

PERSPECTIVE

Evolution in biodiversity policy – current gaps and future needs

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Abstract

The intensity and speed of human alterations to the planet's ecosystems are yielding our static, ahistorical view of biodiversity obsolete. Human actions frequently trigger fast evolutionary responses, affect extant genetic variation and result in the establishment of new communities and co-evolutionary networks for which we lack past analogues. Contemporary evolution interplays with ecological changes to determine the response of organisms and ecosystems to anthropogenic pressures. Examples on wild species include responses to harvest (e.g. fisheries, hunting, angling), habitat loss and fragmentation (e.g. genetic effects of isolation), biotic exchange (e.g. evolutionary responses to control measures), climate change (e.g. local adaptation and its interplay with dispersal processes) and the responses of endangered species to conservation measures. A review of international and EU biodiversity policies showed numerous opportunities for the integration of evolutionary knowledge, with the realistic prospect of improving their efficacy. Such opportunities should be extended to other sectoral policies of direct relevance for biodiversity – notably nature conservation, fisheries, agriculture, water resources, spatial planning and climate change. These avenues for improvement are, however, challenged by the low level of enforcement of biodiversity policies, linked to the nonbinding nature of most biodiversity-policy documents, and the decreasing representation of biodiversity in EU's research policy.

Introduction

Biological diversity is the variability among living organisms and the ecological complexes of which they are part, including diversity within species, between species and of ecosystems (CBD 1992). Traditionally, it is defined at three levels of biological organization (species, ecosystem and genetic diversity), though a fourth level has been recently proposed (molecular diversity; Campbell 2003). It is generally regarded as a key determinant of ecosystem health (Rapport et al. 1998), functioning (Loreau et al. 2001; Naeem 2002) and resilience (Folke et al. 2004). The increasing influence of humans on the Earth's ecosystems has resulted in its abrupt reduction, often referred to as the '6th mass extinction' (Barnosky et al. 2011) because estimated rates of species loss are 100–10 000 times higher than background rates (i.e. those typical in the fossil record; Mace et al. 2006). The main driver of biodiver-

sity loss is land-use change, followed by climate change, nitrogen deposition and biotic exchange (Sala et al. 2000).

The need to conserve biodiversity has become, by now, a broadly acknowledged societal goal – reflected in international, national and local policies and in a wealth of policy documents, educational material and media campaigns. Despite an initial emphasis on moral, ethical or spiritual motivations, often grounded on forceful arguments (e.g. Ehrenfeld 1988), the dominant view emphasizes nowadays the tangible benefits that biodiversity provides to human society, often expressed in economic terms. Indeed, biodiversity is considered the backbone of multiple ecosystem services (e.g. erosion control, soil formation, nutrient cycling, pollination, biological control, as well as the regulation of atmospheric composition, climate, water and disturbances) with an average global value of US\$33 trillion per year (Costanza et al. 1997).

Furthermore, biodiversity loss represents a major threat to health and food security (Chivian and Bernstein 2008; Ostfeld 2009).

In contrast to the dynamic evolutionary flux that characterizes life, our view on biodiversity and ecosystem functioning has been predominantly static, trying to conserve biodiversity as it is and preferably, as it was (Grant et al. 2010). However, the intensity and speed of human alterations to the planet's ecosystems are yielding this view obsolete. Human actions often result in unforeseen evolutionary pressures that trigger fast evolutionary responses, while drastically affecting (most often, depleting) the raw material of short-term evolutionary responses: extant genetic variation. At the same time, the dismantling and reshuffling of existing biotic communities, caused by the combination of habitat, climate and biotic changes, results in the ongoing establishment of new communities and co-evolutionary networks for which we lack past analogues (Williams and Jackson 2007; Stewart 2009; Stralberg et al. 2009). These processes are responsible for the generation, maintenance and (often) erosion of biodiversity in the 'real' (i.e. anthropogenic, rapidly changing, increasingly interconnected) world. The need for effective and cost-efficient policies that steer anthropogenic changes towards sustainability places an increasing emphasis on the generation and transference of evolutionary knowledge.

In this paper, we review recent evidence supporting the need for biodiversity policies that go beyond the identification and conservation of individual habitats, sites or species of high conservation priority, and consider the dynamic nature of the evolutionary processes that generate and maintain diversity. We then examine its significance for international biodiversity policies, evaluate the degree to which it has been incorporated into them, and identify avenues for innovation and improvement. For this purpose, we focus on the Convention on Biological Diversity, which can be considered as the central piece of biodiversity policy across the world, and the European biodiversity policy, because it represents a suitable example of trans-national policy-making.

Evolution and biodiversity

Biodiversity is the result of 3.5 billion years of evolution. Evolutionary diversification, though continuously counterbalanced by extinction (species present today represent only 2–4% of all those that have ever lived; May et al. 1995), is responsible for the continuous increase in biological diversity along the Earth's history – from the unicellular organisms that were its sole inhabitants until 700 million years ago, to an estimated 13–14 million of extant species at present. Evolutionary diversification

eventually leads to the process of speciation, the splitting of a single species lineage. Rates of speciation can vary greatly: it can take place within a single generation (due e.g. to chromosome duplication; Wood et al. 2009), though it generally takes much longer time (millions of years; Mace et al. 2006). As a consequence, there is enormous variation between species in terms of their evolutionary age, and species richness does not vary exclusively over geographical space: it varies also over time.

In general, strong disturbances and other situations resulting in the generation of vacant niches tend to result in accelerated rates of diversification and speciation, which do not simply reoccupy vacated adaptive peaks but explore new opportunities released from previous ecological and/or evolutionary constraints. Mass extinctions represent extreme cases of such ecological opportunities, in which extinction 'can reshape the evolutionary landscape in more creative ways' (Jablonski 2001). Postextinction diversifications, however, lag far behind the initial taxonomic impoverishment and are strongly unpredictable – particularly those following 'pulse extinctions' (rapid, catastrophic events that do not allow adaptive change during the extinction episode; Erwin 1998). Indeed, the interplay between the destructive and generative aspects of extinction and the very different time scales over which they appear to operate remain crucial but poorly understood components of the evolutionary process (Jablonski 2001). At any rate, the existing evidence suggest that evolutionary responses (even rapid ones) will not compensate for the recent and current loss of species within historical times (F. Bonhomme in Grant et al. 2010), though they have contributed already to slow down or mitigate it (Kinnison and Hairston 2007). Adjusting to current rates of environmental change and species loss requires short-term evolutionary responses, which primarily depend on genetic variation rather than the creation of new variation (Frankham 2007). This places the focus on the conservation of present-day genetic variation for safekeeping evolutionary potential (F. Gouyon in Grant et al. 2010).

Unfortunately, most conservation efforts focus at the species level – which often reflects limited resources, rather than a conceptual limitation (as exemplified by the inclusion of infraspecific taxa in international agreements, for example CITES or TRAFFIC, or national legislation, for example in Brazil, Canada, Australia or USA; Haig et al. 2006). Because extinction rates are estimated to be three to eight times higher for populations than for species (Hughes et al. 1997), substantial losses in genetic diversity often occur at the population level before such efforts even take place (Garner et al. 2005). Even actions taken at subspecific level are often addressing the consequences of severe genetic losses caused by range fragmentation and/or population loss during the recent past (e.g.

Florida panther, Gross 2005; Pimm et al. 2006; brown bears, Taberlet et al. 1997; Paetkau et al. 1998; Seychelles' jellyfish tree, Finger et al. 2011).

In addition, the objective of maintaining the evolutionary potential of species or populations may be inadequately served by current management actions primarily aimed at preserving or resurrecting small populations – which (often unwillingly) impose artificial-selection regimes in their efforts to ensure demographic persistence and/or the maintenance of genetic variation (Kinnison et al. 2007). These biases are probably influenced by the array of available technological tools, which emphasize the assessment of neutral genetic variation that primarily reflects stochastic, rather than selective, processes (e.g. Crandall et al. 2000, Leinonen et al. 2008). The improvement in current management procedures may therefore be facilitated by the development of new molecular methods and the associated improvement in bioinformatic tools. Angeloni and Mergeay (2011) provide an illustrative example of how next-generation sequencing (NGS) may be used to improve the estimation of genetic and demographic parameters; clarify the genomic mechanisms of and relationships between neutral, detrimental and adaptive genetic variation; and obtain a better understanding of the genetic basis of interactions among species.

