

Red flags: correlates of impaired species recovery

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Conservation biology research exhibits a striking but unhelpful dichotomy. Analyses of species decline, extinction risk, and threat mitigation typically encompass broad taxonomic and spatial scales. By contrast, most studies of recovery lack generality, pertaining to specific species, populations, or locales. Narrowly focused analyses offer a weak empirical basis for identifying generic recovery correlates across species, particularly in cases where recovery is not effected by an abatement of threats. We present a research framework for multi-species meta-analyses to identify early-warning signals – ‘red flags’ – of impaired recovery that can be used as predictors of recovery potential before recovery efforts are initiated. An empirically comprehensive understanding of the demographic, ecological, evolutionary, and threat-related factors affecting the rate and trajectory of species recovery will strengthen conservation efforts to set recovery priorities, targets, and timelines.

Divergent approaches to conservation biology research

Broad-scale analyses typify much of the current research in conservation biology. Biodiversity loss, for example, is often described and assessed at multiple taxonomic and geographical scales [1–6] [Living Planet Report 2010: biodiversity, biocapacity and development (http://www.panda.org/about_our_earth/all_publications/living_planet_report/)]. Quantitative criteria relating to distribution, abundance, and demography are routinely applied to large numbers of species to identify those at heightened risk of extinction [7–9]. Multiple studies across broad geographic and taxonomic scales have explored the degree to which threats affect species persistence [10,11]. One practical element of these broad-scale analyses is that they allow for identification of general rules and patterns that can be used to help focus conservation efforts when funding is constrained.

Studies of recovery, in contrast, tend to be species- and often population-specific*, reducing their generality and

applicability to other species. Further confounding a generalist approach is the fact that definitions of what constitutes recovery can vary significantly within and among jurisdictions (Box 1). Here, we define recovery as a reversal of declines and achievement of predefined targets relating to metrics of persistence such as abundance or density, range distribution, and genetic/phenotypic variability.

Although sufficient time has elapsed since the first species assessments were undertaken under the auspices of the IUCN Red List (1960s) and the US Endangered Species Act (ESA) (1970s) to allow long-term analysis, multi-species studies of recovery (i.e., analyses of patterns of recovery across species) have been taxonomically limited and few in number [13,16]. Logistic (and often legal) constraints can necessitate a local approach to recovery, given that recovery strategies are often focussed on specific societal responses to the threats affecting a depleted species. However, based on the insights gained from multiple studies of species-independent correlates of decline, threat, and elevated extinction risk, it is reasonable to expect that comparable analyses of recovery would substantially improve our understanding of: (i) the magnitude and nature of variability in species trajectories following decline; and (ii) the drivers of that variability. Such studies could provide a more informed and empirically defensible basis for conservation initiatives and recovery strategies, including setting of recovery priorities, objectives, and targets, and refinement of methods to aid species recovery.

Correlates of species recovery

The scale of the current biodiversity crisis, coupled with the difficulty and increasing expense of species conservation efforts, underscores an acute and growing need for a recovery-correlate template applicable across species and regions [2,17,18]. One emerging reason for such a template is the realization that the amelioration of threats, albeit necessary, is not always sufficient to ensure recovery. An empirically comprehensive understanding of the factors that affect the rate, magnitude, and trajectory of species recovery will strengthen efforts to set recovery targets and timelines, which often are inconsistent and poorly justified [14,19,20]. The need for a more comprehensive

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* The word ‘species’ is used here in a broad sense to include other biological units that might be assessed for conservation or legal-listing purposes, such as subspecies, varieties, and populations or evolutionarily significant units [12].

Box 1. The meaning of 'recovery' across jurisdictions

Recovery is a term with clear biological connotations but no precise, generally accepted definition. It has been used to cover a wide range of scenarios, from simply achieving the minimum conditions for species persistence to full recovery of a species' ecological and evolutionary functionality within its ecosystem [13,14].

Under the US ESA [section 4(f)], for example, recovery plans must incorporate, at a minimum, the following elements: a) a description of site-specific management actions necessary to achieve recovery; b) objective, measurable criteria for delisting; and c) estimates of time and costs required to achieve the stated goals. Recovery plans in the USA have been created for many species, all with the common goal of ensuring species viability and persistence.

