

Rapid and direct recoveries of predators and prey through synchronized ecosystem management

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One of the twenty-first century's greatest environmental challenges is to recover and restore species, habitats and ecosystems. The decision about how to initiate restoration is best-informed by an understanding of the linkages between ecosystem components and, given these linkages, an appreciation of the consequences of choosing to recover one ecosystem component before another. However, it remains difficult to predict how the sequence of species' recoveries within food webs influences the speed and trajectory of restoration, and what that means for human well-being. Here, we develop theory to consider the ecological and social implications of synchronous versus sequential (species-by-species) recovery in the context of exploited food webs. A dynamical systems model demonstrates that synchronous recovery of predators and prey is almost always more efficient than sequential recovery. Compared with sequential recovery, synchronous recovery can be twice as fast and produce transient fluctuations of much lower amplitude. A predator-first strategy is particularly slow because it counterproductively suppresses prey recovery. An analysis of real-world predator-prey recoveries shows that synchronous and sequential recoveries are similarly common, suggesting that current practices are not ideal. We highlight policy tools that can facilitate swift and steady recovery of ecosystem structure, function and associated services.

The unprecedented pace of change in the Anthropocene^{1–3} has added urgency to the task of recovering degraded ecosystems, focusing attention on the time it takes to achieve conservation goals, restoration successes and social-ecological sustainability^{4,5}. Restoration is a global priority of tremendous breadth, with recent international commitments to restore more than half a billion hectares of land⁶ as well as the >3,500 marine fisheries worldwide that remain overexploited⁷. The costliness of prolonged restoration efforts and mandates for rebuilding timelines make it all-the-more pressing to develop practical means to accelerate the speed of recoveries^{7–10}. Remarkably, the pace of recovery is often overlooked in ecosystem restoration. Here, we propose that the temporal sequence in which interventions are implemented can influence the pace of recovery, that this influence is often overlooked in ecosystem restoration, and that it is likely to play a critical role in shaping twenty-first century solutions to environmental issues.

Conventionally, ecosystem restoration was underpinned by the idea that reinstating a plant community would provide habitat for associated animals. There is now increasing appreciation for the roles animals can play in facilitating restoration (for example, nutrient cycling) and the value of considering their dynamics from the outset to achieve desired ecosystem composition¹⁰. Amplified attention to the significance of faunal dynamics in restoration is especially significant, because faunal dynamics have proven key to understanding patterns of ecosystem degradation. People have altered animal communities in a predictable sequence, with species higher on the food chain tending to be depleted before species lower on the food chain, a phenomenon referred to as 'trophic downgrading'¹¹. This predator-first sequence of species loss can

have disproportionate influences on the structure and function of ecosystems, altering food security, economic yields, species invasions, disease prevalence and carbon sequestration^{11–14}. Given the clear ecological and socioeconomic effects of trophic downgrading, a key unanswered question is: does sequence matter when it comes to the recovery of exploited food webs?

Many ecosystems are characterized by declines of one or more predator population and one or more prey population, with restoration actions implemented to counteract these effects. For instance, trophy hunting, the fur trade and industrial fisheries are wholly or partially responsible for population collapses of lions and wildebeest in Africa, Steller sea lions and Pacific herring in the temperate Pacific, and mink and muskrat in North America (Fig. 1). Harvest restrictions and protected-area management are two common strategies used to reverse these effects, resulting in recoveries that follow one of three pathways (Fig. 1): (1) predator-first recovery, (2) prey-first recovery or (3) roughly synchronous predator and prey recovery. Despite the qualitatively distinct characteristics of these recovery pathways, there is little theory or empirical analysis related to restoration sequence (though there are exceptions^{15–19}).

