

## Forum

### An eco-evolutionary perspective on the humpty-dumpty effect and community restoration

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In recent decades, anthropogenic and natural disturbances have increased in rate and intensity around the world, leaving few ecosystems unaffected. As a result of the interactions among these multiple disturbances, many biological communities now occur in a degraded state as collections of fragmented ecological pieces. Restoration strategies are traditionally driven by assumptions that a community or ecosystem can be restored back to a pre-disturbance state through ecological remediation. Yet despite our best efforts, attempts to restore fragmented communities are often unsuccessful. One explanation, the humpty-dumpty effect, suggests that once a community is disassembled, it is difficult to reassemble it even in the presence of all the original pieces. This hypothesis, while potentially useful, often fails to incorporate the multitude of other critical mechanisms that affect our abilities to put fragmented communities back together. Here, we extend the original humpty-dumpty analogy to incorporate eco-evolutionary changes that can hinder successful restoration. A systematic literature review uncovered few studies that have explicitly considered how the original humpty-dumpty effect has affected restoration success in the 30 years since its inception. Using case studies, we demonstrate how the application of our extended eco-evolutionary humpty-dumpty framework may determine the success of restoration actions via ecological and evolutionary changes in fragments of communities. Lastly, given continued anthropogenic disturbances and projected climatic changes, we make five recommendations to facilitate more successful restoration efforts given our revised eco-evolutionary humpty-dumpty effects framework. These guidelines, combined with clearly defined management goals are aimed at both keeping ecological communities as intact as possible while ensuring that future ecosystem restorations might more successfully put the ecological community pieces back together.

Keywords: community conservation, disturbances, eco-evolutionary dynamics, ecosystem management, humpty-dumpty effect, restoration



## Introduction

Anthropogenic disturbances have rippled through natural ecosystems and communities, leaving few in their original state (Kareiva et al. 2007, Staudt et al. 2013). These human-induced disturbances often interact with other anthropogenic and natural disturbances to amplify ecological and evolutionary changes that drive communities further away from their historical states (Palmer et al. 1997, Sanford et al. 2014). Consequently, many communities persist in a disturbed and degraded state, characterized by the loss of biodiversity, structural complexity (e.g. food web complexity), ecological function or evolutionary potential (Moreno-Mateos et al. 2020). Conservation efforts often attempt to restore these modified systems by removing disturbances (e.g. introduced species) and reestablishing key ecosystem components such as reintroducing extirpated species (Palmer et al. 1997, Benayas et al. 2009). These efforts have been traditionally driven by assumptions (explicit or implicit) that the biodiversity, structure and function of a community or ecosystem can be restored back to its pre-disturbance state through ecological remediation (Society for Ecological Restoration 2004, Higgs et al. 2014). Under this restoration approach, historical records detailing earlier 'pre-disturbed' ecological states are commonly used as a guide for determining appropriate restoration actions and end-points (National Research Council 1992, Palmer et al. 1997). Sometimes restoration strategies work well (Lockwood and Pimm 1999), yet despite decades of research and practice, ecological restoration success remains mixed. For example, one synthesis found that 53% of restoration projects were at least partially successful (Alexander and Allan 2007). Yet, oftentimes, restoration attempts and species reintroductions are unsuccessful for reasons that are unknown (Godefroid et al. 2011, Drayton and Primack 2012).

Evaluating and addressing the determinants of restoration outcomes has been at the forefront of restoration ecology for decades with numerous reviews covering the frequencies, causes and solutions to failed attempts. Restoration efforts can fall short of success for many reasons, including socioeconomic or political conflicts (Knight and Cowling 2007, Hjerpe et al. 2009), historical legacies (Cramer et al. 2008, Suding 2011), abiotic or biotic feedback mechanisms (Suding et al. 2004, Cramer et al. 2008) and lack of post-management assessments (Suding 2011). A meta-analysis of 89 studies revealed that rehabilitated ecosystems were often not fully restored relative to undisturbed reference sites (Benayas et al. 2009), and in some situations, differences between restored and reference sites persist for at least a century after restoration efforts were undertaken (Moreno-Mateos et al. 2012, 2017). Lockwood and Pimm (1999) found that while 66% of restoration studies were at least partially successful at restoring species composition (community structure), only 2 of 34 deliberate attempts to restore community composition were successful. The 28% of studies reviewed by Lockwood and Pimm (1999) that did not successfully restore biological communities, alongside those

with only partial success, can provide us with an opportunity to deepen our understanding of how biological communities are constructed, maintained and function – but only if we can identify the underlying causes of success and failures (Jordan et al. 1990). Hence, to develop better restoration and management strategies, we must first understand why restoration efforts so commonly fail to recover the original composition, structural complexity and functioning of ecological communities.

One explanation for the widespread occurrence of restoration failures is the humpty-dumpty effect (Pimm 1991, Drake et al. 1996). This concept, named after the fabled nursery rhyme, suggests that once a community is disassembled, it becomes difficult to reassemble it again from the pre-disturbance species (Pimm 1991, Hang-Kwang and Pimm 1993). This inability to piece a community back together from ecological fragments (also referred to as 'puzzle pieces', Drake et al. 1996) can occur for various reasons. For example, restoration efforts can fail when the re-establishment of a community depends on the timing of species reintroduction (priority effects), if critical species (e.g. keystone species) are missing post-disturbance (Pimm 1991, Hang-Kwang and Pimm 1993, Drake et al. 1996) or a combination of these mechanisms. The humpty-dumpty effect represents a unification of ecological theory and application that could explain historical restoration failures that occurred despite all the ecological components or 'puzzle pieces' being present or restored. However, the degree to which the humpty-dumpty effect can explain restoration failures in the 30 years since its proposal is unknown. Moreover, the existing humpty-dumpty effect ignores other critical mechanisms that could prevent the restoration of post-disturbance communities. For the humpty-dumpty effect to be more broadly applicable in restoration ecology, we need to revise and extend the concept to include additional factors that impact restoration outcomes.

