

Review

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon



Reciprocity in restoration ecology: When might large carnivore reintroduction restore ecosystems?



J.M. Alston^{a,b,c,*}, B.M. Maitland^{a,c}, B.T. Brito^a, S. Esmaeili^a, A.T. Ford^d, B. Hays^a, B.R. Jesmer^e, F.J. Molina^{a,c}, J.R. Goheen^a

^a Department of Zoology & Physiology, 1000 E. University Avenue, University of Wyoming, Laramie, WY 82071, USA

^b Wyoming Natural Diversity Database, 1000 E. University Avenue, Laramie, WY 82071, USA

^c Program in Ecology, University of Wyoming, 1000 E. University Avenue, Laramie, WY 82071, USA

^d Department of Biology, University of British Columbia Okanagan, 1177 Research Road, Kelowna, BC V1V 1V7, Canada

e Max Planck-Yale Center for Biodiversity Movement and Global Change, Yale University, 165 Prospect St., New Haven, CT 06520, USA

A B T I C L E I N F O

Keywords: Apex predator Large carnivore Prediction Reciprocity Restoration Trophic cascade

ABSTRACT

Carnivore reintroduction is often expected to revert community and ecosystem properties to their natural states via risk effects and the direct killing of prey. Because large carnivore extirpation and reintroduction are usually believed to have symmetric and offsetting effects, fulfilling this "assumption of reciprocity" is crucial to realizing the potential of large carnivores to passively restore community structure and ecosystem function. We were unable to find any study in which the assumption of reciprocity was rigorously tested in predator-prey systems featuring large carnivores, their ungulate prey, and primary producers through a comprehensive literature search. We therefore used studies involving (1) the reintroduction of any native apex predator (including but not limited to large mammalian carnivores); and (2) the removal of any introduced apex predator (also including but not limited to large mammalian carnivores) to examine the assumption of reciprocity. Reintroduction of native apex predators did not consistently affect any of four trophic groups (mesopredator, omnivore, herbivore, primary producer) in a positive or negative way, but removal of introduced apex predators consistently increased the abundance and biomass of mesopredators. Further, outcomes of apex predator reintroduction and removal were variable across systems, regardless of system complexity (ranging from single predator-single prey to multiple predator-multiple prey systems). We suggest that the assumption of reciprocity—in which predator extirpation and reintroduction are believed to have consistent, counterbalancing effects-is unsupported by current evidence, and perhaps unrealistic. We discuss potential directions for research that might illuminate when and why the assumption of reciprocity would be valid.

1. Introduction

Predation is one of nature's most important processes, shaping population abundance, community structure, and ecosystem dynamics. Regional distributions of large carnivores have changed in the past century, owing to both the widespread extirpation of some species and subsequent recovery of others (Chapron et al., 2014; Estes et al., 2011; Gompper et al., 2015; Ripple et al., 2014). The reintroduction of large carnivores may trigger trophic cascades by reducing prey densities or altering prey behavior (Bakker and Svenning, 2018; Ripple et al., 2014; Svenning et al., 2016). Attempts to reintroduce large carnivores to ecosystems therefore are heralded not only as an end in themselves, but also for their potential to restore community structure and ecosystem

function via trophic cascades (Andriuzzi and Wall, 2018; Beschta and Ripple, 2009; Newsome and Ripple, 2015; Ordiz et al., 2013).

The assumption that large carnivore reintroductions will result in consistent, cascading effects is critical for realizing any higher-level restorative effects, albeit rarely tested (Allen et al., 2017; Ford and Goheen, 2015). We refer to the notion that large carnivore extirpation and reintroduction have symmetric, counterbalancing effects as the "assumption of reciprocity" (Fig. 1), a special case of resilience (sensu Holling, 1973) in which altered communities, ecosystems, or both return to historical states following reintroduction of large carnivores. Extirpation and reintroduction of large carnivores are often envisioned as natural experiments that mimic removal and addition experiments, thereby providing insight into whether, how, and why large carnivores

* Corresponding author at: Department of Zoology & Physiology, 1000 E. University Avenue, University of Wyoming, Laramie, WY 82071, USA. E-mail address: jalston@uwyo.edu (J.M. Alston).

https://doi.org/10.1016/j.biocon.2019.03.021

Received 1 November 2018; Received in revised form 14 March 2019; Accepted 15 March 2019 0006-3207/ © 2019 Elsevier Ltd. All rights reserved.

J.M. Alston, et al.



Fig. 1. A schematic illustrating the assumption of reciprocity, and alternative scenarios under which the assumption is not met. (A) The assumption of reciprocity. in which lion recovery has an equivalent and counterbalancing effect to lion extirpation. In this example, the ca. 30-year extirpation of lions triggered an increase in their preferred prey (hartebeest); recovery of lions returned hartebeest populations to levels comparable with the historical state. (B) A violation of the assumption of reciprocity (hysteresis), in which lion recovery does not affect hartebeest abundance. In this example, lion extirpation allowed hartebeest populations to increase in size past a threshold below which they were limited top-down. (C) A violation of the assumption of reciprocity (an alternative stable state), in which lion recovery has an anisotropic effect to extirpation. In this example, fire suppression during the

ca. 30-year period of lion extirpation resulted in an increase in tree density, rendering lions more effective at killing hartebeest, and resulting in fewer hartebeest relative to the historical state. Examples based on Ng'weno et al., 2017, Ng'weno et al., in press, and Ng'weno et al., in revision.

impact higher-level ecological patterns and processes (Allen et al., 2017; Ford and Goheen, 2015).