Anthropogenic evolution

To date, biodiversity policy largely rested in the assumption that evolutionary processes take place at a temporal scale that largely exceeds that of most human operations. However, evidence indicating that detectable evolutionary changes commonly occur over ecological time scales has mounted over the last decade (e.g. Thompson 1998). Rapid evolutionary changes often arise in response to new forms of selection caused (directly or indirectly) by human action – termed 'anthropogenic selection', as opposed to natural selection (Palumbi 2001; Stockwell et al. 2003). Anthropogenic evolution is widespread in nature, and numerous recent examples show that anthropogenic trait change in the wild is a global phenomenon, documented in marine, freshwater and terrestrial ecosystems worldwide (Palkovacs 2011). Moreover, and because eco-evolutionary dynamics are inherently bi-directional, contemporary evolution can have important effects on the dynamics of populations, communities and ecosystems; these effects may occur over large spatial scales and impact system-wide processes, such as trophic cascades (Carroll et al. 2007; Palkovacs 2011).

Anthropogenic trait changes take place, in the wild, in two primary contexts: anthropogenic disturbance (especially harvest, but also habitat loss and fragmentation,

pollution/acidification, and climate change) and biotic exchange (Hendry et al. 2008). Harvest is, probably, the most potent agent of anthropogenic trait change. Trait changes associated with the harvest of wild populations are, on average, three times faster than those caused by nonanthropogenic selection (Darimont et al. 2009). Fisheries, for example, drive the evolution of earlier age and smaller size at maturation in target populations, which affects their population persistence and sustainable yield (Hutchings and Fraser 2008) and results in considerable impacts on food-web interactions, trophic cascades and nutrient cycling in aquatic ecosystems (Palkovacs 2011). For example, fisheries of northwest Atlantic cod resulted, between the mid 1950s and the early 1990s, in estimated declines in age at 50% maturity from 6.5–7.0 to 5.0–5.5 years, resulting in an estimated reduction of population growth by 25–30% (Hutchings and Fraser 2008). These evolutionary consequences are often difficult to reverse; in some cases, the reduction or even cessation of fishing does not lead to rapid population recovery, particularly if directional selection continues over protracted periods as fisheries continue to harvest the largest available individuals (Conover 2000; Stockwell et al. 2003). Indeed, one prediction common to all studies of fisheries-induced evolution is that genetic change effected by exploitation will be slow to reverse (Hutchings and Fraser 2008) – as confirmed by the persistence of small size-at-age in some populations of Atlantic cod, for at least 15 years after the cessation of heavy fishing and despite favourable environmental conditions for growth (Swain et al. 2007).

Sport hunting, the main cause of death for prime-aged adults in many populations of ungulates, may result in selective effects that affect their morphological and life-history traits, favouring an earlier reproduction and increased reproductive investment in young adults – particularly when combined with regulations prohibiting the killing of lactating females, which enhance the survival of early-reproducing ones (Festa-Bianchet 2003; Fenberg and Roy 2007). Trophy hunting selects for smaller horn/antler size, delayed horn/antler development and earlier reproduction – influencing male reproductive success and the economic profitability of harvested populations (Festa-Bianchet 2003). Comparable trends may be expected in game-bird species, especially those subjected to trophy hunting (such as capercaillie and black grouse). Even poaching may result in evolutionary pressures that compromise the long-term viability of poached populations – for example, poaching of African elephants for the illegal ivory trade may select for tusklessness (Jachmann et al. 1995).

Habitat loss and fragmentation, the main global driver of biodiversity loss, often result in reduced population

size and increased isolation of the affected biota, which in turn erodes its genetic variation and reduces its evolutionary potential. Small, isolated populations are subject to genetic drift and inbreeding; these processes tend to cause decreased fitness, decreased tolerance to environmental stress, and impeded adaptive responses to changing environmental conditions (K. Bijlsma in Grant et al. 2010). Habitat fragmentation can also impact traits related to migration, movement and habitat selection, with dramatic ecological consequences – such as the reduction of marine-derived subsidies to continental waters, or changed food-web interactions that in turn trigger new evolutionary responses in prey species (see examples in the study by Palkovacs 2011). While the destructive aspects of fragmentation may be accompanied by evolutionary opportunities (e.g. genetic drift may promote evolutionary processes, isolation may promote local adaptation and the rise of evolutionary novelties; F. Boero and F. Bonhomme in Grant et al. 2010), genetic erosion in permanently small, fragmented populations will generally result in decreased adaptive potential, impaired evolutionary processes and local extinctions (K. Bijlsma in Grant et al. 2010). Some species are, however, able to broaden their functional niche and make use of the anthropogenic matrix – a process that may involve evolutionary changes in traits related to both perception and dispersal (Van Dijk 2011).

Climate change is expected to result in shifts in the geographical distribution and phenology of natural populations, as well as in the (local or global) extinction of species unable to counter its speed and magnitude. Rapid evolutionary adaptation can help species counter stressful conditions or realize ecological opportunities arising from climate change, influencing the resulting patterns of colonization, extinction and distribution shifts (Hoffmann and Sgrò 2011). The ‘evolving metacommunity’ framework (Urban 2011) emphasizes that interactions between ecological and evolutionary mechanisms, taking place at both local and regional scales, will drive community dynamics during climate change. In particular, ecological and evolutionary dynamics are likely to interact to produce outcomes different from those predicted based on either mechanism alone. While some of these dynamics have received recent attention (e.g. species interactions may prevent adaptation of other species to new niches, and resident species may adapt to changing climates and thereby prevent colonization by other species; Urban 2011), the realization that we know much more about how climates will change across the globe than about the likely responses of species to these changes and their effects on global biological diversity is profoundly worrisome.

Biotic exchange, by which species are moved beyond the limits of their normal geographical ranges by human

actions – often to produce biological invasions (Blackburn et al. 2011), can also affect the rates and the trajectories of evolutionary change (Shine 2011). Evolutionary responses are important to both predict the likelihood of biological invasions and manage the spread and impact of already-established invaders. These responses are double-sided: invasive species can induce rapid evolutionary responses on native taxa, which may reduce their ecological impact or exploit the opportunities provided by them, but the invasion process itself can cause substantial evolutionary shifts in invader’s traits (Cox 2004; Carroll 2007; Shine 2011). Many of these changes are adaptive, but others may result from nonadaptive evolutionary processes (e.g. spatial sorting; Shine 2011). From an applied point of view, evolutionary changes influencing the invader’s dispersal rate and establishment ability are particularly important.

Evolution in complex systems and co-evolutionary networks

One of the major challenges faced by current and future biodiversity policy relates to the complex interrelationships between the ecological and evolutionary forces at play. On the one hand, research on interaction networks has revealed the existence of topological and structural features that confer them robustness and stability (e.g. nestedness and modularity; Bascompte et al. 2006; Piazzon et al. 2011), and relate to both ecological variables (e.g. phenology, local abundance, geographical range) and past evolutionary history (Bascompte and Jordano 2006). On the other hand, research in geographical mosaics (Thompson 2005, 2009) has revealed that in many species, long-term coevolution is shaped by geographical variation in the structure of selection (‘selection mosaics’), the strength of reciprocal selection (‘co-evolutionary hotspots and coldspots’) and the distribution of traits found within interacting species (resulting from gene flow, random genetic drift and metapopulation dynamics). As a result, species interacting in a geographical mosaic may co-evolve faster and towards different equilibrium states than under panmictic conditions, and may maintain polymorphisms over a longer term than those interacting locally (J. Thompson in Grant et al. 2010, and refs. therein). The ecological underpinnings of the co-evolutionary process are particularly important because humans are increasingly altering the webs of interacting species, adding or eliminating species to ecosystems and imposing direct or indirect genetic changes on populations.

Implications of evolutionary processes for biodiversity policy

The most direct implication of the scientific evidence outlined in the previous sections for biodiversity policy is

one of perception. Viewing biodiversity in dynamic, evolutionary terms would already represent a step forward, particularly in comparison with the static, systematically fixed view that dominates our past and current policies (P.H. Gouyon in Grant et al. 2010). Such perceptual shift could open the way for numerous changes in the way specific problems are addressed at the strategic, operational and technical level (see Table 1). For example, it may result in the refinement or reconsideration of the battery of policies currently in place to regulate the harvest of animal populations – in particular, those encouraging the selective harvest of prime-aged reproductive individuals, as well as those put in place to enforce the conservation of species and habitats – in particular, those primarily focused on rare species and habitats.

