THE ECOLOGY OF DE-EXTINCTION

A mammoth undertaking: harnessing insight from functional ecology to shape de-extinction priority setting

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Summary

1. De-extinction, or the process of resurrecting extinct species, has been advanced as a promising new tool in conservation biology. Most scientific discussion of de-extinction has thus far focused on the methodology and ethics of bringing once-extinct species back to life. We ask: How can de-extinction be strategically shaped into a service that maximally benefits ecological communities and ecosystems?

2. Ecologists often indicate that the worst facet of extinction is the associated loss of ecological function. Several decades of research on defining, classifying and tracking changes in portfolios of ecological function have generated a rich repository of information that should be mined to help guide de-extinction towards a future where its products can meaningfully restore extinction-induced loss of function.

3. Classifications of ecological function remain more subjective than other biological taxonomies. Yet, there is a clear consensus among ecologists that the functions of certain species are less ecologically redundant than others. The loss of such functionally unique species can have proximate and cascading effects on community and ecosystem functioning.

4. We review, from an ecologist's vantage point, efforts underway to use de-extinction to resurrect the woolly mammoth and the passenger pigeon. These iconic case studies illustrate the opportunities and challenges ahead for restoring ecological function using de-extinction.

5. There is great risk that de-extinction could limit itself to the fabrication of products that mimic the biology of extinct species, but fail to resurrect their ecology. We suggest three ways that de-extinction may more meaningfully restore the functioning of once-extinct species: (i) select target species from guilds with low functional redundancy; (ii) concentrate on species that went extinct recently rather than older extinctions; and (iii) only work with species that can be restored to levels of abundance that meaningfully restore ecological function.

Key-words: cascading effect, conservation, de-extinction, diversity, extinction, functional ecology, functional redundancy, mammoth, passenger pigeon, restoration

Introduction

Historically, extinction was permanent in a way that few biological processes are. The binary finality of extinction, however, is being challenged by fast-moving progress in de-extinction science. De-extinction, as reviewed by Seddon, Moehrenschlager & Ewen (2014), is the process of using new developments in ancient DNA sequencing and genetic engineering to resurrect once-extinct species. The pros and cons of de-extinction have been productively debated (Sherkow & Greely 2013; Shapiro 2015a). Here, we endorse neither side of this debate. We instead accept

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the premise that the tools of de-extinction will likely be used in one form or another in the near future to help manage the conservation of biodiversity.

With a few exceptions (Seddon, Moehrenschlager & Ewen 2014; Shapiro 2015a), little attention has been given to whether the products of de-extinction can resurrect the ecological functions of extinct species. As the current pathways of de-extinction are not capable of producing exact replicas of extinct species, the primary focus of de-extinction efforts should be on the production of functionally equivalent proxies (Shapiro 2016). Losses of function can have far-reaching consequences for extant species, can realign the physical and biological functioning of whole ecosystems and can cascade across vast reaches of ecological time (Barnosky *et al.* 2015). To ensure de-extinction does not simply manufacture functionally ineffectual eco-zombies, much more discussion is needed on how de-extinction can meaningfully recover the functions once delivered by extinct species.

To consider if and how de-extinction can be used to fill the functional holes punched in Anthropocene ecosystems, we review how ecological functions and functional diversity are measured, consider how and where functional redundancy occurs and review the challenges and opportunities for recovering function in two rapidly advancing de-extinction case studies: woolly mammoths (*Mammuthus primigenius*) and passenger pigeons (*Ectopistes migratorius*). Through this review, it becomes clear that de-extinction science requires deeper considerations of the ecological uniqueness of target species, ecological hysteresis and interactions between the resurrection of a species' abundance and its ecological function.

Ecological function defined

Here, we define 'ecological function' as the diverse forms of influence an organism has on ecological dynamics (Tilman 2001). Early measures of diversity in ecological communities emphasized species diversity. Interest in measuring functional diversity emerged decades later (Hooper & Vitousek 1997; Tilman 2001). This alternative view of ecological diversity stressed the value of quantifying not only what *kinds of organisms* are present in an ecosystem, but also *what kind of ecological tasks these organisms deliver* and how functional loss influences dynamical properties like community stability (Wardle, Bonner & Barker 2000).