By contrast, in Canada, the government department responsible for implementing the Species At Risk Act defines recovery as 'the process by which the decline of an endangered, threatened, or extirpated species is arrested or reversed and threats are removed or reduced to improve the likelihood of the species' persistence in the wild' [15]. Although the process appears well-defined conceptually, the goals are highly variable, with the recovery target required to achieve species persistence 'ranging from precarious with limited occurrence to highly viable and self-sustaining' [Species at Risk Act Implementation Guidance (<http://www.sfu.ca/biology/courses/bisc309/Info/cws-SARtemplate2.doc>)].

In the EU, Species Action Plans developed by the European Commission define recovery targets to meet short-, medium-, and long-term objectives, with desired values set for specific targets. The short- to medium-term targets are often expressed in relation to IUCN Red List criteria or the EU Habitats Directive (for example, specific population sizes or rates of decline, taking into account generation length) that would result in a classification of the species into a lower category of extinction risk on the IUCN Red List. Long-term objectives are defined in terms of achieving a Favourable Conservation Status (*sensu* Directive 92/43/EEC).

Understanding of recovery has recently been highlighted by the Convention on Biological Diversity's *Strategic Plan for Biodiversity 2011-2020* (<http://www.cbd.int/decision/cop/?id=12268>), which established 20 targets (the Aichi Biodiversity Targets) that serve as aspirations for biodiversity conservation at global, regional, and national levels. Specific objectives include taking measures to ensure that the conservation status of known threatened species 'has been improved and sustained' (Target 12 of the plan) and that 'recovery plans and measures are in place for all depleted species' of 'fish and invertebrate stocks and aquatic plants' (Target 6).

To date, studies of multi-species patterns of recovery have been principally restricted to commercially exploited species [13,16]. One obvious and essential correlate of recovery for such species is reduced exploitation pressure [21]. In addition, some harvested fishes have been found to experience impaired recovery when their magnitude of population reduction is relatively high, their age at maturity is comparatively old, the trophic level at which they feed is high, and their probability of being captured incidentally by different forms of fishing gear is substantial [13,16,22,23].

Threat abatement does not always ensure recovery

Species do not always respond positively, or at the forecasted rate of recovery, to an amelioration of threats. Reductions in abundance, and correlates thereof, can lead to unanticipated and undesirable population trajectories.

There are many examples of species for which threat abatement has not been sufficient to ensure recovery. The

black-footed ferret (*Mustela nigripes*), a species almost entirely dependent on a single species of prey, the black-tailed prairie dog (*Cynomys ludovicianus*), was listed as Endangered in the USA in 1967 [US Fish & Wildlife Service Endangered Species (<http://www.fws.gov/mountain-prairie/species/mammals/blackfootedferret/>)]. The primary threat to the ferret was a severe reduction in the abundance of prairie dogs, long considered a pest by farmers and land managers. Despite the elimination of prairie dog poisoning program and a resultant increase in their abundance, black-footed ferrets have not recovered [US Fish & Wildlife Service Endangered Species (<http://www.fws.gov/mountain-prairie/species/mammals/blackfootedferret/>)]. The Critically Endangered orange-bellied parrot (*Neophema chrysogaster*) of southern Australia faces extinction in the wild within the next 5 years [24], despite extensive recovery efforts and an abatement of threats [Australian Government Department of Sustainability, Environment, Water, Population and Communities (http://www.environment.gov.au/cgi-bin/sprat/public/publicspecies.pl?taxon_id=747#threat_abatement_and_recovery)]. In addition, numerous over-exploited marine fishes have failed to recover despite severe reductions in fishing pressure and an absence of habitat loss (the primary threat to most endangered species [10,11]).

Multi-species approach to recovery*Patterns across species*

We suggest a research framework for multi-species meta-analyses of recovery, with the specific objective of identifying early-warning signals – 'red flags' – of impaired recovery. These red flags can serve a pre-emptive purpose by signifying when urgent measures are needed to prevent species from reaching the point at which recovery is significantly impaired. They can also be used to identify current situations for which species recovery is likely to be slow, presumably costly, and highly uncertain. We believe that the approaches initiated by previous studies of marine species [13,16] can be expanded to identify a suite of recovery correlates, candidate red flags for recovery, and their potential influence, articulated as a series of postulates that lend themselves to hypothesis testing (Table 1) across terrestrial and aquatic species. These recovery correlates can be grouped into four general categories.

