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1 **Title: De-extinction and evolution**

2

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14

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16

17 **Key-words:** De-extinction, conservation translocation, evolutionary processes, adaptation,

18 biocentric conservation ethics, conservation phylogenetics

1 Summary

2

3 1. De-extinction, the process of resurrecting extinct species, is in an early stage of
4 scientific implementation. However, its potential to contribute effectively to
5 biodiversity conservation remains unexplored, especially from an evolutionary
6 perspective.

7 2. We review and discuss the application of the existing evolutionary conservation
8 framework to potential de-extinction projects. We aim to understand how
9 evolutionary processes can influence the dynamics of resurrected populations, and to
10 place de-extinction within micro- and macro-evolutionary conservation perspectives.

11 3. In programs aiming to revive long-extinct species, the most important constraints to
12 the short-term viability of any resurrected population are (1) their intrinsically low
13 evolutionary resilience, and (2) their poor eco-evolutionary experience, in relation to
14 the absence of (co)adaption to biotic and abiotic changes in the recipient
15 environment.

16 4. Assuming that some populations of resurrected species can persist locally, they have
17 the potential to bring substantial benefits to biodiversity if the time since initial
18 extinction is short relative to evolutionary dynamics. The restoration of lost genetic
19 information could lead, along with the re-instatement of lost ecological functions, to
20 the restoration of some evolutionary patrimony and processes, such as adaptation
21 and diversification.

22 5. However, substantial evolutionary costs might occur, including unintended eco-
23 evolutionary changes in the local system, and unintended spread of the species.
24 Further, evolutionary benefits are limited because (1) the use of resurrected

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

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

1 Introduction

2 De-extinction, the idea of bringing back extinct species using back breeding, or cloning and
3 genomic engineering, has generated excitement and controversy (Sherkow & Greely 2013).
4 So far, debates surrounding de-extinction have focused on ecological, ethical, societal and
5 economic issues, but rarely on evolutionary considerations. Evolution is nonetheless one of
6 the most important frameworks with which to describe and understand the effects of
7 human actions on biological processes, and also the primary ethical postulate that justifies
8 conservation research and practices (Soulé 1985). Evolutionary biology has been central to
9 the science of conservation biology since its inception (Hendry et al. 2010) and many
10 evolutionary biologists acknowledge that the current human-driven biotic crisis is likely to
11 disrupt and deplete certain basic processes of evolution (Myers & Knoll 2001). Moreover,
12 conservation biologists have developed theories to understand the evolutionary effects of
13 the main drivers of biodiversity changes (such as habitat destruction, climate change, or
14 invasive species), as well as the expected benefits of conservation actions (such as
15 protection or restoration). The fields of conservation genetics and evolutionary conservation
16 biology address, for instance, short-term genetic deterioration (Coron et al. 2013), future
17 evolutionary potential (Lynch & Lande 1998), and the designation of conservation units and
18 management plans that seek to conserve both evolutionary processes and patterns (Moritz
19 2002). The application of this evolutionary framework to any de-extinction approach is
20 essential, not only to understand how evolutionary processes can favor or constrain the
21 dynamics and ecological consequences of resurrected species, but also to put de-extinction
22 projects, with their potential risks and benefits, into the widest, macro-evolutionary,
23 conservation perspective.

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

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

1 2014). On the other hand, the literature on invasive species has provided insights into
2 populations that are completely exogenous to a given ecological recipient and evolutionary
3 related questions of their success (Facon et al. 2006). Over the last few years, the debate on
4 Pleistocene rewilding has raised the issue of restoration of long-extinct populations of extant
5 species (Rubenstein & Rubenstein 2015) and conservation biologists have developed a
6 feasibility and risk analysis framework for assisted colonization, the intentional movement of
7 organisms outside their indigenous range (IUCN 2013). De-extinction is not simply an
8 intermediate between reintroduction and invasion, but much can be learned from case
9 studies on these topics.

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

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

19

20 **I) Evolutionary constraints on the local success of de-** 21 **extinction projects**

22

23 **1. Discontinuity of biological processes**

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

15

16 **2. Initial genetic diversity and evolutionary resilience**

17 In most conservation translocations, the number of translocated individuals determines the
18 extent of demographic stochasticity occurring during the establishment phase of the
19 population's dynamics and thus influences success (Robert et al. 2015). From a genetic
20 viewpoint, the initial number of individuals partly determines the initial genetic variation and
21 subsequent short-term genetic deterioration and lack of adaptability (Robert, Couvet &
22 Sarrazin 2007). Numbers of released individuals in reintroduction programs typically range
23 from a few tens to a few hundred individuals, and empirical reintroduction surveys suggest
24 that there is a positive relationship between the number of released individuals and program

1 success (Wolf et al. 1996), yet the potential contribution of genetic effects to this pattern
2 has not been clearly established.