For this purpose, generating the necessary, policy-relevant knowledge is still a key priority. Determining the conditions under which evolution may promote versus prevent ecological change, and integrate these into a general framework for predicting which ecologically important traits are most likely to evolve rapidly, should be a top priority in eco-evolutionary research (Palkovacs 2011). Policy-making and development should not wait, however, for the independent accumulation of evidence; instead, it should couple action to the generation of knowledge through adequate planning, monitoring and comparative analysis (a learning cycle that is becoming increasingly established in biodiversity, conservation and resource-use programmes; e.g. Christensen et al. 1996, Folke et al. 2004; Arkema et al. 2006; Seastedt et al. 2008).

Important modifications could already be introduced to the operational goals of conservation programmes, which emphasize demographic persistence and the preservation of (all) genetic variation in ways that are not always compatible with fostering adaptation to current conditions (Stockwell et al. 2003, 2006). On the one hand, programmes that seek to maintain genetic variation often take great measures to shield populations from selective mortality and increase effective population size, superseding adaptive evolution to the tangible present (Stockwell et al. 2006; Frankham 2007). For example, relaxed selection pressure presumably selected for smaller egg size in a hatchery population of chinook salmon (*Oncorhynchus tshawytscha*), and populations supplemented with large numbers of fish from this hatchery showed a reduction in egg size that could be detrimental to fitness (Heath et al. 2003). In steelhead trout (*Oncorhynchus mykiss*), the genetic effects of captive breeding caused a rapid, cumulative reduction of reproductive capabilities (~40% per captive-reared generation) when fish were moved to natural environments (Araki et al. 2007). On the other hand, the creation of refuge

populations as 'genetic replicates' of native populations can be undermined when refuge populations face different selection pressures to which they adapt. If adaptive divergence is substantial, refuge populations may no longer possess adaptive variation suited to the original site; instead, they should be managed as reserves of the evolutionary legacy of the species (see the study by Stockwell et al. 2006 for an example involving genetic and phenotypic changes in New Mexico's White Sands pupfish, *Cyprinodon tularosa*). New ways to balance these goals should be a central research theme of an eco-evolutionary approach to conservation (Kinnison et al. 2007).

The structuring of conservation policies around the protection of rare species and habitats, as well as pristine sites, could also be improved or complemented. For example, the shift from a habitat concept based almost exclusively on vegetation types to a functional habitat concept tailored to the specificities of the different organisms may provide new conservation opportunities. These include a more adequate consideration of human impacts on resource distribution and environmental cues (due e.g. to sensory pollution), and incorporating the potential benefits of niche evolution (e.g. by species that have adapted successfully to anthropogenic environments) into management decisions (Van Dijk 2011). The design and maintenance of current networks of conservation areas could also benefit from an evaluation of the significance of candidate sites and populations in terms of evolutionary potential and/or significance for meta-community dynamics. Conservation planning based on evolutionary significant units (ESU) has received increasing attention over the last two decades, owing largely to its application under the US Endangered Species Act; there is significant controversy, however, over the relative importance that should be given to genetic distinctiveness versus evolutionary potential (see, e.g. Crandall et al. 2000 and Moritz 2002). Along these lines, the introduction of tools that take better account of the underlying evolutionary processes should be used to complement the information about variation in neutral genetic markers currently used to design conservation and management policies, which can be potentially misleading (Leinonen et al. 2008).

The strength and importance of evolutionary effects triggered by selective harvesting also require a re-consideration of current regulatory policies (such as that currently undertaken by the European Union, following decades of regulatory failure; Gray and Hatchard 2003; Daw and Gray 2005; Bretherton and Vogler 2008; COM (2011) 417 final; see below for details). The exploration of new incentives and methods that optimize harvesting yield while mitigating its eco-evolutionary effects represent a fertile field of work in which evolutionary research may go hand in hand with the design, monitoring and

Table 1. Examples of the potential contribution of evolutionary knowledge to existing biodiversity policy.

| Policy sector | Evolutionary process | Policy implications | References |
|--|---|---|--|
| Nature conservation | Disruption of adaptive evolution caused by conservation programmes that shield populations from selective mortality may compromise their future performance | Improved design of <i>in</i> and <i>ex situ</i> conservation programmes | Frankham 2007; Stockwell et al. (2003, 2006) |
| | Genetic diversity involving adaptive traits is determinant to safeguard the adaptive capacity of species and populations. New tools addressing variation in adaptive traits can be used to complement those addressing variation in neutral genetic markers | Improve the design of conservation and management policies | Leinonen et al. (2008) |
| | Local populations and communities often differ in their evolutionary potential and their contribution to meta-population/meta-community dynamics | Improve the design and maintenance of conservation-area networks | Crandall et al. 2000; Moritz 2002 |
| | Functional habitat differs among the different species, and may be disrupted or modified by human action (e.g. sensory pollution) | Complement the structuring of conservation policies around the protection of rare species and habitats | Van Dijk (2011) |
| Fisheries, hunting & angling | Selective harvest of prime-aged reproductive individuals results in selection pressures that may decrease the quantity and quality of harvestable individuals | Modify selective harvest techniques and approaches. Improve the calculation of maximum harvesting yields | Hutchings and Fraser 2008 |
| | Human preference for rarity results in disproportionate risks for over-exploited and endangered populations (anthropogenic Allee effect) | Improve the design of sustainable harvest and conservation programmes | Courchamp et al. 2006 |
| Land-use planning, nature conservation | In fragmented landscapes, gene flow has a dual effect on local populations, increasing genetic variation but limiting local adaptation | Tailor the application of connectivity enhancing and artificial gene-flow measures to the characteristics of target populations | McKay and Latta 2002 |
| Climate change, nature conservation | Local adaptation, dispersal and community ecology interact to determine responses to climate change | Favouring landscape connectivity and gene flow may enhance adaptation to climate change, but effects on the adaptation of resident species and populations are not necessary beneficial | Urban et al. 2011 |
| | Responses to climate change of rare and genetically impoverished species: their limited adaptive capacity will be compounded with low numbers of residents and migrants | To foster evolutionary resilience against climate change, conservation policies should act on target species well before they lose their genetic diversity and evolutionary potential | Urban et al. 2011 |
| Agriculture, forestry, nature conservation | Contemporary evolution may facilitate the establishment and spread of invasive species, exacerbate their impact on native species, and work against attempted control measures | Improvement in the prevention and management of biological invasions, by incorporating knowledge on the evolutionary potential and responses to control measures of invasive species | Frankham 2007; Stockwell et al. (2003, 2006) |
| All sectors | Evolutionary responses are often unpredictable or counterintuitive | Need to learn from action ('policies as experiments', as in adaptive, ecosystem and transition management) | Lee 1993 |

evaluation of the impacts of such measures. These changes should not be restricted to fisheries, but also address angling and hunting. Because the evolutionary effects of selective harvest are likely reinforced by the deleterious consequences of human preference for rarity ('anthropogenic Allee effect', for example Courchamp et al. 2006), they pose a disproportionate risk for over-exploited and endangered populations.

The management of both endangered species and overall landscapes subjected to habitat loss, degradation and fragmentation has also considerable room to benefit from knowledge on evolutionary responses. Here, the double-edged role of gene flow is of key importance (Stockwell et al. 2003). Gene flow increases genetic variation within populations, limiting inbreeding depression and increasing evolutionary potential (genetic rescue; Tallmon et al. 2004); however, it may also limit local adaptation and lead to population declines of locally adapted populations (owing to the introgression of foreign genes). Under habitat degradation and fragmentation, the restoration of population connectivity and gene flow might be a management option. However, uncritical application of artificial gene flow can also have negative consequences – for example if recently fragmented populations have diverged appreciably, efforts to initiate or restore gene flow could result in diminished adaptation and increased risk of extinction. Because the optimal amount of gene flow in a metapopulation will depend on a variety of factors, including the degree to which subpopulations are adapted to local conditions (McKay and Latta 2002), the design of connectivity-enhancement measures would benefit strongly from an explicit consideration (and subsequent monitoring) of the genetic makeup of and evolutionary dynamics in target populations.

The evolving metacommunity framework also has important implications for the interplay between climate change and conservation policies. Because local adaptation, dispersal, and community ecology interact to determine responses to climate change, the impact of management actions affecting any of these components will affect their responses to climate change (Urban 2011). While enhancing landscape connectivity and gene flow probably represents a valid measure to enhance adaptation to climate change (through the shift of spatial ranges and distributions), its effects on the adaptation of resident species and populations are not necessarily beneficial (Urban 2011). More importantly, because conservation policies tend to 'wait' until species are rare and genetically impoverished (owing to the accumulation of population extinctions), their limited adaptive capacity will be compounded with low numbers of residents and migrants – placing them in an almost impossible situation in terms of adapting to new niches, colonizing new sites or monopolizing their local habitat against the entrance

of pre-adapted competitors. The message is that, if the need to foster evolutionary resilience against climate change is taken at heart, conservation policies should act on target species well before these have lost most of their genetic diversity and evolutionary potential.

