De-extinction and evolution

Alexandre Robert, Charles Thévenin, Karine Princé, François Sarrazin, Joanne Clavel

To cite this version:

Alexandre Robert, Charles Thévenin, Karine Princé, François Sarrazin, Joanne Clavel. De-extinction and evolution. Functional Ecology, 2016, 10.1111/1365-2435.12723. hal-01360273

HAL Id: hal-01360273
https://hal.sorbonne-universite.fr/hal-01360273v1

Submitted on 5 Sep 2016

Title: De-extinction and evolution

Authors: Alexandre Robert[1], Charles Thévenin[1], Karine Princé[1], François Sarrazin[2] & Joanne Clavel[1]

[1]UMR 7204 MNHN-CNRS-UPMC Centre d'Ecologie et des Sciences de la Conservation, Muséum National d'Histoire Naturelle, 43, Rue Buffon, 75005 Paris, France

[2]Sorbonne Universités, UPMC Univ Paris 06, Muséum National d'Histoire Naturelle, CNRS, CESCO, UMR 7204, 75005 Paris, France.

Corresponding author: Alexandre Robert, UMR 7204 MNHN-CNRS-UPMC. Muséum National d'Histoire Naturelle, 43, Rue Buffon, 75005 Paris, France. Email: arobert@mnhn.fr. Phone: (33) 1 40 79 57 27. Fax: (33) 1 40 79 38 35.

Running headline: De-extinction and evolution

Key-words: De-extinction, conservation translocation, evolutionary processes, adaptation, biocentric conservation ethics, conservation phylogenetics

Summary

1. De-extinction, the process of resurrecting extinct species, is in an early stage of scientific implementation. However, its potential to contribute effectively to biodiversity conservation remains unexplored, especially from an evolutionary perspective.
2. We review and discuss the application of the existing evolutionary conservation framework to potential de-extinction projects. We aim to understand how evolutionary processes can influence the dynamics of resurrected populations, and to place de-extinction within micro- and macro-evolutionary conservation perspectives.
3. In programs aiming to revive long-extinct species, the most important constraints to the short-term viability of any resurrected population are (1) their intrinsically low evolutionary resilience, and (2) their poor eco-evolutionary experience, in relation to the absence of (co)adaption to biotic and abiotic changes in the recipient environment.
4. Assuming that some populations of resurrected species can persist locally, they have the potential to bring substantial benefits to biodiversity if the time since initial extinction is short relative to evolutionary dynamics. The restoration of lost genetic information could lead, along with the re-instatement of lost ecological functions, to the restoration of some evolutionary patrimony and processes, such as adaptation and diversification.
5. However, substantial evolutionary costs might occur, including unintended eco-evolutionary changes in the local system, and unintended spread of the species. Further, evolutionary benefits are limited because (1) the use of resurrected

populations as « evolutionary proxies » of extinct species is meaningless; (2) their phylogenetic originality is likely to be limited by the selection of inappropriate candidate species, and the fact that the original species might be those for which de-extinction is the most difficult to achieve practically; (3) the resurrection of a few extinct species does not have the potential to conserve as much evolutionary history as traditional conservation strategies, such as the reduction of ongoing species declines and extinction debts.

6. De-extinction is a stimulating idea, which is not intrinsically antagonistic to the conservation of evolutionary processes. However, poor choice of candidate species, and most importantly, too long time scales between a species' extinction and its resurrection are associated with low expected evolutionary benefits and likely unacceptable eco-evolutionary risks.

Introduction

De-extinction, the idea of bringing back extinct species using back breeding, or cloning and genomic engineering, has generated excitement and controversy (Sherkow & Greely 2013). So far, debates surrounding de-extinction have focused on ecological, ethical, societal and economic issues, but rarely on evolutionary considerations. Evolution is nonetheless one of the most important frameworks with which to describe and understand the effects of human actions on biological processes, and also the primary ethical postulate that justifies conservation research and practices (Soulé 1985). Evolutionary biology has been central to the science of conservation biology since its inception (Hendry et al. 2010) and many evolutionary biologists acknowledge that the current human-driven biotic crisis is likely to disrupt and deplete certain basic processes of evolution (Myers & Knoll 2001). Moreover, conservation biologists have developed theories to understand the evolutionary effects of the main drivers of biodiversity changes (such as habitat destruction, climate change, or invasive species), as well as the expected benefits of conservation actions (such as protection or restoration). The fields of conservation genetics and evolutionary conservation biology address, for instance, short-term genetic deterioration (Coron et al. 2013), future evolutionary potential (Lynch & Lande 1998), and the designation of conservation units and management plans that seek to conserve both evolutionary processes and patterns (Moritz 2002). The application of this evolutionary framework to any de-extinction approach is essential, not only to understand how evolutionary processes can favor or constrain the dynamics and ecological consequences of resurrected species, but also to put de-extinction projects, with their potential risks and benefits, into the widest, macro-evolutionary, conservation perspective.

The most important eco-evolutionary peculiarities of resurrected populations will be (1) the discontinuity of biological processes at the scales of the resurrected organisms and populations; (2) the small initial genetic diversity inherent to de-extinction pathways such as cloning; (3) the divergence of evolutionary and environmental trajectories potentially leading to the maladaptation of resurrected species to the rest of the world (biotic, abiotic, from local to global scale). Much of the excitement and controversy associated with de-extinction has focused on the first, qualitative, issue (discontinuity), because it is related to the very definition of de-extinction and what distinguishes it from all other types of conservation translocations (IUCN 2013, 2016). Yet, from an evolutionary perspective, the costs and benefits associated with de-extinction are also linked to the latter two, quantitative, issues. In particular, the divergence issue is critically related to the time elapsed between the extinction of the target species and its resurrection; the temporal scales envisaged for the de-extinction of the Sabre-toothed cat (*Paramachairodus ogygia*) or the Woolly mammoth (*Mammuthus primigenius*) are perhaps the most challenging aspects of these programs.

Although some authors have recently emphasized that de-extinction projects raise new questions in conservation science, some important ecological and evolutionary processes relevant to resurrected species have been studied in other contexts. For example, the reintroduction literature (Seddon, Armstrong & Maloney 2007) has provided a rigorous examination of the eco-evolutionary processes driving the dynamics of (initially small) populations restored into their historic range (Robert et al. 2004, Robert 2009) and some authors have recently argued that the fundamental criteria for selecting appropriate de-extinction candidates for conservation benefit should match selection criteria to those for reintroducing species that have been locally extirpated (Seddon, Moehrenschlager & Ewen

2014). On the other hand, the literature on invasive species has provided insights into populations that are completely exogenous to a given ecological recipient and evolutionary related questions of their success (Facon et al. 2006). Over the last few years, the debate on Pleistocene rewilding has raised the issue of restoration of long-extinct populations of extant species (Rubenstein & Rubenstein 2015) and conservation biologists have developed a feasibility and risk analysis framework for assisted colonization, the intentional movement of organisms outside their indigenous range (IUCN 2013). De-extinction is not simply an intermediate between reintroduction and invasion, but much can be learned from case studies on these topics.