In the 30 years since the humpty-dumpty effect was proposed, it has become clear that evolution can influence ecological dynamics over short timescales (Hendry and Kinnison 1999, Kinnison and Hendry 2001) – a potentially important consideration when conducting ecological restoration. Yet, the traditional humpty-dumpty effect framework ignores eco-evolutionary changes within a community following ecological disturbances. Yet, we know that humans can drive rapid and widespread evolutionary changes in populations (Wood et al. 2021), as exemplified by the increase in antibiotic resistant pathogens and changes to selection regimes due to overharvesting or artificial selection (Palumbi 2001). Recent empirical and theoretical research suggests that eco-evolutionary dynamics can influence the ecology and restoration of communities and ecosystems (Stockwell et al. 2016, Hendry 2019, Moreno-Mateos et al. 2020, Chaparro Pedraza et al. 2021). Consequently, we propose an extended eco-evolutionary humpty-dumpty effect framework that, in addition to missing ecological components, incorporates changes in population abundances, evolution and environments as mechanisms of why restorations fail.

## The eco-evolutionary humpty-dumpty effect framework

Here we extend Pimm's original concept of the humpty-dumpty effect and Drake's (1996) puzzle piece analogy by suggesting that, even if ecological pieces are not lost, they may change size or shape following disturbance events, subsequently preventing the restoration of ecological communities (Fig. 1). In our extended humpty-dumpty effect framework, we consider ecological 'pieces' to represent different populations of species that form the focal community. We define a community as a group of species interacting together in space and time (Fauth et al. 1996, Stroud et al. 2015). We define a change in the size of ecological 'puzzle pieces' as a change in the population abundances of constituent species of the community. We define a change in shape of ecological 'puzzle pieces' as the change of traits either due to evolution or plasticity that influence a population's fitness in the original community. It is these changes in turn that could prevent communities from being restored to original, pre-disturbed states (Fig. 1).

From this perspective, we evaluate the degree to which the humpty-dumpty effect has been applied through empirical studies and identify cases that demonstrate our extended framework. We use case studies to illustrate circumstances

where ecological and evolutionary responses have changed the sizes or shapes of the ecological pieces of a disrupted community in a way that has prevented or may prevent conservationists from piecing the original community composition, structure or function back together. We hope that broadening the concept of the humpty-dumpty effect to include eco-evolutionary responses will enable system managers to maximize the potential of their fragmented communities to attain more successful restoration outcomes.

## Systematic review

We used a systematic literature search to evaluate the empirical evidence for how the humpty-dumpty effect (both by Pimm's original definition and our extended concept) have affected restoration of biological communities. To do this, we gathered literature based on the following search terms in both Web of Science and Scopus: 1) a keyword search: ('evolutionary ecology' or 'eco-evolution\*' or 'adapt\* evolution') and 'restoration', 2) a forward search of the Hang-Kwang and Pimm's (1993) original paper about the humpty-dumpty effect: 'The assembly of ecological communities: a minimalist approach' and 3) forward search of the Lockwood and Pimm's (1999) paper reviewing the concept: 'When does restoration succeed?'. Web of Science search was conducted

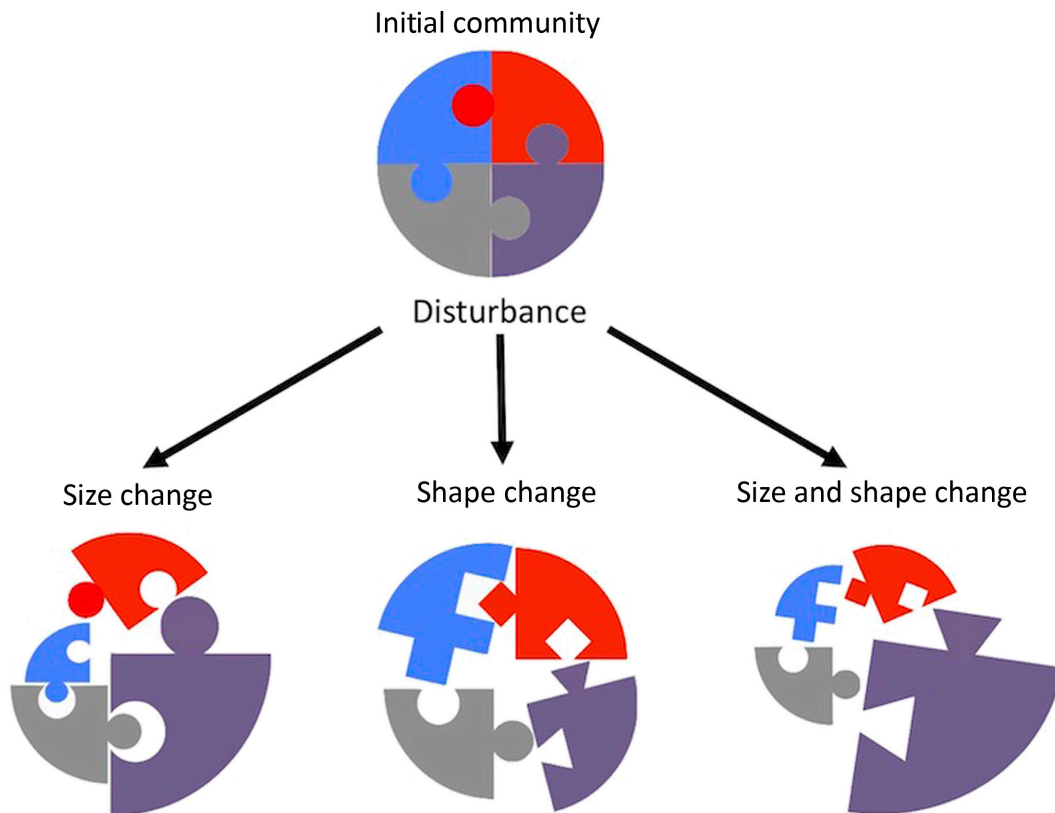


Figure 1. Conceptual framework of the eco-evolutionary humpty-dumpty effects. Even if all ecological pieces (species) that make up a community persist following a disturbance event, these pieces can change size (abundance), shape (evolutionary/plastic shift) or both, which may prevent successful restoration.

