

Evaluating unintended consequences of intentional species introductions and eradications for improved conservation management

Dean E. Pearson^{1,2*}, T.J. Clark³, and Philip G. Hahn⁴

¹ *Rocky Mountain Research Station, U.S. Department of Agriculture Forest Service, Missoula, MT 59801 USA*

² *Division of Biological Sciences, University of Montana, Missoula, MT 59812 USA*

³ *Wildlife Biology Program, Department of Ecosystem and Conservation Sciences, W.A. Franke College of Forestry and Conservation, University of Montana, Missoula, MT 59812 USA*

⁴ *Department of Entomology and Nematology, University of Florida, Gainesville, FL, 32608, USA*

*To whom correspondence may be addressed: dean.pearson@usda.gov

Article impact statement: A global literature review reveals that many unintended outcomes of species introductions and eradications for conservation can be avoided.

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Abstract: Conservation management is deploying increasingly intensive strategies to maintain biodiversity and ecosystem function in response to global anthropogenic threats. These strategies include intentionally introducing and eradicating species around the world via assisted migration, rewilding, biological control, invasive species eradications, and gene drives – management actions which have become highly contentious because of their

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potential for unintended consequences. We conducted a global literature review of these conservation actions to quantify how often unintended outcomes occur and to elucidate their underlying causes. We found that studies reported intended outcomes in 51% of cases, a combination of intended outcomes and unintended outcomes in 26% of cases, and strictly unintended outcomes in 10% of cases. Hence, unintended outcomes were reported in 36% of all cases evaluated. In evaluating overall conservation outcomes (weighing intended vs unintended effects), some unintended effects are fairly innocuous relative to successful conservation objectives whereas others result in serious unintended consequences in recipient communities. Importantly, we also found that studies that assessed a greater number of community interactions with the target species were more likely to report unintended outcomes, suggesting that unintended consequences may be under-reported due to insufficient vetting. Most reported unintended outcomes arose from direct effects (68%) or simple density-mediated, indirect effects (25%) linked to the target species, with only a few documented cases arising from more complex interaction pathways (7%). Therefore, most unintended outcomes involved simple interactions that could potentially be predicted and mitigated through more formal vetting. To address this shortfall, we applied foundational concepts from community ecology to develop a community assessment framework which can be used to systematically screen for potential impacts on nontarget species prior to implementing conservation actions. We propose that incorporating this approach to screen proposed conservation actions could help reduce unintended consequences from intentional species introductions and eradications for conservation.

Introduction

Management of natural systems in the Anthropocene is becoming increasingly intensive. Threats to biodiversity like climate change, species extinctions, and biological invasions are being met with intentional species introductions in the name of assisted migration (Hoegh-Guldberg et al. 2008), rewilding (Corlett 2016), and biological control (Hoddle 2004). In other cases, species are intentionally eradicated, fully or functionally, over large areas where they act as introduced (Zavaleta et al. 2001; Glen et al. 2013) or native pests (Ripple et al. 2011). Moreover, new technologies like gene drives promise even more powerful eradication tools (Webber et al. 2015), with the first gene drive in the U.S. approved in Florida, April 2020 (United States, Environmental Protection Agency, Experimental Use Permit No. 93167-EUP-2). Intentional species introductions and eradications have proven successful in mitigating some very important conservation threats (Gurr & Wratten 2000; Zavaleta et al. 2001; Jones et al. 2016; Brooke et al. 2018; Prior et al. 2018). However, these approaches have also caused unintended consequences to nontarget species with negative, sometimes severe, effects permeating through whole ecosystems (Simberloff & Stiling 1996; Zavaleta et al. 2001; Courchamp et al. 2003; Pearson & Callaway 2006; Doak et al. 2008; Bergstrom et al. 2009; Prior et al. 2018). Such negative outcomes arising from introductions and eradications have generated extensive controversy over the application of each of these conservation strategies (Simberloff & Stiling 1996; Zavaleta et al. 2001; Hoddle 2004; McLachlan et al. 2007; Ricciardi & Simberloff 2009; Lorimer et al. 2015; Webber et al. 2015; Rubenstein & Rubenstein 2016). Yet, despite such warnings and documented impacts, these conservation actions continue, driven by the substantial conservation risks associated with taking no action (e.g., Hoddle 2004; Hoegh-Guldberg et al. 2008; Marvier & Kareiva 2020).

Many unintended outcomes of intentional species introductions and eradications arise from relatively simple two- and three-species interactions that could be predicted from

ecological theory. For example, introduced cats (*Felis catus*) were eradicated from Macquarie Island to alleviate cat predation on native seabirds. However, cat eradication generated an unintended trophic cascade by releasing introduced rabbit (*Oryctolagus cuniculus*) populations from cat predation, allowing rabbit herbivory to devastate native plant communities (Bergstrom et al. 2009; but see Dowding et al.). These herbivore-driven declines in native plants then increased exotic plant populations via apparent competition. In another case, the introduction of red squirrels (*Tamiasciurus hudsonicus*) to Newfoundland island, an action intended to bolster American marten (*Martes americana*) populations via food subsidies, was linked to a serious decline of the endemic Newfoundland red crossbill (*Loxia curvirostris percna*) due to marten-crossbill competition for black spruce (*Picea mariana*) seeds (Benkman 2010). Given that these basic interactions represent well-understood community interactions such as resource competition (Gause 1934), apparent competition (Holt 1977), and trophic cascades (Paine 1980), an important question is, why have these core concepts from community ecology not been better integrated to screen against such unintended outcomes in conservation management?

While many unintended conservation outcomes may result from simple interactions, others can arise from more cryptic and complex pathways associated with longer interaction chains or trait-mediated indirect interactions (see Simberloff & Stiling 1996; Courchamp et al. 2003; Pearson & Callaway 2003; McGregor et al. 2020). Hence, effectively screening for such unintended outcomes requires assessment of multispecies assemblages participating in a variety of direct and indirect interactions (Wootton 2002). Yet, most ecological theory has been built from basic community interactions focusing on only a few species at a time (e.g., Gause 1934; Holt 1977; Paine 1980; Tilman 1980). While pairwise Lotka-Volterra type equations representing such interactions can be integrated into quantitative community-level models (Godoy et al. 2018), they carry high data demands, requiring precise information on

species abundances and interaction coefficients for all key components within a web (but see Adams et al. 2020 for caveats). Hence, ecological theory holds great potential to inform management and conservation decisions, but traditional modeling approaches are commonly too data-hungry to satisfy. Meanwhile, imminent anthropogenic threats are forcing intensive, real-time management actions to be taken with incomplete information. In short, better tools are needed to inform and guide complex conservation management actions.