A focus on sequence provides key insights into across-ecosystem variation in the extent and frequency of documented recoveries^{8,18}. For example, prey may recover more slowly or not at all if abundant predators have strong effects at low prey abundance²⁰. Likewise, slow or failed recoveries may be the result of predator-first approaches in which specialist predators do not have access to a readily available and abundant prey base²¹. Therefore, intuition suggests that prey-first recovery should enhance predator recovery, and thereby

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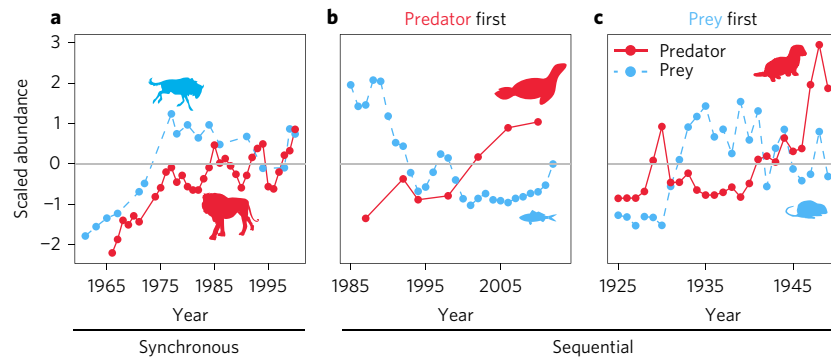


Figure 1 | Example time series illustrating that ecological communities can follow a predictable sequence of recovery to achieve trophic upgrades, following declines in predator and prey populations (trophic downgrades). **a**, Synchronous recovery in Serengeti National Park, Tanzania, where woodlands lions (*Panthera leo*; $n = 12$ counts yr^{-1}) and one of their favoured prey, blue wildebeest (*Connochaetes taurinus*; $n = 1$ count yr^{-1}) recovered at approximately the same time (mid-1970s; ref. 48). **b**, Predator-first recovery in the Northeast Pacific near Haida Gwaii, British Columbia, Canada, where Steller sea lions (*Eumetopias jubatus*; data from $n = 15$ haul-out sites⁴⁹) recovered a decade before their Pacific herring prey (*Clupea pallasii*; based on data from two management regions representing $n = 11$ spawning locations⁵⁰). **c**, Prey-first recovery in Newfoundland, Canada, where muskrat (*Ondatra zibethicus*) recovered about 20 years before predatory mink (*Mustela vison*; reports from $n = 1$ fur trade post⁵¹). Note that all time series were standardized to zero mean and unit variance for the length of the time series presented, and we define recovery as a sustained return to a population size equal to or greater than the long-term mean.

recovery of the full community. However, we are not aware of a theory that has examined these possibilities formally.

Results

We analysed an apex predator–multiple prey model to evaluate the effectiveness and relative cost of synchronous versus sequential reductions in exploitation rates of predators and their prey (Box 1). Surprisingly, we find that synchronous recovery from sustainable exploitation levels produces recoveries of predator and prey populations that are faster than prey-first and predator-first strategies (Figs 2 and 3).

Analytical approximations and numerical sensitivity analysis demonstrate that synchronous recovery is universally the fastest strategy for a wide range of exploitation rates and species' productivity rates (Supplementary Figs 1–4). There is, however, one exception to this conclusion. In the case where the productivity of the focal prey is relatively low and the availability of alternative prey to the predator is relatively high, prey-first recovery is the fastest strategy (Supplementary Fig. 4). While there are certainly examples of this situation in nature²², it is unlikely to be common for the many communities in which prey productivity tends to exceed predator productivity²³.

For most stable and feasible parameter combinations, however, prey-first recovery is not fastest, and because it leads to transient prey release from predation and exploitation, this strategy causes summed predator and prey densities to peak at levels much higher than their eventual equilibria (Figs 2 and 3). In the real world, transient dynamics like these that result from eruptions of prey populations can lead to surprising cascades of ecological interactions and complex but often mismatched management responses¹⁸.