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

6 Although it has been suggested that new genomic editing techniques “*should be able to*
7 *restore heterozygosity pretty easily in living genomes*” (Brand 2014), the amount of initial
8 genetic variation is likely to remain an important issue in de-extinctions. Evolutionary
9 resilience refers to both the ability of populations to persist in their current state and to
10 undergo evolutionary adaptation in response to changing environmental conditions (Sgró,
11 Lowe & Hoffmann 2011). Low genetic variation can affect evolutionary resilience through
12 reduction in population fitness due to increased inbreeding and drift loads (Keller & Waller
13 2002) and through reduced adaptability to future environmental changes (Lankau et al.
14 2011) A population founded with the genetic material from only one or a few individuals will
15 experience similar genetic problems as any natural or captive population experiencing a
16 severe bottleneck, in turn reducing its ability to adapt to changing environments (Frankham
17 et al. 1999). Even assuming that genomic editing can be used, not only to fill gaps, but also to
18 capture a significant fraction of the genetic variation of closely related, extant species, this
19 would necessitate the use of hundreds of distinct individuals of the extant species to avoid
20 such bottleneck effect.

21 On the positive side, although low genetic variation has been shown to increase the
22 extinction risk, there are some documented cases of populations that have persisted over
23 long periods of time at extremely small population sizes prior to recovery (e.g., Groombridge
24 et al. 2000), and both conservation translocation and invasive species literatures provide

1 examples of viable populations founded with very few individuals (Taylor, Jamieson &
2 Armstrong 2005). Furthermore, the science of conservation translocation provides concepts
3 and tools (1) to minimize the loss of genetic variation of captive populations before release
4 into the wild (Lacy 1989) and (2) to maximize post-release survival and population growth
5 through optimal release methods (Hardouin et al. 2014) and through continuing and
6 adaptive management (Swaisgood 2010). Finally, the persistence of small populations is a
7 general concern in conservation biology, and more research on this issue will provide
8 benefits beyond the field of de-extinction. For example, rapid progress in breeding and
9 genetic technologies associated with the de-extinction research may also be applied to the
10 conservation of extant endangered species based on cloning, e.g. to target under-
11 represented genetic lines (Holt, Pickard & Prather 2004) or mitigate the effects of
12 demographic stochasticity.

13

14

15 **3. Evolutionary divergences**

16 Like seed banks or cryogenic zoos, de-extinction raises the issue of evolutionary freezing
17 (Simmonds 1962), which might imply strong divergence between the target species and its
18 target environment. Such evolutionary divergence is primarily a matter of time. The times
19 since extinction of the twenty de-extinction candidate species proposed following the
20 TEDxDeExtinction conference (see Seddon, Moehrensclager & Ewen 2014) range from a
21 few years to more than 10,000 years, which means that, in some cases, several hundreds or
22 thousands of generations might have elapsed since the original extinction (see Table 1). As a
23 comparison, in the case of reintroductions, times between local extinction and the planned
24 release range from a few years to a few hundred years (Fig. 1). Thus, although the time

1 scales of de-extinction and reintroduction largely overlap, the temporal horizon envisaged
2 for some “deep de-extinction” projects (as coined by Sandler 2014) is likely to be several
3 orders of magnitude longer than for any reintroduction project.

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

16 These dramatic environmental changes can be associated with particularly strong and rapid
17 selection, as many populations have the capacity to respond to, e.g., climate change within a
18 time frame of tens of years (Hendry, Farrugia & Kinnison 2008). Such adaptive changes are
19 generally considered much more rapid than non-adaptive changes (Stockwell, Hendry &
20 Kinnison 2003), and most phenotypic differences observed among natural populations are
21 likely adaptive (Hendry et al. 2010). Thus, recent temporal environmental changes and
22 associated contemporary evolution are likely to generate strong levels of divergence
23 between the environment and a de-extinct population that has not had the opportunity to

1 adapt to (1) human induced environmental changes, (2) biotic changes in response to these
2 changes, or (3) biotic changes in response to the original extinction of the target species.

