## Succession

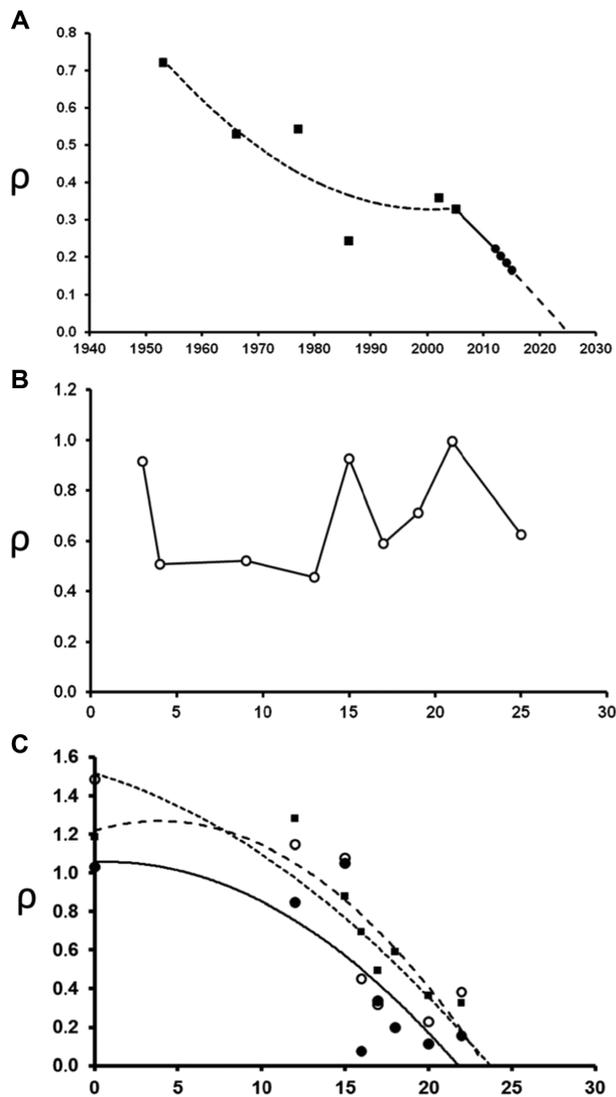
Successional stages affect the rate of restoration and produce trajectories similar to those for alternative states, at least temporarily. Midsuccessional vegetation stages, or competition from successive colonists, could depress or even exclude early colonists until a later successional stage occurs. The recolonization of reptile communities on old bauxite mine sites in dry eucalypt forests of southwestern Australia (Craig *et al.* 2012; Triska *et al.* 2016) show this pattern during regeneration (Figure 4B) relative to undisturbed control areas. Early-stage sunny sites suitable for reptiles later became shady with thick regenerating vegetation unsuitable for reptiles. Reptile species thus increase initially but then decline again. Eventually, mature woodland will establish with patches of both shaded woodland and open sunny glades containing the full complement of reptiles.

## Restoring ecosystem processes

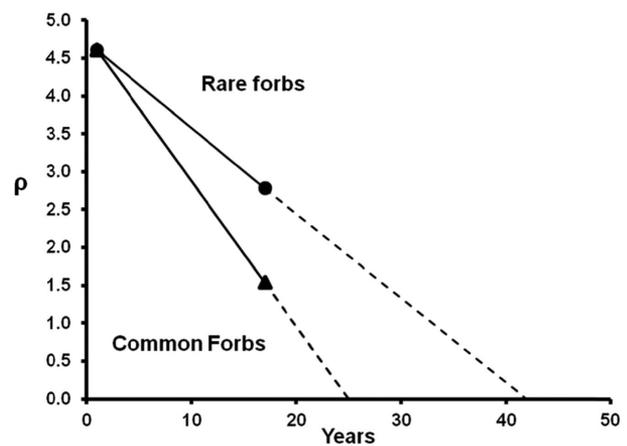
Restoration is not just concerned with biota: it is also relevant to the renewal of ecosystem processes both biotic, e.g., pollination, and abiotic, e.g., water flow and soil erosion (Herrick *et al.* 2006). This is observed in the return of nitrogen in different trophic levels on the Mercury islands in northern New Zealand (Figure 4C). After removal of rats, which had invaded the islands centuries ago, nitrogen concentrations in soils, plants, and spiders returned after 22 years to levels found on control islands that never had rats (Jones 2010). Similar accelerating curves are seen in the return of dissolved oxygen in the Forth Estuary of Scotland (Cloern 2001), and groundwater aquifers at Windhoek, Namibia, (T.J.E. Sinclair, unpublished data). (Figures S1, S2).