Unlike prey-first recovery, our model suggests that both predator and prey recover directly to their unexploited equilibria in the case of predator-first recovery (that is, transient volatility is zero; Fig. 3), just over a longer time period. The increase in community return time occurs because the recovery of the predators increases prey mortality while they continue to be exploited.

The synchronous recovery strategy achieves a compromise between these two extremes, leading to considerably lower volatility than prey-first recovery (Fig. 3). Analytical approximations and numerical sensitivity analysis show that, irrespective of exploitation rates and species' productivity rates, predator-first recovery is always best at damping out transient dynamics, while

prey-first recovery always leads to the greatest community volatility (Supplementary Figs 1–4).

Thus, in ecological terms, restoration of exploited communities is generally predicted to be faster and more direct under synchronous recovery. On the social side, an analysis of foregone harvest yields suggests that synchronous recovery is no worse—and in several cases better—than the sequential recovery strategies (see Supplementary Fig. 5).

Our model therefore implies that both ecological and social goals tend to be best served via synchronous recovery efforts, yet empirical evidence from a comprehensive database of marine fisheries²⁴ shows that synchronous recoveries are not the rule. Rather, there are approximately equal numbers of synchronous and sequential recoveries in exploited marine ecosystems, with predator-first recoveries being less common than prey-first recoveries (Supplementary Tables 2 and 3 and Supplementary Figs 6–8). This analysis includes iconic examples, such as the Baltic, where predatory Baltic cod recovered (2011) only following their herring prey (2007); along the west coast of Vancouver Island, Canada, where Pacific cod recovered (2002) before their preferred Pacific herring prey (2008); and the Gulf of Maine, where predatory Atlantic cod and Acadian redfish, which are regular prey for Atlantic cod, both recovered in 2008 following decades of overdepletion (Supplementary Tables 2 and 3).

Discussion

Comparing theory to data. On the one hand, the disconnect between our theory and observed restoration patterns implies an opportunity for improvement in the more than half of empirical cases of sequential recovery, even in the context of multiple restoration goals such as long-term economic value, biological sustainability of multiple species, and short- and long-term harvest opportunities^{7,10,16,25,26}. On the other hand, these results are encouraging, because predator-first recovery—the slowest strategy according to our theory—is less common than prey-first recovery.

It is worth noting that the database we analysed did not include case studies with an explicit focus on spatial management measures such as protected areas, which might alter the frequency of synchronous and sequential recoveries compared with what we assessed. For example, marine protected areas may relax harvest pressure on all species in a community, or preferentially on a relatively sedentary predator while more mobile prey remain partially exposed to harvest outside the protected area²⁷. Furthermore, our empirical

Box 1 | Apex predator–multiple prey model with harvest.

We analyse a model of a generalist predator and its prey to evaluate the effectiveness of synchronous versus sequential community recovery in terms of rates and volatility of recovery to an unexploited community state. We extend a model^{25,45} that consists of a generalist predator (*P*, in number of individuals) consuming one explicitly modelled prey (*X*, the focal prey, in number of individuals) as well as a non-dynamical other-prey group (*Y*, in number of individuals). This focus on a three-node community module allows for tractability and is appropriate, as many food webs are characterized by few strong and many weak interactions³². As in Gordon–Schaefer fishery models, we assume that both the predator and focal prey experience logistic population growth such that:

$$\frac{dX}{dt} = r_X X \left(1 - \frac{X}{K_X} \right) - a_X P X - h_X X \quad (1)$$

$$\frac{dP}{dt} = P [c(a_X X + a_Y Y) - d_p] \left(1 - \frac{P}{K_p} \right) - h_p P \quad (2)$$