In an effort to better understand and address the challenge of unintended consequences of conservation management, we first drew from theoretical and empirical work in community ecology to develop a community assessment framework for thinking about how species introductions and eradications can influence recipient communities. Next, we conducted a global literature review of large-scale studies to quantify unintended outcomes arising from intentional species introductions (assisted migration, rewilding, and biological control) and eradications (invasive species removal and gene drives). While these conservation strategies represent a range of disparate conservation objectives, they all share a critical commonality: by manipulating an entire species (whether adding or removing them) each strategy serves as a community-level perturbation with the potential to profoundly affect other organisms via similar community interaction pathways. Hence, community ecology holds potential to inform and improve each of these practices similarly. Collating the results from the literature review allowed us to assess the rate of unintended outcomes arising from these conservation actions and identify the types of interaction pathways commonly associated with unintended outcomes to inform conservation management. Applying the community assessment framework to hundreds of case studies from aquatic and terrestrial ecosystems around the globe illustrates its potential as a tool for systematically considering and mapping out the relevant recipient community interaction web to screen for species most susceptible to unintended consequences and mitigate against such outcomes.

Methods

A framework for assessing community-level effects of species manipulations

In community ecology and network theory (May 1972; Wootton 1994; Godoy et al. 2018), there are four basic components that make up a community interaction web: 1) the species in the web (i.e., network nodes), 2) the linkages connecting interacting species/nodes, 3) the type (e.g., predation, mutualism) and hence directionality of the linkages (i.e., positive or negative), and 4) the strength of the interactions (May 1972; Wootton 1994). With information on each of these components, it is theoretically possible to model community interactions using a standard community interaction matrix to determine the effects of changing the abundance (or presence) of one community member on the remaining community components (May 1972; Ramsey & Veltman 2005). While abundance information can be important for modelling, it is not essential for determining community outcomes, so we focus on these four elements. Hence, these are the basic elements required for understanding a community's response to perturbations like species introductions and eradications. Building from these basic elements, the next step is to determine which of the multitude of species and interactions within the recipient community are most likely to be affected by introducing or removing a species targeted for management (hereafter, target species). Fortunately, empirical studies in community ecology demonstrate that most communities are comprised of many weak and few strong interactions (Paine 1992; Neutel et al. 2002). Hence, most interactions and species can be ignored, but determining which ones should be included to best capture substantive changes within the community becomes a challenging and potentially subjective process.

To address this problem, we draw from the wealth of research in community ecology to construct a community assessment framework for systematically considering the types of interaction linkages most relevant to the species targeted for management action (Fig. 1). While there are a multitude of specific types of community interactions, most biotic interactions fall into the broad categories of: resource uptake (consumption or intake of foods, nutrients, energy), competition (resource and interference competition), consumption (including herbivory and predation), parasitism (pathogen-host interactions), and mutualism (Wootton 1994). In addition, ecosystem engineering is a powerful interaction by which engineers may strongly interact with many community members (Jones et al. 1997). Of course, anthropogenic factors, including management, can greatly influence organisms and their interactions, and should be considered. Finally, all organisms have physical requirements which explicitly define their fundamental niches and determine their realized niches as a function of biotic interactions that are often environmentally conditioned (Hutchinson 1957). By outlining the basic components of a community interaction web, this framework provides a tool for systematically considering the range of interactions directly linking a target species to other community members in order to identify the key nodes of the community interaction web and determine the nature and strength of their linkages - the essential components for understanding community outcomes. Further, assuming that strong interactions are those most likely to perpetuate indirect effects (e.g., Paine 1980), this same process can be repeated for any organisms presumed to be strongly directly linked to the target species in order to incorporate potentially important indirect interactions. In sum, the community assessment framework provides a tool for understanding community interactions and for systematically constructing a community interaction web relevant to the management action that can help to elucidate past outcomes and vet proposed actions.

Literature Review

To quantify the prevalence of unintended outcomes across a range of management actions and better understand the community interaction pathways by which they arise, we conducted a global literature search to generate a sample of peer-reviewed publications addressing proposed or executed conservation-driven management actions involving intentional species introductions (assisted migration, rewilding, and biocontrol) or eradications (invader removal or gene drive). We used the Web of Science All Databases search engine to generate a preliminary list of papers on our five focal categories related to intentional species introductions (assisted migration, rewilding and biocontrol) or eradications (invader removal or gene drive). Our search was conducted on 11 April 2019. For all four searches, we included a subject search term to focus on environmental sciences and ecology (SU=Environmental Sciences & Ecology) plus additional search terms to screen titles and topics for each of our four focal categories. For assisted migration and rewilding we included the following terms: TI=('rewilding' OR 'assisted migration' OR 'assisted colonization') AND TS=("propos*" OR outcome OR result OR consequence). This generated a list of 131 papers. For biocontrol introduction, we included the following terms: TI=(biocontrol OR 'biological control') AND TS=('intro*') AND TS=(plant OR insect OR invertebrate) AND TS=(propos* OR outcome OR result OR consequence) NOT TS=(crop OR "agri*" OR pathogen OR lab* OR greenhouse). This generated a list of 179 papers. For invader removals, we included the following terms: TI=('remov*') AND TI=('inva*' OR exotic OR introduced) AND TS=("propos*" OR outcome OR result OR consequence). This generated a list of 156 papers. For gene drives used to eradicate pest species, we included the following search terms: TI=('gene drive') AND TS=('control'). This generated a list of 87 papers.

We further screened the preliminary list of 553 papers from the above search results to include in our literature review. We screened each paper to ensure that each study either proposed or executed a species introduction or eradication and that it was conducted at a large-enough scale to be considered a realistic community-level management action. We included studies that were conducted on whole ecosystems (e.g., ponds, islands) or a minimum of 1-hectare scale. Studies were not included, for example, if an invasive species was experimentally removed within small plots (e.g., 1 m² plots) or potential biocontrol insects were screened on host plants in a lab. In addition, executed actions were restricted to those that effectively established the introduced species (for biological control = establishing the control agent) or effected some reduction of the species targeted for eradication to ensure that we only included studies that achieved the minimal objective with the target organism. A small number of papers included multiple cases, which we included as independent observations. In total, this resulted in 172 cases from 140 papers of our original list of 553 potential papers. For papers that met the above criteria, we classified each case based on management action (introduction or eradication), management status (proposed or executed), and management category (assisted migration, biocontrol, gene drive, invasive species removal, or rewilding).