Despite the frequent assumption of reciprocity, however, a number of contextual factors may reorganize communities and ecosystems in ways that prevent reversion to a historical state (discussed below; see Ford et al., 2015; Marshall et al., 2013). These factors include shifts in environmental conditions, shifts in land-use patterns, or conservation interventions during the period of carnivore reintroduction. For example, although most agree that the reintroduction of wolves into the Greater Yellowstone Ecosystem begat a series of trophic cascades that altered Yellowstone's biotic communities (Beschta and Ripple, 2016; Ripple and Beschta, 2012), wolf reintroduction coincided with increased drought (Middleton et al., 2013), regeneration after an expansive series of wildfires (Romme et al., 2011), and recolonization by beavers (Smith and Tyers, 2012), rendering it difficult to determine precisely the extent to which subsequent changes to Yellowstone's biotic communities can be attributed to wolves. As a result, a nuanced view of the restorative potential for large carnivores via cascading trophic effects is required: predators can have different effects at different times and in different places (Haswell et al., 2017; Paine, 1966; Vaughn and Young, 2010). Our ability to predict the impacts of large carnivore reintroduction should thus depend on a host of contextual details (Agrawal et al., 2007; Ford and Goheen, 2015; Heithaus et al., 2009; Ritchie et al., 2012).

One such source of contingency is the degree of reticulation in food webs. Reticulate food webs involve at least some functional overlap, wherein reduced consumption of prey (i.e., animals for predators, plants for herbivores) stemming from predator extirpation is compensated for by other, functionally redundant, predators in the community (Polis and Strong, 1996; Strong, 1992). In predator-prey systems defined by multiple species of large carnivores, multiple species of prey, or both, any cascading effects of large carnivore extirpation or reintroduction are likely dampened relative to simpler systems lacking reticulation (i.e., food chains with a single large carnivore and a single species of prey; Borer et al., 2005; Shurin et al., 2002; Trussell et al., 2017). Reintroduction of large carnivores should therefore have the most pronounced impacts in relatively simple predator-prey systems, or in predator-prey systems where extirpated large carnivores or the herbivorous prey on which they depend exhibit minimal functional overlap with those large carnivores or herbivorous prey that persist (Otieno et al., 2019; Pringle et al., 2016).

Assuming that large carnivore extirpation alleviates top-down

control on at least some species of prey, three conditions must be true for the assumption of reciprocity to be upheld:

Condition 1: prey populations (typically ungulate populations, with respect to large carnivores) decrease or redistribute themselves on the landscape when large carnivores are reintroduced (Creel et al., 2005; Elmhagen and Rushton, 2007; Fortin et al., 2005).

Condition 2: biomass, growth, survival, or composition of primary producers shifts when prey become rare or redistribute themselves on the landscape in response to large carnivore reintroduction (Ford et al., 2014; Hebblewhite et al., 2005; Morris and Letnic, 2017). In other words, a trophic cascade is triggered by the reintroduction of large carnivores.

Condition 3: the trophic cascade arising from Conditions 1 and 2 yields a return to one or more historical states (or "reference points"; Sinclair et al., 2018) that existed before large carnivores were extirpated.

In the simplest cases (one species of large carnivore, one species of ungulate prey, primary producers), reciprocity occurs when Condition 1, 2, and 3 are true (i.e., a trophic cascade occurs, and the magnitude of its effects are sufficient to return the community or ecosystem to its historical state; Fig. 1A). Alternatively, the reintroduction of a large carnivore may not result in reciprocity because of hysteresis. Hysteresis—in this context, the existence of variable abundances or compositions of prey and primary producers given the presence of the same species of large carnivore—occurs when neither Condition 1 nor Condition 2 are true (Stier et al., 2016; Young et al., 2005; Fig. 1B). An alternative state may occur when either Condition 1 or Condition 2 is true, or when both Condition 1 and Condition 2 are true, but the effect of one or both differs from their historical effects (Ford et al., 2015; Marshall et al., 2013; Ng'weno et al., 2017; Fig. 1C).

To understand whether the assumption of reciprocity is upheld following large carnivore reintroductions, we conducted a meta-analysis on data derived from keyword searches on the published literature to identify studies involving the removal or addition of large carnivores. Specifically, we sought studies on reintroductions of extirpated species of large carnivores to parts of their historical ranges. Such studies were rare, however (n = 6 from our literature search; see below), so we extended our search to include other apex predators, which we defined operationally as any predator not consumed by other predators in the focal study. Because reciprocity assumes symmetric and opposing effects of carnivore addition and removal, we also included studies involving the removal of exotic apex predators from their introduced ranges. We expected to find support for the aforementioned three conditions (i.e., that effects induced by the reintroduction of native predators or the removal of invasive predators were reciprocal to extirpation and introduction, respectively). Specifically, (1) reintroduction of native apex predators reduces the abundance of their prey (distinguishing between herbivores, omnivores, and mesopredators), in turn leading to increased primary producer abundance; and (2) removal of introduced apex predators results in increased prey abundance and decreased abundance of primary producers. We expected the strongest support for the assumption of reciprocity to exist in cases involving a single species of predator consuming a single species of prey, with multiple species of predators, prey, or both dampening any indirect effects of carnivores (Otieno et al., 2019; Polis and Strong, 1996).