Here, r_x is the prey’s intrinsic per-capita growth rate (units: yr⁻¹), K_x is the prey’s logistic growth carrying capacity (units: number of individuals), d_p is the predator’s per capita mortality rate (units: yr⁻¹) and K_p is the predator’s carrying capacity (units: number of individuals) reflecting limiting factors other than prey availability, such as habitat¹⁴. The predator feeds on prey *X* and *Y* with linear type I functional responses at per-capita rates a_x and a_y , respectively (units: number of individuals⁻¹ × yr⁻¹), the relative magnitude of which reflects its preference for the two prey, and converts these to predator biomass at rate *c* (units: prey per predator). The predator and focal prey are harvested at constant per-capita rates, h_p and h_x (units: yr⁻¹). Additional details on simulating recovery strategies are in the Methods, and analytical solutions appear in the Supplementary Information.

analysis focused exclusively on fish stocks without attention to the likely common situations where threatened/endangered species and carnivore protection have facilitated recoveries of predatory mammals and birds before their less charismatic prey (Table 1, and references therein, and Fig. 1).

The contrast between our theory and observed restoration patterns may also suggest a need to incorporate further complexities into the theory—such as stage structure or additional interactions between a greater number of species—to explain why synchronous and sequential recoveries are equally common in fisheries (see Supplementary Discussion for potential extensions). Perhaps the most important social consideration will be the relative economic value of predator versus prey species and the losses incurred by ceasing harvest on one or both¹⁹.

Implications for synchronous and sequential policy actions.

Several policy mechanisms exist for shifting to synchronous recovery strategies (Table 1). One that has not been implemented often involves temporary and purposeful increases in exploitation of one species (that is, culling) to promote the recovery of another. In the context of fisheries, this approach could even involve purposefully overfishing abundant predators to transition sequential rebuilding of stocks to synchronous rebuilding (for example, via catch-quota balancing²⁸, under the rubric of a mixed-stock exception^{29,30}). This possibility has been raised recently in the California Current ecosystem, where lingcod and rockfishes benefited from US legislation provoking synchronous rebuilding. However, less desirable lingcod recovered faster than their rockfish prey because

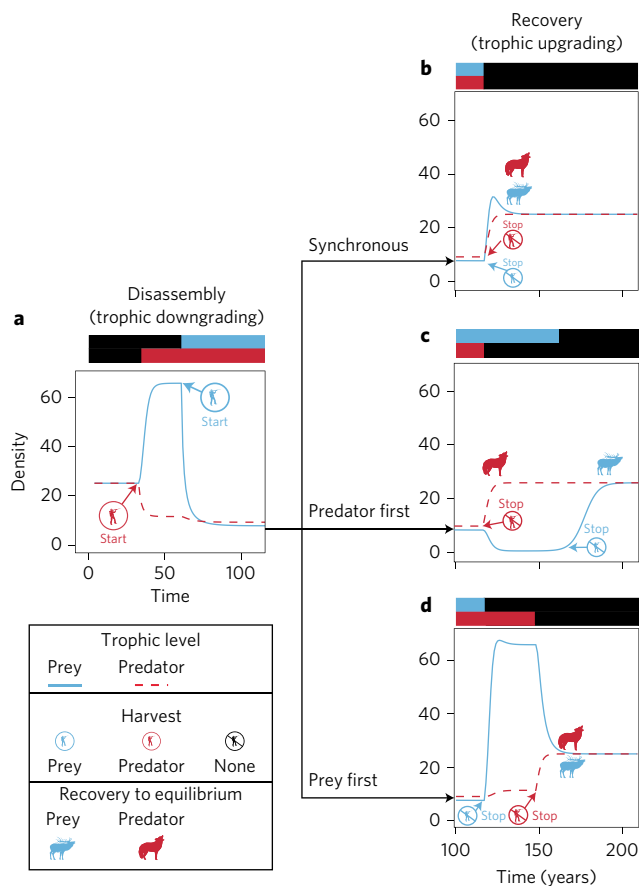


Figure 2 | Time series panels showing predator and prey densities during community disassembly and recovery. **a**, Community disassembly. **b–d**, Three community recovery scenarios: synchronous (**b**), predator first (**c**) and prey first (**d**). In the bars above each panel, black indicates no harvest over the corresponding time period (years), blue indicates prey harvest and red indicates predator harvest. Note that recovery time is defined as the time from when recovery begins—when exploitation is reduced to zero for at least one species—until it is completed, when harvest pressure is zero for both predator and prey and their densities (number of individuals per unit area) remain within 10% of their long-term equilibria. However, the analytical results show that relaxing this assumption to eliminate the time between cessation of predator harvest and cessation of prey harvest does not change the qualitative conclusions (see Supplementary Information for details). See Methods for parameter values.