## Resilience of ecosystems

Maintaining or improving resilience of ecosystems is often one of the main policy objectives of conservation. Resilience is a term that refers to the ability of ecosystems to tolerate or rebound from disturbance, such as from human exploitation or climate change (Holling 1973;



**Figure 4** A) Alternative communities occur when the original species community can no longer be recovered. The restoration trajectory indicates this situation when it levels out and does not reach the baseline, as seen for the major carnivores in the Serengeti ecosystem since 1953 (squares, dotted line) (data from Durant *et al.* 2011, A. Brooks, E. Eblate, E. Masenga and A. Sinclair unpublished) because wild dogs went extinct in 1992. Wild dogs were reintroduced to the ecosystem starting in 2012 (circles). The subsequent restoration trajectory (solid line) can predict if this will succeed and when the trajectory reaches zero (broken line). B). Vegetation succession also modifies the restoration trajectory. Recolonization of old bauxite mine sites by reptiles in Western Australia. Recent sites, with little vegetation cover, are recolonized in the first 10 years. As succession proceeds denser vegetation produces cooler environments and reptiles leave again (Triska *et al.* 2016). C). Restoration of ecosystem processes as illustrated by the return of nitrogen at three trophic levels on the Mercury Islands, New Zealand, after rat removal. Soils (solid circles, full line), plants (squares, broken line) and spiders (open circles, dotted line) all show accelerating return (data from Jones 2010).



**Figure 5** Resilience of an ecosystem can be predicted by the estimated time required for the restoration index (recovering from a disturbance) to reach the endpoint on the x-axis, a fragile system taking longer than a resilient system for the same disturbance. In the South African montane grassland returning from the disturbance of a pine plantation common forbs (triangles) return faster and so are more resilient than rare forbs (circles) which are more fragile (Data from Zaloumis & Bond 2011).

Walker 1995; Kareiva & Fuller 2016). Resilience can be measured by the rate at which an ecosystem recovers from a disturbance; a fragile ecosystem taking longer to return than a resilient one that undergoes the same disturbance. Resilience is easily determined from the slope of the restoration trajectory. For example, in a montane grassland with many rare forbs in South Africa a portion was converted to a pine plantation (Zaloumis & Bond 2011). It was later decided to return the area to the original indigenous community. After 17 years of restoration, Zaloumis and Bond recorded the species that had returned relative to adjacent undisturbed sites in six categories of plants. The restoration index showed common forbs have a fast rate of return and are more resilient than rare forbs, which are, therefore, less resilient (Figure 5).

### Discussion

We have outlined an approach to predicting the outcome of restoration activities, and assessing its progress using a restoration index, irrespective of whether such progress occurs through natural processes or by active management. This approach applies to any chosen goal, including reference sites that act as controls for human impacts. Sites may recover at different rates and with different degrees of acceleration. If earlier arrival of species impedes later arrivals, a restoration trajectory will be concave, or complex if these are successional stages. If earlier species facilitate the establishment of others, then an accelerating

rate of species return is indicated by convex restoration trajectories.