## Measuring ecological function and linkages to extinction

Plant functional trait taxonomies have a longer history of study and are frequently characterized based on morphological and life-history attributes. Animal functional traits are more often based on the trophic interactions and behavioural traits (see Table S1, Supporting Information). Rubrics for defining plant functional traits are becoming increasingly standardized, but the process of systematically defining traits for animals is still dynamically evolving (Blaum *et al.* 2011). By far the largest number of species that have been submitted for consideration as targets for de-extinction are animal species (Fig. 1). This bias means de-extinction scientists will need to grapple with an as yet rapidly evolving set of complex principles for defining faunal function.

Understanding the relationship between species diversity and functional diversity is essential to understanding how extinction erodes function and, importantly, if, when and how de-extinction may best promote the recovery of such function. Across very large spatial scales, a strong positive, but saturating, relationship has often been observed between species diversity and functional diversity across a wide range of taxa (Lamanna *et al.* 2014). At smaller spatial scales, however, there is more variation in the relationship between species diversity and functional diversity: some systems lose functional diversity much *faster* than species diversity (D'Agata *et al.* 2014), and others show no relationship or exhibit an inverse pattern (Villéger, Mason & Mouillot 2008; Edwards *et al.* 2013).

Functional uniqueness of species

Are all species created equal in regard to their contribution to ecosystem functioning? Several studies have explored the patterns and distribution of functional redundancy
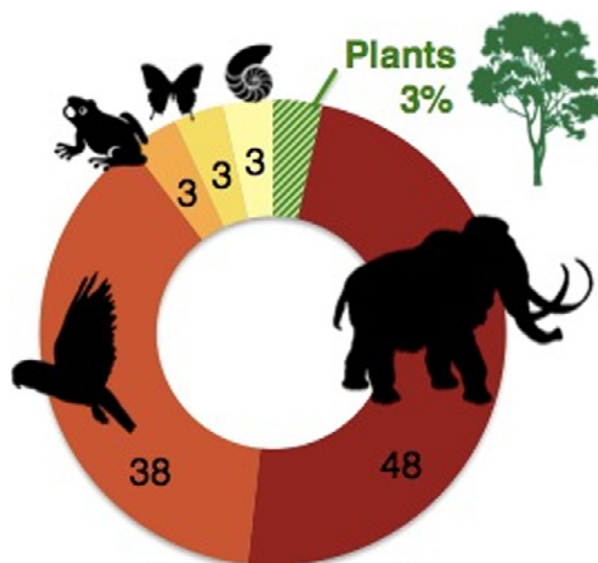
Fig. 1. Taxonomic breakdown of species (animals subdivided by class) located in a literature review of named candidates for de-extinction (see Table S2 for full species list and references). De-extinction considerations have disproportionately focused on animals (solid colours) with emphasis on vertebrates. Plants (green, hashed colours), as yet, have been little acknowledged in the de-extinction literature. Numbers indicate the absolute number of species. Red = Mammalia; dark orange = Aves; light orange = Amphibia; dark yellow = Insecta; light yellow = Gastropoda.

within different ecosystems (Micheli & Halpern 2005; Mouillot *et al.* 2014), with the common result that the amount of redundancy varies by functional group. It seems, however, universally clear that some functional groups are very species-depauperate, and consequently, many systems contain species which deliver unique and unreplicated functions (Halpern & Floeter 2008; Hoey & Bellwood 2009; Mouillot *et al.* 2014).

Determining where low levels of functional redundancy are situated taxonomically and geographically can help make de-extinction more ecologically strategic. Redundancy tends to be lower in systems with lower species richness. Because diversity is associated with both latitude and habitat, levels of redundancy may be proportionally lower (and levels of functional uniqueness higher) in higher latitude temperate regions and other lower diversity systems (e.g. insular ecosystems). It is worth noting, however, that a number of iconic examples of functionally unique species, such as elephants (Asner *et al.* 2009) and bumphead parrotfish (McCauley *et al.* 2014), are drawn from speciose tropical ecosystems.

Most candidate species proposed in the de-extinction literature thus far are terrestrial (see Table S2). This terrestrial bias may derive both from the much lower rates of human-associated marine extinctions (McCauley *et al.* 2015) and from heightened awareness of terrestrial extinction. Low levels of functional redundancy, however, are well known for marine communities (Halpern & Floeter 2008), and numerous extinct and near-extinct marine species have been classified as functionally unique (McCauley *et al.* 2014; Estes, Burdin & Doak 2016).