of high natural productivity. Along with partners, The Nature Conservancy (www.pcouncil.org/wp-content/uploads/2015/11/12_Sup_Att6_EFP_TNC_GearInnovations_Nov2015BB.pdf) is now exploring the possibility that a selective lingcod fishery may enhance rebuilding of rockfishes²⁷. Similar approaches have been proposed in terrestrial systems to limit predation on threatened prey while they are recovering³¹.

The exact tactics used to shift to synchronous recovery strategies would require careful study, as culling of predators can have unexpected consequences³². Other more passive restoration approaches with longer histories focus on umbrella species³³ or protected-area management. However, these tools may be inefficient if restoration objectives have a sharp focus on short-term gains of a particular subset of species (for example, ref. ³⁴) or if strategic interventions are necessary to accommodate differences in life histories within an ecosystem, even though they have the benefit of being able to affect recoveries at small spatial scales where necessary^{10,35}.

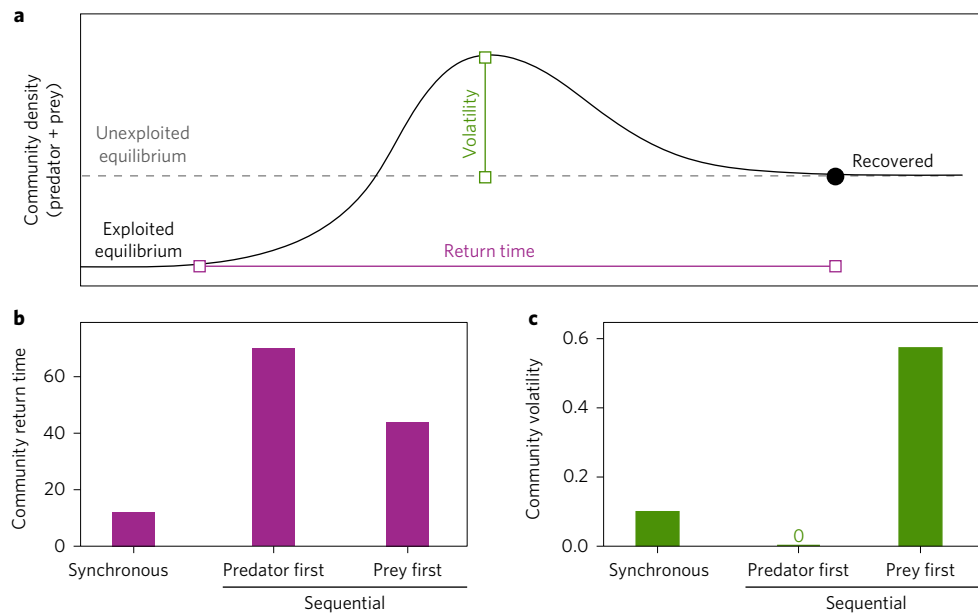


Figure 3 | Community return time and volatility for three recovery scenarios. **a**, Schematic illustrating the two recovery metrics, community return time and community volatility, used to analyse the effectiveness of alternative recovery strategies. **b, c**, Community return times (years) (**b**) and community volatilities (dimensionless) (**c**) for the baseline case under three recovery scenarios. See Methods for parameter values and definitions of recovery metrics. Note that these patterns are generally robust even if the lag time between recovery of the predator (prey) and cessation of exploitation of the other species is eliminated (see Supplementary Information).