Knowledge on the evolutionary potential and actual responses of exotic species is critically important to predict the likelihood of biological invasions and manage their spread and impact. Besides facilitating the invasion process and exacerbating its impact on native species, contemporary evolution often works against attempted control measures. Without the inclusion of treatments that reduce evolutionary potential in the target species, traditional control measures (such as the application of herbicides and pesticides to control weeds) may exert strong selection on the target species and result in the evolution of resistance (Stockwell et al. 2003). In addition, and depending on whether increased gene flow is expected to increase or decrease the rate of contemporary adaptation, control programmes could either target the disconnection or the interconnection of local populations of established invaders (Stockwell et al. 2003).

The Convention on Biological Diversity

The Convention on Biological Diversity (CBD hereafter) can be considered as the central piece of biodiversity policy across the world. Signed at the Rio Summit (UNCED) in 1992, it came into effect at the end of 1993. Once considered 'one of the most significant and far-reaching environmental treaties ever to have been developed' (Heywood 1995), it has achieved a moderate success, at best. From its very onset, the discrepancy between its objectives and resources was broadly acknowledged. Conservationists were painfully aware that they were 'far from able to assist all species under threat, if only for lack of funding' (Myers et al. 2000). Despite the broad scope of the convention, for example in defining the various levels at which biological diversity can be addressed (Convention on Biological Diversity 1992), funding limitations and knowledge gaps forced biodiversity conservation to focus, at the operational level, on the static definition of species still predominant in biological sciences – considered to be 'the most prominent and readily recognizable form of biodiversity', as opposed to 'populations or other taxa' (Myers et al. 2000). The management of genetic variation has also been circumscribed to crop/livestock diversity, the impact of GMOs, and the occasional assessment of genetic erosion in endangered species with small or fragmented populations (GBO Secretariat of the Convention on Biological Diversity 2010).

Ten year after its inception, political leaders meeting at the 2002 World Summit on Sustainable Development

(held in Johannesburg, South Africa) agreed 'to achieve by 2010 a significant reduction of the current rate of biodiversity loss at the global, regional and national level' (COP 6 Decision VI/26, <http://www.cbd.int/decision/cop>). This decision presented conservation scientists with one of their most significant challenges. This challenge was not circumscribed to the design and implementation of the policies necessary to achieve his goal; it also included the necessity to incorporate an independent, transparent, credible and robust scientific assessment of the potential success of such policies – that is how rates of biodiversity loss changed from 2002 to 2010. Scientist recognized at the time that measuring biodiversity several times within such period would be rarely possible (most habitats, species, populations and ecosystem services had not been assessed even once); furthermore, available data were 'biased towards the charismatic vertebrate species' which 'supply minimal services to the human economy' (Dobson 2005).

By 2010, the global community acknowledged that it had failed to achieve the Biodiversity Target (CBD Press Brief 2010). The 3rd Global Biodiversity Outlook provided evidence that despite the efforts made, pressures on biodiversity have increased overall. In response to this failure, the CBD adopted a new Strategic Plan for Biodiversity at the 10th Conference of the Parties in Nagoya, Japan. The Strategic Plan has a detailed series of goals and milestones, as well as capacity-development elements, including resource mobilization. A detailed analysis of such goals reveals numerous opportunities to introduce policy-relevant evolutionary thinking (summarized in Table 2). Given the importance of fostering evolutionary resilience in the face of global change, however, a more strategic step would be to incorporate such topic as one of the Cross-Cutting Issues (which develop work on key matters of relevance to the seven thematic programmes established by the Conference of the Parties; see Appendix S1 for details). The creation of a CCI for eco-evolutionary processes could certainly boost a major change of perspective in biodiversity policy, broadening its scope from the reactive conservation of rare and endangered species to the proactive management of the network of eco-evolutionary processes that may ensure their long-term survival in the face of global change.

Diversitas and the IPBES

One of the most important difficulties faced during the implementation of the CBD, as the experience of the last 20 years eloquently shows, is the lack of a coherent interface between science and policy. Two recent initiatives try to address this issue: Diversitas and Intergovernmental Platform on Biodiversity and Ecosystem Services

(IPBES). Diversitas is an international programme of biodiversity science, aimed at providing the scientific basis for the conservation and sustainable use of biodiversity. It was initially established in 1991 by three international organizations (UNESCO, SCOPE and IUBS). Its science plan, launched in 2002, is implemented through seven projects, including one aimed at 'providing an evolutionary framework for biodiversity science' (BioGENESIS). BioGENESIS addresses the areas of evolutionary investigation of direct significance to understanding and managing biodiversity. Activities are largely in line with a number of topics highlighted here (e.g. evolutionary change in biodiversity, the evolution of functional traits, rapid evolution and co-evolutionary dynamics, evolutionary ecosystem management, evolution and climate change), though the emphasis is more on fostering research within these topics than in promoting their incorporation into current policies and management practices.

The IPBES (<http://ipbes.net>) aims at becoming a global interface between the scientific community and policy-makers. It is born from the realization that despite the proliferation of organizations and initiatives that contribute to the science-policy interface on biodiversity and ecosystem services, there is no ongoing global mechanism that brings information together and synthesizes it for decision-making. It will function as an independent intergovernmental body administered by the United Nations and will respond to requests for scientific information from Governments, relevant multilateral environmental agreements and United Nations bodies, as well as other relevant stakeholders. Given that its main functions include the identification of key scientific information needed for policy-makers, the identification of policy-relevant tools and methodologies, and the prioritization of key capacity-building needs to improve the science-policy interface, IPBES could be instrumental in taking proactive action to review the importance of evolutionary processes for biodiversity policy and catalyse its inclusion into current policies and management practices.

EU biodiversity policy

The European Union can be taken as an example of continental policy-making involving multiple states. We can distinguish two strands in EU biodiversity policy: the implementation of international agreements signed by the Member States, such as the CBD (see Appendix S1 for details), and the environmental legislation contained in the *acquis communautaire*. Within the later, the key European policies related to biodiversity are nature conservation, water resources and land use.

Table 2. Potential contribution of evolutionary knowledge to the fulfilment of CBD's Aichi Biodiversity Targets.