In this paper, we review and discuss de-extinctions from an evolutionary perspective and address two questions:

1. Could de-extinction programs result in long-term viable and self-sustainable populations despite potential ecological and evolutionary factors limiting their dynamics, and if so, would they have the evolutionary potential to locally re-establish lost ecological functions in their recipient ecosystem? In other words, does de-extinction have the potential to be successful at the local scale?
2. Assuming that some de-extinct species are locally successful, would they constitute a benefit to biodiversity at a global and macro-evolutionary scale?

I) Evolutionary constraints on the local success of de-extinction projects

1. Discontinuity of biological processes

A first difference between de-extinctions and other types of conservation translocations (although shared with cloning of extant species) is the discontinuity or breakdown of some molecular, cellular, behavioral and ecological processes. Such discontinuity is mainly related to the non-genetic transmission of a proportion of the heritable biological and cultural information (Danchin et al. 2011), which might be disrupted by cloning protocols (Tsunoda & Kato 2002; Shapiro 2016). This includes epigenetic make-up, vertically transmitted symbionts, physiological effects, and cultural transmission. Such discontinuities are potentially associated with demographic problems. For example, somatic cell nuclear transfer protocols can be associated with epigenetic drift of the embryonic genome, leading to developmental constraints on the clones, and potential post natal mortality (Loi, Galli & Ptak 2007). Recent ecological research also showed that imperfect vertical transmission of symbionts can affect population dynamics (Yule, Miller & Rudgers 2013). Other examples include missing parental effects, such as antibodies transmission or behavioral care, which are likely to affect juvenile survival and, in turn, population dynamics.

2. Initial genetic diversity and evolutionary resilience

In most conservation translocations, the number of translocated individuals determines the extent of demographic stochasticity occurring during the establishment phase of the population’s dynamics and thus influences success (Robert et al. 2015). From a genetic viewpoint, the initial number of individuals partly determines the initial genetic variation and subsequent short-term genetic deterioration and lack of adaptability (Robert, Couvet & Sarrazin 2007). Numbers of released individuals in reintroduction programs typically range from a few tens to a few hundred individuals, and empirical reintroduction surveys suggest that there is a positive relationship between the number of released individuals and program success (Wolf et al. 1996), yet the potential contribution of genetic effects to this pattern has not been clearly established.

One peculiarity of de-extinction with respect to initial genetic variation is that initial numbers of individuals and initial genetic variation can be completely decoupled in cases the operations are based on e.g. multiple clones from a single source (see Steeves et al. 2016).

Although it has been suggested that new genomic editing techniques "*should be able to restore heterozygozity pretty easily in living genomes*" (Brand 2014), the amount of initial genetic variation is likely to remain an important issue in de-extinctions. Evolutionary resilience refers to both the ability of populations to persist in their current state and to undergo evolutionary adaptation in response to changing environmental conditions (Sgró, Lowe & Hoffmann 2011). Low genetic variation can affect evolutionary resilience through reduction in population fitness due to increased inbreeding and drift loads (Keller & Waller 2002) and through reduced adaptability to future environmental changes (Lankau et al. 2011) A population founded with the genetic material from only one or a few individuals will experience similar genetic problems as any natural or captive population experiencing a severe bottleneck, in turn reducing its ability to adapt to changing environments (Frankham et al. 1999). Even assuming that genomic editing can be used, not only to fill gaps, but also to capture a significant fraction of the genetic variation of closely related, extant species, this would necessitate the use of hundreds of distinct individuals of the extant species to avoid such bottleneck effect.

On the positive side, although low genetic variation has been shown to increase the extinction risk, there are some documented cases of populations that have persisted over long periods of time at extremely small population sizes prior to recovery (e.g., Groombridge et al. 2000), and both conservation translocation and invasive species literatures provide examples of viable populations founded with very few individuals (Taylor, Jamieson & Armstrong 2005). Furthermore, the science of conservation translocation provides concepts and tools (1) to minimize the loss of genetic variation of captive populations before release into the wild (Lacy 1989) and (2) to maximize post-release survival and population growth through optimal release methods (Hardouin et al. 2014) and through continuing and adaptive management (Swaisgood 2010). Finally, the persistence of small populations is a general concern in conservation biology, and more research on this issue will provide benefits beyond the field of de-extinction. For example, rapid progress in breeding and genetic technologies associated with the de-extinction research may also be applied to the conservation of extant endangered species based on cloning, e.g. to target under-represented genetic lines (Holt, Pickard &Prather 2004) or mitigate the effects of demographic stochasticity.

3. Evolutionary divergences

Like seed banks or cryogenic zoos, de-extinction raises the issue of evolutionary freezing (Simmonds 1962), which might imply strong divergence between the target species and its target environment. Such evolutionary divergence is primarily a matter of time. The times since extinction of the twenty de-extinction candidate species proposed following the TEDxDeExtinction conference (see Seddon, Moehrenschlager & Ewen 2014) range from a few years to more than 10,000 years, which means that, in some cases, several hundreds or thousands of generations might have elapsed since the original extinction (see Table 1). As a comparison, in the case of reintroductions, times between local extinction and the planned release range from a few years to a few hundred years (Fig. 1). Thus, although the time scales of de-extinction and reintroduction largely overlap, the temporal horizon envisaged for some "deep de-extinction" projects (as coined by Sandler 2014) is likely to be several orders of magnitude longer than for any reintroduction project.

Although the effect of the time since local extinction on the success of reintroduction programs has, to our knowledge, not been formally, empirically assessed, Osborne and Seddon (2012) recently pointed out that the longer this time, the greater the chance that suitable habitat will no longer be available. The environment is continually changing at different rates and scales, and humans are main drivers of these changes (Corlett 2015; Hofman et al. 2015). The main human drivers of rapid evolutionary responses are harvesting (Uusi-Heikkilä et al. 2015), invasive species (Mooney & Cleland 2001), habitat degradation (Macnair 1987), and ongoing climate change (Hof et al. 2011). Thus, in many regions of the world, conditions under which a 200-year-old tree established are likely to be quite different to those existing today (Sgró, Lowe & Hoffmann 2011), and the ecological context of a species that went extinct even only 100 years ago, such as the passenger pigeon (*Ectopistes migratorius*), has changed dramatically (Sherkow & Greely 2013; Peers et al. 2016).

These dramatic environmental changes can be associated with particularly strong and rapid selection, as many populations have the capacity to respond to, e.g., climate change within a time frame of tens of years (Hendry, Farrugia & Kinnison 2008). Such adaptive changes are generally considered much more rapid than non-adaptive changes (Stockwell, Hendry & Kinnison 2003), and most phenotypic differences observed among natural populations are likely adaptive (Hendry et al. 2010). Thus, recent temporal environmental changes and associated contemporary evolution are likely to generate strong levels of divergence between the environment and a de-extinct population that has not had the opportunity to adapt to (1) human induced environmental changes, (2) biotic changes in response to these changes, or (3) biotic changes in response to the original extinction of the target species.