using the following databases from the Web of Science Core Collection: science citation index expanded (1900–present), social sciences citation index (1900–present) and arts and humanities citation index (1975–present). These searches were conducted on 23 November 2021, and, when combined, produced 271 unique articles (Table 1, Supporting information). We assigned each article produced by our literature search to one of four categories: 1) community pieces have changed size (i.e. species abundance), 2) community pieces have changed shape (i.e. evolution/eco-evolution/plasticity), 3) the community is missing piece(s) (a species in the system is now absent – thus affecting restoration) or 4) the article did not fit the humpty-dumpty framework (e.g. the article was not an empirical study, no changes were observed in community pieces, changes were purely environmental or abiotic, simulations or methods papers, books, etc.). For the three categories that fit our revised humpty-dumpty effect framework, we further classified the restoration status of each article either as 1) a successful restoration example, 2) an unsuccessful restoration example or 3) an example where restoration was only proposed and not attempted, or restoration success was not assessed. In a few situations, articles represented more than one category ( $n=1$ ) or restoration status ( $n=2$ ) and therefore appear more than once in Table 1.

Of the 271 unique articles obtained through our literature search, we found 14 articles where populations changed in abundance (community pieces changed in size), 8 articles where populations had evolved (community pieces had changed shape) and 9 articles where populations or species were removed or extirpated (missing community pieces) (Table 1). Approximately half of these studies ( $n=14$ ) reported successful community restoration while the remaining studies either reported failed restoration ( $n=7$ ) or did not implement or assess the outcome of community restoration ( $n=12$ ). Although this review identified numerous papers that discussed, simulated or reviewed theory supporting the original, or our extended eco-evolutionary humpty-dumpty effect framework (Nemergut et al. 2013,

Moreno-Mateos et al. 2020, Tielke et al. 2020, Chaparro Pedraza et al. 2021), our systematic review shows that very few studies have explicitly evaluated if and how populations have changed in ways that may inhibit community restoration in accordance with the humpty-dumpty effect. Nevertheless, our review indicated that eco-evolutionary humpty-dumpty effects can influence the trajectory of restoration, suggesting this framework might be useful when considering actions to restore the biodiversity, structural complexity or functions of ecosystems in the future. Using case studies, we next highlight how ecological, evolutionary and joint eco-evolutionary alterations can drive changes in the sizes and shapes of community pieces, which in turn can prevent them from fitting back into the original community framework.

### Change in size (abundance) of community pieces

Disturbances often change the size of community pieces by altering either the relative or absolute abundances of populations in a community. A classic example of this is the overexploitation of populations, e.g. due to overfishing (Hutchings 2000). Reducing harvesting pressure seems like the obvious road to recovery; however, such reductions do not always result in population and community recovery, and when it does, recovery is often slower than expected (Hutchings 2000, Murawski 2010, Hutchings and Kuparinen 2017). One way that community restoration might fail, despite reduced harvesting pressure, is if increased natural mortality replaces anthropogenic-driven mortality. For example, ground fish abundance in the Gulf of St Lawrence and Scotian Shelf collapsed in the 1980s and 1990s due to overfishing, and many species have not recovered despite a fishing moratorium enacted in 1992 (Swain et al. 2011, Sinclair et al. 2015, Neuenhoff et al. 2019). Failed recovery is likely due, in part, to increased natural mortality via predation by grey seals

Table 1. Community restoration articles that follow the humpty-dumpty effect framework. Full list of articles resulting from the systematic literature search ( $n=271$ ) is provided in the Supporting information. The asterisk (\*) denotes articles that apply to more than one category of community change or restoration status.

Type of community 'piece' change	Restoration status	Number of articles	References
Change in size (abundance)	Successful	6	Wassenaar et al. 2005*, Graf et al. 2006, Summerville et al. 2007, Laughlin et al. 2008, Gould et al. 2013, Sun et al. 2018.
	Unsuccessful	5	Wassenaar et al. 2005*, Summerville et al. 2006, Hansen et al. 2010, Tognetti et al. 2010, Strommer and Conant 2018.
	Proposed/not attempted/not assessed	4	Dickson and Busby 2009, Harwell et al. 2010, Simler-Williamson et al. 2019, Pomeranz et al. 2020*.
Change in shape (evolution or plasticity)	Successful	2	Michels et al. 2007, Lo Cascio Sætre et al. 2017
	Unsuccessful	0	
	Proposed/not attempted/not assessed	6	Lemaire et al. 2012, Turlure et al. 2013, Ensslin et al. 2015, Silliman et al. 2018, Magnoli 2020, Ma et al. 2021
Piece loss (extinction)	Successful	6	Cione et al. 2002, Warren et al. 2003*, Redi et al. 2005, Sutton 2015, Brown et al. 2016, Moyer and Brewer 2018.
	Unsuccessful	2	Warren et al. 2003*, Schreiber and Rittenhouse 2004.
	Proposed/not attempted/not assessed	2	Gratton and Denno 2006, Pomeranz et al. 2020*

(Chouinard et al. 2005, Benoit and Swain 2008, Swain et al. 2011, Hammill et al. 2014, Neuenhoff et al. 2019). Grey seals were hunted to near extirpation in the early 1900s and their abundance remained low into the 1980s when fishing pressure was high (Bowen et al. 2003, Savenkoff et al. 2007). However, grey seal abundance has been increasing exponentially since the 1980s (Bowen et al. 2003). When the fishing moratorium was enacted, annual consumption of ground fish by grey seals exceeded commercial fish landings, and by 2010, grey seal consumption was seven times higher than pre-moratorium landings (Sinclair et al. 2015). This provides a clear example of how changes in the sizes of community pieces can prevent post-harvesting recovery.