General categories of recovery correlates

Demographic correlates pertain to multiple factors, including: rate, magnitude, and trajectory of abundance decline; life-history traits; the age class or developmental stage most affected by the threat; and changes in population growth rate (r), and the variance in r , with changes in abundance (e.g., Allee effects). Ecological correlates include those that affect intra- and interspecific interactions, such as competition, predation, and parasitism. Evolutionary correlates involve changes in heritable trait variation, magnitude of natural selection, and human-induced alterations to gene frequencies, such as those hypothesized to result from harvesting or artificial propagation [25–27]. A fourth category, threat correlates, might include variables such as threat magnitude (a product of scope and severity), the number and diversity of threats,

Table 1. Examples of potential correlates and red flags of species recovery amenable to empirical evaluation

Correlate	Red flag	Postulated influence on recovery
Magnitude of reduction in abundance or distribution	Numerical or distributional declines in excess of 50% ^a	Greater reductions are associated with slower recovery
Rate of decline in abundance or distribution	Numerical or distributional declines >30% during the greater of three generations or 10 years ^b	Faster rates of decline are associated with slower rates of recovery
Temporal trajectory of decline in abundance or distribution ^c	Large concavity in the shape of trajectories of abundance or distribution	Shift in trajectory; rate of recovery declines as trajectories in abundance or distribution shift from highly convex to highly concave shapes
Life history traits ^d	Advanced age at maturity; large size at maturity; long generation time; slow individual growth rate (ectotherms); low fecundity (excluding teleost fish); low dispersal ability	Trait combinations that reduce <i>r</i> will retard recovery; reduced among-population variation might reduce recovery rate (reduced portfolio effect) ^e
Allee effect (depensation, positive density dependence)	Reductions in <i>r</i> with declining abundance	Populations that fall below the threshold at which Allee effects are expressed will have slower, more uncertain recovery
Variance in <i>r</i>	Increases in the variance of <i>r</i> , particularly when associated with population decline	The greater the variance in <i>r</i> , the greater the uncertainty in the trajectory of recovery
Interspecific interactions	Increases in the relative abundance of negatively interacting species (e.g., predators, competitors, parasites, pathogens); decreases in the relative abundance of positively interacting species (e.g., prey, mutualists)	The greater the proportional change in abundances of interacting species, the slower the recovery
Threats	Increases in number and magnitude of threats, particularly those with high irreversibility	Intense threats (or combinations of threats) and highly irreversible threats will impair recovery
Evolutionary responses to anthropogenic threats	Genetic changes in fitness-related traits; loss of genetic diversity within and between populations; reversibility of selection responses	The greater the selection response, and the greater the loss of genetic variability, the slower the recovery
Conservation action	Lack of effective implementation of conservation interventions within one species generation of a species qualifying for elevated conservation concern	The sooner remedial action is taken, the greater the rate and probability of recovery

^a[23].^bGuidelines for Using the IUCN Red List Categories and Criteria (<http://www.iucnredlist.org/documents/RedListGuidelines.pdf>).^c[7].^d[16,35,36].^e[37].

degree of threat reversibility, and societal willingness to undertake conservation actions to mitigate threats.

Examples of research questions

Although threat correlates have long been recognized and studied for species of conservation concern, the same is not true for demographic, ecological, and evolutionary correlates of species recovery. For these three general categories of correlates, the information in Table 1 raises a number of key questions concerning recovery that can be profitably addressed by multi-species analysis (Figure 1).

Demographic correlates

From a single-species perspective, demographic correlates of recovery are paramount. To what degree is recovery (as measured by future trends in abundance or distribution) affected by the magnitude or rate of reduction in abundance or distribution during the period of decline [13,16] (Figure 1a)? Rate (but not absolute magnitude) of decline, over the longer period of 10 years or three generations, is a criterion used in many risk-evaluation frameworks, such as the IUCN Red List (<http://www.iucnredlist.org/documents/RedListGuidelines.pdf>). However, few studies [16] have evaluated what happens to species after they have experienced various rates of decline over these (and other) time frames. This question could be addressed by an analysis of population trajectories following various rates of change, standardized by generation length.

Do the shape characteristics of a species' abundance or distribution trajectory during decline (e.g., convex, concave, linear, highly fluctuating, minimally fluctuating) influence the shape of a species' trajectory during recovery (Figure 1b)? How does the variance in *r*, a key [28], if understudied, component of extinction risk, vary with population size? A study of Spanish ibex (*Capra pyrenaica*) suggests that thresholds for the variance in *r* exist, such that extinction risk increases considerably once these thresholds have been exceeded [29]. Furthermore, how might *r* and its variance during recovery be affected by prior population abundance, changes in age/size structure (Figure 1c) [30], and reductions in distribution extent?