Despite the availability of synchronous restoration approaches, it seems likely that many of the tools with the strongest legal underpinnings and in most widespread use result in sequential management actions that produce sequential recoveries (Table 1). Sequential recovery allows for continued exploitation of some species while harvest is discontinued for another. In addition, it is not necessarily concerned with coordinated management actions aimed at different species and potentially different sectors^{4,36}. While these social benefits are appealing in the near term, in the long term our findings indicate greater social and ecological benefits of synchronous recovery. Regardless of the exact intervention employed to achieve it, the critical component is to embrace systems-level thinking for restoration policy and practice.

Conclusions. Our study highlights how and why the sequence of restoration operations matters when one target of restoration

is eaten by another. We bridge community assembly and food web theories^{37–39} to improve restoration practice by demonstrating that synchronous recoveries of predators and prey are generally rapid and direct. In contrast, predator-first recoveries are slow and potentially risky because they can introduce a double jeopardy situation for prey, due to the combination of continued exploitation of prey populations and increased mortality from the recovering predator population.

These findings add emphasis to recent calls for coordinating management and restoration actions at the ecosystem level^{4,19,36}, while underscoring the central role of transient dynamics in making inferences about social-ecological systems^{18,40}. Moreover, we highlight the ready availability of key policies as opportunities to achieve restoration goals in ecosystems experiencing increasing exploitation demands as human populations continue to grow. In 1992, E.O. Wilson wrote, “The next century will, I believe, be

Table 1 | Relationship between policy or management actions and community recovery strategies.

Management approach	Terrestrial or aquatic system	Recovery strategy	Description	References
Protected area	Terrestrial, aquatic	Synchronous	Complete or partial protection of all species within a fixed area.	52–54
Mixed stock management	Aquatic	Synchronous	Single species management that regulates fisheries to account for and prevent low productivity or overexploited stocks from being overexploited.	22,55,56
Umbrella species management	Terrestrial	Synchronous	Single species management that focuses on a single species with a large home range to protect a broader community or ecosystem.	57,58
Threatened/endangered species actions	Terrestrial, aquatic	Sequential	Predator- or prey-first: single species focus reducing or eliminating exploitation of species that are at risk of extinction.	59–61
Carnivore protection	Terrestrial	Sequential	Predator-first: focus on the preservation of charismatic, higher-trophic-level species.	62,63
Pre-emptive single fishery closure	Aquatic	Sequential	Prey-first: allocation of lower-trophic-level species for dependent predators.	64,65

the era of restoration in ecology.” We are well into this era of restoration, but there remains an unambiguous need to advance theory and practice to meet its demands. Our work clearly shows how careful consideration of trophic-upgrade strategies provides a useful step towards the goal of reversing overexploitation at the top of the food chain.

Methods

The theory developed here is grounded in the notion that restoration relies on any actions that will re-establish a self-sustaining system, including all aspects of the environment required for constituent organisms^{6,9}. We define synchronous recovery of an exploited community as the simultaneous release of all trophic levels from harvest pressure, and sequential recovery as the release of predators from harvest before prey (predator-first recovery) or the release of prey from harvest before predators (prey-first recovery). Our primary interest is in the transient dynamics⁴⁰ expected following the implementation of a community recovery strategy. We develop this theory via both numerical simulation and analytical approximations (see Supplementary Information for details).

Using the model described in Box 1, we focus on how each of the recovery strategies affects the rates and volatility of recovery to an unexploited community state, as well as cumulative yields. For our simulations, community return time is the time from when recovery begins—when exploitation is reduced to zero for at least one species—until it is completed, when harvest pressure is zero for both predator and prey, and their densities remain within 10% of their long-term equilibria^{41,42}. Community volatility captures the magnitude by which the recovery strategies cause the summed predator and prey densities to exceed the unexploited community equilibrium. Specifically, we define it as the proportional difference between the maximum community density achieved during the transient period of recovery and the unexploited equilibrium⁴³. We define a recovery with lower community volatility as more direct because, in the limit, zero volatility indicates a monotonic return to equilibrium. As reductions in exploitation rates come at a cost of lost yields, we track the cumulative yields across all T years of the simulations ($\sum_{t=1}^T h_X X_t$, $\sum_{t=1}^T h_P P_t$ and $\sum_{t=1}^T h_X X_t + h_P P_t$) as well as yields per unit time t when exploitation is non-zero.