Sometimes changes in the relative sizes of community pieces following disturbance go farther than just changes in population sizes and push ecosystems into an alternative stable state, which can prevent restoration attempts (Suding et al. 2004). This situation can happen when a previously rare or entirely new predator species enters the community and prevents the return of native prey species, or when a previously rare species becomes dominant and prevents the return of its competitors (Allen et al. 1995, Palmer et al. 1997, Bradshaw and Waller 2016). One clear example of this is observed in Jamaican coral reefs. Historically, these reefs have re-established fairly rapidly following frequent disturbance by hurricanes. However, changes in the relative sizes of community pieces due to overfishing has severely hindered the reefs' natural resilience (Hughes 1994). On Jamaican reefs, the overfishing of herbivorous fish enabled the proliferation of the herbivorous echinoid *Diadema antillarum* that became solely responsible for controlling algal populations (Hughes 1994). Following the outbreak of disease (a secondary disturbance), which caused the population of *D. antillarum* to crash, the reef lacked herbivorous fish (in this case, missing suitable ecological pieces) to control algal populations (Hughes 1994). As a result, thicker algal mats coated the surface of rocks and coral following the disturbances by hurricanes, preventing coral larvae from re-establishing the reef, which shifted the system into an alternative stable state of macroalgae dominance (Hughes 1994). Similar transitions to alternative states, including the well-known transitions from kelp forests to urchin barrens, are observed worldwide (Filbee-Dexter and Scheibling 2014). Furthermore, these shifts driven by overharvesting have been observed in other kelp forests around the world, including in Tasmania (Ling et al. 2009), southern California (Dayton et al. 1998, Hamilton and Caselle 2015) and Maine (Steneck et al. 2004). These case studies highlight how changes in the size of one or more ecological pieces following either 'natural' or anthropogenic disturbance event(s) compromise the ability to restore the diversity, structure and dynamics of natural systems to pre-disturbance conditions.

## Changes in the shape of ecological pieces

Evolutionary and plastic changes during community declines that alter the 'shapes' of ecological pieces can also explain

why degraded communities are unable to be restored back to their original or target state. Altered selection or genetic drift during degradation can change the evolutionary trajectory of systems by modifying population-level dynamics or the adaptive capacity of species. Here we define adaptive capacity (or adaptive potential) as the ability for a population to evolve adaptively (via additive genetic variation) in response to selection (Hoffmann et al. 2017, Kardos et al. 2021). Some of these evolutionary changes (e.g. shifts in selection regimes) can have cascading community-wide impacts that may prevent successful restoration, for example by altering the ecological interactions between species (e.g. competition or predator-prey cycles), decreasing the likelihood that communities will shift back to desired states, or reducing the adaptive potential of populations to disturbances (Hendry 2019, Moreno-Mateos et al. 2020, Chaparro Pedraza et al. 2021). One way that evolutionary changes can be induced within communities is by the introduction of non-native species (Leger 2008, Leger and Espeland 2010). When communities evolve in response to introduced species, removal of the original disturbance (i.e. the introduced organism) might not be effective in restoring the native community. Similarly, introduced species might possess adaptive capacity to novel environmental change, providing an ecological edge over native species that may allow non-native species to dominate the system (Matsubara and Sakai 2016).

One case study that illustrates the effect of evolution is the introduction of novel fish predators such as brown trout *Salmo trutta* to freshwater streams in New Zealand. The introduction of these non-native fish not only altered the ecological dynamics of these systems via shifts in nutrient cycling and predation (Flecker and Townsend 1994, McIntosh and Townsend 1996, McIntosh et al. 2010), but also induced evolution in the foraging behaviors of invertebrate prey species such as siphonurid mayfly larvae *Nesameletus ornatus* (McIntosh and Townsend 1996, Townsend 1996). Aquatic diurnal insects such as *N. ornatus* are an important prey resource to New Zealand galaxias *Galaxias vulgaris*, a native fish that forages diurnally for these invertebrates in the water column. In streams without introduced brown trout, *N. ornatus* larvae forage during the day, making them available as prey to native galaxias. In contrast, mayfly larvae in streams with brown trout switch to foraging at night, making them unavailable to native diurnal predators (McIntosh and Townsend 1996). This behavioral switch in *N. ornatus* larvae from trout-invaded streams persists in the laboratory regardless of the presence or absence of either native or introduced predatory fish, suggesting this behavioral shift is at least partially genetically determined. The inflexibility in this behavior contrasts against the behavior of *N. ornatus* larvae from uninvaded streams, which do alter their foraging behavior in the laboratory depending on the presence or absence of fish predators (McIntosh and Townsend 1996). Hence, in the absence of a rapid evolutionary reversal in larval behavior, this evolutionary change from diurnal to nocturnal behavior in mayfly larvae from invaded streams will likely prevent the restoration of these river communities to a historical

pre-disturbance state if or when New Zealand management priorities shift from supporting this trout fishery to conservation of native river communities (Jones and Closs 2018).