2. Methods

2.1. Literature search

We searched peer-reviewed publications for manipulative or natural experiments that quantified responses of both prey and primary producers to native predator reintroduction or to the removal of invasive predators. We used the Web of Science Core Collection and the search terms: ((((carnivor* OR predator*) AND (communit* OR ecosystem) AND (*coloniz* OR reintroduc* OR removal* OR eradicat* OR restor* OR introduc* OR invas* OR exotic*) AND (multiple state* OR multiple stable state* OR ecosystem function* OR alternate state* OR alternative stable state* OR recover* OR resilience* OR stable state* OR regime shift* OR hysteresis OR trophic cascade*)))). The initial search resulted in 1816 articles published up to May 2018. We refined this list of papers to a final dataset comprising responses to reintroduction and removal events (Tables A.1, A.2) based on the following criteria: (1) reintroduction of an extirpated native apex predator or removal of an introduced apex predator; and (2) abundance or biomass data of both prey and primary producers for at least two of the following three consecutive time steps: before extirpation or introduction of an apex predator, during extirpation or invasion of apex predator, and after reintroduction or removal of apex predator. Data were extracted from tables, text, and figures. All resulting data consisted of the latter two time steps (i.e., during and after extirpation or invasion). Following Shurin et al. (2002), we used the final sampling date as a proxy for the cumulative effects of predators. For studies that reported the effects on multiple species of prey and primary producers in the same article, we extracted data for each taxon at the finest possible resolution. Most data are therefore for species, but some are for higher taxonomic levels. We then categorized studies as either apex predator reintroduction or apex predator removal and classified taxa into trophic groups (primary producers [terrestrial plants and algae], herbivores, omnivores, or mesopredators). We defined apex predators as any predator in a food web that is not consumed by any other species in that food web. Therefore, our operational definition of "apex predator" encompassed species that otherwise could qualify as mesopredators in the presence of other species that consume them.

2.2. Meta-analysis

Because the historical states from the study systems in our dataset were not quantified, we assumed that trophic responses by prey and primary producers would follow the patterns laid out in the final paragraph of our Introduction: that (1) reintroduction of native apex predators reduces the abundance of their prey (distinguishing between herbivores, omnivores, and mesopredators), in turn leading to increased primary producer abundance; and (2) removal of introduced apex predators results in increased prey abundance and decreased abundance of primary producers. Predictions that follow these patterns are pervasive in the literature on large carnivore reintroduction (e.g., Beschta and Ripple, 2009; Callan et al., 2013; Licht et al., 2010; Malhi et al., 2016; Soule et al., 2003). To quantify our predicted trophic responses, we calculated the effects of apex predator reintroduction or apex predator removal as the log response ratio (LRR) of primary producer and prey densities (Hedges et al., 1999). The LRR is calculated as $[\ln(Y_{treatment}) / (Y_{control})]$, where $Y_{control}$ is the density or abundance of a species of primary producer or prey prior to apex predator reintroduction or removal, and $Y_{treatment}$ is the density or abundance of primary producer or prey following the reintroduction or removal of apex predators. The log ratio represents the proportional change in a response variable, where a positive LRR indicates that the reintroduction or removal of an apex predator increases the abundance or biomass of prey or plants. We regressed LRRs against study duration to ensure the final (cumulative) effects reported in studies did not represent transient dynamics (Hastings, 2004).

Although the precision of LRR estimates varied between studies in our data set, we did not weight values by their precision, nor did we scale LRRs to the duration of experiments for the reasons articulated by Shurin et al. (2002). Namely, 9 of 20 studies in our data set were unreplicated, and 7 others did not report variance or other metrics of variability. Eliminating studies without variance estimates would have reduced our sample size and possibly biased our data set (Englund et al., 1999). Using unweighted LRR estimates would weaken our power to detect differences among systems (i.e., inflating Type II error), but does not bias our estimates of effect sizes (Gurevitch and Hedges, 1999; Hedges et al., 1999).

To assess variation in responses among taxa, we first split the data into two treatments (reintroduction studies and removal studies) and visualized the LRR across trophic groups. We then tested for differences in LRRs among trophic groups within each treatment type using oneway Kruskal-Wallis rank sum tests and tested whether the median LRR for trophic groups was significantly different from zero using Wilcoxon rank sum tests and Bonferroni corrections for multiple comparisons.

Next, we examined changes in LRRs among trophic groups within four types of predator-prey systems (single predator/single prey, single predator/multi-prey, multi-predator/single prey, and multi-predator/ multi-prey systems). Differences in LRRs among trophic groups within each treatment × study system combination were evaluated with oneway Kruskal-Wallis non-parametric rank sum tests. We then tested whether the average LRR for trophic groups within each treatment × study system combination was significantly different from zero using Wilcoxon rank sum tests and Bonferroni corrections for multiple comparisons.

Finally, we related LRRs among trophic groups within each treatment to the time since apex predator reintroduction or removal using ordinary least-squares linear regression. We also related LRRs of both prey species and primary producers to the number of prey species in each system using ordinary least-squares regression.

3. Results

The final dataset included 142 observations from 20 studies (Table A.1). The 20 studies were distributed among 6 ecosystem types (islands, deserts, forests, grasslands, lentic freshwater, and marine), comprised 7 reintroduction studies and 13 removal studies, and represented 124 unique taxa ranging from primary producers to mesopredators. Log response ratios were unrelated to the time elapsed following reintroduction or removal efforts (Fig. A.1).

Both reintroduction and removal studies were characterized by a high degree of variability (Fig. 2), suggesting idiosyncratic responses of trophic groups to the reintroduction of native apex predators or to the removal of introduced apex predators. Within treatments, we found no statistically significant differences in LRR among trophic groups (Fig. 3; reintroduction studies: H = 6.48, df = 3, P = 0.09; removal studies: H = 6.42, df = 3, P = 0.09), indicating that trophic groups do not consistently differ in their response to the reintroduction or removal of apex predators. No trophic group responded directionally to the



Fig. 2. Log response ratios (LRRs) of individual species, categorized into four trophic groups (primary producer, herbivore, omnivore, mesopredator), following the (A) reintroduction of native apex predators; or (B) removal of introduced apex predators. In panel A, the LRR is calculated as [In (Y_{reintroduction}) / (Y_{extirpation})], such that positive LRRs indicate a positive response of abundance or biomass of the individual species or trophic group following the reintroduction of native apex predators. In panel B, the LRR is calculated as [ln(Y_{removal}) / (Y_{invaded})], such that positive LRRs indicate a positive response of abundance or biomass of the individual species or trophic group following the removal of introduced apex predators. The observed variability in LRR suggests idiosyncratic responses of trophic groups to the reintroduction of native apex predators and to the removal of introduced apex predators.