One legitimate critique of the study of ecological function that deserves to be kept at the forefront of discussions on applying this science to de-extinction is that such functions are often ambiguously defined (Petchey & Gaston 2006). While such concerns about the subjectivity of ecological function are clearly important, there appears to be a consensus among ecologists that functional redundancy varies meaningfully and that functionally unique species shape critical processes in ecology.

The takeaway for de-extinction planning seems clear: speciose functional groups will benefit less from de-extinction efforts, whereas functional groups with only a few species may benefit disproportionately.

Functional uniqueness within species

We are becoming increasingly aware of ecologically significant functional variation between conspecific individuals and between different populations of the same species. For example, when exposed to a food-limiting environment, California sea otter (*Enhydra lutris nereis*) diet and foraging behaviour differed substantially between individuals. Intraspecific variation in behaviour can be observed at the population level as well. Both California sea otters and lake trout (*Salvelinus namaycush*) have been found to have significant within- and among-population differences in

trophic level (Vander Zanden *et al.* 2000; Tinker, Bentall & Estes 2008).

De-extinction operates by recovering individuals of extinct taxa. Such individuals, however, may represent an ecologically idiosyncratic and constrained view of the historic breadth of intraspecific variability. This science suggests that de-extinction may need to manage for intraspecific bottlenecks in ecological function along with genetic bottlenecks (see Steeves *et al.* 2016).

Functional extinction and abundance

Functional extinctions can (and often do) occur long before a species goes extinct globally. We use the term functional extinction to demarcate the point at which a species fails to perform its historical functional role (McCauley *et al.* 2015). Species of tuna, sawfish, sea otters, tigers and birds are all examples of taxa that are biologically extant, but have been determined to be functionally extinct (Estes *et al.* 2011). In some instances only very slight decreases in abundance can precipitate a functional extinction – as in the case of large-bodied, high-trophic-level species (Saterberg, Sellman & Ebenman 2013). De-extinction practitioners must be mindful of such nonlinearities when determining target abundance levels needed to meaningfully resurrect ecological function (Winfree *et al.* 2015). Including a focus on recovery of abundance in de-extinction planning also holds open the option of resuming sustainable harvest for such species, should this eventually prove desirable.

Cascading effects of functional extinction

Communities and ecosystems operate as intimately interconnected living networks (McCauley *et al.* 2012). The loss of a single species, particularly a functionally important one, often triggers a cascade of secondary extinctions, each with potential for secondary functional impacts (Dunne & Williams 2009). These changes can ripple through ecosystems, causing whole-scale state change (Estes *et al.* 2011). De-extinction would be most impactful in scenarios where the tool can be used to nip incipient cascading change in the bud.

One frequently discussed group known to drive such disassembly are top predators. For instance, localized extinctions of sea otters are widely believed to trigger cascading effects on ecosystems, converting highly productive kelp forests to urchin barrens via a classic trophic cascade (Estes & Duggins 1995). The cascading effects of this functional loss impact not only prey species (urchins), but also myriad other species (e.g. from starfish to bald eagles) and ecological functions (e.g. carbon storage) (Wilmers *et al.* 2012).

Other classes of species with similarly outsized functional roles can also drive cascades. Herbivores, particularly megaherbivores, have been shown to elicit cascading change (Pringle 2008; Ripple *et al.* 2015). For example, in

modern African savanna communities, we find that the loss of megaherbivores can change vegetation communities, alter fire regimes and transform ecosystem composition and structure (Hempson, Archibald & Bond 2015; Bakker *et al.* 2016), with cascading effects on a wide range of other taxa (e.g. from snakes to fleas; McCauley *et al.* 2006, 2008; Keesing & Young 2014) and a diverse set of functions (e.g. disease dynamics; Young *et al.* 2014).

Species that physically engineer ecosystems (e.g. beavers, termites, elephants) are also likely to have transformative cascading effects on ecosystem functioning. Likewise, whenever foundation species (e.g. forest building trees, coral reefs) are impacted, we expect chains of functional consequences (McCauley *et al.* 2012). Species that perform services critical to reproduction of other species (e.g. pollination or dispersal) should be similarly predicted to have disproportionate functional effects (Potts *et al.* 2010). For instance, the recent decline of large frugivorous birds and the historic decline of island tortoises are both thought to have much altered vegetation structure and dynamics (Galetti *et al.* 2013; Hansen 2015).