We recognize here that the published literature may not represent a comprehensive assessment of all the factors and interactions considered prior to each management action, because not all conservation actions are published in peer-reviewed journals (e.g., Wainwright et al. 2017). Many conservation actions around the world are documented in part or whole in the gray literature of government outlets or may go undocumented. However, because the rules and regulations governing conservation management differ by local and national governments, as do the processes for documenting such efforts, it is logistically infeasible to acquire a globally representative, comprehensive accounting of all such actions.

This problem has been noted by others who have gone on to demonstrate the value of reviewing the published literature for advancing conservation, despite these limitations (e.g. Wainwright et al. 2017). Accordingly, our inferences are based on the assumption that our survey of the peer-reviewed scientific literature established from our targeted key-word search of this topic provides an index representative of the underlying efforts and the types of outcomes that occur, rather than an exhaustive evaluation of the underlying case studies.

Quantifying Outcomes from the Literature Review

To understand the extent to which each management action resulted in intended vs unintended outcomes, we scored the outcomes of the management action based on the objectives of the effort and/or assessments of the authors as follows. We scored an outcome as 'intended' when the management action successfully accomplished the management goal (e.g., an exotic pest was successfully extirpated from an island). We scored an outcome as 'unintended' when the authors reported an outcome had occurred that was not part of the management objective, i.e. there was a change in a nontarget species abundance or other community component. When the authors reported both intended and unintended outcomes of the management action, we scored the outcome as 'mixed', and when no detectable effect of the action was reported, we scored the outcome as 'neutral'. If an unintended or mixed outcome was reported, we also recorded the nature of the unintended effects (density-mediated or trait-mediated) and indicated whether it was a direct or indirect effect, including the number of nontarget species involved (e.g., a direct density-mediated effect = D1, an indirect trait-mediated effect = T2) whenever possible.

In our assessment, we define the terms “unintended effects” and “unintended outcomes” (used synonymously) in an ecological context relative to the intended

management action and the reported response of nontarget species or system components. An unintended effect is deemed to be negative or positive as measured by the response of the nontarget organism or system component (e.g., if a nontarget species declines, the effect is negative; if it increases, it is positive). Hence, unintended effects are objectively, ecologically defined relative to the intended management goals. In contrast, interpreting whether the overall conservation outcome is successful or deleterious, i.e. evaluating the sum of the intended and unintended effects, is far more subjective. For example, the Macquarie Island case (Bergstrom *et al.* 2009) discussed in the Introduction might be seen as a success by those focused on mitigating impacts on seabirds, but those focused on the native plant response might consider this a case of deleterious unintended consequences. Due to this subjectivity, we do not attempt to judge the overall conservation outcome for each case study. Rather, we highlight in the Discussion the general types of overall outcomes observed, reserving term “unintended consequences” for deleterious overall outcomes, as distinct from specific unintended effects within a case study.

In order to understand the extent to which community-level interactions may have been considered for each management action, as reflected by the published literature, we also evaluated the degree to which each study addressed the critical elements of a basic community interaction web (Fig. 1). We examined each paper/case to determine the number of types of interactions with the target organism that were addressed (0-8) as well as the number of associated interaction strengths that were at least qualitatively considered (0-8) as identified in the community assessment framework (Fig. 1). Since the direction of the interaction was almost always defined in the context of its linkage to the target species (e.g., predation is negative for the prey), we did not separately track this element. Finally, since the quantification of community interactions could range from none to highly quantitative, we accounted for the sophistication of the analysis of the community components as follows: no

model = 0, qualitative model = 1 (e.g., verbal model or path diagram), quantitative model = 2 (e.g., linear model); mechanistic model = 3 (e.g., Lotka-Volterra models.). Summing the scores across these categories provided a scale for evaluating results from the literature review across management actions and management categories (range = 0-19: 0-8 interaction types, 0-8 interaction strengths, and an analytical score 0-3). Obviously, there can be many species and linkages represented within a single interaction type; e.g., a target species could have many competitors. However, we did not account for multiple interactions within a single interaction type, because our primary objective was to understand the degree to which the range of key elements of a basic community interaction web were addressed to account for potential unintended outcomes. Accounting for only one interaction type, no matter how many interactions within that type are addressed, will not sufficiently account for the breadth of unintended outcomes that might arise from a species-level community perturbation.

Data Analysis

We carried out analyses in R (R Core Team 2019). To understand the relationship between the extent to which different community components were addressed and the likelihood and nature of unintended outcomes reported, we modeled the unintended impacts categorical variables, which described the nature and complexity of unintended effects (see above), as a function of the community assessment score, using multinomial log-linear models with the “nnet” R package (Venables & Ripley 2002). To control for confounding differences between each study in our statistical analysis, we also included the variables: management status and category, taxa (e.g. plant vs invertebrate vs mammal), habitat, and region of the target organism. We did not include management action in this analysis due to collinearity with management category (e.g., rewilding involves intentional introductions not eradications).

Starting with a model containing all candidate explanatory variables and interactions, we simplified models using backwards selection until we minimized the AIC, retaining only the top model (Burnham & Anderson 2003). Additionally, we generated summary statistics ($\bar{x} \pm SE$) for management action and management categories using the scores for each community element.