Fig. 3. Summary of log response ratios (LRRs) among four trophic groups (primary producer, herbivore, omnivore, mesopredator) following the (A) reintroduction of native apex predators, or (B) removal of introduced apex predators. Within treatments, we found no statistically significant differences in LRR among trophic groups using one-way Kruskal-Wallis rank-sum tests. *P*-values given in figure correspond to results from non-parametric Wilcoxon signed rank tests and indicate that mesopredators and herbivores exhibit a positive numerical response to predator removal actions.

reintroduction of native apex predators (Fig. 3A), but mesopredators responded positively to the removal of introduced apex predators (Z = 287, P = 0.01; Fig. 3B).

Of the 20 studies in our dataset, 7 were single predator, single prey systems, 13 involved a single predator and multiple prey species, and none involved multiple predators and multiple prey systems or systems with multiple predators with a single species of prey (Table A.1). The number of prey species in a system had no effect on the magnitude of either prey or primary producer LRRs (Fig. A.2). Within each treatment × study system combination, we found no significant differences in LRR among trophic groups (Fig. 4). Further, Wilcoxon signed-rank tests revealed that only mesopredators in removal studies with single predator-multiple prey systems had mean LRR values significantly different from zero (Z = 254, P = 0.003; Fig. 4). Together, these results suggest that outcomes of apex predator reintroduction and removal are highly variable across both simple and multi-species predator-prey systems.

4. Discussion

Responses of trophic groups to the reintroduction and removal of native and apex predators varied widely. We quantified responses of four trophic groups—mesopredators, omnivores, herbivores, and primary producers—to the reintroduction of native apex predators, and to the removal of introduced apex predators. Mesopredators responded most strongly to removal and reintroduction of apex predators, although assessment of responses by mesopredators to the reintroduction of apex predators was limited by sample size (Fig. 2B). Among species interactions, this "mesopredator release" is unusual in its universality: it occurs almost invariably when apex predators are removed from a system (Prugh et al., 2009). If functional overlap occurs between apex predators and mesopredators, responses of herbivores and primary producers may be dampened following removal (or introduction) of apex predators. In contrast, because only apex predators are capable of consuming mesopredators, mesopredators may be the only trophic group that responds consistently to removal (or introduction) of apex predators.

Contingent outcomes of species interactions are common, and our results demonstrate that they are pervasive following reintroduction and removal of apex predators. Though we were unable to test for the full assumption of reciprocity because of a shortage of historical reference point data, predicting the direction of trophic responses is a necessary first step toward reaching that goal. Our study demonstrates that simply predicting the direction of trophic responses is challenging—responses by lower trophic levels to apex predator removal and reintroduction are often not predictable (Figs. 1, 2). For example, Trophic Group # Producer # Herbivore # Omnivore # Mesopredator



Fig. 4. Summary of log response ratios (LRRs) for trophic groups across predator-prey system types from simple predator-prey systems (single species of predator, single species of prey), versus more complex predator-prey systems (those with multiple species of predators, multiple species of prey, or both) following (A) the reintroduction of native apex predators; and (B) the removal of introduced apex predators. Within treatments, one-way Kruskal-Wallis rank-sum tests found significant differences in LRR among trophic groups only in removal studies with a single predator and multiple prey (H = 7.68, df = 3, P = 0.05). Asterisks in the figure correspond to results from non-parametric Wilcoxon signed rank tests and indicate that only mesopredators in removal studies with single predator-multiple prey systems (Z = 301, P < 0.001) and herbivores in removal studies with multiple predators-multiple prey systems (Z = 27, P = 0.03), had mean LRRs significantly different from zero.

recolonization of Laikipia, Kenya by African wild dogs (Lycaon pictus) suppressed densities of primary prey (Guenther's dik-dik [Madoqua guentheri]) which suppressed growth of some species of trees, but wild dog recolonization did not translate to a trophic cascade. Ford et al. (2015) hypothesized that some combination of increased rainfall and compensatory browsing by other ungulates attenuated the effects of wild dog recolonization on these trees. Similarly, Marshall et al. (2013) demonstrated that shifts in stream hydrology driven by beaver extirpation prevented the restoration of willows (Salix spp.) in many areas following the return of wolves to the Greater Yellowstone Ecosystem. Although wolf (Canis lupus) reintroduction reduced elk (Cervus elaphus) abundance, a lowered water table and resulting changes in nutrient availability gave rise to an alternative stable state in beaver-free areas that was resilient to shifts in elk abundance stemming from wolf reintroduction. In sum, pinpointing the effects of apex predator reintroduction and removal is often complicated by shifting abiotic conditions.