Ecosystem managers have successfully restored prior ecological states by recovering the function of once-rare species (Hay & Rasher 2010). However, undoing regime shifts, once ecological tipping points have been crossed, can be extremely challenging (Selkoe *et al.* 2015). Often it is insufficient to restore one aspect of a system and expect a state shift (Suding, Gross & Houseman 2004). These issues of hysteresis necessitate that de-extinction practitioners adopt a realistic appreciation for the difficulty of reversing cascading functional change.

De-extinction and ecological time

The extent to which ecology abhors extinction-induced functional vacuums is highly relevant to de-extinction; that is, analogous to vegetational succession following treefalls, does community level eco-evolutionary succession eventually fill in functional gaps created by extinction? There is certainly evidence that other species, both native and non-native, can and do fill such gaps, making it difficult for de-extinction to attempt to fill such perceived gaps. This ecological niche filling can be biologically solidified by adaptive radiations that retune the phenotypes of extant species to capitalize upon extinction-generated opportunity.

Consider the case of the African elephant (*Loxodonta africana*), an icon of functional uniqueness. Field experiments that have removed elephants from savannas have noted post-removal increases in abundance of smaller mammals (Keesing & Young 2014). Eventually, the small herbivores may partially fill the functional voids created by the loss of elephants. For example, the conspicuous influence that elephant feeding has on woody cover and landscape structural diversity (Asner *et al.* 2009) could, over very long time periods, be partially compensated by predation on tree seeds and seedlings by expanding populations of small herbivores (Goheen *et al.* 2004). These noted expansions of small herbivores parallel observations of ecological expansion of mesopredators following local and global extinctions of large carnivores (Prugh *et al.* 2009).

In addition to the possibility that other species will partially fill in extinction-created functional voids, there will also be scenarios in which functional gaps would widen via cascading extinction. Janzen & Martin (1982), for example, consider instances in neotropical landscapes in which large-fruited trees previously dispersed by Pleistocene megafauna have become increasingly rare. Similar effects may be underway elsewhere (Galetti *et al.* 2013). In such regions, recovering long extinct megafauna via de-extinction would not immediately restore their role as dispersal agents of large-seeded trees if these trees were absent or rare.

A view of these dynamic system-level responses to functional voids suggests that de-extinction may be most effective at restoring function when used to recover recently extinct species. Reaching too far back in time to select de-extinction candidates increases the likelihood that such efforts will result in the production of functionally anachronistic species.

De-extinction within de-extinction

Most species are themselves communities that host diverse assemblages of symbiotic microbes. We have become increasingly aware of the important role that the microbiome plays in shaping the ecology and health of hosts, including influencing diet, metabolism and immune function. Various modes of herbivory, for example, are made possible by gut microbes that can rapidly digest particular types of complex plant carbohydrates. Can de-extinction be used to restore the microbiomes of extinct species, thereby recovering host species function with greater integrity?

Few de-extinction papers have addressed this issue (Sherkow & Greely 2013; Shapiro 2015b). There are several methods that could potentially be used to reconstruct a microbiome, such as utilizing coprolites, dental plaques or specimens frozen in permafrost (Orlando 2015; Ravin, Prokhortchouk & Skryabin 2015). Similar microbiomes could also be partially acquired from extant close relatives, again highlighting the value of selecting de-extinction targets for which this opportunity remains.

Of mammoths and pigeons

Two of the highest profile de-extinction candidate species are the woolly mammoth (*Mammuthus primigenius*) and the passenger pigeon (*Ectopistes migratorius*) (Church & Regis 2014). Research teams at multiple institutions are actively working on the revival of both species (e.g. 'The Long Now Foundation' http://longnow.org/revive/). These two case studies provide an opportunity to consider how de-extinction may best engage the complex challenges and opportunities for restoring ecological function.

Case study 1: woolly mammoth

While the extinction of mammalian megafauna, like mammoths, was likely caused by a variety of drivers, humans almost certainly played a role in their demise (Koch & Barnosky 2006). Mammoths, like other proboscideans, have been hypothesized to have delivered a diverse and inimitable set of ecological functions. These functions derive from the observation that mammoths consumed a lot, defecated a lot and travelled long distances (Fig. 2).