### Policy implications for managers

Desired endpoints for restoration involve a range of societal values and policies (Baker & Eckerberg 2016). Whatever goal is chosen, an endpoint must be specified in advance in order to assess whether it is being achieved. Measuring the return rate of a community or process toward that endpoint is essential in order to estimate how long active management should continue (Figure 1B, C). A return to a pristine, prehuman biotic community is not required; managers can choose a pragmatic sustainable level of human influence as an endpoint. For example, reconstruction of lost landscapes at Oostvaardersplassen in Holland incorporates ancient varieties of cattle as surrogates for the aurochs (F. Vera in Marris 2009). Restoration is in progress at this site, but assessment of future recolonization of other ecosystem components such as plant, insect, amphibian, and bird communities toward a stated endpoint is still required. There is debate concerning the endpoint in such habitats (Birks 2005); should it be closed canopy woodland or a mosaic of open glades and closed canopy? Baselines are required to test (using our method) both hypotheses and assess whether either (or both as alternative stable states) are resilient and persistent in the contemporary environmental regime. To evaluate this outcome, one essential baseline is the restoration of trophic structure in some areas.

Second, the specified endpoint can include foreign species if they do not radically alter ecosystem integrity and function (e.g., European starlings (*Sturnus vulgaris*) in North America; Koenig 2003). However, invasive species that impede restoration and distort trophic structures need to be removed beforehand, as seen in fenced eco-sanctuaries on mainland New Zealand (Innes *et al.* 2012) or in Australia where competing exotic black rats (*Rattus rattus*) must be removed to allow recolonization of native bush rats (*Rattus fuscipes*; Stokes *et al.* 2009).

Third, managers can monitor progress toward an endpoint using a variety of parameters depending on what is available to them. Species presence lists, species abundances (Figures 1D, 4A), and processes such as nutrient flow and hydrologic function are all suitable (Figures 4C, S1, S2).

Fourth, the restoration index trajectory allows managers to determine whether their chosen endpoint is being achieved, or is instead moving to an alternative state due to excessive disturbance, extinction of species, the presence of invasive species or an unstable combination of novel species. Strategies for active restoration (e.g., reintroductions; control of invasive species) can then be

instituted if appropriate. In some areas, carnivores are undesirable and may be removed from the endpoint list. In other areas, they can be actively reintroduced and monitored (Figure 4A).

Fifth, all stable ecosystems require a mosaic of successional and terminal biotic communities, which means managers need to identify suitably large areas to maintain this mosaic. The restoration index can be used to detect the effects of successional processes on ecosystem recovery (Figure 4B). Finally, managers can determine quantitatively the resilience of components of their restored ecosystem (Figure 5), which allows them to focus resources on the more vulnerable and fragile ones.

### Conclusion

It is becoming increasingly clear that conservation of the world's ecosystems and biota will require restoration to reverse the pervasive threats from human exploitation. Restoration requires first the monitoring of progress toward any chosen goals, set by human values and policies, to determine their resilience and persistence, and second to conduct in a comparable adjacent area but with less human impact the restoration of trophic structures and ecosystem processes to act as reference systems (controls) for these chosen goals. We present here the rationale and a method for quantifying the progress of restoration toward predetermined endpoints, for building resilience in human-dominated systems and, potentially, for constructing novel ecosystems. Endpoints must be defined in advance, these being the stated set of species or processes to be achieved. Our restoration index further highlights critical needs for documenting baseline data, and for long-term monitoring.

### Acknowledgments

Funding for this work was provided by Canadian NSERC grants to ARES, RT, JMF, and KM, and by the New Zealand Ministry of Business, Innovation and Employment for RPP and AEB through core funding to Crown Research Institutes. We thank Philip Ashmole and the Carrifran Wildwood Project for their data and support, and Sarah Durant, Alan Brooks, Ernest Eblate, and Emmanuel Masenga for data on Serengeti carnivores.

### Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's web site:

**Figure S1.** Restoration trajectories for dissolved oxygen in the Forth Estuary, Scotland. The reversal of oxygen improvement in the mid-1970s delayed the predicted return to original conditions from 1976 to 1990 as shown by regressions for the pre- (open circles) and postreversal periods (closed circles). Data from Cloern (2001).

**Figure S2.** Restoration trajectories for ground aquifer levels in Windhoek, Namibia. Original data were ground water levels returning to normal after draw-down from overuse. Data show an accelerated rate of return (T.J.E. Sinclair, unpublished data).

## References

- Arthur, A.D., Catling, P.C. & Reid, A. (2012). Relative influence of habitat structure, species interactions and rainfall on the post-fire population dynamics of ground-dwelling vertebrates. *Austral. Ecol.*, **37**, 958-970.
- Baker, S. & Eckerberg, K. (2016). Ecological restoration success: a policy analysis understanding. *Restor. Ecol.*, **24**, 284-290.
- Birks, H.J.B. (2005). Mind the gap: how open were European primeval forests? *Trends Ecol. Evol.*, **20**, 154-156.
- Brashares, J.S., Arcese, P., Sam, M.K., Coppolillo, P.B., Sinclair, A.R.E. & Balmford, A. (2004). Bushmeat hunting, wildlife declines, and fish supply in West Africa. *Science*, **306**, 1180-1183.
- Choi, Y.D. (2007). Restoration ecology to the future: a call for new paradigm. *Restor. Ecol.*, **15**, 351-353.
- Cloern, J.E. (2001). Our evolving conceptual model of the coastal eutrophication problem. *Mar. Ecol. Prog. Ser.*, **210**, 223-253.
- Craig, M.D., Hardy, G.E.S.J., Fontaine, J.B., *et al.* (2012). Identifying unidirectional and dynamic habitat filters to faunal recolonisation in restored mine-pits. *J. Appl. Ecol.*, **49**, 919-928.
- Ehrlich, P. & Walker, B. (1998). Rivets and redundancy. *Bioscience*, **48**, 387-387.
- Estes, J.A., Terborgh, J., Brashares, J.S., *et al.* (2011). Trophic downgrading of planet Earth. *Science*, **333**, 301-306.
- Fraser, L.H., Harrower, W.L., Garriss, H.W., *et al.* (2015). A call for applying trophic structure in ecological restoration. *Restor. Ecol.*, **23**, 503-507.
- Fukami, T. & Nakajima, M. (2011). Community assembly: alternative stable states or alternative transient states? *Ecol. Lett.*, **14**, 973-984.
- Herrick, J.E., Schuman, G.E. & Rango, A. (2006). Monitoring ecological processes for restoration projects. *J. Nat. Conserv.*, **14**, 161-171.
- Hobbs, R.J., Higgs, E.S. & Hall, C.M. (2013). Introduction: why novel ecosystems?, in: Hobbs, R.J., Higgs, E.S., Hall, C.M. (Eds.) *Novel Ecosystems: Intervening in the New Ecological World Order*, John Wiley & Sons, Ltd, Chichester, UK. <https://doi.org/10.1002/9781118354186.ch1>
- Holling, C.S. (1973). Resilience and stability of ecological systems. *Annu. Rev. Ecol. Syst.*, **4**, 1-23.
- Innes, J., Lee, W.G., Burns, B., *et al.* (2012). Role of predator-proof fences in restoring New Zealand's biodiversity: a response to Scofield *et al.* (2011). *N.Z. J. Ecol.*, **36**, 232-238.
- Jepson, P. (2016). A rewilding agenda for Europe: creating a network of experimental reserves. *Ecography (Cop.)*, **39**, 117-124.
- Jones, H.P. (2010). Seabird islands take mere decades to recover following rat eradication. *Ecol. Appl.*, **20**, 2075-2080.
- Kareiva, P. & Fuller, E. (2016). Beyond resilience: how to better prepare for the profound disruption of the anthropocene. *Global Policy*, **7**, 107-118.
- Koenig, W.D. (2003). European starlings and their effect on native cavity-nesting birds. *Conserv. Biol.*, **17**, 1134-1140.
- Lorimer, J., Sandom, C., Jepson, P., Doughty, C., Barua, M. & Kirby, K.J. (2015). Rewilding: science, practice, and politics. *Annu. Rev. Environ. Resour.*, **40**, 39-62.
- MacDougall, A.S., McCann, K.S., Gellner, G. & Turkington, R. (2013). Diversity loss with persistent human disturbance increases vulnerability to ecosystem collapse. *Nature*, **494**, 86-89.
- Malhi, Y., Doughty, C.E., Galetti, M., Smith, F.A., Svenning, J. & Terborgh, J.W. (2016). Megafauna and ecosystem function from the pleistocene to the anthropocene. *Proc. Natl. Acad. Sci. USA*, **113**, 838-846.
- Marris, E. (2009). Conservation biology: reflecting the past. *Nature*, **462**, 30-32.
- Marris, E. (2011). *Rambunctious garden: saving nature in a post-wild world*. Bloomsbury, New York, NY.
- Martínez, M.L. & López-Barrera, F. (2008). Special issue: restoring and designing ecosystems for a crowded planet. *Ecoscience*, **15**, 1-5.
- Maxwell, S.L., Fuller, R.A., Brooks, T.M. & Watson, J.E.M. (2016). The ravages of guns, nets and bulldozers. *Nature* **536**, 143-145.
- Ricciardi, A., Hoopes, M.F., Marchetti, M.P. & Lockwood, J.L. (2013). Progress toward understanding the ecological impacts of nonnative species. *Ecol. Monogr.*, **83**, 263-282.
- Savory, C.J. (2016). Colonization by woodland birds at Carrifran Wildwood: the story so far. *Scottish Birds*, **36**, 135-149.
- Sinclair, A.R.E., Mduma, S.A.R., Hopcraft, J.G.C., Fryxell, J.M., Hilborn, R. & Thirgood, S. (2007). Long-term ecosystem dynamics in the Serengeti: lessons for conservation. *Conserv. Biol.*, **21**, 580-590.
- Stokes, V.L., Banks, P.B., Pech, R.P. & Spratt, D.M. (2009). Competition in an invaded rodent community reveals black rats as a threat to native bush rats in littoral rainforest of south-eastern Australia. *J. Appl. Ecol.*, **46**, 1239-1247.
- Svenning, J.-C., Pedersen, P.B.M., Donlan, J., *et al.* (2015). Science for a wilder anthropocene: synthesis and future