4. Community processes

Evolutionary processes occurring at the level of the biological community further complicate patterns of divergence between de-extinct populations and their recipient environment. There is abundant evidence that ecological interactions drive rapid evolution and can change the direction of evolution compared to adaptation in isolation (Liow, Van Valen & Stenseth 2011; Lawrence et al. 2012). Coevolutionary processes occurring at the community level partly determine ecosystem functions (Bailey et al. 2009) and community response to climate (Reusch et al. 2005; Sgró, Lowe & Hoffmann 2011).

In the context of de-extinction, another potentially important factor of rapid evolutionary and ecological changes in the local community is the initial extinction of the target species itself, which is expected to affect eco-evolutionary feedbacks and in turn, community and ecosystem stability (de Mazancourt 2008). Based on experiments, Lawrence et al. (2012) showed that, after the extinction of a species providing important functions, surviving species tended to restore (rather than further disrupt) those functions at relatively short time scales (70 generations). The ecological consequences of phenotypic change are expected to be particularly important in species with large per capita ecological roles or those that are very abundant or rapidly evolving (e.g., some pathogens). For example, the loss of a predator can have manifold effects on the remainder of the community (Reznick, Ghalambor & Crooks 2008), such as the rapid growth of prey populations, changes in their age structure and population dynamics, and a restructuring of the lower trophic levels (Pace *et al.* 1999). Predators can have a profound effect on the evolution of other species.

Processes such as antipredator behavior can develop over relatively short timescales (Blumstein & Daniel 2005), and thus disappear similarly quickly if they are costly (e.g., vigilance).

These ecology-evolution interactions can be formalized thanks to the concept of eco-evolutionary experience (Saul & Jeschke 2015), which emphasizes that (1) during evolution, species adapt to biotic interactions in their native environment and thereby accumulate eco-evolutionary experience; and (2) this heritable experience might be applicable in new ecological contexts, e.g. when species are introduced to non-native environments. The degree to which a species can actually apply its experience in new ecological contexts depends on the ecological similarity between previous interactions and those in the new contexts, and significantly influences a species' proficiency to persist with its new interaction partners (Cox & Lima 2006).

Thus, although there is some evidence that species reintroduction can lead to local community and ecosystem recovery (Ripple & Beschta 2012), in the cases of long extinct populations, eco-evolutionary experience must be accommodated if the reconstruction of communities is to be successful.

5. Maladaptation and local success

The most important and immediate cost of such divergence and maladaptation is likely to be a demographic cost: the re-extinction of the resurrected population (Steeves et al. 2016). Theory has demonstrated that the capacity of a population to survive an episode of selection will be determined more by whether or not the population can survive the initial increase in mortality rate than by whether or not it can evolve in response to selection (Gomulkiewicz &

Holt 1995). In the case of invasive species, demographic costs of initial maladaptation are implied in the observation that introduced species (1) usually fail to become established (Sax & Brown 2000), (2) do so only after a lag period, which is often accompanied by phenotypic changes (Facon et al. 2006), and that (3) relatedness to native species can influence the success of invasive species (Strauss, Webb & Salamin 2006).

Phenotype plasticity tends to relax conditions under which such extinction is inevitable unless the costs of plasticity are high (Chevin, Lande & Mace 2010). However, both the discontinuity of biological and cultural processes and the loss of evolutionary and ecological histories might affect the effectiveness of plasticity in de-extinct populations. For example, at an individual level, organisms that evolved under variable climates tend to have much broader physiological tolerances for temperature than those that evolved in aseasonal zones (Tewksbury, Huey & Deutsch 2008). History might be especially important for phenotypically plastic responses, in which an individual uses specific environmental cues to elicit a phenotypic change (in morphology, behavior, etc., Lankau et al. 2011). In de-extinction programs, “rapid” environmental changes can alter the relationship between cue and future condition, such that the normal phenotypic response to certain cues is no longer adaptive (Schlaepfer, Runge & Sherman 2002).

II) Restoration of evolutionary trajectories

1) Phylogeny of de-extinct species

A. Evolutionary history of de-extinct species

Evolutionary history has been argued to capture the diversity of life better than simple measures of species richness (Purvis 2008). Since the 1990s, a phylogenetic approach to conservation has been proposed, in order to prioritize the protection of evolutionary distinct groups or of geographic areas. For example, at the level of a group of several species, a common measure used to quantify evolutionary history is phylogenetic diversity (Faith 1992), which is the minimum total length of all the phylogenetic branches required to connect the species in a phylogenetic tree. At the level of the individual species, indices of evolutionary distinctiveness quantify how few relatives a species has and how phylogenetically distant they are (Veron et al. 2015).

Phylogenetic diversity is sometimes used as a proxy of (integrative) functional diversity. It has been argued that, at the species level, evolutionarily distinct species exhibit rare functional traits (Pavoine, Ollier & Dufour 2005, but see Winter, Devictor & Schweiger 2012). Another important property is that both extinction rates and the prevalence of threatened species are non-neutral with respect to phylogenies (Diniz-Filho 2004). This knowledge of evolutionary history is increasingly used to set conservation priorities (Lankau et al. 2011; Hendry et al. 2010; Jetz et al. 2014), for example by identifying species which are at the same time both evolutionarily distinct and globally endangered (Isaac et al. 2007).

Can this framework be applied to the selection of de-extinction candidates? From the perspective of evolutionary conservation biology, one might consider that the “moral imperative” (Seddon, Moehrenschlager & Ewen 2014) to reverse species extinction caused by humans should be translated into an imperative to reintroduce their extinct genomes into the global gene pool (Church & Regis 2012), or even to restore evolutionary trajectories interrupted by humans. Because de-extinction is primarily a species-based approach, the use of evolutionary distinctiveness measures to select candidates might seem pertinent. Restoring evolutionary-distinct extinct species should, in theory, maximize the restoration of evolutionary history. However, resurrections of long-extinct species raise problems that do not exist for other types of conservation translocation, related to DNA degradation and imperfect knowledge of evolutionary relationships between species. In this context, it has been suggested that the same next generation DNA sequencing technologies that make de-extinction technologically feasible should be first applied to make new inferences on evolutionary relationships between species using ancient genomes (Shapiro & Hofreiter 2014), which offers promising potential to assess the evolutionary stakes of de-extinction initiatives.

B. Unintended phylogenetic bias

Despite the existence of an operational phylogenetical framework, the selection of candidate species for (classical) translocations is generally made without respect for phylogenetic considerations, although candidate selection can paradoxically (and unintentionally) lead to a reduced coverage of the phylogenetic tree of life. The decision and feasibility of translocating a particular extant species depends on multiple factors, including the conservation status of the species, the availability of individuals to be translocated, accurate translocation site, funds, public and political support, etc. Obviously, most of these constraints are non-neutral with respect to taxonomy. In the case of reintroductions, for example, Seddon, Soorae & Launay (2005) showed that vertebrate projects are over-represented with respect to their prevalence in nature. In the cases of rewilding programs aiming at re-establishing ecological functions (IUCN 2013), strong functional biases are expected. These taxonomic and functional biases will translate into phylogenetic biases.