Evolutionary changes within communities can also be induced by other habitat alterations including the construction (or removal) of anthropogenic structures such as walls, buildings or dams. Dams are among the most widespread, habitat-altering anthropogenic structures, creating migratory and dispersal barriers for many freshwater species, while simultaneously altering selection regimes, including physical conditions, nutrient dynamics and predator–prey interactions (Palkovacs and Post 2008, Fan et al. 2015, Giery et al. 2015). The removal of dams is often implemented as a restoration strategy, aimed at restoring these impacted ecosystems to pre-dam conditions (Palkovacs and Post 2008, Palkovacs et al. 2008, Post et al. 2008, Apgar et al. 2017). However, local adaptation can influence the outcome of dam removal restoration projects, particularly if remaining populations have become maladapted to restoration conditions (Palkovacs et al. 2008, Palkovacs and Post 2009, Fan et al. 2015, Apgar et al. 2017). Trait evolution alters the shape of community components in ways that may hinder restoration efforts. Examples of dam-induced evolution in population traits are observed in freshwater systems worldwide. In the northeastern United States, populations of alewife *Alosa pseudoharengus* separated by dams have evolved trait differences in anadromy, body size, feeding strategies and spawning preferences (Palkovacs et al. 2008, Jones et al. 2013, Littrell et al. 2018). Similarly, in the Lancang-Mekong River, China, fish life-history traits have shifted toward smaller bodied, earlier maturing individuals following dam installation compared to pre-dam population traits (Fan et al. 2015). Shifts in life history traits, such as towards earlier and smaller maturation in fish, can destabilize ecosystems (Kuparinen et al. 2016), which may make it more difficult to achieve restoration success. This effect can occur via shifts in size-related predation and due to changes in behavior (e.g. reduction in boldness) associated with smaller body sizes (Biro and Post 2008, Kuparinen and Festa-Bianchet 2017). Similarly, evolutionary shifts in population-level traits can have broader effects on ecosystem structure and function via cascading effects on food webs stability and temporal changes in environmental oscillations (Rouyer et al. 2012). Thus, evolution in population traits driven by initial ecological disturbances can continue to affect the success of restoration attempts long after the initial disturbance to the system is removed.

Finally, phenotypic plasticity can also induce changes in the shape of populations, and developmentally or environmentally induced changes in population traits can affect restoration efforts. These changes can occur when plasticity alters traits such as foraging behavior or population age structure, which in turn affect population dynamics (Hendry 2019). These plastic effects can result in community-level shifts in food web structure, ecological processes or trophic interactions, and may even lead to evolution if cryptic variation within populations is exposed and followed by divergent selection (Pfennig and Pfennig 2009). For example,

captive-reared fish from hatcheries are often used to help restore wild fish populations (Jonsson and Fleming 1993, Brown and Day 2002). Yet in many cases, ecological traits, such as the development rate and behavior of hatchery-raised fish, are substantially different from their wild counterparts – even when genetic identities are the same, indicating a role for phenotypic plasticity (Chittenden et al. 2010, Larsson et al. 2011). Restoration consequences caused by this developmental-induced mismatch are seen in hatchery raised Atlantic salmon *Salmo salar* as hatchery smolts forage less than wild smolts (Larsson et al. 2011) and often fail to reach suitable breeding habitats as adults. Hatchery-reared fish also exhibit reduced antipredator behaviors, increased levels of conspecific aggression and larger bodies (Chittenden et al. 2010). As a result, when they are released into the wild, these hatchery-raised fish often behave differently than their wild counterparts, which can hinder the success of restoration projects. For example, the reduced antipredator behaviors observed in hatchery fish results in higher predation rates, meaning that most of these fish can die before reaching the sea (Olla et al. 1998, Jackson and Brown 2011). Indeed, Henderson and Letcher (2003) demonstrated that trout and older salmon consumed up to 60% of re-introduced native Atlantic salmon fry over a two-day period in the Connecticut river. These behavioral and ecological changes, in turn, can affect the rest of the river community structure as the few hatchery-sourced populations that do survive are morphologically and behaviorally different from the original wild populations. These physical and behavioral shifts exemplify plastic changes that alter the shape of ecological pieces under our revised humpty-dumpty effect framework, which in turn might explain some failed restorations.

## Changes in both size and shape of community pieces

Changes in the sizes and shapes of community pieces are not mutually exclusive. Indeed, given enough time, changes in the sizes of ecological pieces (e.g. a decrease in population size) can lead to those pieces changing shape (e.g. because of genetic bottleneck or drift). Similarly, a change in shape through evolution or plasticity can affect population size through effects on fitness. In these situations, successful restoration relies on a combination of ecological and evolutionary restoration strategies.

The introduction of non-native species is one way to alter both the sizes and shapes of the pieces of disrupted communities. A common example of this is when native herbivores evolve to rely primarily or solely on non-native plant species rather than their original native hosts. Such resource switches are frequently observed in Lepidoptera species. For example, at least 34% of butterfly species found in California now rely on introduced plant taxa for feeding or oviposition (Graves and Shapiro 2003), such as the Edith's checkerspot butterflies *Euphydryas editha* in Nevada (Singer et al. 1993). Historically, *E. editha* butterflies preferred the native *Collinsia*

*parviflora* as their sole host. However, the butterfly now prefers the invasive ribwort plantain *Plantago lanceolata* in locations where it has been introduced by cattle ranchers, and this change is at least partially due to evolution (Singer et al. 1993). Initially, butterflies attained higher fitness on the novel host versus the native host but fed on both species. By 2007, however, the butterflies living in cattle fields had evolved to reject their ancestral host completely and only occurred on the invasive host (Singer and Parmesan 2018). When cattle ranching ceased and the return of native grasses reduced the density of invasive ribwort plantain hosts, the fitness of the butterflies which were now adapted to the introduced host also declined, resulting in the extirpation of the population in two years (Singer and Parmesan 2018). Following a natural reduction in native grass length caused by limited nutrient availability, ancestral hosts became suitable again and were colonized by a nearby butterfly population that still preferred the ancestral host. Related butterfly species made the same switch in Europe and are now declining as agricultural fields become wild again – possibly too quickly for adaptation to other hosts to occur (Singer et al. 1993). This case study illustrates that although the inclusion of exotic species in the diets of native herbivores may provide a buffer for some species, such dietary switches can also modify the sizes and shapes of community pieces to such an extent that they are difficult to restore to their historical conditions following the removal of the introduced species.