- directions for rewilding research. *Proc. Natl. Acad. Sci. USA*, **113**, 1-7.
- Terborgh, J. & Estes, J.A. (2010). *Trophic cascades: predators, prey, and the changing dynamics of nature*. Island Press, Washington, DC.
- Triska, M., Craig, M.D., Stokes, V., Pech, R. & Hobbs, R.J. (2016). Reptile recolonization of sites post-mining: the relative influence of in situ and neighborhood variables. *Restor. Ecol.*, **24**, 517-527.
- Turkington, R., John, E., Watson, S. & Seccombe-Hett, P. (2002). The effects of fertilization and herbivory on the herbaceous vegetation of the boreal forest in north-western Canada: a 10-year study. *J. Ecol.*, **90**, 325-337.
- Walker, B. (1995). Conserving biological diversity through ecosystem resilience. *Conserv. Biol.*, **9**, 747-752.
- Zaloumis, N.P. & Bond, W.J. (2011). Grassland restoration after afforestation: no direction home? *Austral. Ecol.*, **36**, 357-366.
- Zedler, J.B., Doherty, J.M. & Miller, N.A. (2012). Shifting restoration policy to address landscape change, novel ecosystems, and monitoring. *Ecol. Soc.*, **17**, 36. <https://doi.org/10.5751/ES-05197-170436>