3

4 **4. Community processes**

5 Evolutionary processes occurring at the level of the biological community further complicate
6 patterns of divergence between de-extinct populations and their recipient environment.

7 There is abundant evidence that ecological interactions drive rapid evolution and can change
8 the direction of evolution compared to adaptation in isolation (Liow, Van Valen & Stenseth
9 2011; Lawrence et al. 2012). Coevolutionary processes occurring at the community level
10 partly determine ecosystem functions (Bailey et al. 2009) and community response to
11 climate (Reusch et al. 2005; Sgró, Lowe & Hoffmann 2011).

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

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

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

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

17

18

19 **5. Maladaptation and local success**

20 The most important and immediate cost of such divergence and maladaptation is likely to be
21 a demographic cost: the re-extinction of the resurrected population (Steeves et al. 2016).

22 Theory has demonstrated that the capacity of a population to survive an episode of selection
23 will be determined more by whether or not the population can survive the initial increase in
24 mortality rate than by whether or not it can evolve in response to selection (Gomulkiewicz &

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

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

18

19 **II) Restoration of evolutionary trajectories**

20 **1) Phylogeny of de-extinct species**

21 A. *Evolutionary history of de-extinct species*

22 Evolutionary history has been argued to capture the diversity of life better than simple
23 measures of species richness (Purvis 2008). Since the 1990s, a phylogenetic approach to

1 conservation has been proposed, in order to prioritize the protection of evolutionary distinct
2 groups or of geographic areas. For example, at the level of a group of several species, a
3 common measure used to quantify evolutionary history is phylogenetic diversity (Faith
4 1992), which is the minimum total length of all the phylogenetic branches required to
5 connect the species in a phylogenetic tree. At the level of the individual species, indices of
6 evolutionary distinctiveness quantify how few relatives a species has and how
7 phylogenetically distant they are (Veron et al. 2015).

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

16 Can this framework be applied to the selection of de-extinction candidates? From the
17 perspective of evolutionary conservation biology, one might consider that the “moral
18 imperative” (Seddon, Moehrensclager & Ewen 2014) to reverse species extinction caused
19 by humans should be translated into an imperative to reintroduce their extinct genomes into
20 the global gene pool (Church & Regis 2012), or even to restore evolutionary trajectories
21 interrupted by humans. Because de-extinction is primarily a species-based approach, the use
22 of evolutionary distinctiveness measures to select candidates might seem pertinent.
23 Restoring evolutionary-distinct extinct species should, in theory, maximize the restoration of
24 evolutionary history. However, resurrections of long-extinct species raise problems that do

1 not exist for other types of conservation translocation, related to DNA degradation and
2 imperfect knowledge of evolutionary relationships between species. In this context, it has
3 been suggested that the same next generation DNA sequencing technologies that make de-
4 extinction technologically feasible should be first applied to make new inferences on
5 evolutionary relationships between species using ancient genomes (Shapiro & Hofreiter
6 2014), which offers promising potential to assess the evolutionary stakes of de-extinction
7 initiatives.

8

9

10 *B. Unintended phylogenetic bias*

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

23 The selection of candidate species for de-extinction projects is undoubtedly influenced by
24 the biases that exist for other conservation translocations: a bias towards species with a

1 supposedly important functional impact on ecosystems (such as grazers or predators), and
2 more than ever a bias towards large, charismatic species. However, it is also very likely that
3 these phylogenetic filters will differ, at least quantitatively in the case of de-extinction. First,
4 because the list of known species extinctions since 1500AD is incomplete and biased (Purvis
5 2008), and, as the time scale increases, additional constraints on data and biological material
6 availability are likely to amplify existing phylogenetic biases or engender new biases on
7 candidate species (Alroy et al. 2001). Second, because the economic cost of de-extinction is
8 intuitively far higher than for any other type of conservation translocation, any economic
9 filter on the choice of candidate species (Tisdell & Nantha 2007) will be amplified.
10 Finally, the evolutionary benefit of any de-extinction program relies on the phylogenetic
11 distinctness of the target species. However, the technical feasibility of a program is critically
12 linked to the existence of organisms of phylogenetically closely related extant species to be
13 used as egg donors, surrogates or references for genome reconstruction. This paradox
14 questions the potential evolutionary benefits of de-extinction because evolutionary distinct
15 species might be those for which de-extinction is least feasible.