Mammoths and their congeners are believed to have shaped decomposition and nutrient turnover by consuming mass amounts of vegetation (Zimov *et al.* 1995; Doughty *et al.* 2015). This pathway was especially important in cold climates where turnover often occurs slowly. The consumption of plant material by mammoths also prevented leaf litter build-up, which would insulate the soil and reduce fertility (Zimov *et al.* 1995; Zimov 2005). The mobility of mammoths allowed the consumed nutrients to be transported far from nutrient hot spots before they were defecated (Zimov *et al.* 1995; Doughty *et al.* 2015). It is estimated that when Pleistocene megafauna, including mammoths, went extinct, the global mean nutrient distribution capacity of terrestrial animals dropped to about 8% of pre-extinction values (Doughty *et al.* 2015), which precipitated a 90–95% decline in lateral nutrient transport in the Americas (Doughty, Wolf & Malhi 2013).

Additionally, mammoths are believed to have exerted important mechanical and landscape-level engineering impacts on ecosystems. The trampling and aggressive feeding of these 6-tonne mammals are thought to have created disturbances that allowed less-competitive grasses to grow where moss or woodland would otherwise be dominant. Barnosky *et al.* (2015) concluded that the loss of such megafaunal ecosystem engineers likely contributed to ecological state shifts in North America: there was a noted increase in dense woody understorey and deciduous forests across North America (Haynes 2012) and, in higher latitudes, a shift from steppe grassland mosaic to moss-dominated tundra.

Woolly mammoth: challenges and opportunities

Can de-extinction recover the unique functions of the mammoth? According to Zimov, Zimov & Chapin (2012), there are areas in the Arctic that have both the climatic parameters necessary for the mammoth steppe ecosystem and grassland source populations. State shift reversal, however, may be challenging. For instance, no de-extinction studies have addressed the influence of soil pH on the return of grasslands. In the past 10 000 years, soils in this region may have become too acidic as a result of increased soil moisture to support the return of grassland ecosystems (Gough *et al.* 2000).
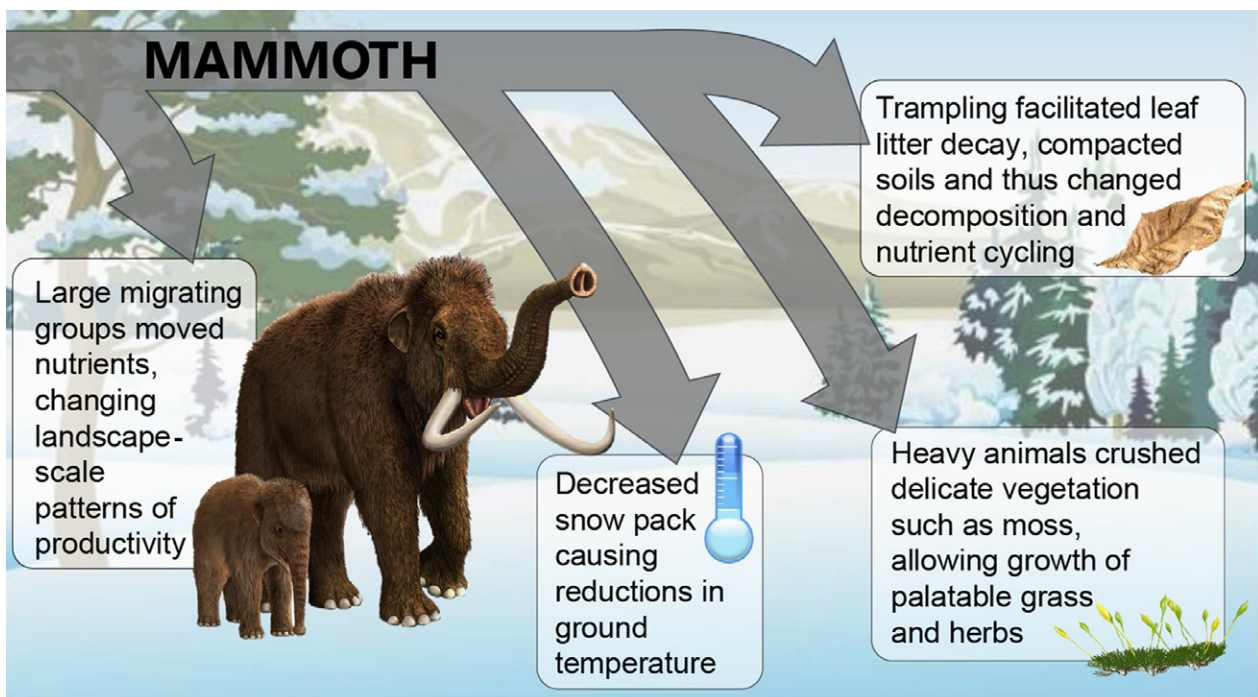
Fig. 2. The extinction of the woolly mammoth (*Mammuthus primigenius*) was associated with the extinction of a diverse set of ecological functions. De-extinction programmes currently targeting the resurrection of mammoths can be made more ecologically meaningful by endeavouring to recover both the biological and the ecological integrity of this species. Functions depicted were derived from the following literature: migration and nutrient transport (Zimov, Zimov & Chapin 2012; Doughty *et al.* 2015); decreased snowpack (Zimov 2005); increased grass and herb growth (Zimov *et al.* 1995; Barnosky *et al.* 2015); and trampling impacts on nutrient cycling (Zimov *et al.* 1995; Barnosky *et al.* 2015).