Results

Our screening of papers from the literature search generated 28 assisted migration, 15 rewilding, 63 biocontrol, 13 gene drive, and 53 invasive species removal cases (Appendix S1). These cases were widely, although not evenly, distributed globally (North America = 91, Australia = 22, Islands including New Zealand = 15, Europe = 13, Asia = 9, South America = 8, Africa = 7, Antarctica = 1, and 6 encompassed arctic regions of both Europe and North America). Overall, when outcomes from these management actions were documented, 51% (57 of n=111 cases which documented management outcomes) were classified as strictly intended effects, 10% as strictly unintended effects, and 26% as mixed (with the remaining cases assigned to neutral outcomes = 6%, where biocontrol introductions neither reduced the target nor impacted nontarget species, or unknown outcomes = 6%; Fig. 2A). Hence, 36% of cases reported some unintended outcomes. For those unintended effects reported, most arose from simple density-mediated direct effects of the manipulated species on a community member (68%), followed by simple density-mediated indirect effects (25%), with only unintended effects arising from more complex trait-mediated indirect interactions (7%; Fig. 2B). However, most documented unintended outcomes arose from invader removal and biocontrol cases, a result linked to the fact that these management actions have been executed far more often than the newer management actions: assisted migration, rewilding, and gene

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drives. Notably, higher community assessment scores correlated with increased probabilities of unintended outcomes (Appendix S2, S3), a result that was unaffected by potentially confounding factors such as taxa or geographic region (Appendix S2), suggesting that our results are conservative and more comprehensive screening would identify additional unintended outcomes. Regarding the breadth of interaction types reported on, 51% of studies addressed ≥ 2 interaction types, 39% mentioned only one type of interaction, and 10% of studies did not address any interactions between nontarget species and recipient community members (Fig. 3A). Fewer studies yet discussed interaction strengths, even qualitatively, with 42% percent of studies making no mention of interaction strength (Fig. 3B). Finally, few studies offered quantitative evaluation of community outcomes (Fig. 3C). Overall, eradication efforts touched on more components than introduction efforts (sum of the scores for total number of interaction types, interaction strengths, and modeling scores was $\bar{x} \pm SE = 4.7 \pm 0.3$ vs. 3.2 ± 0.3 ; respectively), whereas proposed actions addressed fewer components than executed actions (2.7 ± 0.3 vs. 4.5 ± 0.2 , respectively), providing little evidence that newly proposed actions are doing more to consider unintended outcomes. The published literature suggests that the extent to which community components were considered was fairly limited across all conservation action categories (3.8 ± 0.2 ; range = 0 – 13; Fig. 3C), with longer-standing fields like invasive species removal and biological control tending to address more components (mean $\pm SE$: IR = 5.0 ± 0.3 , BC = 4.3 ± 0.3 , GD = 3.5 ± 0.5 , RW = 2.9 ± 0.8 , AM = 1.1 ± 0.3).

Discussion

Management actions proposing intentional species introductions and eradications for conservation purposes are controversial due to risks to nontarget species (Doak et al. 2008; Hoegh-Guldberg et al. 2008; Ricciardi & Simberloff 2009; Webber et al. 2015; Rubenstein &

Rubenstein 2016). However, these debates are largely founded in anecdotes and inference about such risks because outcomes are not well quantified. Our literature review found that collectively these conservation actions generate intended outcomes most of the time, but unintended outcomes were common side-effects of success, and sometimes the sole outcome of well-intended efforts. Of course, understanding whether unintended effects result in deleterious unintended consequences in the context of the overall conservation outcome requires consideration of the relative strength of intended and unintended effects. While many unintended effects are minor and can be written off as acceptable collateral damage relative to overall benefits (Johnson & Cushman 2007; Ferrero et al. 2013; Leege & Kilgore 2014; ; Lindenmayor et al. 2017), others may result in serious unintended consequences, including substantial declines in native species populations (Bergstrom et al. 2009; Bateman et al. 2015; Darrah & van Riper 2018), secondary invasion following invader removal (Dickie et al. 2014; reviewed in Pearson et al. 2016), and increased disease risk to humans (Pearson & Callaway 2006). Such strong unintended effects are particularly concerning if the intended outcome is not achieved or is fully offset by the unintended effects (Pearson et al. 2016). Whereas some have suggested that unintended consequences are visages of past conservation failures from the 1960-70s (Marvier & Kareiva 2020), most of the cases we reviewed have taken place since that time (up through 2019). Moreover, we found the likelihood of unintended outcomes being reported increased as studies addressed more interaction types, suggesting that unintended outcomes may be under-reported because they are under-vetted. Most importantly, our finding that most unintended outcomes arose from simple direct effects (68%), instead of more complex interactions, suggests that many unintended effects could potentially be identified by more formal screening.

The finding that 51% (87 of n=172) of the cases that we reviewed addressed two or more types of interactions with the target species (with multiple sets of interactions within an

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interaction type commonly considered), suggests that conservation management is attempting to account for unintended outcomes much of the time. However, 10% of the papers mentioned no interactions with nontarget species and 39% addressed only a single type of interaction with the target organism. If we assume that most organisms targeted for conservation management experience at minimum resource requirements, competitors, and top-down interactions (e.g. a consumer, predator, or parasite), then we might expect most organisms to have at minimum three substantive types of interactions within the affected community that should be considered. Our finding that studies reporting on more interaction types with the target species also reported more unintended outcomes, suggests that more formal vetting of these conservation actions prior to their enactment may help to highlight and plan for unintended consequences.

Our review of the published scientific literature provides evidence that conservation management is attempting to address nontarget species and unintended outcomes. However, our results indicate that potentially important nontarget species (e.g. an important predator or competitor of the target species) and system components are commonly not considered.

Lacking is a systematic means for both vetting potential unintended outcomes and documenting this process in a transparent manner. For example, even in the most comprehensive and well-quantified assessments of intentional species eradications, where multiple potential direct and indirect interactions are identified and outcomes are predictively modeled (e.g., Raymond et al. 2011; Dexter et al. 2012), it is often unclear what process was used to identify the system components that were assessed, which ones were evaluated and disregarded as irrelevant, and which were not considered due to oversight. Even in classical biological control of exotic plants using introduced insects, a field with arguably the most rigorous and well-documented prescreening testing of any of the conservation actions we assessed (e.g., Briese 2005), only one type of interaction is normally considered – the direct

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attack or consumption of nontarget species by the target (but see Todd et al. 2020). Yet, many unintended outcomes of these biological control introductions have arisen through other interaction pathways (Pearson & Callaway 2003; Carvalheiro et al. 2008; Veldtman et al. 2011). Finally, certain types of interactions that can be among the most important may not be recognized or considered for their potential to cause strong unintended outcomes. For example, introducing artificial water sources to facilitate the rewilding of tortoises on desert islands (Falcón & Hansen 2018) could strongly affect other endemic and/or nonnative species in such water limited systems. A framework for systematically and objectively considering the range of biotic, abiotic, and anthropogenic factors that may strongly link a species targeted for management to other community members could provide a simple tool for identifying potential unintended outcomes for further consideration before introductions as well as provide a means for consistently documenting this process.