## When the environment changes and the pieces do not

So far, we have discussed when puzzle pieces (populations) change size (abundance) and shape (traits). Now we explore what happens when the environment changes in more than one way, when not all the environmental changes can be reversed, and the community members do not change their shape to match. Even the most sophisticated restoration plans can fail if abiotic factors such as climate or nutrient conditions shift away from those required by the original native community (Jackson and Hobbs 2009, Mora et al. 2013). Such abiotic changes could result from regional climatic shifts or by the interactions of species that are currently, or have previously (e.g. legacy effects), been a part of the community (Corbin and D’Antonio 2012). For example, areas colonized previously by nitrogen-fixing lupines *Lupinus arboreus* in California are characterized by a distinct soil biogeochemistry, which lead to differences in aboveground biomass and species composition compared to non-lupine sites (Maron and Jefferies 1999). These abiotic effects can persist for years following lupine removal or decline, with lupine-induced changes in soil characteristics influencing future plant community assemblages. For example, these changed soil conditions can facilitate invasive-dominated plant communities compared to non-lupine sites (Maron and Jefferies 1999).

When environmental changes happen, restoring communities back to their original location and composition may be difficult, if not impossible. Interactions between ecological and evolutionary changes can create unanticipated ecological mismatches in disturbed communities, which can alter important community dynamics such as predator–prey cycles or nutrient cycling (Legrand et al. 2017). Failure to recognize such mismatches in advance can prohibit successful management, particularly in systems strongly affected by environmental change. For example, in species with seasonal color molts like snowshoe hares *Lepus americanus* and mountain hares *Lepus timidus*, ecological mismatch between coat color and background color leads to increased mortality (Zimova et al. 2016). Without considering such ecological mismatches, restoring predators to disturbed communities can have unanticipated consequences (Reznick et al. 2008). For example, mountain hares in northeast Scotland did not adapt their molt phenology to decreasing snow cover and currently experience a nearly two-fold increase in camouflage mismatch since the 1950s (Zimova et al. 2020). However, hares persist in these areas likely because their predators, including golden eagles *Aquila chrysaetos* and red foxes *Vulpes vulpes*, are functionally extinct (Thompson et al. 2016). Although camouflage mismatch currently incurs minimal fitness costs, sudden changes in predation risk might have dire consequences for those hare populations (Zimova et al. 2016). Therefore, future restorations, such as reintroductions of natural predators of hares, must be carefully planned to prevent population extirpations. Additionally, reintroduction of individuals that are already preadapted to the altered habitat (i.e. hares that evolved molt phenology with shorter snow seasons, Mills et al. 2018) is likely to improve restoration success.

## Moving forward with restoration in the Anthropocene

Evaluating both if and how to manage and restore ecological communities involves a delicate balance between limitations such as time, resources and socio-economic conflicts (Geist and Galatowitsch 1999, Knight and Cowling 2007). In the age of rapid global environmental change, careful thought must also be given to the future viability of restoration efforts given the expected impacts of future climate and land use change. Below we describe five guidelines that we believe will help facilitate current and future successful restoration efforts, given the potential widespread impacts of eco-evolutionary humpty-dumpty effects.

- 1) *Understand all the ecological pieces.* A critical starting point to understanding community restoration is knowing the presence, size and shape of the existing ecological puzzle pieces. This goal, however, is a monumental task in even the least diverse ecosystems. Hence, it will often be necessary to prioritize gathering knowledge about the identity

and roles that different species play in the functioning and structure of communities and ecosystems. These data can be collected through a combination of approaches including field-based observational work, manipulative field and laboratory experiments (e.g. mesocosms), or through dynamic models (e.g. models of metacommunity dynamics proposed by Montoya 2021).

Often, these important community pieces are top predators (Sergio et al. 2005, 2008, Ritchie and Johnson 2009, Zarnetske et al. 2012, Urban et al. 2017) or keystone species (Mills and Doak 1993, Power et al. 1996). For example, non-native feral pigs *Sus scrofa* on the Channel Islands of California facilitated the colonization and expansion of an unnaturally large population of golden eagles *Aquila chrysaetos*, a top terrestrial predator and protected species (Roemer et al. 2001, 2002). Understanding that hyperpredation by golden eagles (driven by feral pigs) was the underlying cause of endemic island fox *Urocyon littoralis* population crashes was crucial for saving the endemic island fox from extinction during the removal of invasive feral pigs (Roemer et al. 2001, 2002, Courchamp et al. 2003). This is one example of a situation where restoration cannot simply be achieved through the removal of a primary disturbance in a system (invasive pigs), and now paradoxically the successful conservation of the island fox populations is contingent on the control of the golden eagle population (Courchamp et al. 2003). Another example can be found in Dutch populations of the butterfly *Boloria aquilonaris*, which are experiencing metapopulation collapse (Turlure et al. 2013). Translocation of *B. aquilonaris* from stable Belgian metapopulations could be one restoration strategy to save the declining Dutch populations, however Dutch sites support lower quality host plants compared to Belgian sites. This difference may prevent successful restoration using this translocation approach as Belgian butterflies are unable to survive on the low-quality Dutch host plants (Turlure et al. 2013). As a result, future efforts to conserve declining Dutch butterfly populations would need to consider the mechanisms underlying differences in Belgian butterfly performance between low- and high-quality hosts, potentially facilitating local adaptation of Belgian individuals to low quality hosts prior to translocation efforts (Turlure et al. 2013).