Post-glacial shifts towards warmer climate regimes in lower latitudes have similarly altered vegetation, likely prohibiting the return of the mammoths. Additionally, it would be hard or infeasible to introduce mammoths to lower latitudes in North America due to inevitable human–mammoth conflict. The areas of the Arctic with the necessary climatic parameters proposed by Zimov, Zimov & Chapin (2012) are less densely populated, but steps would need to be taken to prevent the overlap of mammoths and humans, as much for the sake of the mammoths as for the humans. The high frequency of elephant–human conflict in Africa provides some indication of how poorly humans and proboscideans coexist even in rural settings. Some of these complications associated with regional-scale programmes for the de-extinction of mammoths could potentially be circumvented by programmes focused on smaller, fenced landscapes. De-extinction run at smaller scales could recover some (e.g. woody plant suppression) but not all of the ecological functions (e.g. long-range nutrient transport) historically provided by mammoths.

As previously discussed, properly restoring function requires abundance levels high enough to begin to recover ecological function. Given the challenges associated with restoring mammoth populations anywhere near to functionally meaningful abundance levels, it is less clear how hopeful we can be about reversing large-scale ecological state shifts and recovering lost nutrient transport services.

Case study 2: passenger pigeon

A variety of factors are believed to have contributed to driving passenger pigeons from numbering in the billions during population peaks to becoming completely extinct. Human hunting along with episodic shifts in resource abundance and waves of deforestation (Pimm & Askinst 1995) played an unambiguously important role (Hung *et al.* 2014).