| Aichi Biodiversity Targets – By 2020... | Potential contribution of evolutionary knowledge |
|---|--|
| T1. People are aware of the values of biodiversity and the steps they can take to conserve and use it sustainably | Emphasize the dynamic nature of biodiversity, and the contribution of evolutionary processes to its genesis and maintenance |
| T2. Biodiversity values have been integrated into national and local development and poverty reduction strategies and planning processes and are being incorporated into national accounting, as appropriate, and reporting systems | Explore the potential contribution of genetic resources to local development and poverty alleviation |
| T3. Incentives, including subsidies, harmful to biodiversity are eliminated, phased out or reformed to minimize or avoid negative impacts, and positive incentives for the conservation and sustainable use of biodiversity are developed and applied, consistent and in harmony with the Convention and other relevant international obligations, taking into account national socio economic conditions | Pay due attention to the contribution of evolutionary processes to the (positive or negative) effects of certain incentives and regulations – concerning, for example, hunting and angling, pest and invasive-species control, and captive breeding programmes |
| T4. Governments, business and stakeholders at all levels have taken steps to achieve or have implemented plans for sustainable production and consumption and have kept the impacts of use of natural resources well within safe ecological limits | Incorporate knowledge on evolutionary effects to the design of sustainable fisheries and agricultural practices |
| T5. The rate of loss of all natural habitats, including forests, is at least halved and where feasible brought close to zero, and degradation and fragmentation is significantly reduced | Inform policies with knowledge about the effect of landscape structure and matrix characteristics on the connectivity, gene flow, genetic structure and associated evolutionary processes of target species or populations |
| T6. All fish and invertebrate stocks and aquatic plants are managed and harvested sustainably, legally and applying ecosystem-based approaches, so that overfishing is avoided, recovery plans and measures are in place for all depleted species, fisheries have no significant adverse impacts on threatened species and vulnerable ecosystems, and the impacts of fisheries on stocks, species and ecosystems are within safe ecological limits | Incorporate knowledge on evolutionary effects (e.g. of the removal of prime-aged reproductive individuals) to the design of sustainable fishing practices and policies |
| T7. Areas under agriculture, aquaculture and forestry are managed sustainably, ensuring conservation of biodiversity | Incorporate knowledge on evolutionary effects (e.g. of pest control and harvest practices) to the design of sustainable practices and policies in the agriculture, aquaculture and forestry sectors |
| T8. Pollution, including from excess nutrients, has been brought to levels that are not detrimental to ecosystem function and biodiversity | Pay due attention to the effect of emergent contaminants, particularly those acting as genetic or endocrine disruptors |
| T9. Invasive alien species and pathways are identified and prioritized, priority species are controlled or eradicated, and measures are in place to manage pathways to prevent their introduction and establishment | Incorporate knowledge on the evolutionary responses of exotic species to the design of protocols for the prevention (e.g. species banning) and management (e.g. control measures) of biological invasions |
| T10. The multiple anthropogenic pressures on coral reefs, and other vulnerable ecosystems impacted by climate change or ocean acidification, are minimized, so as to maintain their integrity and functioning | |
| T11. At least 17 per cent of terrestrial and inland water, and 10 per cent of coastal and marine areas, especially areas of particular importance for biodiversity and ecosystem services, are conserved through effectively and equitably managed, ecologically representative and well connected systems of protected areas and other effective area-based conservation measures, and integrated into the wider landscapes and seascapes | Inform nature-conservation policies with knowledge on the evolutionary potential of target populations and/or the effect of (natural and artificial) gene flow thereupon |
| T12. The extinction of known threatened species has been prevented, and their conservation status, particularly of those most in decline, has been improved and sustained | Inform in and ex situ conservation programmes for threatened species with small population numbers, so that measures taken to maintain genetic variation do not supersede adaptive evolution to present conditions. Provide techniques and processes allowing for the consideration of adaptive genetic variation in conservation policies |

Table 2. Continued.

| Aichi Biodiversity Targets – By 2020... | Potential contribution of evolutionary knowledge |
|--|---|
| T13. The genetic diversity of cultivated plants and farmed and domesticated animals and of wild relatives, including other socio-economically as well as culturally valuable species, is maintained, and strategies have been developed and implemented for minimizing genetic erosion and safeguarding their genetic diversity | Incorporate the maintenance of (and best practices for) artificial-selection processes responsible for the generation and preservation of existing genetic variation in domesticated species and wild relatives, to current strategies for the conservation of their genetic diversity |
| T14. Ecosystems that provide essential services, including services related to water, and contribute to health, livelihoods and well-being, are restored and safeguarded, taking into account the needs of women, indigenous and local communities, and the poor and vulnerable | Consider the link between ecosystem degradation and emergent diseases, and the evolutionary processes involved in the latter (e.g. host shifts, changes in infectiousness or virulence) |
| T15. Ecosystem resilience, and the contribution of biodiversity to carbon stocks, has been enhanced, through conservation and restoration, including restoration of at least 15% of degraded ecosystems, thereby contributing to climate change mitigation and adaptation and to combating desertification | Inform adaptation policies with knowledge on the eco-evolutionary responses of key or target organisms (e.g. based on the evolving metacommunity framework), particularly concerning the need to safeguard their evolutionary potential in the face of global change |
| T16. The Nagoya Protocol on Access to Genetic Resources and the Fair and Equitable Sharing of Benefits Arising from their Utilization is in force and operational, consistent with national legislation | Base the access and use of genetic resources on the co-responsible safeguarding of the evolutionary potential of focal organisms, and not merely on the shared exploitation of the benefits provided by them |
| T17. Each Party has developed, adopted as a policy instrument, and has commenced implementing an effective, participatory and updated national biodiversity strategy and action plan | Target the conservation of genetic diversity. Develop and incorporate the necessary knowledge on key evolutionary processes, and make explicit links to sectoral policies affecting and being affected by them (e.g. fisheries, agriculture, hunting and angling, pollution prevention and control) |
| T18. The traditional knowledge, innovations and practices of indigenous and local communities relevant for the conservation and sustainable use of biodiversity, and their customary use of biological resources, are respected, subject to national legislation and relevant international obligations, and fully integrated and reflected in the implementation of the Convention with the full and effective participation of indigenous and local communities, at all relevant levels | Support and fund, as required, the generation and transference of knowledge on evolutionary processes of direct relevance for biodiversity policy |
| T19. Knowledge, the science base and technologies relating to biodiversity, its values, functioning, status and trends, and the consequences of its loss, are improved, widely shared and transferred, and applied | |
| T20. The mobilization of financial resources for effectively implementing the Strategic Plan for Biodiversity 2011–2020 from all sources, and in accordance with the consolidated and agreed process in the Strategy for Resource Mobilization, should increase substantially from the current levels. This target will be subject to changes contingent to resource needs assessments to be developed and reported by Parties | |

Nature conservation

Nature conservation is based on two Directives: the Birds Directive and the Habitats Directive (Table 3). The most important practical objective of the Habitats Directive has been the creation of ‘Natura 2000’, a network composed of the Special Protection Areas for wild birds and Special Areas of Conservation for natural habitats and threatened fauna and flora. The directive lists ‘priority natural habi-

tat types’ and ‘priority species’, which member countries should specifically consider when designating special areas of conservation. In most European countries, the establishment of Natura 2000 network has therefore been based on local species lists and mappings of habitat types. Genetic studies of local populations have seldom been used in justification of new conservation areas (exceptions include the Lake Saimaa seal in Finland; Wilson et al. 2001; Sipilä 2003; T. Vuorisalo in Grant et al. 2010).

Table 3. Examples of references made to genetic diversity and/or evolutionary processes in EU biodiversity policy, and proposed innovations to such policies.

| Policy sector | Policy document | References to genetic diversity and/or evolutionary processes | Proposed innovations |
|---------------------|---|--|--|
| Nature conservation | Guidance Document on Hunting under the Birds Directive (Council Directive 79/409/EEC) | The only reference made to the 'genetic diversity' of target species in one of the arguments advanced by the Belgian authorities to allow the capture of wild birds protected by the Directive (based on the 'risk to successful captive breeding posed by a lack of genetic diversity in captive breeding stocks'). However, Article 10 of the Birds Directive (requiring Member States to encourage research and 'any work required as a basis for the protection, management and use of the population of all species of birds referred to in Article 1') has to be transposed and implemented in national legal orders | Amend the GDH to recommend the explicit evaluation of the effects of hunting on trait selection and genetic diversity of target species |
| | Habitats Directive (Council Directive 92/43/EEC) | Genetically distinct populations within species are not specifically mentioned. However, Annex III requires taking into account the 'global ecological value of the site for the biogeographical regions concerned' and the degree of isolation of priority species for the assessment of Natura 2000 sites. Member States are encouraged to improve the ecological coherence of the Natura 2000 network by 'encouraging the features of the landscape which are important for wild fauna and flora', such as 'those which... are essential for the migration, dispersal and genetic exchange of wild species' (Article 10) | Introduce the conservation status of genetically distinct local populations and their respective contribution to the species' evolutionary potential as criteria for declaring the conservation status of species and justifying new conservation areas. Make the application of Article 10 mandatory |
| Fisheries | Biodiversity Action Plan on Fisheries (Communication COM/2001/0162 final) | Numerous references to the potential impacts of fisheries on genetic diversity. Adheres to a fairly broad definition of biological diversity (which includes genetic, species and ecosystem diversity, as well as 'the variability in the size/age and reproductive quality of the species'). Refers explicitly to the 'genetic effects of decades of high and size selective fishing pressure'. Stresses the necessity to guarantee 'genetic sustainability' and safeguard genetic stocks | Address explicitly the relationships between selective fishing and trait selection, and its potential effects on the quality and quantity of harvestable stocks |
| Agriculture | Biodiversity Action Plan on Agriculture (Communication COM/2001/0162 final) | Direct reference to anthropogenic evolution taking place in semi-natural and natural landscapes. Section on genetic resources (Sectoral Objective 1) implemented through the first programme on the conservation, characterization, collection and utilization of genetic resources in agriculture (Regulation EC 1467/94), focused on <i>ex situ</i> conservation (mainly gene-bank collections). The second programme 'should make a major contribution to <i>in situ</i> conservation and on farm management' that 'permits populations of plant species to be maintained in their natural or agricultural habitat, allowing the evolutionary processes that shape the genetic diversity and adaptability of plant populations to continue to evolve' | Address the effect that current agricultural practices have on the (co)evolution of associated animal and plant species - notably pests and weeds, but also their predators and parasites |