We found no evidence that functional redundancy among prey

species affects either prey or primary producer responses to the reintroduction or removal of apex predators (Fig. 2.A), but this may result from studies centering on relatively common species rather than uncommon ones. In predator-prey systems characterized by large carnivores and multiple species of ungulate prey, prey communities tend to be comprised of one or a few species that are sufficiently numerous to escape top-down control and several less common species for which predation limits abundance (e.g., Chirima et al., 2013; Georgiadis et al., 2007; Owen-Smith et al., 2005; Sinclair and Fryxell, 1985). Because numerically dominant species strongly influence community structure and ecosystem function, the reintroduction of large carnivores may simply reduce populations of secondary species of prey that already were uncommon before large-carnivore reintroductions and are less likely than common species to control plant populations. Researchers also have a strong tendency to simplify complex systems when studying trophic relationships (Montgomery et al., 2019), and uncommon species are less likely to be included in studies of trophic relationships due to logistical concerns (e.g., added difficulty and cost in surveying

Table 1

Outstanding questions regarding the ecology of large carnivore rei	introductions.
--	----------------

Outstanding	questions	in	large	carnivore	reintroduction	

Under what conditions do large carnivore removal and reintroduction have offsetting (reciprocal) effects on ecosystem structure or function?

- Which regions and ecological processes are most sensitive to changing large carnivore abundance? Which are most resistant?
- Do risk effects persist following removal of large carnivores, and for how long? What functional traits of large carnivores and prey mediate the impacts of top-down control?
- How does variation in environmental conditions and landscape characteristics mediate the impacts of top-down control?

Under what conditions does bottom-up control supersede top-down control?

individuals and accurately estimating abundance). Both of these phenomena could yield the muted outcomes from apex predator reintroduction or removal we observed (Figs. 2, 3).

Our inferences regarding the assumption of reciprocity are constrained by a lack of experimental evidence involving both large carnivores and trophic cascades (Allen et al., 2017; Ford and Goheen, 2015), as well as more tractable mesocosm manipulations. To properly evaluate the assumption of reciprocity, data on large carnivores (or other apex predators), prey, and primary producers are required for three distinct time steps: one in which native apex predators exist (i.e., a historical state), a time step in which native apex predators have been extirpated, and a time step in which apex predators have been reintroduced and attain population sizes comparable to the historical state. The vast majority of studies in the literature focus on the latter two time steps and did not report historic reference point data prior to apex predator reintroduction (or removal, in the case of introduced apex predators). Though baseline data on historical reference points is very challenging to quantify in most systems, it is occasionally possible to generate reasonable estimates of important variables-e.g., tree density using historical photographs of known landscapes. Filling this knowledge gap is critical for understanding whether extirpation and reintroduction have symmetrical, offsetting impacts.

Shifts in environmental conditions are increasingly likely as the time periods over which apex predators are extirpated increase, and it may take some time for altered environmental conditions to revert to historical reference points after predator reintroduction. Consequently, there is strong potential for transient dynamics during the extirpation and reintroduction of apex predators, where populations within trophic groups will have not yet reached equilibrial abundances at the end of a study (Hastings, 2001). The extent to which the assumption of reciprocity is upheld should therefore depend on the amount of time over which a native apex predator is extirpated or, conversely, an introduced apex predator is present. In an attempt to address the possibility of transient (non-equilibrial) dynamics, we analyzed responses of trophic groups as a function of time elapsed since the reintroduction or removal of apex predators. We found no evidence that the effects of apex predator reintroduction or removal are influenced by time in the studies in our data set (Fig. A.1), indicating that the results reported for the majority of studies in our meta-analysis do not reflect transient dynamics.

Reintroduction of large carnivores can inject optimism into conservation efforts typically characterized by reactive approaches. Many questions concerning the ecology of large carnivore reintroduction remain unanswered (see Table 1), however, particularly concerning the consistency (and thus predictability) of higher-level effects generated by such reintroductions. Professionals in our field might consider the conservation importance of large carnivore reintroduction (which few ecologists would question) as distinct from the cascading impacts of large carnivore reintroduction, which can be significant (Letnic et al., 2009; Ripple and Beschta, 2012), muted (Elmhagen and Rushton, 2007; le Roux et al., 2018), or virtually non-existent (Ford et al., 2015). Removing or reintroducing apex predators from ecosystems does not appear to have predictable restorative effects, but solid confirmation will require additional rigorous tests of this assumption of reciprocity. Supplementary data to this article can be found online at https://

doi.org/10.1016/j.biocon.2019.03.021.

Acknowledgements

JMA, BMM, and JRG led in organization and analysis of this manuscript. All other authors made major contributions in all phases of manuscript preparation and are listed in alphabetical order. We thank R. Montgomery for inviting us to participate in this feature and three anonymous reviewers for their helpful comments on our manuscript.