Passenger pigeons contributed a diverse set of ecological functions that shaped ecosystems across North America (Fig. 3). Recent evidence suggests that passenger pigeon population sizes fluctuated dramatically and that almost certainly some of the ecological functions of this species were regulated by their often high abundances (Hung *et al.* 2014). Passenger pigeons fed heavily on seeds, particularly tree nuts. They are believed to have been a major force of seed dispersal due to their propensity for high abundance, long-distance movement and delayed digestion (Webb 1986). Their influence as seed consumers and dispersers is hypothesized to have had an important influence on forest composition (Ellsworth & McComb 2003). This same mass consumption of seeds may have had an important influence on the population dynamics of seed-consuming faunal competitors, for example deer, squirrel and turkey (Neumann 1985). Alterations in competitive dynamics of passenger pigeons and mammalian forest species have even
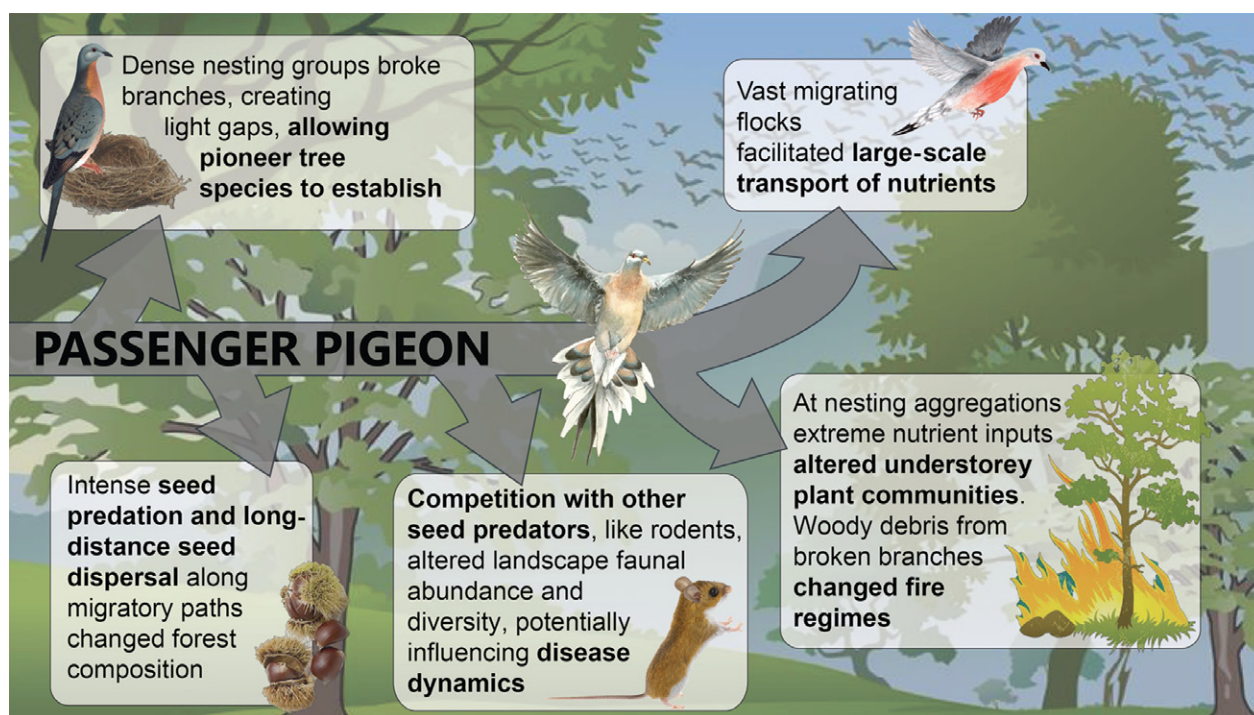
Fig. 3. Passenger pigeons (*Ectopistes migratorius*), driven extinct in 1914, had diverse functional roles in ecosystems. The ecological functions illustrated here were derived from the following literature: disturbances caused by dense nesting (Audubon 1831; Schorger 1955; Ellsworth & McComb 2003; Fuller 2014); nutrient transport (Webb 1986; Ellsworth & McComb 2003); seed predation and dispersal (Schorger 1955; Webb 1986; Ellsworth & McComb 2003); competition with other seed predators and disease dynamics (Neumann 1985; Blockstein 1998); and nutrient inputs from nesting aggregations (Audubon 1831; Schorger 1955; Ellsworth & McComb 2003).

been speculated to have influenced landscape-level disease dynamics (Blockstein 1998).

The high concentration and volume of nutrients in the defecation of passenger pigeon flocks shaped biogeochemical processes by both distributing (e.g. during migration) and concentrating (e.g. during roosting/nesting) nutrients. Avian control over the spatial distribution of nutrients is known to shape a wide range of ecological properties from food chain length (Young *et al.* 2013) to animal behaviour (McCauley *et al.* 2012). Less is known about the change elicited by passenger pigeons, but there are reports that vegetation communities under stable roosting sites were dramatically altered by the mass excretion of flocks (Audubon 1831; Ellsworth & McComb 2003).

Passenger pigeons, when amassed in extremely large roosting and nesting flocks, also exerted mechanical impacts on tree canopy architecture. Aggregations of roosting pigeons would break branches and topple smaller trees, leaving canopy gaps that likely promoted the establishment of partial shade-tolerant plant species (Schorger 1955; Ellsworth & McComb 2003). A secondary outcome of pigeons downing branches and trees was increased loading of wood fuel, which may have influenced fire regimes with knock-on effects on ecosystem functioning (Ellsworth & McComb 2003).

Passenger pigeon: challenges and opportunities

The hypersociality and large flocks that contribute to marking passenger pigeons as functionally unique create major barriers to restoring their functions. Passenger pigeon fitness may be impaired when they are not in massive flocks and lack social momentum to make decisions about navigation or are sufficiently abundant to detect and swamp predators (Stephens & Sutherland 1999; Hung *et al.* 2014). Even presuming passenger pigeons were able to survive in smaller numbers, many of the functions so intimately linked to mass abundance might be muted to the point of irrelevance. The prospect of producing millions or billions of passenger pigeons via de-extinction is daunting. Even if this is achieved, questions remain about whether their pre-extinction ecological functions were genetically programmed or learned.