Ecological correlates

Recovery can be influenced by ecological factors associated with species habitat and with food web related changes in species interactions. For example, how is the abundance or distribution trajectory during recovery affected by habitat fragmentation and/or changes to population connectivity during decline? How might changes in the relative abundance of interacting species (e.g., predators:prey, hosts:parasites, competitors, mutualists) influence recovery? Exponentially increasing numbers of grey seals (*Hali-choerus grypus*) in eastern Canada are hypothesized to be significantly retarding the recovery of one of their prey, Atlantic cod (*Gadus morhua*) [31,32]. The yucca moth

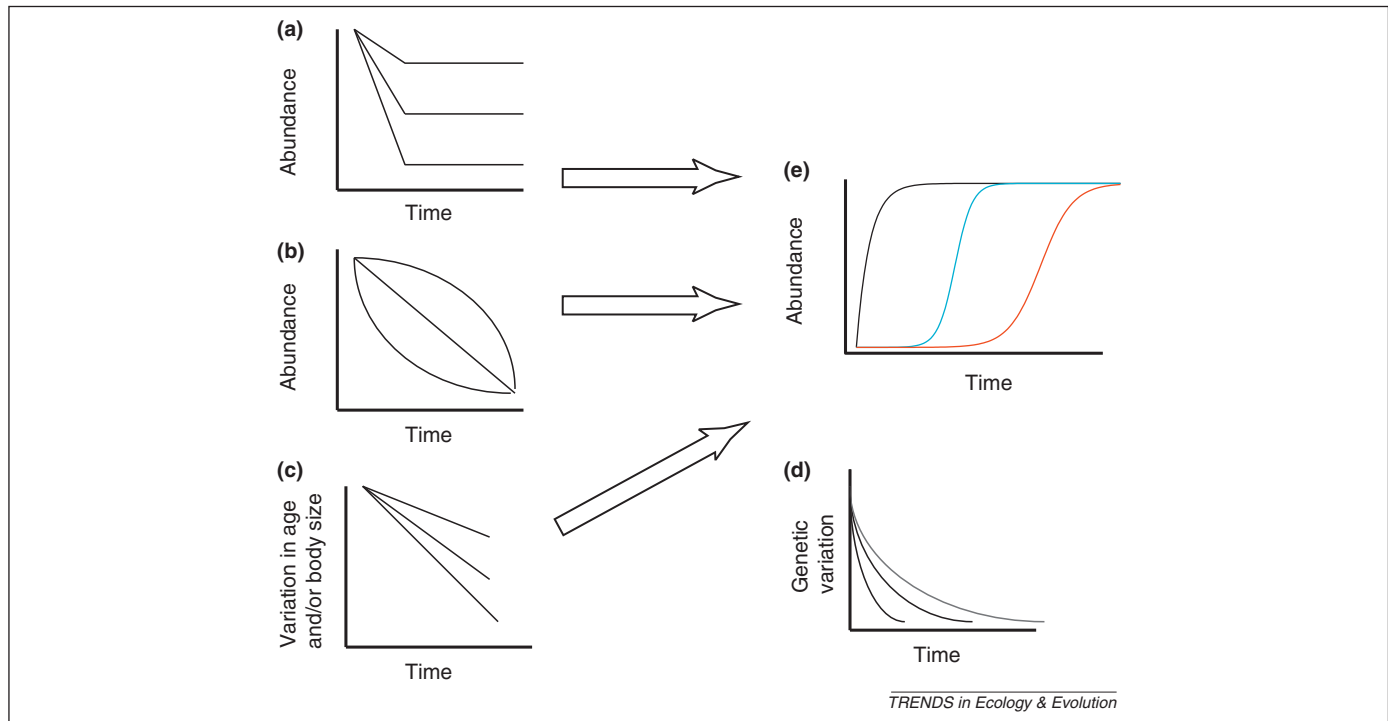


Figure 1. Schematic diagram of some potential correlates (a–d) of the rate and trajectory of species recovery (e). Recovery correlates illustrated here include: (a) magnitude and rate of decline in abundance; (b) trajectory of abundance decline; (c) reductions in individual variability in age and/or body size; and (d) trajectory of losses in genetic variation. These correlates could influence (e) the trajectory of recovery, depicted here as being rapid (black line), intermediate (blue line), or slow (red line). We note that the set of recovery trajectories shown here represent one possible set of outcomes (for example, the asymptotes of the curves could vary as well); the realized trajectories will need to be determined by empirical evaluation. We also note that recovery can be quantified in terms of other variables, such as distributional area.