Table 3. Continued.

| Policy sector | Policy document | References to genetic diversity and/or evolutionary processes | Proposed innovations |
|-------------------|---|---|--|
| Natural resources | Biodiversity Action Plan on the Conservation of Natural Resources (Communication COM/2001/0162 final) | Links to sectoral legislation (see rows below) | |
| Water resources | Water Framework Directive (WFD; Directive 2000/60/EC) | One action of the BAP on the Conservation of Natural Resources (see previous row) aims at ensuring that River Basin Management Plans (mandated by the WFD) reflect biodiversity concerns by, among others, 'establishing a string of aquatic ecosystems with restored or improved ecosystem function, which may function as aquatic ecological corridor' | Expand this reference by addressing the effect of connectivity on metacommunity and metapopulation processes. Address other processes that may affect the evolutionary dynamics of aquatic organisms, such as pollution (e.g. with endocrine disruptors) or angling (including re-stocking with captive-bred fishes) |
| Land use | European Spatial Development Perspective (European Commission, 1999) Territorial Agenda of the EU | Acknowledges explicitly the need to avoid the isolation of protected areas and the importance of a successful development of European ecological networks for the conservation and development of biodiversity Section II ('Challenges and potentials for territorial development') and III ('Territorial Priorities for the Development of the European Union') of the Agenda include specific Subsections on, respectively, the 'Loss of biodiversity, vulnerable natural, landscape and cultural heritage' and 'Managing and connecting ecological, landscape and cultural values of regions' | Use these references to pay due consideration to the evolutionary processes that shape biodiversity at the local and landscape scale, particularly those related to gene flow and genetic structuring in fragmented or naturally isolated landscapes |
| Climate change | White Paper on Adaptation Framework (COM(2009) 147 final) | Includes a number of actions for which knowledge on eco-evolutionary responses is highly relevant: (i) epidemiological surveillance and disease prevention in human and animal health; (ii) evaluation of the impact of climate change on the management of Natura 2000 sites; (iii) initiatives to ensure the diversity of and connectivity between natural areas, and to allow for species migration and survival when climate conditions change; (iv) actions to introduce adaptation in coastal and marine areas to the reform of the Common Fisheries Policy | Rise the profile of evolutionary knowledge in the technical groups (e.g. Impact and Adaptation Steering Group) and knowledge-base instruments (e.g. Clearing House Mechanism) set up within the Adaptation Framework |

Although a key criterion for declaring the favourable conservation status of a species is the long-term viability of its populations, its assessment is at best based on demographic analyses; hence, it disregards the conservation status of genetically distinct local populations and their respective contribution to the species' evolutionary potential (e.g. Salducci et al. 2004). Indeed, the conservation of genetically distinct populations, races or subspecies is not specifically mandated in the Habitats Directive, and although the Directive supports it to a certain extent (see

Table 3), the greatest obstacle has been lack of financing and enforcing interest by Member States (T. Vuorisalo in Grant et al. 2010).

Natura 2000 aims to be 'a coherent European ecological network of special areas of conservation,' and Member States are encouraged to improve such ecological coherence by maintaining and developing appropriate landscape features (see Table 3). This is completely coherent with the maintenance of gene flow and, more broadly, evolutionary processes across the mosaic of anthropogenic

and natural landscapes. However, while the designation of special sites is clear and compulsory (European Commission, 2000), the maintenance of or improvement in their ecological coherence is left to the judgement of the Member States – a potential loophole, given the reluctance of several Member States to implement this Directive (Paavola 2004) and the ensuing shift in emphasis from the fulfilment of its ambitious goals to the procedural aspects of decision-making (Beunen 2006).

The Birds Directive recognizes the legitimacy of hunting of wild birds as a form of sustainable use. However, hunting is limited to certain species and restricted by a series of ecological principles and legal requirements, which application has been surrounded by fierce controversy. In an attempt to provide guidelines for the regulation of the hunting sector, the European Commission launched the Sustainable Hunting Initiative (SHI) in 2001. Its documentation includes the Guidance Document on Hunting under the Birds Directive (GDH), a nonbinding document that explains the ecological principles that underpin the management of hunting under the Directive. The GDH makes no reference to the evolutionary effects of hunting (including the management and translocation of game and fowl populations) or its effects on genetic diversity. This absence is particularly worrying given the strong selection effects of hunting procedures targeting prime-aged reproductive individuals and their potential effect of estimations of ‘viable population’ sizes and ‘optimal sustainable yield’. The case law of the Court of Justice has indicated, however, the importance of using the best available scientific information as a basis for implementing the Directive and the obligation of carrying out the research programmes required to generate it (see Table 3). Based on it, knowledge on the evolutionary effect of current practices could be incorporated to hunting regulation and exploitation plans.

Biodiversity action plans

Most examples of contemporary, anthropogenic evolution affecting wild species do not take place in nature-conservation areas, but in those subjected to intensive human use – such as agriculture, fisheries or hunting. The incorporate current evolutionary knowledge to biodiversity and sustainability policies, therefore, requires changes in the corresponding sectoral legislation. The 2010 Biodiversity Strategy aimed at ensuring the required level of policy integration by including the development of Biodiversity Action Plans for agriculture, fisheries, development and economic co-operation, and the conservation of natural resources (Communication COM/2001/0162 final).

The BAP on fisheries makes numerous references to the potential impacts of fisheries on genetic diversity and

stresses the necessity to guarantee ‘genetic sustainability’ and safeguard genetic stocks (see Table 3). However, these concerns are solely framed in terms of depletion versus conservation of the genetic resources, with little mention to the associated evolutionary processes. The difference is significant, because an explicit consideration of the underlying evolutionary processes would shift the emphasis from tailoring fishing pressure to safeguard a given level of genetic diversity, to modifying the current suite of techniques, incentives and regulations as to prevent the evolutionary consequences of harvesting prime-quality reproductive individuals. To the extent that such evolutionary consequences include reductions in the population persistence and sustainable yield of target species (see for example the study by Hutchings and Fraser 2008), halting or mitigating them can represent a shortcut towards achieving the long-term objective of sustainable harvesting yields.

The BAP on agriculture includes a direct reference to anthropogenic evolution taking place in semi-natural and natural landscapes. The section on genetic resources has resulted already in a 5-year programme focused on *ex situ* conservation and indicates that a future programme will focus *in situ* conservation and on farm management (see Table 3). The aim of such programme includes ‘allowing the evolutionary processes that shape the genetic diversity and adaptability of plant populations to continue to evolve’. This reference could be broadened and reinforced by addressing the effect that current agricultural practices have on the (co)evolution of associated animal and plant species (notably pests and weeds, but also their predators and other species).

Finally, the BAP for the conservation of natural resources states clearly that ‘as the preservation of biodiversity requires actions not only within designated areas but also across the whole territory, the Action Plan also has a focus on land-use-related environmental initiatives... and the integration of biodiversity in other sectors’. Point 3 of the Plan focuses on reversing the current trends of biodiversity loss related to management of water, soil, forest and wetlands, and establishes explicit links to the corresponding sectoral legislation.

It is, however, worth stressing that in spite of their strategic importance, the Communications that lay down the Biodiversity Strategy and Action Plans are only guidelines; hence, contrary to legislative documents (regulations, directives and decisions), they are not binding for Member States. Given the contrasting willingness shown by different Member States when it comes to adhering to the targets and objectives included in these Communications, it is fair to expect a highly heterogeneous implementation across the whole EU. Indeed, it is tempting to suggest that the failure to achieve a substantial progress

in the target of reducing the loss of biodiversity by 2010 was strongly related to the lack of direct legislative support provided to this target.

Water resources

The BAP for the conservation of natural resources relies heavily on the Water Framework Directive (WFD, see Appendix S2 for details) for the conservation and sustainable use of biodiversity at river-basin level. It pays due attention to the maintenance of connectivity –for example one specific Action aims at ensuring that River Basin Management Plans reflect biodiversity concerns by, among others, ‘establishing a string of aquatic ecosystems with restored or improved ecosystem function, which may function as aquatic ecological corridor’. However, there is a conspicuous absence of references to both the role of dispersal mechanisms (e.g. waterfowl and fish migration) in maintaining connectivity and its effect on the metacommunity and metapopulation processes responsible for maintenance of species and genetic diversity (Amezaga et al. 2002). Other processes that may also affect the evolutionary dynamics of key aquatic organisms, such as pollution (e.g. with endocrine disruptors) or angling (including re-stocking with captive-bred fishes), should also be addressed in future modifications of this BAP.