The community assessment framework we developed for elucidating how species introductions and eradications might affect recipient communities (Fig 1) provides a formal assessment tool that could be applied to more holistically consider how an organism proposed for conservation action interacts with other species in the community and how these interactions might permeate through the ecosystem. Because the framework is built from foundational ecological theory reinforced by decades of empirical work, it provides a generic tool for systematically evaluating the basic components common to all communities to identify which components may be most relevant to a specific conservation action. In conducting our review and applying this framework to a variety of systems from saltwater to freshwater to terrestrial ecosystems, ranging from deserts to tropical forests, we found it to be widely applicable. This tool can be readily implemented by using natural history information, available literature, and, if available, empirical data from the system to systematically assess the range of possible interactions that might strongly link the target organism to other

community members. This process can be used to quickly generate a community interaction web that highlights strong direct and indirect interactions linking the target organism to other community members, thereby identifying potential unintended outcome pathways (Fig. 1).

While this method is more systematic and objective than the various approaches we observed in the literature, it is still a subjective process to decide which interactions are “strong enough” to consider. This sort of subjectivity can be further addressed by gathering managers, subject experts, and stakeholders as appropriate to assimilate the relevant information and define the community interaction in a consensus approach (e.g., Özesmi & Özesmi 2004). Once the interaction web is completed, the risks associated with potential unintended outcomes can then be weighed against the potential benefits of taking the conservation action (*sensu* Marvier & Kareiva 2020) through consensus decision or additional research can be conducted to explicitly assess the identified risks prior to action in order to determine whether the proposed action is warranted or not. While this strategy does not completely remove subjectivity, it established a process for broader input that can help to overcome subjective bias, and it establishes a formal, systematic and transparent process that can be clearly defined and defended on the grounds that important factors are considered and documented and stakeholders have opportunity for input.

Another limitation of the tool as presented above is that it provides a purely qualitative back-of-the-envelope approach to map and identify possible community outcomes. While our literature review suggests that simply formalizing this mapping approach could help to reduce many fairly obvious unintended outcomes in conservation management (68% were simple direct effects), qualitative modeling tools have been developed that can incorporate the basic information derived from applying the framework in Fig. 1 to formally evaluate the potential for the various interactions to play out (Hobbs et al.

2002; Ramsey & Veltman 2005; Ramsey & Norbury 2009; Raymond et al. 2011; Ramsey et al. 2012; Baker et al. 2018; Geary et al. 2020; Baker & Bode 2020). These approaches greatly add objectivity to the process and are highly recommended. However, as noted above, identifying the community interaction web to be applied in these models remains fairly arbitrary, with the types of interactions evaluated, species selected, and the depth to which the web is extended into the community not always clearly justified or systematically applied. For example, in one of the more rigorous qualitative modeling attempts to vet unintended effects of a conservation action, Raymond et al. (2011) state, “Our particular situation is further complicated by another form of ambiguity: model structure uncertainty (there are a number of interactions that could potentially be included or excluded from the model)”, a problem they addressed by “considering a large number of model structures, encompassing all possible combinations of unknown interactions”. We propose that the community assessment framework that we introduce here provides an ecologically based and systematic means for delineating the community interaction web that is prerequisite to such modeling approaches. Hence, whether the community assessment is used to map out the relevant community interaction web for purely qualitative evaluation or as the basis for applying modeling approaches, this tool provides a mechanism for systematically assessing the community of interest in a manner that is more ecologically grounded, systematic, and reproducible than current methods.

In summary, our literature review reveals that unintended outcomes commonly arise from intentional species introductions and eradications in conservation management. While many unintended outcomes may be relatively minor, some are quite serious. Importantly, most documented cases of unintended outcomes arise from basic direct and simple indirect interactions that could potentially be identified and managed for by formal vetting of proposed management actions prior to execution. Toward this end, we drew from community

ecology theory to develop a community assessment framework that provides a generic tool for systematically defining the community interaction web most strongly linked to the target organism in order to highlight potential unintended effects on nontarget community members. We propose that applying this simple tool in conservation planning is not overly burdensome and doing so could greatly reduce unintended outcomes, while also providing a methodology that is more transparent and defensible for executing these conservation actions. Finally, this tool also provides a systematic approach for developing the information necessary for more formal modeling of both intended and unintended outcomes, thereby delineating a pathway toward more advanced conservation management to reduce unintended consequences.

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Supporting Information

Database of case studies (Appendix S1), AIC model results Tables 1 (Appendix S2) and model parameter coefficients Table 2 (Appendix S3) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

Literature Cited

Adams, M.P., S.A. Sisson, K.J. Helmstedt, C.M. Baker, M.H. Holden, M. Plein, J. Holloway,

K.L. Mengersen and E. McDonald-Madden. 2020. Informing management decisions for ecological networks, using dynamic models calibrated to noisy time-series data. *Ecology Letters* 23:607-619.

Baker CM, Bode, M. 2020. Recent advances of quantitative modeling to support invasive species eradication on islands. *Conservation Science and Practice*, e246.

Baker CM, Holden MH, Plein M, McCarthy MA, Possingham HP. 2018. Informing network management using fuzzy cognitive maps. *Biological Conservation* 224:122–128. Elsevier. Available from <https://doi.org/10.1016/j.biocon.2018.05.031>.

Bateman, H. L., Merritt, D. M., Glenn, E. P., & Nagler, P. L. (2015). Indirect effects of biocontrol of an invasive riparian plant (*Tamarix*) alters habitat and reduces herpetofauna abundance. *Biological invasions*, 17(1), 87-97.

Benkman CW. 2010. Diversifying Coevolution between Crossbills and Conifers. *Evolution: Education and Outreach* 3:47–53. Available from <https://evolution-outreach.biomedcentral.com/articles/10.1007/s12052-009-0190-8>.

Bergstrom DM, Lucieer A, Kiefer K, Wasley J, Belbin L, Pedersen TK, Chown SL. 2009. Indirect effects of invasive species removal devastate World Heritage Island. *Journal of Applied Ecology* 46:73–81.

Briese DT. 2005. Translating host-specificity test results into the real world: The need to harmonize the yin and yang of current testing procedures. *Biological Control* 35:208–214.