References

- Agrawal, A.A., Ackerly, D.D., Adler, F., Arnold, A.E., Cáceres, C., Doak, D.F., Post, E., Hudson, P.J., Maron, J., Mooney, K.A., Power, M., Schemske, D., Stachowicz, J., Strauss, S., Turner, M.G., Werner, E., 2007. Filling key gaps in population and community ecology. Front. Ecol. Environ. 5, 145–152. https://doi.org/10.1890/ 1540-9295(2007)5[145:FKGIPA]2.0.CO;2.
- Allen, B.L., Allen, L.R., Andrén, H., Ballard, G., Boitani, L., Engeman, R.M., Fleming, P.J.S., Ford, A.T., Haswell, P.M., Kowalczyk, R., Linnell, J.D.C., David Mech, L., Parker, D.M., 2017. Can we save large carnivores without losing large carnivore science? Food Webs 12, 64–75. https://doi.org/10.1016/j.fooweb.2017.02.008.
- Andriuzzi, W.S., Wall, D.H., 2018. Soil biological responses to, and feedbacks on, trophic rewilding. Phil. Trans. R. Soc. B 373, 20170448. https://doi.org/10.1098/rstb.2017. 0448.
- Bakker, E.S., Svenning, J.-C., 2018. Trophic rewilding: impact on ecosystems under global change. Phil. Trans. R. Soc. B 373, 20170432. https://doi.org/10.1098/rstb.2017. 0432.
- Beschta, R.L., Ripple, W.J., 2009. Large predators and trophic cascades in terrestrial ecosystems of the western United States. Biol. Conserv. 142, 2401–2414. https://doi. org/10.1016/j.biocon.2009.06.015.
- Beschta, R.L., Ripple, W.J., 2016. Riparian vegetation recovery in Yellowstone: the first two decades after wolf reintroduction. Biol. Conserv. 198, 93–103. https://doi.org/ 10.1016/j.biocon.2016.03.031.
- Borer, E.T., Seabloom, E.W., Shurin, J.B., Anderson, K.E., Blanchette, C.A., Broitman, B., Cooper, S.D., Halpern, B.S., 2005. What determines the strength of a trophic cascade? Ecology 86, 528–537. https://doi.org/10.1890/03-0816.
- Callan, R., Nibbelink, N.P., Rooney, T.P., Wiedenhoeft, J.E., Wydeven, A.P., 2013. Recolonizing wolves trigger a trophic cascade in Wisconsin (USA). J. Ecol. 101, 837–845. https://doi.org/10.1111/1365-2745.12095.
- Chapron, G., Kaczensky, P., Linnell, J.D.C., Arx, M. von, Huber, D., Andrén, H., López-Bao, J.V., Adamec, M., Álvares, F., Anders, O., Balčiauskas, L., Balys, V., Bedő, P., Bego, F., Blanco, J.C., Breitenmoser, U., Brøseth, H., Bufka, L., Bunikyte, R., Ciucci, P., Dutsov, A., Engleder, T., Fuxjäger, C., Groff, C., Holmala, K., Hoxha, B., Iliopoulos, Y., Ionescu, O., Jeremić, J., Jerina, K., Kluth, G., Knauer, F., Kojola, I., Kos, I., Krofel, M., Kubala, J., Kunovac, S., Kusak, J., Kutal, M., Liberg, O., Majić, A., Männil, P., Manz, R., Marboutin, E., Marucco, F., Melovski, D., Mersini, K., Mertzanis, Y., Mysłajek, R.W., Nowak, S., Odden, J., Ozolins, J., Palomero, G., Pannović, M., Persson, J., Potočnik, H., Quenette, P.-Y., Rauer, G., Reinhardt, I., Rigg, R., Ryser, A., Salvatori, V., Skrbinšek, T., Stojanov, A., Swenson, J.E., Szemethy, L., Trajce, A., Tsingarska-Sedefcheva, E., Váňa, M., Veeroja, R., Wabakken, P., Wölfl, M., Wölfl, S., Zimmermann, F., Zlatanova, D., Boitani, L., 2014. Recovery of large carnivores in Europe's modern human-dominated landscapes. Science 346, 1517–1519. https://doi.org/10.1126/science.1257553.
- Chirima, G.J., Owen-Smith, N., Erasmus, B.F.N., Parrini, F., 2013. Distributional niche of relatively rare sable antelope in a South African savanna: habitat versus biotic relationships. Ecography 36, 68–79. https://doi.org/10.1111/j.1600-0587.2012. 07333.x.
- Creel, S., Winnie, J., Maxwell, B., Hamlin, K., Creel, M., 2005. Elk alter habitat selection as an antipredator response to wolves. Ecology 86, 3387–3397. https://doi.org/10. 1890/05-0032.
- Elmhagen, B., Rushton, S.P., 2007. Trophic control of mesopredators in terrestrial ecosystems: top-down or bottom-up? Ecol. Lett. 10, 197–206. https://doi.org/10.1111/j. 1461-0248.2006.01010.x.
- Englund, G., Sarnelle, O., Cooper, S.D., 1999. The importance of data-selection criteria: meta-analyses of stream predation experiments. Ecology 80, 1132–1141. https://doi. org/10.1890/0012-9658(1999)080[1132:TIODSC]2.0.CO;2.
- Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Carpenter, S.R., Essington, T.E., Holt, R.D., Jackson, J.B.C., Marquis, R.J., Oksanen, L., Oksanen, T., Paine, R.T., Pikitch, E.K., Ripple, W.J., Sandin, S.A., Scheffer, M., Schoener, T.W., Shurin, J.B., Sinclair, A.R.E., Soulé, M.E., Virtanen, R., Wardle, D.A., 2011. Trophic downgrading of planet Earth. Science 333, 301–306. https://doi.org/10.1126/ science.1205106.
- Ford, A.T., Goheen, J.R., 2015. Trophic cascades by large carnivores: a case for strong inference and mechanism. Trends Ecol. Evol. 30, 725–735. https://doi.org/10.1016/ j.tree.2015.09.012.
- Ford, A.T., Goheen, J.R., Otieno, T.O., Bidner, L., Isbell, L.A., Palmer, T.M., Ward, D., Woodroffe, R., Pringle, R.M., 2014. Large carnivores make savanna tree communities less thorny. Science 346, 346–349. https://doi.org/10.1126/science.1252753.