Land use

One of the essential problems of implementing EU environmental policies encompassing the whole territory is that land-use policies are determined by Member States. The European Spatial Development Perspective (ESDP, see Appendix S2 for details) acknowledges explicitly the need to avoid the isolation of protected areas with a broader land-use policy and the importance of a successful development of European ecological networks for the conservation and development of biodiversity. In May 2007, it was complemented by the Territorial Agenda of the EU, which makes an explicit mention to ‘the fragmentation of natural habitats and ecological corridors’, underlines the common responsibility for ensuring the ‘well-functioning, protection and enhancement of ecological systems and the cultural and natural heritage’, and supports ‘the integration of ecological systems and areas protected for their natural values into green infrastructure networks’. These explicit references to the spatial aspects of biodiversity and ecosystem function offer ample room for incorporating the evolutionary processes that shape them at the local and landscape scale – particularly those related to gene flow and genetic structuring in fragmented or naturally isolated landscapes.

EU climate change policy

Evolutionary responses may also be relevant for policies seeking to enhance EU’s adaptive potential in the face of to climate change. Measures aimed at mainstreaming adaptation into EU policies (point 2 of the Adaptation Framework, see Appendix S2 for details) include a review, ‘based on solid scientific and economic analysis made for each policy area’, of how policies could be re-focused or amended to facilitate adaptation, as well as early action in sectors with strong EU policy involvement for which adaptation strategies ‘would generate net social and/or economic benefits irrespective of uncertainty in future forecasts (no-regret measures)’. These include a number of actions for which the eco-evolutionary responses described earlier are likely to be highly relevant – such as epidemiological surveillance and disease prevention in the field of human and animal health; initiatives to factor in the impact of climate change into the management of Natura 2000 sites, to ensure the diversity of and connectivity between natural areas, and to allow for species migration and survival when climate conditions change; and actions to ensure that adaptation in coastal and marine areas is taken into account in the reform of the Common Fisheries Policy. Rising the profile of evolutionary knowledge in the technical groups (such as the Impact and Adaptation Steering Group, see Appendix 2) and knowledge-base instruments (such as the Clearing House Mechanism, see Appendix 2) set up within the Adaptation Framework forward would also contribute to address the numerous unpredictabilities surrounding the impacts of and responses to future climate.

EU research policy

A last word is due concerning the knowledge required to support the policy initiatives outlined earlier and the role of EU research policy in generating such knowledge. Along this paper, frequent references were made to the importance of policy-relevant, proactive research for the generation of knowledge needed to design, implement and evaluate biodiversity, climate change, and other sectoral policies. This is particularly true when it comes to introducing new knowledge and perspectives (such as the incorporation of evolutionary processes) into already-established policy fields. Unfortunately, neither the reality of current EU research policy nor its future prospects are any encouraging. Despite the lip service paid to the key importance of research and knowledge in the Biodiversity Strategy and the Adaptation Framework, the forthcoming Framework Programme for Research and Innovation ‘Horizon 2020’ (outlined in the Green Paper

COM (2011) 48; see MEMO/11/435) will be dominated by a narrow focus on industrial, technological and end-of-point social innovation, complemented by increases in the funding of blue-sky research through the European Research Council (see also EC 2011). In summary, EU funding of policy-relevant research in biodiversity will be severely cut.

These budget cuts culminate a decade-long trend towards decreasing innovation in biodiversity research. Framework programme projects have simultaneously increased their size and narrowed their scope during the last decade (notably, within the 6th and 7th FPs) – a decision motivated by the need to reduce the cost and trouble involved in the evaluation and management of the projects, rather than by the drive to improve research quality. This trend was combined with a sharp decrease in transparency during the preparation of the calls – which are increasingly based in proposals derived from ‘expert meetings’ dominated by the very same research teams that subsequently apply for the projects. The result has been a decrease in the originality of FP research projects, which reduced critically the possibility of incorporating innovative knowledge to current and future EU policy. The question remains of whether future ERC projects – a clear success of the 7th FP, attending to their originality and quality – will do the trick. Despite their numerous virtues, ERC projects are granted to single researchers and generally oblivious of (if not openly alien to) EU policy needs. In our view, coupling research to policy initiatives will probably be exceedingly difficult within such funding framework.

Conclusions

The intensity and speed of human alterations to the planet’s ecosystems are yielding our static, ahistorical view of biodiversity obsolete. Human actions frequently trigger fast evolutionary responses, drastically affect extant genetic variation (most often, depleting it), and result in the ongoing establishment of new communities and co-evolutionary networks for which we lack past analogues. Our review of international (CBD) and EU biodiversity policy showed numerous opportunities for the integration of evolutionary knowledge, with the realistic prospect of improving their efficacy. Such opportunities should be extended to several sectoral policies of direct relevance for biodiversity – notably, nature conservation, fisheries, agriculture, water resources, spatial planning and climate change. These avenues for improvement are, however, challenged by the low level of enforcement of biodiversity policies and by the decreasing emphasis paid to biodiversity in EU’s research policy.

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Literature cited

- Amezaga, J. M., L. Santamaría, and A. J. Green. 2002. Waterfowl-mediated dispersal and wetland connectedness: supporting a new approach to wetland policy. *Acta Oecologica* **23**:213–222.
- Angeloni, F., C. A. M. Wagemaker, P. Vergeer, and N. J. Ouborg. 2012. Genomic toolboxes for conservation biologists. *Evolutionary Applications* **5**:128–141.
- Araki, H., B. Cooper, and M. S. Blouin. 2007. Genetic effects of captive breeding cause a rapid, cumulative fitness decline in the wild. *Science* **318**:100.
- Arkema, K. K., S. C. Abramson, and B. M. Dewsbury. 2006. Marine ecosystem-based management: from characterization to implementation. *Frontiers in Ecology and the Environment* **4**:525–532. doi: 10.1890/1540-9295(2006)4[525:MEMFCT]2.0.CO;2.
- Barnosky, A. D., N. Matzke, S. Tomiya, G. O. U. Wogan, B. Swartz, T. B. Quental, C. Marshall *et al.* 2011. Has the Earth’s sixth mass extinction already arrived? *Nature* **471**:51–57.
- Bascompte, J., and P. Jordano. 2007. Plant-animal mutualistic networks: the architecture of biodiversity. *Annual Review of Ecology, Evolution, and Systematics* **38**:567–593.
- Bascompte, J., P. Jordano, and J. M. Olesen. 2006. Asymmetric coevolutionary networks facilitate biodiversity maintenance. *Science* **312**:431–433.
- Beunen, R. 2006. European nature conservation legislation and spatial planning: for better or for worse? *Journal of Environmental Planning and Management* **49**:605–619.
- Blackburn, T. M., P. Pyšek, S. Bacher, J. T. Carlton, R. P. Duncan, V. Jarosik, J. R. U. Wilson, and D. M. Richardson. 2011. A proposed unified framework for biological invasions. *Trends in Ecology and Evolution* **26**:333–339.
- Bretherton, C., and J. Vogler. 2008. The European Union as a Sustainable Development Actor: the Case of External Fisheries Policy. *Journal of European Integration* **30**:410–417.
- Campbell, A. K. 2003. Save those molecules: molecular biodiversity and life. *Journal of Applied Ecology* **40**:193–203.
- Carroll, S. P. 2007. Facing change: forms and foundations of contemporary adaptation to biotic invasions. *Molecular Ecology* **17**:361–372.
- Carroll, S. P., A. P. Hendry, D. N. Reznick, and C. W. Fox. 2007. Evolution on ecological time-scales. *Functional Ecology* **21**:387–393.
- CBD Press Brief. 2010. The strategic plan for the CBD. <http://www.cbd.int/cop10> (accessed on 18 January 2012).