16

17 **2) Evolutionary benefits of de-extinctions**

18 *A. Evolutionary proxies?*

19 This is perhaps one of the biggest paradoxes about de-extinction: although primarily based
20 on the manipulation of genetic information, the potential evolutionary benefit of these
21 operations is non-trivial, unlike their ecological benefit. Many authors acknowledge that de-
22 extinction could have potentially important ecological benefits (although these benefits are
23 complex to characterize and should be balanced against potential ecological risks). These
24 benefits rely on the concept of ecological proxy, i.e., a substitute entity, which carries out

1 similar ecological functions as the lost entity. Contrary to ecological proxy, the notion of
2 « evolutionary proxy » is meaningless. In other words, while nature's functions and services
3 can be synthesized (Redford, Adams & Mace 2013), nature, by definition, cannot be. In
4 contrast to functional diversity that can potentially be recovered through recurrent
5 selection, historically isolated lineages cannot be recovered and historically isolated but
6 ecologically exchangeable populations should be considered as distinct significant
7 evolutionary units (Moritz 2002). Furthermore, one major component of biodiversity – that
8 is both a component of the evolutionary history and the main driver of evolutionary
9 processes - is intra-species genetic diversity, which is expected to be extremely low in most if
10 not all species resurrected through cloning. Thus, while both the species as seen as a
11 typological entity and its functional ecological role can indeed be resurrected (or at least be
12 replaced by proxies), the evolutionary loss associated with the initial species decline and
13 extinction, is irreversible (Ehrlich 2014).

14

15 *B. Balance of costs and benefits*

16 What might the evolutionary benefits of de-extinctions be? At the scale of the local
17 biological system, assuming that a given program (1) can reasonably be considered to be a
18 short-term response to short-term human effects (see below), and (2) can restore a
19 significant fraction of lost genetic information of the extinct species, expected benefits are
20 the same as those expected from any other type of translocation: the restoration of some
21 evolutionary patrimony and processes, such as adaptation and diversification. Further
22 assuming that local restoration leads to the re-instatement of lost ecological functions, this
23 could contribute, at the global scale, to the improvement of functional and genetic diversity.
24 Even assuming that de-extinction does not restore a significant fraction of lost genetic

1 information, it has been suggested that it could also contribute to the global evolutionary
2 resilience of current biodiversity: some programs might directly benefit the conservation of
3 particular phylogenetic groups by widening the ecological niche of the groups and their
4 geographic ranges. For example, releasing elephants expressing mammoth genes into cold
5 habitats can be seen as a means to extend the geographical distribution of elephants beyond
6 their current declining, warm habitats (Shapiro 2015).

7 And what could be the evolutionary costs, assuming that the resurrected population is
8 viable? Most, if not all evolutionary costs are probably mediated by ecological costs: (1)
9 profound, unintended eco-evolutionary changes in the local system (including hysteretic
10 phenomena, in which irreversible catastrophic shift occurs, see e.g., van Nes & Scheffer
11 2004), (2) unintended spread of the species, which is likely in the case of mismatch between
12 historic and current or future habitat suitability (Peers et al. 2016), (3) sudden changes in
13 local human pressures (e.g., increase of tourism following the resurrection of a highly
14 charismatic species). These ecological costs, which are similar to some of the well-known
15 consequences of invasive species and local environmental degradation, can have major
16 unintended evolutionary consequences (Hendry et al. 2010).

17

18 **3) Alternatives to de-extinctions**

19 *A. A restoration perspective*

20 Since most of the arguments in favor of de-extinction are linked to the concept of ecological
21 proxy, the best alternative to the resurrection of extinct species could be the selection and
22 release of extant ecological replacements (IUCN 2013). Using existing species as alternatives
23 deserves to be considered (IUCN 2016), not only from an ecological perspective, but also

1 from an evolutionary perspective (see an example in the Pyrenean wild goat (*Capra p.*
2 *pyrenaica*) in Garcia-Gonzalez & Margalida 2014).