The selection of candidate species for de-extinction projects is undoubtedly influenced by the biases that exist for other conservation translocations: a bias towards species with a supposedly important functional impact on ecosystems (such as grazers or predators), and more than ever a bias towards large, charismatic species. However, it is also very likely that these phylogenetic filters will differ, at least quantitatively in the case of de-extinction. First, because the list of known species extinctions since 1500AD is incomplete and biased (Purvis 2008), and, as the time scale increases, additional constraints on data and biological material availability are likely to amplify existing phylogenetic biases or engender new biases on candidate species (Alroy et al. 2001). Second, because the economic cost of de-extinction is intuitively far higher than for any other type of conservation translocation, any economic filter on the choice of candidate species (Tisdell & Nantha 2007) will be amplified.

Finally, the evolutionary benefit of any de-extinction program relies on the phylogenetic distinctness of the target species. However, the technical feasibility of a program is critically linked to the existence of organisms of phylogenetically closely related extant species to be used as egg donors, surrogates or references for genome reconstruction. This paradox questions the potential evolutionary benefits of de-extinction because evolutionary distinct species might be those for which de-extinction is least feasible.

2) Evolutionary benefits of de-extinctions

A. Evolutionary proxies?

This is perhaps one of the biggest paradoxes about de-extinction: although primarily based on the manipulation of genetic information, the potential evolutionary benefit of these operations is non-trivial, unlike their ecological benefit. Many authors acknowledge that de-extinction could have potentially important ecological benefits (although these benefits are complex to characterize and should be balanced against potential ecological risks). These benefits rely on the concept of ecological proxy, i.e., a substitute entity, which carries out similar ecological functions as the lost entity. Contrary to ecological proxy, the notion of « evolutionary proxy » is meaningless. In other words, while nature's functions and services can be synthesized (Redford, Adams & Mace 2013), nature, by definition, cannot be. In contrast to functional diversity that can potentially be recovered through recurrent selection, historically isolated lineages cannot be recovered and historically isolated but ecologically exchangeable populations should be considered as distinct significant evolutionary units (Moritz 2002). Furthermore, one major component of biodiversity – that is both a component of the evolutionary history and the main driver of evolutionary processes - is intra-species genetic diversity, which is expected to be extremely low in most if not all species resurrected through cloning. Thus, while both the species as seen as a typological entity and its functional ecological role can indeed be resurrected (or at least be replaced by proxies), the evolutionary loss associated with the initial species decline and extinction, is irreversible (Ehrlich 2014).

B. Balance of costs and benefits

What might the evolutionary benefits of de-extinctions be? At the scale of the local biological system, assuming that a given program (1) can reasonably be considered to be a short-term response to short-term human effects (see below), and (2) can restore a significant fraction of lost genetic information of the extinct species, expected benefits are the same as those expected from any other type of translocation: the restoration of some evolutionary patrimony and processes, such as adaptation and diversification. Further assuming that local restoration leads to the re-instatement of lost ecological functions, this could contribute, at the global scale, to the improvement of functional and genetic diversity. Even assuming that de-extinction does not restore a significant fraction of lost genetic information, it has been suggested that it could also contribute to the global evolutionary resilience of current biodiversity: some programs might directly benefit the conservation of particular phylogenetic groups by widening the ecological niche of the groups and their geographic ranges. For example, releasing elephants expressing mammoth genes into cold habitats can be seen as a means to extend the geographical distribution of elephants beyond their current declining, warm habitats (Shapiro 2015).

And what could be the evolutionary costs, assuming that the resurrected population is viable? Most, if not all evolutionary costs are probably mediated by ecological costs: (1) profound, unintended eco-evolutionary changes in the local system (including hysteretic phenomena, in which irreversible catastrophic shift occurs, see e.g., van Nes & Scheffer 2004), (2) unintended spread of the species, which is likely in the case of mismatch between historic and current or future habitat suitability (Peers et al. 2016), (3) sudden changes in local human pressures (e.g., increase of tourism following the resurrection of a highly charismatic species). These ecological costs, which are similar to some of the well-known consequences of invasive species and local environmental degradation, can have major unintended evolutionary consequences (Hendry et al. 2010).

3) Alternatives to de-extinctions

A. A restoration perspective

Since most of the arguments in favor of de-extinction are linked to the concept of ecological proxy, the best alternative to the resurrection of extinct species could be the selection and release of extant ecological replacements (IUCN 2013). Using existing species as alternatives deserves to be considered (IUCN 2016), not only from an ecological perspective, but also from an evolutionary perspective (see an example in the Pyrenean wild goat (*Capra p. pyrenaica*) in Garcia-Gonzalez & Margalida 2014).

The functional arguments put forward to justify de-extinction projects apply to the translocation of both living and any potentially resurrected species. However, from an evolutionary view-point, the translocation of a resurrected species cannot be equivalent to the translocation of a living species, even in the case where the latter is exotic. Living species participate in the evolutionary process in the broad sense, for instance because they undergo speciation, because they engage in coevolutionary arms race or trench-warfare with their cohort of pathogens (van Valen 1973), and because they continue to accumulate mutations, embedded in complex networks of gene flow. The eco-evolutionary factors that were driving the evolution of extinct species are just as extinct as the species themselves, and they can hardly be restored.

B. A conservation perspective

A common reaction against de-extinction is to ask “why would we spend all this energy and effort to bring back ancient animals but let so many others just disappear?” (Jamie Rappapaport Clark, quoted in Gross 2013). Is this heuristic argument consistent with our knowledge on the potential respective benefits on evolutionary processes and patrimony of conserving extant species versus resurrecting extinct species? It is estimated that one-fifth of vertebrate species are now threatened with extinction (Hoffmann *et al.,* 2010). However, one important point is that the vast majority of species threatened with extinction are not extinct (Barnosky et al. 2011), and this is also true for phylogenetic diversity (review in Veron et al. 2015). Thus, the recent loss of species is dramatic and serious but does not yet qualify as a mass extinction in the paleontological sense of the Big Five (Barnosky et al. 2011); and there is still much of the world’s biodiversity left to save, but doing so will require the reversal of the well-known Anthropogenic threats which are responsible for the ongoing declines (Ehrlich 2014). Thus, at a phylogenetic level, the potential benefits of saving threatened species and populations and reducing extinction debts is much more important than the likely benefits of resurrecting a few extinct species. This should be considered especially if one believes that there can exist a trade-off (e.g., economic) between de-extinction and other conservation approaches (see Iacona et al. 2016).