Brooke MDL et al. 2018. Seabird population changes following mammal eradications on islands. *Animal Conservation* 21:3–12.

- Burnham KP, Anderson D. 2003. Model selection and multimodel inference: a practical information-theoretic approach. Spring Science & Business Media, New York, NY, U.S.A.
- Carvalho LG, Buckley YM, Ventim R, Fowler S V., Memmott J. 2008. Apparent competition can compromise the safety of highly specific biocontrol agents. *Ecology Letters* **11**:690–700.
- Corlett RT. 2016. Restoration, Reintroduction, and Rewilding in a Changing World. *Trends in Ecology and Evolution* **31**:453–462. Elsevier Ltd. Available from <http://dx.doi.org/10.1016/j.tree.2016.02.017>.
- Courchamp F, Woodroffe R, Roemer G. 2003. Removing Protected Populations to Save Endangered Species. *Science* **302**:1532–1532. Available from <http://www.sciencemag.org/cgi/doi/10.1126/science.1089492>.
- Darrah AJ, van Riper C. 2018. Riparian bird density decline in response to biocontrol of Tamarix from riparian ecosystems along the Dolores River in SW Colorado, USA. *Biological Invasions* **20**:709–720. Springer International Publishing.
- Dexter N, Ramsey DSL, MacGregor C, Lindenmayer D. 2012. Predicting Ecosystem Wide Impacts of Wallaby Management Using a Fuzzy Cognitive Map. *Ecosystems* **15**:1363–1379.
- Dickie, I. A., St John, M. G., Yeates, G. W., Morse, C. W., Bonner, K. I., Orwin, K., & Peltzer, D. A. (2014). Belowground legacies of *Pinus contorta* invasion and removal result in multiple mechanisms of invasional meltdown. *AoB plants*, 6.
- Doak D, Estes J, Halpern B, Ute J. 2008. Understanding and Predicting Ecological Dynamics: Are Major Surprises Inevitable? *Ecology* **89**. Available from

http://opensiuc.lib.siu.edu/zool_pubs (accessed September 14, 2017).

- Dowding JE, Murphy EC, Springer K, Peacock AJ, & Krebs CJ (2009). Cats, rabbits, Myxoma virus, and vegetation on Macquarie Island: a comment on Bergstrom et al.(2009). *Journal of Applied Ecology* **46**:1129-1132.
- Falcón W, Hansen DM. 2018. Island rewilding with giant tortoises in an era of climate change. *Philosophical Transactions of the Royal Society B: Biological Sciences* **373**.
- Ferrero V, Castro S, Costa J, Acuña P, Navarro L, Loureiro J. 2013. Effect of invader removal: Pollinators stay but some native plants miss their new friend. *Biological Invasions* **15**:2347–2358.
- Gause GF. 1934. Experimental analysis of Vito Volterra's mathematical theory of the struggle for existence. *Science* **79**:16–17.
- Geary W, Bode M, Doherty T, Fulton E, Nimmo D, Tulloch A, Tulloch V, Ritchie E. 2020. A guide to ecosystem models and their environmental applications. *Nature Ecology & Evolution* 4(11), 1459-1471.
- Glen AS, Atkinson R, Campbell KJ, Hagen E, Holmes ND, Keitt BS, Parkes JP, Saunders A, Sawyer J, Torres H. 2013. Eradicating multiple invasive species on inhabited islands: the next big step in island restoration ? *Biological Invasions* **15**:2589–2603.
- Godoy O, Bartomeus I, Rohr RP, Saavedra S. 2018. Towards the Integration of Niche and Network Theories. *Trends in Ecology and Evolution* **33**:287–300. Elsevier Ltd. Available from <http://dx.doi.org/10.1016/j.tree.2018.01.007>.
- Gosse JW, Hearn BJ. 2005. Seasonal diets of Newfoundland Martens, *Martes americana atrata*. *Canadian Field-Naturalist* **119**:43–47.

- Gurr G, Wratten S. 2000. Biological control: measures of success. Kluwer Academic Publishers, Dordrecht, NE.
- Hobbs BF, Ludsin SA, Knight RL, Ryan PA, Ciborowski JJH. 2002. Fuzzy Cognitive Mapping As a Tool To Define Management. *Ecological Applications* **12**:1548–1565.
- Hodde MS. 2004. Restoring Balance: Using Exotic Species to Control Invasive Exotic Species. *Conservation Biology* **18**:38–49.
- Hoegh-Guldberg O, Hughes L, McIntyre S, Lindenmayer DB, Parmesan C, Possingham HP, Thomas CD. 2008. Assisted Colonization and Rapid Climate Change. *Science* **321**:345–346. Available from <http://dx.doi.org/10.1126/science.1157897>.
- Holt R. 1977. Predation, apparent competition, and the structure of prey communities. *Theoretical Population Biology* **12**. Available from <https://people.clas.ufl.edu/rdholt/files/001.pdf> (accessed September 28, 2017).
- Hutchinson G. 1957. Concluding remarks. Pages 75–96 Cold Spring Harbour Symposium on Quantitative Biology.
- Johnson BE, Cushman JH. 2007. Influence of a large herbivore reintroduction on plant invasions and community composition in a California grassland. *Conservation Biology* **21**:515–526.
- Jones CG, Lawton JH, Shachak M. 1997. Positive and Negative Effects of Organisms as Physical Ecosystem Engineers. *Ecology* **78**:1946–1957.
- Jones HP et al. 2016. Invasive mammal eradication on islands results in substantial conservation gains. *Proceedings of the National Academy of Sciences of the United States of America* **113**:4033–8. National Academy of Sciences. Available from

<http://www.ncbi.nlm.nih.gov/pubmed/27001852> (accessed January 5, 2017).