(*Tegeticula yuccasella*) and the soapweed plant (*Yucca glauca*) are mutualists; moth larvae feed only on soapweed seeds, and in turn the soapweed is able to produce seeds only if the plant is pollinated by yucca moths. Factors that limit access to soapweed constitute the primary threat to the Endangered yucca moth in Canada [Government of Canada Species at Risk Public Registry (http://www.sararegistry.gc.ca/species/speciesDetails_e.cfm?sid=715)]. The example of the black-footed ferret demonstrates how reductions in prey can significantly increase the extinction probability of a specialist predator.

Evolutionary correlates

Correlates of recovery can be evolutionary in nature and related in myriad ways to threat mitigation. How might the trajectory of loss of genetic variation influence the recovery trajectory (Figure 1d)? An evolved specificity in prey selection, and a concomitant inability to shift to alternative prey, has been hypothesized to negatively affect the recovery of Spanish imperial eagles (*Aquila adalberti*) and Iberian lynx (*Lynx pardinus*) [33]. How is the trajectory of recovery affected by human-induced genetic change (e.g., evolutionary responses to exploitation and artificial propagation, inbreeding depression, habitat alteration)? Evolutionary correlates of recovery could be particularly important to elucidate, because a species that has experienced human-mediated evolutionary change (through alteration of selective regimes experienced by the species) might have a different response to threat amelioration than one that has declined solely because of, say, habitat loss.

Relevance for recovery efforts and conservation planning

Ideally, by articulating a range of probable recovery trajectories, the recovery correlate, red flag approach advocated here would be relevant from a policy and statute implementation perspective. The red flags that emerge from the envisaged multi-species meta-analyses could be used to inform recovery planning processes and to increase the transparency and accountability associated with these processes. For a given set of conditions, the analyses should be able to distinguish the range of probable recovery trajectories from the range of possible trajectories for a depleted species. Of course, the ranges of possible and probable trajectories of recovery will ultimately depend on how recovery is defined, and this can vary considerably with the recovery goals and objectives articulated by conservation organizations, government policies, national statutes, and international agreements (Box 1).

We anticipate that it will be helpful for conservation planners, before recovery efforts have begun, to avail themselves of scientific advice that is better able to distinguish the range of probable recovery trajectories from the range of possible trajectories for a recovering species, particularly from the perspective of setting expectations for recovery time frames. For example, it is likely that a taxonomically broad examination of recovery trajectories would have dampened the societal expectations generated by the initially forecasted 2-year recovery period for northern Atlantic cod off Newfoundland, Canada – a population that today remains at less than 10% of its abundance in the early 1960s, despite dramatically reduced fishing mortality [33].

Concluding remarks

We have argued that a dearth of multi-species studies of recovery hinders efforts to achieve a general understanding of the factors that affect population trajectories during the recovery phase. To address this deficiency, we outlined a research framework for studying patterns of recovery across species that should serve to strengthen the scientific basis of recovery priorities and strategies for species of conservation concern. The increased availability of large, multi-species databases comprising temporal data on population and species abundance will facilitate research efforts to address the research questions posed here. Some databases include information on hundreds of populations for species of marine fishes [34], European birds [European Bird Census Council (<http://www.ebcc.info/index.php?ID=476>)], and a broad taxonomic range of terrestrial and marine mammals [6].

The key element to the research framework proffered here is that the analyses be used to identify metrics that could serve as early warning signals for impaired recovery potential across a broad suite of taxa under a range of different scenarios. Such red flags could relate to demographic, ecological, evolutionary, or threat-related characteristics of population trajectories during depletion. Using them would help to set priorities for recovery efforts (both within and between species), assist in determining better-informed targets and recovery objectives, and allow more informed decision making regarding the trade-offs to species and to society associated with immediate versus delayed recovery actions. A strengthened scientific underpinning of efforts to recover species, populations, and their distributions will be increasingly important as the scale of the biodiversity crisis continues to grow.

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