4) Evolutionary values

A. Ethics and values

Assuming that a de-extinction program results in a demographically viable population, and assuming that this population has led to the re-establishment of lost ecological functions. Do the conservation benefits of this program go beyond such functional aspects? The first functional aspect completed by de-extinction is a cultural service: the return of charismatic, popular species and a sort of reverence for the power of technology to resuscitate life. The second aspect completed by de-extinction is to restore functional services such as regulation, provisioning, or supporting. In conservation sciences, biodiversity services are prominently associated with utilitarian conservation values. Do we intend to resurrect the species that we have led to extinction in the past in order only to benefit from associated biodiversity services? Would this be ethically acceptable?

Acknowledging that change is the basis of life (Dobzhansky 1973) implies a fundamental change from an anthropocentric to a biocentric philosophy in which biodiversity has its own participant role and history independently of human beings (Maris 2010). Thus, many biologists agree that maintaining evolutionary potential and processes is a primary concern of conservation science (Soulé 1985; Myers & Knoll 2001), and conserving evolutionary trajectories might constitute a challenging major evolutionary transition inducing a deliberate overcoming of the Anthropocene (Sarrazin & Lecomte 2016).

In agreement with these general principles, many ecological restoration approaches do not aim to return to some arbitrary historical state but instead focus on the re-instatement of functions to restore degraded ecosystems (IUCN 2013) and promote adaptation (Aitken & Whitlock 2013). De-extinction, by essence, is not antagonistic with these efforts aiming at restoring or maintaining functional variation. However, it is questionable whether de-extinction has the potential to restore the evolutionary values of lost biodiversity. Sandler (2014) recently argued that deep de-extinction does not restore the natural-history properties of species, nor their wildness or independence from humans, because it results only in organisms whose genetic makeup most resembles that of species that went extinct long ago, and for whom we have reconstructed the genome. We agree that the potential of de-extinctions to reestablish lost (evolutionary) value is questionable, and we advocate that Sandler (2014)’s reasoning be extended below and beyond the species level and be focused on the evolutionary processes themselves, rather than the products of these processes. Evolution operates through changes in the frequency of alleles across generations and not instant heritable changes in the properties of individuals themselves. Species traits or functions are not intrinsic drivers of evolution. Thus, although de-extinction has the potential to restore some historical patterns that might in turn influence future evolution, the impossibility of restoring past dynamics of co-evolution between the target organisms and their environments is the main limitation to the evolutionary value of de-extinct populations.

B. Saving species to restore evolutionary trajectories: time scale and ethical justifications

Species are operational or ontological concepts useful to biologists rather than fixed categories within a continuum of biodiversity (Hey 2006). Although ultimate conservation goals are directed towards general processes, rather than products or entities (such as particular species), saving particular species from extinction is a pragmatic way to reduce the global rate of *untimely*, human-induced extinctions (Soulé 1985). This implies, however that the strong and essential discrepancy between the time scale of macro-evolutionary processes and the time scale of human influence is clearly acknowledged. De-extinction makes sense only if it constitutes responses to short-term (at the evolutionary scale) human influence: a few tens or hundreds of generations since the extinction of the target species, which represents only a small fraction of the average longevity of species (Jenkins 1992). Moreover, this also implies that causes of extinction are identified as being anthropogenic, which might be ambiguous for distant extinctions (Stuart 2015). Archaeogenomics based on ancient DNA has an important role in helping resolve both the causes and effects of these distant extinction events (Hofman et al. 2015), and thus provide evolutionary and ethical justification to de-extinctions.

Conclusion

De-extinction is a stimulating idea, which has raised, and will continue to raise debates among scientists. Focusing on ethical aspects, Sandler (2014) recently concluded that de-extinction is not intrinsically problematic, although it is in many respects a luxury. From an evolutionary view-point, we agree with Sandler's view and believe that critics from ecologists and evolutionary biologists do not need to focus on de-extinction *per se* but rather on its potential excesses, such as irrelevant choice of target species, potential of invasive impact on ecosystems, or unreasonable time scales. In particular, one of the most important scientific arguments against de-extinction could be an evolutionary one: extinct species do not evolve, but the rest of the world does. While some recent translocation practices aim at finding genotypes that can match future environments (Aitken & Whitlock 2013), de-extinction involves the risk that resurrected species are not adapted to the present, Anthropocene environment.

As the time elapsed since the extinction of the target species becomes longer, (1) the eco-evolutionary experience of the target species to its local environment will become lower and ecological functions provided by the target species will have more chance to have been fulfilled by evolutionary changes having occurred in the community; (2) the technical difficulty will increase due to DNA degradation, in turn increasing the necessity of using phylogenetically closely related extant species for genome reconstruction (Shapiro 2016); (3) our knowledge of the past ecological context and evolutionary history of the target species becomes fragmentary and our responsibility in the initial extinction becomes uncertain.

Both feasibility assessment and selection of species for de-extinction programs should include these considerations. Candidate species should have gone extinct recently, have high evolutionary distinctiveness, and their original environment should be well described.

Although species' traits are likely to influence de-extinction success, determining what life history or ecological traits can mitigate demographic problems associated with small population size, lack of genetic variation and maladaptation is not trivial. As in the case of invasive species, it is likely that barriers and filtering at various stages of de-extinction programs will shape complex relationships between species traits and success (Capellini et al. 2015).

Feasibility assessments and comparisons should rely on thorough interdisciplinary modeling and comparative analysis. Within the last decades, an array of empirical and theoretical modeling techniques have been developed to project past and future environmental, ecological and evolutionary dynamics, such as niche modeling, (no-)analog ecosystem projection, predictive evolutionary modeling and population viability analysis. Embracing these techniques is essential to select best candidate species, optimize release methods, and assess the chance of success and potential evolutionary benefits of de-extinction programs.

Acknowledgments

J.C. is supported by a grant from CG-77 Seine et Marne. We thank Phil Seddon for his invitation to write this article and for helpful suggestions, and two anonymous reviewers for their constructive comments.

References

Aitken, S.N., Whitlock, M.C. (2013) Assisted gene flow to facilitate local adaptation to climate change. *Annual Review of Ecology, Evolution, and Systematics,* **44**, 13.1–13.22.

Alroy, J., Marshall, C.R., Bambach, R.K., Bezusko, K., Foote, M., Fürsich, F.T., Hansen, T. A., Holland, S.M., Ivany, L.C., Jablonski, D., Jacobs, D.K., Jones, D.C., Kosnik, M.A., Lidgard, S., Low, S., Miller, A. I., Novack-Gottshall, P.M., Olszewski, T.D., Patzkowsky, M.E., Raup, D.M., Roy, K., Sepkoski J.J. Jr, Sommers, M., G. Wagner, P.J. & Webber A. (2001) Effects of sampling standardization on estimates of Phanerozoic marine diversification. *Proceedings of the National Academy of Sciences USA*, **98**, 6261–6266.

Bailey, J., J. Schweitzer, F. Ubeda, J. Koricheva, C. LeRoy, M. Madritch, B. Rehill et al. (2009) From genes to ecosystems: a synthesis of the effects of plant genetic factors across levels of organization. *Philosophical Transactions of the Royal Society B*, **362**, 1607–1616.