We first analyse a single baseline case that depresses the predator and prey population densities to levels resembling common sustainable exploitation goals (for example, target densities that are 30–40% of unexploited levels⁴⁴). In this baseline case, focal prey (X) productivity is higher than that of the predator (P), the exploitation rate of the focal prey ($h_X = 0.65$) exceeds that of the predator ($h_P = 0.325$), and the predator is a generalist such that the other-prey group (Y) constitutes the majority of the predator diet ($Y = 500$). This baseline other-prey density and the predator attack rates (identical for focal and alternative prey, $a_X = a_Y = 0.03$), predator conversion rate ($c = 0.05$), carrying capacities of the predator ($K_P = 25$) and focal prey ($K_X = 100$), intrinsic per-capita growth rate of the focal prey ($r_X = 1$) and death rate of the predator ($d_P = 0.25$) represent reasonable intermediate values that allow for coexistence of the predator and focal prey under a range of predator and prey productivity rates and harvest rates⁴⁵.

We also evaluate how variation in two major characteristics of the exploited predator–prey system influences inferences: (1) the intrinsic productivity rates of the predator and the prey, and (2) the legacy of exploitation in the community. We explore all combinations of prey intrinsic productivity rates ($r_X = [0.5, 1.5]$) and predator attack rates ($a_X = a_Y = [0.02, 0.05]$), reflecting the predator intrinsic productivity that allow both predator and prey to coexist under a range of predator and prey harvest rates (see Supplementary Discussion and Supplementary Fig. 2 for parameter combinations that allow coexistence). Harvest rates span a range of values corresponding to three exploitation levels: underexploited, sustainably exploited and overexploited ($h_X = [0, 0.8]$ and $h_P = [0, 0.6]$). All other parameter values are identical to the baseline case.

In addition to conducting numerical simulations of synchronous and sequential community recovery, we determine the equilibrium solutions to the model (Box 1) analytically and assess community responses under the three recovery strategies based on those analytical solutions. We also examine the sensitivity of responses to changes in the per-capita rates with which predator and prey are harvested, increased intrinsic growth rate of the focal prey population (from $r_X = 1$ to $r_X = 5$) and increased availability of other prey (from $Y = 500$ to $Y = 1,000$), which effectively increases the intrinsic growth rate of the predator population. See the Supplementary Information for details.

To determine whether real-world community recoveries tend to be synchronous or sequential (predator first or prey first), we rely on a meta-analysis²⁴ of a global database of marine fisheries (RAM legacy stock assessment database⁴⁶). This meta-analysis provides a comprehensive source of recoveries of exploited species analysed and reported in a standardized format. We are unaware of a similarly comprehensive database of recoveries in exploited terrestrial communities.

To analyse the database, we use chi-squared tests to determine whether (1) synchronous community recovery case studies occur with equal frequency

to sequential community recovery case studies, and (2) synchronous, predator-first, and prey-first community recovery case studies occur with equal frequency (see Supplementary Information for details). We determine statistical significance via Monte Carlo simulation using `chisq.test` in R v3.0.3⁴⁷.

Data availability. The data from this study supporting our findings are available from the corresponding author on reasonable request.

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Author contributions

J.F.S., A.C.S., P.S.L. and M.N. designed the study. J.F.S., A.C.S., M.N. and S.M.H. collected and analysed all data. J.F.S., A.C.S., P.S.L., B.S.H. and M.N. jointly wrote the manuscript.

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Competing interests

The authors declare no competing financial interests.

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