- Leege LM, Kilgore JS. 2014. Recovery of foredune and blowout habitats in a freshwater dune following removal of invasive Austrian pine (*Pinus nigra*). *Restoration Ecology* **22**:641–648.
- Lewis S, Titus K, Fuller M. 2006. Northern Goshawk Diet During the Nesting Season in Southeast Alaska. *Journal of Wildlife Management* **70**:1151–1160.
- Lorimer J, Sandom C, Jepson P, Doughty CE, Barua M, Kirby K. 2015. Rewilding: Science, Practice, and Politics. *Annual Review of Environmental Resources*.
- Marvier, M., & Kareiva, P. (2020). It is time to rebalance the risk equation. *Frontiers in Ecology and the Environment* doi:10.1002/fee.2256
- May R. 1972. Will a Large Complex System be Stable? *Nature* **238**. Available from <https://www.nature.com/articles/238413a0.pdf> (accessed December 6, 2017).
- McGregor H, Moseby K, Johnson CN, Legge S. 2020. The short-term response of feral cats to rabbit population decline :Are alternative native prey more at risk ? *Biological Invasions* **22**:799–811. Springer International Publishing. Available from <https://doi.org/10.1007/s10530-019-02131-5>.
- McLachlan JS, Hellmann JJ, Schwartz MW. 2007. A framework for debate of assisted migration in an era of climate change. *Conservation Biology* **21**:297–302.
- Menge BA. 1978. Effect of an Algal Canopy, Wave Action and Desiccation on Predator Feeding Rates. *Oecologia* **35**:17–35.
- Neutel A-M, Heesterbeek JAP, Ruiters PC De. 2002. Stability in Real Food Webs: Weak Links in Long Loops. *Science* **296**:1120–1123.

- Özesmi U, Özesmi S. 2004. Ecological models based on people's knowledge: a multi-step fuzzy cognitive mapping approach. *Ecological Modelling* **176**:47–59.
- Paine R. 1992. Food-web analysis through field measurement of per capita interaction strength. *Nature* **355**:73–75.
- Paine RT. 1980. Food Webs: Linkage, Interaction Strength and Community Infrastructure. *Journal of Animal Ecology* **49**:666–685.
- Pearson DE, Callaway RM. 2003. Indirect effects of host-specific biological control agents. *Trends in Ecology and Evolution* **18**:456–461.
- Pearson DE, Callaway RM. 2006. Biological control agents elevate hantavirus by subsidizing deer mouse populations. *Ecology Letters* **9**:443–450.
- Pearson, D. E., Ortega, Y. K., Runyon, J. B., & Butler, J. L. (2016). Secondary invasion: the bane of weed management. *Biological Conservation*, 197, 8-17.
- Prior KM, Adams DC, Klepzig KD, Hulcr J. 2018. When does invasive species removal lead to ecological recovery? Implications for management success. *Biological Invasions* **20**:267–283. Springer International Publishing.
- Ramsey D, Veltman C. 2005. Predicting the effects of perturbations on ecological communities: What can qualitative models offer? *Journal of Animal Ecology* **74**:905–916.
- Ramsey DSL et al. 2012. An approximate Bayesian algorithm for training fuzzy cognitive map models of forest responses to deer control in a New Zealand adaptive management experiment. *Ecological Modelling* **240**:93–104. Elsevier B.V. Available from <http://dx.doi.org/10.1016/j.ecolmodel.2012.04.022>.

- Ramsey DSL, Norbury GL. 2009. Predicting the unexpected: Using a qualitative model of a New Zealand dryland ecosystem to anticipate pest management outcomes. *Austral Ecology* **34**:409–421.
- Raymond B, McInnes J, Dambacher JM, Way S, Bergstrom DM. 2011. Qualitative modelling of invasive species eradication on subantarctic Macquarie Island. *Journal of Applied Ecology* **48**:181–191.
- Ricciardi A, Simberloff D. 2009. Assisted colonization is not a viable conservation strategy. *Trends in Ecology and Evolution* **24**:248–253.
- Ripple WJ et al. 2011. Status and Ecological Effects of the World's Largest Carnivores. *Science*. Available from <http://ir.library.oregonstate.edu/xmlui/bitstream/handle/1957/46657/RippleWilliamFores+tEcosystemsSocietyStatusEcologicalEffects.pdf?sequence=1> (accessed July 3, 2017).
- Roth JD, Marshall JD, Murray DL, Nickerson DM, Steury TD. 2007. Geographical gradients in diet affect population dynamics of Canada lynx. *Ecology* **88**:2736–2743.
- Rubenstein DR, Rubenstein DI. 2016. From pleistocene to trophic rewilding: A Wolf in sheep's clothing. *Proceedings of the National Academy of Sciences of the United States of America* **113**:E1.
- Simberloff D, Stiling P. 1996. How Risky is Biological Control? *Ecology* **77**:1965–1974.
- Smith CC. 1970. The Coevolution of Pine Squirrels (*Tamiasciurus*) and Conifers. *Ecological Monographs* **40**:349–371.
- Smithers BL, Boal CW, Andersen DE. 2005. Northern Goshawk Diet in Minnesota: An Analysis Using Video Recording Systems. *Journal of Raptor Research* **39**:264–273.

- Tilman D. 1980. A Graphical-Mechanistic Approach to Competition and Predation. *The American Naturalist* **116**:362–393.
- Todd JH, Pearce BM, Barratt BIP. 2020. Using qualitative food webs to predict species at risk of indirect effects from a proposed biological control agent. *BioControl* **7**. Springer Netherlands. Available from <https://doi.org/10.1007/s10526-020-10038-7>.
- Veldtman R, Lado TF, Botes A, Procheş Ş, Timm AE, Geertsema H, Chown SL. 2011. Creating novel food webs on introduced Australian acacias: Indirect effects of galling biological control agents. *Diversity and Distributions* **17**:958–967.
- Venables W, Ripley B. 2002. *Modern Applied Statistics with S*, 4th edition. Springer, New York, NY, U.S.A.
- Webber BL, Raghu S, Edwards OR. 2015. Opinion: Is CRISPR-based gene drive a biocontrol silver bullet or global conservation threat? *Proceedings of the National Academy of Sciences of the United States of America* **112**:10565–10567.
- Wootton JT. 1994. The Nature and Consequences of Indirect Effects in Ecological Communities. *Annual Review of Ecology and Systematics* **25**:443–466.
- Wootton JT. 2002. Indirect effects in complex ecosystems: Recent progress and future challenges. *Journal of Sea Research* **48**:157–172.
- Zavaleta ES, Hobbs RJ, Mooney HA, Zavaleta E, Mooney HA. 2001. Viewing invasive species removal in a whole-ecosystem context. *Trends in Ecology & Evolution* **16**:454–459.