Barnosky A.D., Matzke N., Tomiya S., Wogan G.O.U., Swartz B., Quental T.B., Marshall C., McGuire J.L., Lindsey E.L., Maguire K.C., Mersey B. & Ferrer E.A. (2011) Has the Earth's sixth mass extinction already arrived? *Nature*, **471**, 51–57.

Blumstein D.T. & Daniel J.C. (2005) The loss of anti-predator behavior following isolation on islands. *Proceedings of the Royal Society of London B*, **272**, 1663–1668.

Brand, S. (2014) The Case for De-Extinction: Why We Should Bring Back the Woolly Mammoth. http://e360.yale.edu/feature/the_case_for_de-extinction_why_we_should_bring_back_the_woolly_mammoth/2721/

Capellini, I., Baker, J., Allen, W., Street, S., Venditti, C. (2015) The role of life history traits in mammalian invasion success. *Ecology Letters*, **18**, 1099–1107.

Chevin, L.-M., Lande, R. & Mace, G. M. (2010). Adaptation, plasticity, and extinction in a changing environment: towards a predictive theory. *PLoS Biology* **8**, e1000357.

Church, G. & Regis, E. (2012) Regenesis – How Synthetic Biology Will Reinvent Nature and Ourselves. New York: Basic Books.

Corlett, R.T. (2015) The Anthropocene concept in ecology and conservation. *Trends in Ecology & Evolution*, **30**, 36-41.

Coron, C., Porcher, E. Méléard, S. & Robert, A. (2013) Quantifying the mutational meltdown in diploid populations. *American Naturalist*, **181**, 623-636.

Cox, J.G. & Lima, S.L. (2006) Naivete and an aquatic-terrestrial dichotomy in the effects of introduced predators. *Trends in Ecology and Evolution*, **21**, 674–680.

Danchin, E., Charmantier, A., Champagne, F.A., Mesoudi, A., Pujol, B. & Blanchet, S. (2011) Beyond DNA: integrating inclusive inheritance into an extended theory of evolution. *Nature Reviews in Genetics*, **12**, 475–486.

de Mazancourt, C., Johnson, E. & Barraclough, T.G. (2008) Biodiversity inhibits species' evolutionary responses to changing environments. *Ecology Letters*, **11**, 380–388.

Diniz-Filho, J.A.F. (2004) Phylogenetic autocorrelation analysis of extinction risks and the loss of evolutionary history in felidae (Carnivora: Mammalia). *Evolutionary Ecology*, **18**, 273–282.

Dobzhansky, T. (1973) Nothing in Biology Makes Sense Except in the Light of Evolution. *The American Biology Teacher*, **35**, 125–129.

Ehrlich, P.R. (2014) The Case Against De-Extinction: It's a Fascinating but Dumb Idea. http://e360.yale.edu/feature/the_case_against_de-extinction_its_a_fascinating_but_dumb_idea/2726/

Facon, B., Genton, B.J., Shykoff, J., Jarne, P., Estoup, A. & David, P. (2006) A general eco-evolutionary framework for understanding bioinvasions. *Trends in Ecology and Evolution*, **21**, 130–135.

Faith, D.P. (1992) Conservation evaluation and phylogenetic diversity. *Biological Conservation*, **61**, 1–10

Frankham, R., Lees, K., Montgomery, M.E., England, P.R., Lowe, E. & Briscoe, D.A. (1999) Do population size bottlenecks reduce evolutionary potential? *Animal Conservation*, **2**, 255–260.

Garcia-Gonzalez, R. & Margalida, A (2014) The Arguments against Cloning the Pyrenean Wild Goat. *Conservation Biology*, **28**, 1445–1446.

Gomulkiewicz, R. & Holt, R.D. (1995) When does evolution by natural selection prevent extinction? *Evolution*, **49**, 201–207.

Groombridge, J.J., Jones, C.G., Bruford, M.W., Nichols, R.A. (2000) Conservation biology - 'Ghost' alleles of the Mauritius kestrel. *Nature*, **403**, 616.

Gross, L. (2013) De-Extinction Debate: Should Extinct Species Be Revived? KQED Science. NPR. link: http://blogs.kqed.org/science/2013/06/05/deextinction-debate-should-extinct-species-be-revived/ webcite

Hardouin, L., Robert, A., Nevoux, M., Gimenez, O., Lacroix, F., Hingrat, Y. (2014) Meteorological conditions influence short-term survival and dispersal in a reinforced long-lived bird population. *Journal of Applied Ecology*, **51**, 1494–1503.

Hendry, A. P., Lohmann, L. G., Conti, E., Cracraft, J., Crandall, K. A., Faith, D. P., Hauser, C. et al. (2010) Evolutionary biology in biodiversity science, conservation, and policy: a call to action. *Evolution*, **64**, 1517–1528.

Hendry, A. P., Farrugia, T. J. & Kinnison, M. T. (2008) Human influences on rates of phenotypic change in wild animal populations. *Molecular Ecology*, **17**, 20–29.

Hey, J. (2006) On the failure of modern species concepts *Trends in Ecology and Evolution*, **21**, 447-450.

Hof, C. , Levinsky I., Araújo, M.B. & Rahbek, C. (2011) Rethinking species' ability to cope with rapid climate change. *Global Change Biology*, **17**, 2987–2990.

Hoffmann, M., Hilton-Taylor, C., Angulo, A., Böhm, M., Brooks, T.M., Butchart, S.H.M. et al. (2010) The impact of conservation on the status of the world's vertebrates. *Science*, **330**, 1503–1509.

Hofman C. A., Rick, T.C., Fleischer, R. C. & Maldonado, J.E. (2015) Conservation archaeogenomics: ancient DNA and biodiversity in the Anthropocene. *Trends in Ecology and Evolution*, **30**, 540–549.

Holt, W.V., Pickard, A.R., Prather, R.S. (2004) Wildlife conservation and reproductive cloning. *Reproduction*, 127, 317–324.

Iacona, G., Maloney, R.F., Chades, I., Bennett, J.R., Seddon, P.J., Possingham, H.P. (2016) Prioritising revived species: What are the conservation management 1 implications of de-extinction? *Functional Ecology* (this issue)

Isaac, N.J.B., Turvey, S.T., Collen, B., Waterman, C. & Baillie, J.E.M. (2007) Mammals on the EDGE: conservation priorities based on threat and phylogeny. *PLoS ONE*, 2, e296.

IUCN/SSC (2013) Guidelines for Reintroductions and Other Conservation Translocations. Version 1.0. Gland, Switzerland. Available from www.issg.org/pdf/publications/RSG_ISSG-Reintroduction-Guidelines-2013.pdf

IUCN/SSC (2016) IUCN SSC Guiding principles on Creating Proxies of Extinct Species for Conservation Benefit. Version 1.0. Gland, Switzerland: IUCN Species Survival Commission.

Jenkins, M. (1992) Species extinction. Pp 192-233 in Groombridge, B., ed. Global biodiversity: Status of the Earths' living resources. Chapman & Hall, London.