- Ford, A.T., Goheen, J.R., Augustine, D.J., Kinnaird, M.F., O'Brien, T.G., Palmer, T.M., Pringle, R.M., Woodroffe, R., 2015. Recovery of African wild dogs suppresses prey but does not trigger a trophic cascade. Ecology 96, 2705–2714. https://doi.org/10. 1890/14-2056.1.
- Fortin, D., Beyer, H.L., Boyce, M.S., Smith, D.W., Duchesne, T., Mao, J.S., 2005. Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. Ecology 86, 1320–1330. https://doi.org/10.1890/04-0953.
- Georgiadis, N.J., Ihwagi, F., Olwero, J.G.N., Romañach, S.S., 2007. Savanna herbivore dynamics in a livestock-dominated landscape. II: ecological, conservation, and management implications of predator restoration. Biol. Conserv. 137, 473–483. https://doi.org/10.1016/j.biocon.2007.03.006.
- Gompper, M.E., Belant, J.L., Kays, R., 2015. Carnivore coexistence: America's recovery. Science 347, 382–383. https://doi.org/10.1126/science.347.6220.382-b.
- Gurevitch, J., Hedges, L.V., 1999. Statistical issues in ecological meta-analyses. Ecology 80, 1142–1149. https://doi.org/10.1890/0012-9658(1999)080[1142:SIIEMA]2.0. CO;2.
- Hastings, A., 2001. Transient dynamics and persistence of ecological systems. Ecol. Lett. 4, 215–220. https://doi.org/10.1046/j.1461-0248.2001.00220.x.
- Hastings, A., 2004. Transients: the key to long-term ecological understanding? Trends Ecol. Evol. 19, 39–45. https://doi.org/10.1016/j.tree.2003.09.007.
- Haswell, P.M., Kusak, J., Hayward, M.W., 2017. Large carnivore impacts are contextdependent. Food Webs 12, 3–13. https://doi.org/10.1016/j.fooweb.2016.02.005.
- Hebblewhite, M., White, C.A., Nietvelt, C.G., McKenzie, J.A., Hurd, T.E., Fryxell, J.M., Bayley, S.E., Paquet, P.C., 2005. Human activity mediates a trophic cascade caused by wolves. Ecology 86, 2135–2144. https://doi.org/10.1890/04-1269.
- Hedges, L.V., Gurevitch, J., Curtis, P.S., 1999. The meta-analysis of response ratios in experimental ecology. Ecology 80, 1150–1156. https://doi.org/10.1890/0012-9658(1999)080[1150:TMAORR]2.0.CO;2.
- Heithaus, M.R., Wirsing, A.J., Burkholder, D., Thomson, J., Dill, L.M., 2009. Towards a predictive framework for predator risk effects: the interaction of landscape features and prey escape tactics. J. Anim. Ecol. 78, 556–562. https://doi.org/10.1111/j.1365-2656.2008.01512.x.
- Holling, C.S., 1973. Resilience and stability of ecological systems. Annu. Rev. Ecol. Evol. Syst. 4, 1–23. https://doi.org/10.1146/annurev.es.04.110173.000245.
- Letnic, M., Koch, F., Gordon, C., Crowther, M.S., Dickman, C.R., 2009. Keystone effects of an alien top-predator stem extinctions of native mammals. Proc. R. Soc. Lond. B Biol. Sci. 276, 3249–3256. https://doi.org/10.1098/rspb.2009.0574.
- Licht, D.S., Millspaugh, J.J., Kunkel, K.E., Kochanny, C.O., Peterson, R.O., 2010. Using small populations of wolves for ecosystem restoration and stewardship. BioScience 60, 147–153. https://doi.org/10.1525/bio.2010.60.2.9.
- Malhi, Y., Doughty, C.E., Galetti, M., Smith, F.A., Svenning, J.-C., Terborgh, J.W., 2016. Megafauna and ecosystem function from the Pleistocene to the Anthropocene. PNAS 113, 838–846. https://doi.org/10.1073/pnas.1502540113.
- Marshall, K.N., Hobbs, N.T., Cooper, D.J., 2013. Stream hydrology limits recovery of riparian ecosystems after wolf reintroduction. Proc. R. Soc. Lond. B Biol. Sci. 280, 20122977. https://doi.org/10.1098/rspb.2012.2977.
- Middleton, A.D., Kauffman, M.J., McWhirter, D.E., Cook, J.G., Cook, R.C., Nelson, A.A., Jimenez, M.D., Klaver, R.W., 2013. Animal migration amid shifting patterns of phenology and predation: lessons from a Yellowstone elk herd. Ecology 94, 1245–1256. https://doi.org/10.1890/11-2298.1.
- Montgomery, R.A., Moll, R.J., Say-Sallaz, E., Valeix, M., Prugh, L.R., 2019. A tendency to simplify complex systems. Biol. Conserv. 233, 1–11. https://doi.org/10.1016/j. biocon.2019.02.001.
- Morris, T., Letnic, M., 2017. Removal of an apex predator initiates a trophic cascade that extends from herbivores to vegetation and the soil nutrient pool. Proc. R. Soc. Lond. B Biol. Sci. 284, 20170111. https://doi.org/10.1098/rspb.2017.0111.
- Newsome, T.M., Ripple, W.J., 2015. A continental scale trophic cascade from wolves through coyotes to foxes. J. Anim. Ecol. 84, 49–59. https://doi.org/10.1111/1365-2656.12258.
- Ng'weno, C.C., Maiyo, N.J., Ali, A.H., Kibungei, A.K., Goheen, J.R., 2017. Lions influence the decline and habitat shift of hartebeest in a semiarid savanna. J. Mammal. 98, 1078–1087. https://doi.org/10.1093/jmammal/gyx040.
- Ordiz, A., Bischof, R., Swenson, J.E., 2013. Saving large carnivores, but losing the apex predator? Biol. Conserv. 168, 128–133. https://doi.org/10.1016/j.biocon.2013.09. 024.
- Otieno, T.O., Goheen, J.R., Webala, P.W., Mwangi, A., Osuga, I.M., Ford, A.T., 2019. Human- and risk-mediated browsing pressure by sympatric antelope in an African

savanna. Biol. Conserv. 232, 59–65. https://doi.org/10.1016/j.biocon.2019.01.028.