- 2) *Maintain ecological pieces in situ*. When possible, maintaining the ecological components of communities in situ can help minimize the impact of the humpty-dumpty effect on future restoration attempts. Maintaining ecological pieces as part of their natural communities may include the construction of ecological sanctuaries, which exclude unwanted predators or competitors (Burns et al. 2012, Bombaci et al. 2018) or prioritizing management of areas supporting genetically diverse populations or high phylogenetic community diversity (Winter et al. 2013). Preserving or restoring sites with high phylogenetic diversity may also be an effective bet-hedging strategy to help current or future restoration attempts succeed at restoring the ecological functions of a community (Cadotte et al.

2012, Kettenring et al. 2014), as more phylogenetically diverse communities show increased functional stability (due to increased redundancy) and ecological complementarity via greater niche partitioning (Kettenring et al. 2014). Similarly, maintaining sites that support populations with high levels of genome-wide diversity could also be effective for preserving adaptive potential of populations, as greater additive genetic variation (typically present in larger populations) may facilitate more rapid adaptive responses to future selection regimes (Kardos et al. 2021).

Strategies for maintaining ecological pieces in situ could also include targeted population management aimed at preserving declining species or declining population genetic diversity using species-targeted approaches such as the installation of nest boxes, closure of breeding areas and improving population or habitat connectivity (Eadie et al. 1998, Lindsay et al. 2008, Krosby et al. 2010). Wherever possible, managers should focus on conserving connectivity between the potentially isolated pieces (Krosby et al. 2010). Maintaining connectivity may facilitate the preservation of populations and species that contribute to biodiversity and ecological functions or services in situ and may also allow for a species to return to an area from where it was lost. This approach may also enhance adaptive capacity of the system by increasing the additive genetic diversity of in situ populations (Kardos et al. 2021). Management actions that facilitate dispersal among natural areas include establishment of landscape corridors or stepping-stone reserves or actions that increase matrix permeability. If natural migration is not an option, assisted migration or translocations (Aitken and Whitlock 2013) can also help preserve species and populations in situ. However, caution should be used when determining the frequency and source location of such restoration actions (Weeks et al. 2011, Pérez et al. 2012, Furlan et al. 2020), as decisions regarding the source of individuals for translocations can influence the evolutionary trajectory and adaptive potential of communities (e.g. if translocated individuals are adapted to different environmental conditions) (Stockwell et al. 2016).

- 3) *Maintain ecological pieces ex situ*. Multiple reasons can prevent the persistence of all ecological pieces within their natural location. For example, increases in sea level are likely to prevent the in situ preservation of crucial species in coastal communities (Ross et al. 2009, Bayard and Elphick 2011). In such cases, managers should focus on maintaining the missing pieces elsewhere, either outside of their current/native range or in captivity, to create a reserve to restore the fragmented community in an appropriate time or place in the future. Ideally, ecological pieces maintained ex situ might be able to be connected (e.g. via migration corridors) to current populations at a future time period (Krosby et al. 2010). Populations maintained ex situ should also be managed to preserve as much genetic diversity as possible to maximize adaptive potential (Kardos et al. 2021). If managers are unable to create other populations outside of the current range,



they should focus on managing habitats that remain less changed by disturbance through time, e.g. climate change refugia (Sgrò et al. 2011, Keppel and Wardell-Johnson 2012, Morelli et al. 2016). For species and populations in which wild populations cannot be established outside of the current species range, ex situ conservation via captivity, for example in zoos, botanic gardens or aquaria may be considered (Bowkett 2009, Conde et al. 2011). Many risks are associated with captive breeding programs (e.g. adaptation to captivity, loss of genetic diversity as discussed previously) that may hamper future restoration efforts (Snyder et al. 1996, Mathews et al. 2005). Therefore, unless a species is facing imminent extinction, managers should view ex situ conservation as the final resort. If ex situ conservation via captivity is used, extensive and ongoing management efforts are needed to ensure captive environments closely match the ecological, evolutionary and environmental conditions in wild systems to avoid genetic loss or adaptation to captive conditions (Ensslin et al. 2015, Stockwell et al. 2016).

4) *Manage systems to promote adaptive capacity.* The restoration and recovery of viable wild populations and communities may be facilitated via adaptation to current and future ecological conditions (Hampe and Petit 2005, Stockwell et al. 2016). Given that genetic variation provides the raw material for evolution, sufficient genetic variation is critical for evolutionary change and adaptive responses to occur. Loss of genetic variation can occur as locally adapted populations become extirpated or as the numbers of breeding individuals in existing populations decrease to levels at which inbreeding and drift begin to reduce genetic diversity (McKay et al. 2005, Lopez et al. 2009).

Genetic diversity can also have important community- and ecosystem-level effects (Bailey et al. 2009, Des Roches et al. 2018). These effects include promoting stability of eco-evolutionary processes such as predator–prey dynamics or nutrient cycling, maximizing population growth rates and increasing resilience to environmental changes by reducing ecological mismatches between populations and the community (Smith et al. 2014, Des Roches et al. 2018). Adaptive responses, however, can also lead to trophic cascades that might alter community pieces. For example, Madritch and Lindroth (2011) showed that shifts in aspen tree genotypes induce changes in microbial communities, which in turn alter soil processes leading to ecological cascades in the broader plant community.