Jetz, W., Thomas, G. H., Joy, J. B., Redding, D. W., Hartmann, K. & Mooers, A. O. (2014) Global distribution and conservation of evolutionary distinctness in birds. *Current Biology*, **24**, 919–930.

Keller, L.F. & Waller, D.M. (2002) Inbreeding effects in wild populations. *Trends in Ecology and Evolution*, **17**, 230–241.

Lacy, R.C. (1989) Analysis of founder representations in pedigrees: Founder equivalents and founder genome equivalents. *Zoo Biology*, **8**, 111–123.

Lankau, R. A., Jørgensen, P. S., Harris, D. J. & Sih, A. (2011) Incorporating evolutionary principles into environmental management and policy. *Evolutionary Applications*, **4**, 315–325.

Lawrence, D. et al. (2012). Species interactions alter evolutionary responses to a novel environment. *PLoS Biology*, **10**, e1001330.

Liow L. H, Van Valen L & Stenseth N. C (2011) Red Queen: from populations to taxa and communities. *Trends in Ecology and Evolution*, **26**, 349–358.

Loi, P., Galli, C. & Ptak, G. (2007) Cloning of endangered mammalian species: any progress? *Trends in Biotechnology*, **25**, 195–200.

Lynch, M. & Lande, R. (1998) The critical effective size for a genetically secure population. *Animal Conservation*, **1**, 70–72.

Macnair, M. (1987) Heavy metal tolerance in plants: a model evolutionary system. *Trends in Ecology and Evolution*, **2**, 354–359.

Maris, V. (2010) Philosophie de la biodiversité, Petite éthique pour une nature en peril, Paris, Buchet-Chastel.

Mooney, H.A. & Cleland, E.E. (2001) The evolutionary impact of invasive species. *Proceedings of the National Academy of Sciences*, **98**, 5446-5451.

Moritz, C. (2002) Strategies to protect biological diversity and the evolutionary processes that sustain it. *Systematic Biology*, **51**, 238–254.

Myers, N. & Knoll, A.H. (2001) The biotic crisis and the future of evolution. *Proceedings of the National Academy of Sciences USA*, **98**, 5389 -5392.

Osborne, P.E. & Seddon, P.J. (2012) Selecting suitable habitats for reintroductions: variation, change and the role of species distribution modelling. In: Ewen, J.G., Armstong, D.P., Parker, K.A., Seddon, P.J. (Eds.), Reintroduction Biology, Integrating Science and Management. Blackwell Publishing Ltd., West Sussex.

Pace, M.L., Cole, J.J., Carpenter, S.R. & Kitchell, J.F. (1999) Trophic cascades revealed in diverse ecosystems. *Trends in Ecology and Evolution*, **14**, 483–488.

Pavoine, S., Ollier, S. & Dufour, A. B. (2005). Is the originality of a species measurable? *Ecology Letters*, **8**, 579–586.

Peers, M.J.L., Thorntonb, D.H.c, Majchrzaka, Y.N, Bastille-Rousseaud, G., Murraya, D.L (2016) De-extinction potential under climate change: Extensive mismatch between historic and future habitat suitability for three candidate birds. *Biological Conservation*, **197**, 164-170.

Purvis, A. (2008) Phylogenetic approaches to the study of extinction. *Annual Review of Ecology, Evolution, and Systematics*, **39**, 301–319.

Redford, K.H., Adams, W. & Mace, G.M. (2013) Synthetic Biology and Conservation of Nature: Wicked Problems and Wicked Solutions. *PLoS Biology*, **11**, e1001530. doi:10.1371/journal.pbio.1001530

Reusch, T.B., Ehlers, A., Hammerli, A. & Worm, B. (2005) Ecosystem recovery after climatic extremes enhanced by genotypic diversity. *Proceedings of the National Academy of Sciences USA*, **102**, 2826–2831.

Reznick, D.N., Ghalambor, C.K. & Crooks, K. (2008) Experimental studies of evolution in guppies: a model for understanding the evolutionary consequences of predator removal in natural communities. *Molecular Ecology*, **17**, 97–107.

Ripple, W.J., Beschta, R.L. (2012) Trophic cascades in Yellowstone: the first fifteen years after wolf reintroduction. *Biological Conservation*, **145**, 205–213.

Robert, A, Couvet, D. & Sarrazin, F. (2007) Integration of demography and genetics in population restorations. *Ecoscience*, **14**, 463-471.

Robert, A, Sarrazin, F., Couvet, D. & Legendre, S. (2004) Releasing adults versus young in reintroductions: interactions between demography and genetics. *Conservation Biology*, **18**, 1078-1087.

Robert, A. (2009) Captive breeding genetics and reintroduction success. *Biological Conservation*, **142**, 2915-2922.

Robert, A., Colas, B., Guigon, I., Kerbiriou, C., Mihoub, J.-B., Saint Jalme, M. & Sarrazin, F. (2015) Defining reintroduction success using IUCN criteria for threatened species: a demographic assessment. *Animal Conservation*, **18**, 397–406.

Rubenstein, D. & Rubenstein, D. (2015) From Pleistocene to trophic rewilding: A wolf in sheep's clothing. *Proceedings of the National Academy of Sciences USA*, **113**: E1.

Sandler, R. (2014) The ethics of reviving long extinct species. *Conservation Biology*, **28**, 354–360.

Sarrazin, F. & Lecomte, J. (2016) Evolution in the Anthropocene. *Science*, **351**, 922-923.

Saul, W.C. & Jeschke, J.M. (2015) Eco-evolutionary experience in novel species interactions. *Ecology Letters*, **18**, 236–45.

Sax, D. F. & Brown, J. H. (2000) The paradox of invasion. *Global Ecology and Biogeography*, **9**, 363–371.

Schlaepfer, M.A., Runge, M.C. & Sherman, P.W. (2002) Ecological and evolutionary traps. *Trends in Ecology and Evolution*, **17**, 474–480.

Seddon, P.J., Moehrenschlager, A. & Ewen, J. (2014) Reintroducing resurrected species: selecting deextinction candidates. *Trends in Ecology and Evolution*, **29**, 140–147.

Seddon, P.J., Soorae, P.S. & Launay, F. (2005) Taxonomic bias in reintroduction projects. *Animal Conservation*, **8**, 51–58.

Seddon, P.J., Armstrong, D.P. & Maloney, R.F. (2007) Developing the Science of Reintroduction Biology. *Conservation Biology*, **21**, 303–312.

Sgró, C. M., Lowe, A. J. & Hoffmann, A.A. (2011) Building evolutionary resilience for conserving biodiversity under climate change. *Evolutionary Applications*, **4**, 326–337.

Shapiro, B. & Hofreiter, M.A. (2014) paleogenomic perspective on evolution and gene function: new insights from ancient DNA. *Science*, **343**, 1236573.

Shapiro, B. (2015) Long live the Mammoth. http://www.popsci.com/de-extinction-long-live-mammoth

Shapiro, B. (2016) Pathways to de-extinction: How close can we get to resurrection of an extinct species? *Functional Ecol*ogy (this issue)

Sherkow, J.S. & Greely, H.T. (2013) What if extinction is not forever? *Science*, **340**, 32–33.