Owen-Smith, N., Mason, D.R., Ogutu, J.O., 2005. Correlates of survival rates for 10 African ungulate populations: density, rainfall and predation. J. Anim. Ecol. 74, 774–788. https://doi.org/10.1111/j.1365-2656.2005.00974.x.

- Paine, R.T., 1966. Food web complexity and species diversity. Am. Nat. 100, 65–75. https://doi.org/10.1086/282400.
- Polis, G.A., Strong, D.R., 1996. Food web complexity and community dynamics. Am. Nat. 147, 813–846. https://doi.org/10.1086/285880.
- Pringle, R.M., Prior, K.M., Palmer, T.M., Young, T.P., Goheen, J.R., 2016. Large herbivores promote habitat specialization and beta diversity of African savanna trees. Ecology 97, 2640–2657. https://doi.org/10.1002/ecy.1522.
- Prugh, L.R., Stoner, C.J., Epps, C.W., Bean, W.T., Ripple, W.J., Laliberte, A.S., Brashares, J.S., 2009. The rise of the mesopredator. BioScience 59, 779–791. https://doi.org/10. 1525/bio.2009.59.9.9.
- Ripple, W.J., Beschta, R.L., 2012. Trophic cascades in Yellowstone: the first 15 years after wolf reintroduction. Biol. Conserv. 145, 205–213. https://doi.org/10.1016/j.biocon. 2011.11.005.
- Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P., Schmitz, O.J., Smith, D.W., Wallach, A.D., Wirsing, A.J., 2014. Status and ecological effects of the world's largest carnivores. Science 343, 1241484. https://doi.org/10.1126/science.1241484.
- Ritchie, E.G., Elmhagen, B., Glen, A.S., Letnic, M., Ludwig, G., McDonald, R.A., 2012. Ecosystem restoration with teeth: what role for predators? Trends Ecol. Evol. 27, 265–271. https://doi.org/10.1016/j.tree.2012.01.001.
- Romme, W.H., Boyce, M.S., Gresswell, R., Merrill, E.H., Minshall, G.W., Whitlock, C., Turner, M.G., 2011. Twenty years after the 1988 Yellowstone fires: lessons about disturbance and ecosystems. Ecosystems 14, 1196–1215. https://doi.org/10.1007/ s10021-011-9470-6.
- le Roux, E., Kerley, G.I.H., Cromsigt, J.P.G.M., 2018. Megaherbivores modify trophic cascades triggered by fear of predation in an African savanna ecosystem. Curr. Biol. 28, 2493–2499.e3. https://doi.org/10.1016/j.cub.2018.05.088.
- Shurin, J.B., Borer, E.T., Seabloom, E.W., Anderson, K., Blanchette, C.A., Broitman, B., Cooper, S.D., Halpern, B.S., 2002. A cross-ecosystem comparison of the strength of trophic cascades. Ecol. Lett. 5, 785–791. https://doi.org/10.1046/j.1461-0248.2002. 00381.x.
- Sinclair, A.R.E., Fryxell, J.M., 1985. The Sahel of Africa: ecology of a disaster. Can. J. Zool. 63, 987–994. https://doi.org/10.1139/z85-147.
- Sinclair, A.R.E., Pech, R.P., Fryxell, J.M., McCann, K., Byrom, A.E., Savory, C.J., Brashares, J., Arthur, A.D., Catling, P.C., Triska, M.D., Craig, M.D., Sinclair, T.J.E., McLaren, J.R., Turkington, R., Beyers, R.L., Harrower, W.L., 2018. Predicting and assessing progress in the restoration of ecosystems. Conserv. Lett. 11, e12390. https://doi.org/10.1111/conl.12390.
- Smith, D.W., Tyers, D.B., 2012. The history and current status and distribution of beavers in Yellowstone National Park. Northwest Sci 86, 276–289. https://doi.org/10.3955/ 046.086.0404.
- Soule, M.E., Estes, J.A., Berger, J., Del Rio, C.M., 2003. Ecological effectiveness: conservation goals for interactive species. Conserv. Biol. 17, 1238–1250. https://doi.org/ 10.1046/j.1523-1739.2003.01599.x.
- Stier, A.C., Samhouri, J.F., Novak, M., Marshall, K.N., Ward, E.J., Holt, R.D., Levin, P.S., 2016. Ecosystem context and historical contingency in apex predator recoveries. Sci. Adv. 2, e1501769. https://doi.org/10.1126/sciadv.1501769.
- Strong, D.R., 1992. Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. Ecology 73, 747–754. https://doi.org/10.2307/1940154.
- Svenning, J.-C., Pedersen, P.B.M., Donlan, C.J., Ejrnæs, R., Faurby, S., Galetti, M., Hansen, D.M., Sandel, B., Sandom, C.J., Terborgh, J.W., Vera, F.W.M., 2016. Science for a wilder Anthropocene: synthesis and future directions for trophic rewilding research. PNAS 113, 898–906. https://doi.org/10.1073/pnas.1502556112.
- Trussell, G.C., Matassa, C.M., Ewanchuk, P.J., 2017. Moving beyond linear food chains: trait-mediated indirect interactions in a rocky intertidal food web. Proc. R. Soc. Lond. B Biol. Sci. 284, 20162590. https://doi.org/10.1098/rspb.2016.2590.
- Vaughn, K.J., Young, T.P., 2010. Contingent conclusions: year of initiation influences ecological field experiments, but temporal replication is rare. Restor. Ecol. 18, 59–64. https://doi.org/10.1111/j.1526-100X.2010.00714.x.
- Young, T.P., Petersen, D.A., Clary, J.J., 2005. The ecology of restoration: historical links, emerging issues and unexplored realms. Ecol. Lett. 8, 662–673. https://doi.org/10. 1111/j.1461-0248.2005.00764.x.