Also significantly, the North American forests into which passenger pigeons would be reintroduced have changed considerably in the past one hundred years. Notably, tree species composition has changed: red oak (*Quercus rubra*) has replaced the once-dominant white oak (*Quercus alba*), and the American chestnut (*Castanea dentata*), a favourite food of the passenger pigeon, is all but extinct as a result of chestnut blight in its native range (Abrams & Ruffner 1995). Furthermore, the ecosystems of north-eastern North America contain many more humans than they did in a century ago. Accounts of passenger pigeons describe widespread damage to human estates as much as the forests, raiding crops and damaging property (Fuller 2014). Just as in the case of mammoths, it is hard to imagine that full-blown restoration would not also restore conflict between passenger pigeons and humans.

Conclusions

Examination of the pathways and roadblocks to restoring the ecological functions of once-extinct species using de-extinction provides a healthy opportunity to set expectations for what this new tool can and cannot promise for conservation and ecology. De-extinction may be deemed a success in many scientific circles if it is able to generate products that are genetically and morphologically similar to extinct species. Yet, from the vantage point of many ecologists, the viability of de-extinction as a conservation tool will hinge upon the success of bringing function back from the dead. Ecologists are likely to be a demanding audience: a resurrected mammoth counts as mammoth only if it looks like a mammoth *and* consumes, defecates, tramples and migrates like a mammoth.

Based on our review of the science of ecological function, we offer three primary suggestions to assist de-extinction practitioners in making their efforts more ecologically meaningful:

1. *Preferentially select de-extinction candidate species that have low levels of functional redundancy.* Greater impact can be made by resurrecting species that deliver functions that are poorly replicated by other species. Searches for low levels of functional redundancy among extinct taxa must be made amid a disconcerting amount of subjectivity, yet remain worthwhile.

2. *Prioritize species for de-extinction that went extinct recently.* Attempts to reintroduce lost functions via de-extinction can be ineffectual if too much time has elapsed. Like species, ecological communities evolve both structurally and dynamically such that resurrected species and their recovered functions mesh poorly with extant ecological networks. Chain reactions of post-extinction cascading functional change may be hard or impossible to reverse. Neglecting the complexities of eco-systemic evolution will relegate de-extinction to operating like a futile attempt to integrate a piston from a 1910 Model T Ford into a 2017 Tesla electric car. It may also be beneficial to proactively focus de-extinction efforts on species that are perilously approaching extinction but have not yet crossed the extinction threshold.

3. *Concentrate on the resurrection of species that can be returned to functionally meaningful abundance levels.* The delivery of ecological functions is often an abundance-dependent process. Even functionally important species can be resurrected via de-extinction without meaningful ecological benefits, if there are barriers preventing a return to ecologically meaningful densities. Barriers to numerical restoration via de-extinction can be diverse, ranging from changing dynamics in policy, disease, climate, basal system productivity and

predator–prey dynamics. Engaging in the resurrection of species for which such barriers are insurmountable may prove an exercise in ecological frustration.

It is worthwhile noting that both of the de-extinction case studies that we review here, the woolly mammoth and the passenger pigeon, measure up poorly against each of these three selection guidelines. A wide range of more 'ecologically smart' de-extinction choices are conceivable. The Christmas Island pipistrelle bat (*Pipistrellus murrayi*), the Reunion giant tortoise (*Cylindraspis indica*) and the lesser stick-nest rat (*Leporillus apicalis*), for example, would all be choices that better conform to the three recommendations we offer (see other examples in Table S3).

Final selections for de-extinction candidate species must responsibly attend to the differing views of how well a resurrected species fits into a particular social–ecological context. We, however, do see a need for careful internal evaluation of whether the maturation of de-extinction science will be more heavily shaped by ideas from ecology and conservation biology or by popular pressures.

Soberly considering where de-extinction will have the greatest and least success at restoring function provides a healthy way to advance de-extinction science and to properly set expectations. There is little to be gained for ecologists by having de-extinction simply manufacture biological curiosities for display in laboratories and zoolike spaces. Incorporating lessons from functional ecology into the DNA of de-extinction science provides a potentially promising pathway towards helping it achieve more meaningful goals.

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Data accessibility

This manuscript does not use data.

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Supporting Information

Additional Supporting Information may be found online in the supporting information tab for this article:

Table S1. Examples of functional traits assigned to plants and animals derived via literature review.

Table S2. Species enumerated in the scientific literature as potential candidates for de-extinction.

Table S3. List of example species that could serve as ecologically responsible targets for de-extinction.