Simmonds, N.W. (1962) Variability in crop plants, its use and conservation. *Biological Reviews*, **37**, 422-465.

Soulé, M. E. (1985) What is conservation biology? *BioScience*, **35**, 727–734.

Steeves, T.E., Johnson, J.A., Hale, M.L. (2016) A conservation genetic perspective on de-extinction: Maximising evolutionary potential in functional proxies for extinct species is imperative. *Functional Ecology* (this issue)

Stockwell, C.A., Hendry, A.P. & Kinnison, M.T. (2003) Contemporary evolution meets conservation biology. *Trends in Ecology and Evolution*, **18**, 94–101.

Strauss, S. Y., Webb, C. O. & Salamin, N. (2006) Exotic taxa less related to native species are more invasive. *Proceedings of the National Academy of Sciences of the United States of America*, **103**, 5841–5845.

Stuart, A.J. (2015) Late Quaternary megafaunal extinctions on the continents: a short review. *Geological Journal*, **50**, 338–363.

Swaisgood, R.R. (2010) The conservation-welfare nexus in reintroduction programs: A role for sensory ecology. *Animal Welfare*, **19**, 125–137.

Taylor, S.S., Jamieson, I.G., Armstrong, D.P. (2005) Successful island reintroductions of New Zealand robins and saddlebacks with small numbers of founders. *Animal Conservation*, **8**, 415–420.

Tewksbury, J.J., Huey, R.B. & Deutsch, C.A. (2008) Ecology – Putting the heat on tropical animals. *Science*, **320**, 1296–1297.

Tisdell, C. & Nantha, H.S. (2007) Comparison of funding and demand for the conservation of the charismatic koala with those for the critically endangered wombat *Lasiorhinus krefftii*. *Vertebrate Conservation and Biodiversity*, **16**, 435–4555.

Tsunoda, Y. & Kato, Y. (2002) Recent progress and problems in animal cloning. *Differentiation*, **69**, 158-161.

Uusi-Heikkilä, S., Whiteley, A.R., Kuparinen, A., Matsumura, S., Venturelli, P.A., Wolter, C., Slate, J., Primmer, C.R., Meinelt, T. Killen, S.S., Bierbach, D., Polverino, G., Ludwig, A. & Arlinghaus, R. (2015) The evolutionary legacy of size-selective harvesting extends from genes to populations. *Evolutionary Applications*, **8**, 597-620.

Van Nes, E.H. & Scheffer, M. (2004) Large species shifts triggered by small forces. *American Naturalist*, **164**, 255–266.

Van Valen, L. (1973) A new evolutionary law. *Evolutionary Theory*, **1**, 1-30.

Veron S., Davies, T.J., Cadotte, M.W., Clergeau, P. & Pavoine, S. (2015) Predicting loss of evolutionary history: where are we? *Biological Reviews*, DOI: 10.1111/brv.12228

Winter, M., Devictor, V. & Schweiger, O. (2012) Phylogenetic diversity and nature conservation: where are we? *Trends in Ecology and Evolution*, **28**, 199–204.

Wolf, C.M., Griffith, B., Reed, C. & Temple, S.A. (1996) Avian and mammalian translocations: update and reanalysis of 1987 survey data. *Conservation Biology*, **10**, 1142–1154.

Yule, K.M., Miller, T.E.X. & Rudgers, J.A. (2013) Costs, benefits, and loss of vertically transmitted symbionts affect host population dynamics. *Oikos*, **122**, 1512–1520.

Legends of figures and tables

Table 1: Generation length (GL) estimates for the 20 candidate species for de-extinctions. GL estimates for the Ivory-billed woodpecker, the Baiji and the Spanish Ibex (as the Bucardo is a subspecies) were taken from the BirdLife (http://www.birdlife.org) and IUCN (http://www.iucnredlist.org) websites. For the rest of the candidate species we used close relative living species as proxies to estimate GL values (see details and references in Table S1 of Supporting Information). The estimated number of generations since extinction is calculated as the time since extinction (in years) divided by GL.

Figure 1: Distribution of time since extinction (logarithmic scale) for de-extinction candidate species (white bars, n=20), compared to the time elapsed since local extinction for several reintroduction programs in Europe (grey bars, n=35, see Table S2 for details). Median time since extinction: 129.5 years (de-extinctions) and 38 years (reintroductions).

Table 1

ID	**Common name**	**Scientific name**	**Extinction**	**Time since extinction (years)**	**Generation length (years)**	**Reference (Generation length)**	**Nb. of generations since extinction**
1	Passenger pigeon	*Ectopistes migratorious*	1914	101	6,9	BirdLife 2015	14.64
2	Carolina parakeet	*Conuropis carolinensis*	1918	97	6,67	BirdLife 2015	14.54
3	Cuban red macaw	*Ara tricolor*	1864	151	12,7	BirdLife 2015	11.89
4	Ivory-billed woodpecker	*Campephilus principalis*	1944	71	6,5	BirdLife 2015	10.92
5	O'o	*Moho nobilis*	1934	81	5,6	BirdLife 2015	14.46
6	Elephant bird	*Aepyornis sp/Mullerornis sp*	1800s	215	10,5	BirdLife 2015	20.48
7	Moa	*Dinornis spp.*	1400s	615	10,5	BirdLife 2015	58.57
8	Huia	*Heteralocha acutirostris*	1907	108	12,5	BirdLife 2015	8.64
9	Dodo	*Raphus cucullatus*	1662	353	6,6	BirdLife 2015	53.48
10	Great auk	*Pinguinis impennis*	1852	163	13,6	BirdLife 2015	11.99
11	Auroch	*Bos primigenius*	1627	388	6	Murray et al. 2010	64.67
12	Pyrenean ibex, Bucardo	*Capra pyrenaica pyrenaica*	2000	15	6,77	Pacifici et al. 2013	2.22
13	Thylacine, Tasmanian tiger	*Thylacinus cynocephalus*	1936	79	4,67	Pacifici et al. 2013	16.92
14	Woolly mammoth	*Mammuthus primigenius*	6400 yr before present	6400	22	Pacifici et al. 2013	500
15	Mastodon	*Mammut spp.*	10 000 yr before present	10000	22	Pacifici et al. 2013	290.9
16	Saber-toothed cat	*Smilodon*	11 000 yr before present	11000	6	Pacifici et al. 2013	1833.3
17	Steller's sea cow	*Hydrodamalis gigas*	1768	247	28,07	Pacifici et al. 2013	9.51
18	Caribbean monk seal	*Monachus tropicalis*	1952	63	15	Pacifici et al. 2013	4.2
19	Baiji, Chinese river dolphin	*Lipotes vexillifer*	2006	9	13,26	Pacifici et al. 2013	0.68
20	Xerces blue butterfly	*Glaucopsyche xerces*	1941	74	1	Arnold 1987	74