Unfortunately, conservation decisions may not always protect important genetic variants, especially if the species' decline was not recognized early enough. Similarly, conservation measures that aim to preserve genetic diversity only in certain adaptive traits may inadvertently decrease the overall fitness and adaptive potential of a species by reducing genetic diversity elsewhere in a species' genome (Kardos et al. 2021). Given the widespread ecological and evolutionary impacts of human actions

and environmental changes, successful future ecological restoration will often require explicit consideration of current processes (e.g. priority and legacy effects) that could influence community development and assembly in the future. Management decisions should therefore aim to protect as much genetic diversity in as many critical or declining species as possible (Kardos et al. 2021) and create suitable conditions for evolution to recreate both lost genetic variation and particular adaptive traits. For example, intraspecific genetic diversity can be maintained by managing for a metapopulation where populations occur in a diversity of environments (either natural or created). This design can promote the persistence of adaptive differences within and between populations rather than allowing all individuals to adapt to the subset of remaining habitats or artificial conditions (Leibold et al. 2004). Another recommendation is to create the largest, most genetically diverse populations and most phylogenetically diverse communities possible during recovery. This could be achieved by connecting existing fragmented populations and communities (for example via wildlife bridges or tunnels, Smith et al. 2014) or using genetically and phylogenetically diverse seed banks for revegetation (Kettenring and Tarsa 2020). These management actions can improve the adaptive evolutionary potential in restored systems because larger populations tend to have higher genetic variance (Frankham 1996) and higher probabilities of beneficial mutations arising (Frankham et al. 2011, Weeks et al. 2011). Finally, additional genetic variation can be generated when individuals of varying genetic backgrounds reproduce and recombine alleles to create new genetic combinations via outbreeding or hybridization (Arnold 2004, Tallmon et al. 2004, Barrett and Schluter 2008). Thus, a basic recommendation would be to use genetic assays to identify the most divergent individuals to seed new populations or contribute to genetic diversity in captive breeding programs. The potential downside of genetic mixing is the possibility of decreasing local adaptation of an existing population by creating maladaptive gene flow or outbreeding depression (McKay et al. 2005, Frankham et al. 2011) or the genetic extinction of native taxa due to introgressive hybridization (Taylor et al. 2006, Kleindorfer et al. 2014). Therefore, genetic mixing is best applied following studies into adaptive genomics and risk assessments (Edmands 2007, Weeks et al. 2011).

5) *Substitute missing pieces with analogous pieces.* Restoring the biodiversity, structure or function of ecosystems through community-level management is harder when key pieces are unavailable or extinct. Taxa substitution aims to restore essential functions such as seed dispersal, grazing and bioturbation using extant species that are functionally equivalent to those lost by extinction or extirpation (Griffiths et al. 2011). For example, de-extinction through artificial selection is being employed to reconstitute ancestral phenotypes and ecological roles in domesticated cattle and horses (Stokstad 2015, Lundgren et al. 2018). However, in most situations, domesticated descendants are

unlikely to exist, necessitating a different solution such as taxa substitution or ecological replacement. For example, to restore functions lost to extinction, nonnative species of giant tortoise were introduced to areas around the world where original tortoise species went extinct (Hansen et al. 2010, Griffiths et al. 2013, Hunter et al. 2013, Falcón and Hansen 2018). These strategies, imperfect and controversial as they are (Nogués-Bravo et al. 2016, Rubenstein and Rubenstein 2016, Svenning et al. 2016), ultimately rely on an extant pool of biodiversity. This dependency highlights the need to knowingly conserve genetic and species diversity, not just for in situ conservation efforts, but also for the restoration of foreign and/or future communities and landscapes with functionally analogous pieces.

## Speculations

Despite our examples demonstrating how eco-evolutionary humpty-dumpty effects could prevent restoration success, our review returned little empirical evidence for these effects. We speculate this may be due to three factors. First, financial and time constraints often restrict restoration actions to overly simplistic goals that focus on species rather than whole community restoration and likely ignore eco-evolutionary humpty-dumpty effects. Second, inaccurate, or unavailable historical data, coupled with experimental challenges associated with testing eco-evolutionary dynamics in nature and in the lab (Hendry 2019) make explicitly testing for eco-evolutionary humpty-dumpty effects in communities difficult or costly. Thirdly, despite an increasing focus on theoretical knowledge pertaining to eco-evolutionary processes affecting restoration, evaluations of restoration outcomes are still grossly understudied. Clearer definitions of restoration ‘success’, increased post-restoration monitoring and additional research into both restoration successes and failures that includes eco-evolutionary dynamics will be necessary to understand and predict the humpty-dumpty effect in the future. We believe that the eco-evolutionary humpty-dumpty metaphor is useful for organizing our thoughts on restoration practices, but still needs a fuller development into an explicit theoretical framework. We hope that our empirical review is a first step towards supporting and developing such a theoretical framework.

## Conclusion

We showed that many unsuccessful restoration attempts are affected by the humpty-dumpty effect, whereby fragmented communities are difficult to reassemble from the species and populations that remain post-disturbance. Our systematic literature search however, showed that few studies have explicitly considered how the humpty-dumpty effect has

affected restoration success in the 30 years since the original concept was proposed. To incorporate other factors that affect restoration success we extended the humpty-dumpty analogy to suggest that changes in ecological and evolutionary dynamics may also alter the remaining ecological fragments, thus limiting our ability to reassemble the ecological pieces. We demonstrated how ecological and/or evolutionary changes can potentially inhibit restoration even if all ecological components are present. Given our revised eco-evolutionary humpty-dumpty effect framework, we provided five guidelines to facilitate successful restoration efforts including: 1) understanding all the ecological pieces that comprise a focal community, 2) maintaining ecological pieces in situ when possible or 3) maintain ecological pieces ex situ if necessary, 4) managing systems to promote adaptive capacity and 5) substituting missing pieces with analogous pieces to facilitate restoration of important community structures (e.g. food web complexity) or functions. Careful consideration of these guidelines, including benefits and caveats associated with the eco-evolutionary humpty-dumpty effect, combined with well-defined restoration goals, might facilitate ecosystem restoration outcomes in the future that more successfully put the ecological community pieces together again.

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## Data availability statement

This paper contain no original data.

## Supporting information

The supporting information associated with this article is available from the online version.

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