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

13

14 *B. A conservation perspective*

15 A common reaction against de-extinction is to ask “why would we spend all this energy and
16 effort to bring back ancient animals but let so many others just disappear?” (Jamie
17 Rappaport Clark, quoted in Gross 2013). Is this heuristic argument consistent with our
18 knowledge on the potential respective benefits on evolutionary processes and patrimony of
19 conserving extant species versus resurrecting extinct species? It is estimated that one-fifth of
20 vertebrate species are now threatened with extinction (Hoffmann *et al.*, 2010). However,
21 one important point is that the vast majority of species threatened with extinction are not
22 extinct (Barnosky *et al.* 2011), and this is also true for phylogenetic diversity (review in Veron
23 *et al.* 2015). Thus, the recent loss of species is dramatic and serious but does not yet qualify
24 as a mass extinction in the paleontological sense of the Big Five (Barnosky *et al.* 2011); and

1 there is still much of the world's biodiversity left to save, but doing so will require the
2 reversal of the well-known Anthropogenic threats which are responsible for the ongoing
3 declines (Ehrlich 2014). Thus, at a phylogenetic level, the potential benefits of saving
4 threatened species and populations and reducing extinction debts is much more important
5 than the likely benefits of resurrecting a few extinct species. This should be considered
6 especially if one believes that there can exist a trade-off (e.g., economic) between de-
7 extinction and other conservation approaches (see lacona et al. 2016).

8

9 **4) Evolutionary values**

10 A. Ethics and values

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

21 Acknowledging that change is the basis of life (Dobzhansky 1973) implies a fundamental
22 change from an anthropocentric to a biocentric philosophy in which biodiversity has its own
23 participant role and history independently of human beings (Maris 2010). Thus, many
24 biologists agree that maintaining evolutionary potential and processes is a primary concern

1 of conservation science (Soulé 1985; Myers & Knoll 2001), and conserving evolutionary
2 trajectories might constitute a challenging major evolutionary transition inducing a
3 deliberate overcoming of the Anthropocene (Sarrazin & Lecomte 2016).

4 In agreement with these general principles, many ecological restoration approaches do not
5 aim to return to some arbitrary historical state but instead focus on the re-instatement of
6 functions to restore degraded ecosystems (IUCN 2013) and promote adaptation (Aitken &
7 Whitlock 2013). De-extinction, by essence, is not antagonistic with these efforts aiming at
8 restoring or maintaining functional variation. However, it is questionable whether de-
9 extinction has the potential to restore the evolutionary values of lost biodiversity. Sandler
10 (2014) recently argued that deep de-extinction does not restore the natural-history
11 properties of species, nor their wildness or independence from humans, because it results
12 only in organisms whose genetic makeup most resembles that of species that went extinct
13 long ago, and for whom we have reconstructed the genome. We agree that the potential of
14 de-extinctions to reestablish lost (evolutionary) value is questionable, and we advocate that
15 Sandler (2014)'s reasoning be extended below and beyond the species level and be focused
16 on the evolutionary processes themselves, rather than the products of these processes.
17 Evolution operates through changes in the frequency of alleles across generations and not
18 instant heritable changes in the properties of individuals themselves. Species traits or
19 functions are not intrinsic drivers of evolution. Thus, although de-extinction has the
20 potential to restore some historical patterns that might in turn influence future evolution,
21 the impossibility of restoring past dynamics of co-evolution between the target organisms
22 and their environments is the main limitation to the evolutionary value of de-extinct
23 populations.

24

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

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

18

19 **Conclusion**

20 De-extinction is a stimulating idea, which has raised, and will continue to raise debates
21 among scientists. Focusing on ethical aspects, Sandler (2014) recently concluded that de-
22 extinction is not intrinsically problematic, although it is in many respects a luxury. From an
23 evolutionary view-point, we agree with Sandler's view and believe that critics from
24 ecologists and evolutionary biologists do not need to focus on de-extinction *per se* but rather

1 on its potential excesses, such as irrelevant choice of target species, potential of invasive
2 impact on ecosystems, or unreasonable time scales. In particular, one of the most important
3 scientific arguments against de-extinction could be an evolutionary one: extinct species do
4 not evolve, but the rest of the world does. While some recent translocation practices aim at
5 finding genotypes that can match future environments (Aitken & Whitlock 2013), de-
6 extinction involves the risk that resurrected species are not adapted to the present,
7 Anthropocene environment.

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

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

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

1 Feasibility assessments and comparisons should rely on thorough interdisciplinary modeling
2 and comparative analysis. Within the last decades, an array of empirical and theoretical
3 modeling techniques have been developed to project past and future environmental,
4 ecological and evolutionary dynamics, such as niche modeling, (no-)analog ecosystem
5 projection, predictive evolutionary modeling and population viability analysis. Embracing
6 these techniques is essential to select best candidate species, optimize release methods, and
7 assess the chance of success and potential evolutionary benefits of de-extinction programs.
8

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5

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1 **Legends of figures and tables**

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

9

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

14

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

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