Figure legends

Fig. 1. The community assessment framework provides a skeleton for generating a community interaction web to understand how a target species intentionally introduced or eradicated for conservation purposes might influence community outcomes. The schematic lays out standard interactions that may link the target species to other network nodes (species or system components) to identify the species most likely to be affected by the action, the nature of each interaction linkage (i.e., positive or negative), and the strength of each interaction. These are the basic components of a community interaction web necessary to understand and model community outcomes. Of course, there can be multiple sets of interactions within any one interaction type (e.g., multiple competitors of the target species) that may need to be considered. The initial community assessment focuses on immediate linkages to the target species likely to be strong enough to substantively alter the abundance or function of other system components. If this assessment indicates that the target species is likely to have strong effects on particular community members, then the same process should be applied to the affected species/node to extend the web and include indirect effects, under the assumption that most strong indirect effects derive from strong direct effects. Hence, this approach systematically identifies and follows out strong linkages until they become weak, thereby delineating the relevant community of concern.

Figure 2. Proportion of studies identified from a global literature review that executed species introductions or eradications for conservation purposes for which management outcomes were reported split out by management category (AM = assisted migration; BC = biocontrol; GD = gene drive; IR = invader removal; RW = rewilding) for **(a)** outcome category (Mixed = both intended and unintended outcomes, Unintend = strictly unintended outcomes, Neutral = no changes among nontarget species (all cases where a biocontrol agent established but neither controlled the target nor impacted nontarget species), Intend = strictly intended outcomes, Unknown = outcome unclear) and **(b)** interaction web distance to unintended management outcome (D1 = density-mediated direct effects, D2 = density-mediated indirect effect, 2T = trait-mediated indirect effect).

Figure 3. Results from a global literature review of studies proposing or executing species introductions or eradications for conservation purposes. Case studies are broken out by **(a)** interaction types (e.g. competition vs predation), **(b)** interaction strengths, and **(c)** level of model sophistication (no model = 0, qualitative model = 1, quantitative model = 2; mechanistic model = 3]) to show the proportion of cases addressing each category (e.g. the proportion of studies addressing 0,1,... or 6 interaction types) and split by management category (AM = assisted migration; BC = biocontrol; GD = gene drive; IR = invader removal; RW = rewilding).



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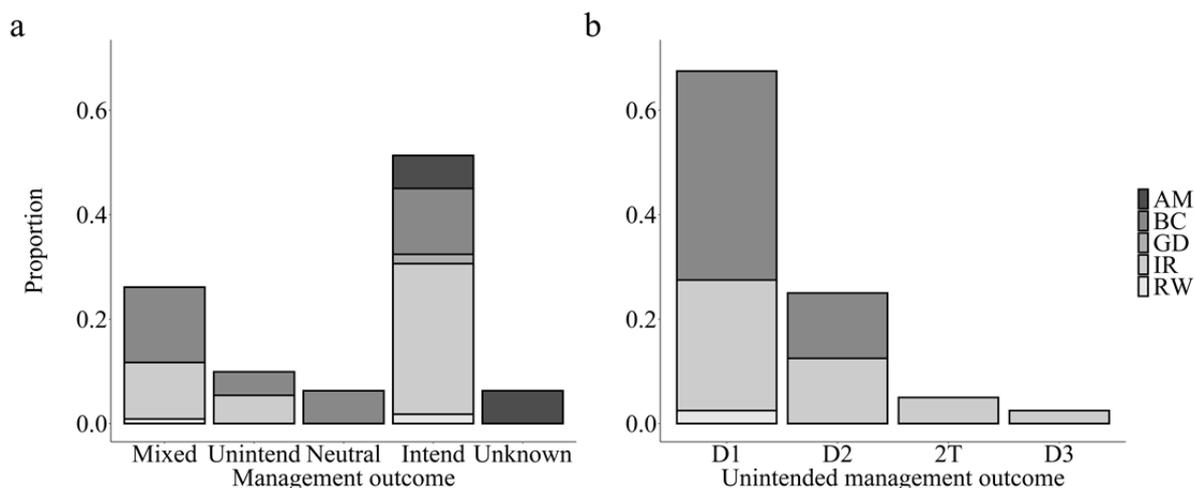


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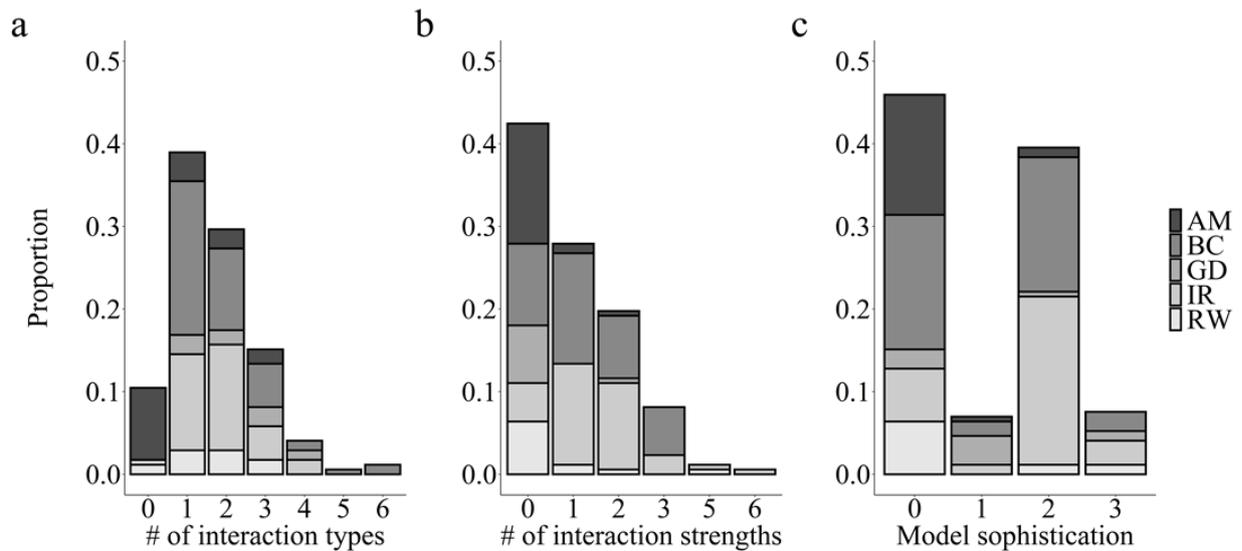


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