- Chivian, E., and A. Bernstein, eds. 2008. *Sustaining Life: How Human Health Depends on Biodiversity*. Oxford University Press, Oxford.
- Christensen, N. L., A. M. Bartuska, J. H. Brown, S. Carpenter, C. D'Antonio, R. Francis, J. F. Franklin *et al.* 1996. The Report of the Ecological Society of America Committee on the Scientific Basis for Ecosystem Management. *Ecological Applications* **6**:665–691.
- Conover, D. 2000. Darwinian fishery science. *Marine Ecology Progress Series* **208**:299–313.
- Convention on Biological Diversity. 1992. <http://www.cbd.int/doc/legal/cbd-en.pdf> (accessed on 16 January 2012).
- Costanza, R., R. D'arge, R. De Groot, S. Farber, M. Grasso, B. Hannon, K. Limburg *et al.* 1997. The value of the world's ecosystem services and natural capital. *Nature* **387**:253–260.
- Courchamp, F., E. Angulo, P. Rivalan *et al.* 2006. Rarity value and species extinction: the anthropogenic allee effect. *PLoS Biology* **4**:e415. doi: 10.1371/journal.pbio.0040415.
- Cox, G. W. 2004. *Alien Species and Evolution*. Island Press, Washington.
- Crandall, K. A., O. R. P. Bininda-Emonds, G. M. Mace, and R. K. Wayne. 2000. Considering evolutionary processes in conservation biology. *Trends in Ecology & Evolution* **15**:290–295.
- Darimont, C. T., S. M. Carlson, M. T. Kinnison, P. C. Paquet, T. E. Reimchen, and C. C. Wilmers. 2009. Human predators outpace other agents of trait change in the wild. *Proceedings of the National Academy of Sciences* **106**:952–954.
- Daw, T., and T. Gray. 2005. Fisheries science and sustainability in international policy: a study of failure in the European Union's Common Fisheries Policy. *Marine Policy* **29**:189–197.
- Dobson, A. 2005. Monitoring global rates of biodiversity change: challenges that arise in meeting the Convention on Biological Diversity (CBD) 2010 goals. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* **360**:229–241.
- Ehrenfeld, D. 1988. Why put a value on biodiversity. In E. O. Wilson, and F. M. Peter, eds. *Biodiversity*, pp. 212–216. National Academy Press, Washington, DC.
- Erwin, D. H. 1998. The end and the beginning: recoveries from mass extinctions. *Trends in Ecology & Evolution* **13**:344–349.
- European Commission. 1999. *European Spatial Development Perspective*. Office for Official Publications of the European Communities, Luxembourg.
- European Commission. 2011. *Common Strategic Framework for EU Research and Innovation Funding*. Analysis of public consultation. Publications Office of the European Union, Luxembourg. doi: 10.2777/58706.
- Fenberg, P. B., and K. Roy. 2007. Ecological and evolutionary consequences of size-selective harvesting: how much do we know? *Molecular Ecology* **17**:209–220.
- Festa-Bianchet, M. 2003. Exploitative wildlife management as a selective pressure for life-history evolution of large mammals. In M. Festa-Bianchet, and M. Apollonio, eds. *Animal Behavior and Wildlife Conservation*, pp. 191–207. Island Press, Washington, DC.
- Finger, A., C. J. Kettle, C. N. Kaiser-Burnbury, T. Valentin, D. Doude, D. Matatiken, and J. Ghazoul. 2011. Back from the brink: potential for genetic rescue in a critically endangered tree. *Molecular Ecology* **20**:3773–3784.
- Folke, C., S. Carpenter, B. Walker, M. Scheffer, T. Elmqvist, L. Gunderson, and C. S. Holling. 2004a. Regime shifts, resilience, and biodiversity in ecosystem management. *Annual Review of Ecology, Evolution and Systematics* **35**:557–581.
- Frankham, R. 2007. Genetic adaptation to captivity in species conservation programs. *Molecular Ecology* **17**:325–333.
- Garner, A., J. L. Rachlow, and J. F. Hicks. 2005. Patterns of genetic diversity and its loss in mammalian populations. *Conservation Biology* **19**:1523–1739.
- Grant, F., J. Mergeay, L. Santamaría, J. Young, and A. D. Watt, eds. 2010. *Evolution and biodiversity: the evolutionary basis of biodiversity and its potential for adaptation to global change*. Report of an e-conference. <http://www.epbrs.org/event/show/27> (accessed 16 January 2012).
- Gray, T., and J. Hatchard. 2003. The 2002 reform of the Common Fisheries Policy's system of governance—rhetoric or reality? *Marine Policy* **27**:545–554.
- Gross, L. 2005. Why not the best? How science failed the Florida panther. *PLoS Biology* **3**:e333. doi: 10.1371/journal.pbio.0030333.
- Haigi, S. M., E. A. Beever, S. M. Chambers, H. M. Draheim, B. D. Dugger, S. Dunham, E. Elliott-Smith, *et al.* 2006. Taxonomic Considerations in Listing Subspecies Under the U.S. Endangered Species Act. *Conservation Biology* **20**:1584–1594.
- Heath, D. D., J. W. Heath, C. A. Bryden, R. M. Johnson, and C. W. Fox. 2003. Rapid evolution of egg size in captive salmon. *Science* **299**:1738–1740.
- Hendry, A. P., T. J. Farrugia, and M. T. Kinnison. 2008. Human influences on rates of phenotypic change in wild animal populations. *Molecular Ecology* **17**:20–29.
- Heywood, V. H., ed. 1995. *The Global Biodiversity Assessment*. United Nations Environment Programme. Cambridge University Press, Cambridge.
- Hoffmann, A. A., and C. M. Sgrò. 2011. Climate change and evolutionary adaptation. *Nature* **470**:479–485.
- Hughes, J. B., G. C. Daily, and P. R. Ehrlich. 1997. Population diversity: its extent and extinction. *Science* **278**:689–692.
- Hutchings, J. A., and D. J. Fraser. 2008. The nature of fisheries- and farming-induced evolution. *Molecular Ecology* **17**:294–313.
- Jablonski, D. 2001. Lessons from the past: evolutionary impacts of mass extinctions. *Proceedings of the National Academy of Sciences* **98**:5393–5398.
- Jachmann, H., P. S. M. Berry, and H. Imae. 1995. Tuskslessness in African elephants: a future trend. *African Journal of Ecology* **33**:230–235.
- Kinnison, M. T., and N. G. Hairston Jr. 2007. Eco-evolutionary conservation biology: contemporary evolution and the dynamics of persistence. *Functional Ecology* **21**:444–454.
- Kinnison, M. T., A. P. Hendry, and C. A. Stockwell. 2007. Contemporary evolution meets conservation biology II: impediments to integration and application. *Ecological Research* **22**:947–954.
- Lee, K. N. 1993. *Compass and Gyroscope: Integrating Science and Politics for the Environment*. Island Press, Washington, DC.
- Leinonen, T., R. B. O'Hara, J. M. Cano, and J. Merilä. 2008. Comparative studies of quantitative trait and neutral marker divergence: a meta-analysis. *Journal of Evolutionary Biology* **21**:1–17.
- Loreau, M., S. Naeem, P. Inchausti *et al.* 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science* **294**:804–808.
- Mace, G., H. Masundire, J. Baillie *et al.* 2006. Biodiversity. In R. M. Hassan, R. Scholes, and N. Ash, eds. *Ecosystems and Human Well-Being: Current State and Trends*. Findings of the Condition and Trends Working Group of the Millennium Ecosystem Assessment, pp. 79–115. Island Press, Washington, DC.

- May, R. M., J. H. Lawton, and N. E. Stork. 1995. Assessing extinction rates. In J. H. Lawton, and R. M. May, eds. *Extinction Rates*, pp. 1–24. Oxford University Press, Oxford.
- McKay, J. K., and R. G. Latta. 2002. Adaptive population divergence: markers, QTL and traits. *Trends in Ecology and Evolution* 17:285–291.
- Moritz, C. 2002. Strategies to protect biological diversity and the evolutionary processes that sustain it. *Systematic Biology* 51:238–254.
- Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. B. da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403:853–858.
- Naeem, S. 2002. Ecosystem consequences of biodiversity loss: the evolution of a paradigm. *Ecology* 83:1537–1552.
- Ostfeld, R. S. 2009. Biodiversity loss and the rise of zoonotic pathogens. *Clinical Microbiology and Infection* 15:40–43.
- Paavola, J. 2004. Protected areas governance and justice: theory and the European Union's Habitats Directive. *Environmental Sciences* 1:59–77.
- Paetkau, D., L. P. Waits, P. L. Clarkson, L. Craighead, E. Vyse, R. Ward, and C. Strobeck. 1998. Variation in genetic diversity across the range of North American brown bears. *Conservation Biology* 12:418–429.
- Palkovacs, E., M. T. Kinnison, C. Correa, C. M. Dalton, and A. Hendry. 2012. Ecological consequences of human-induced trait change: fates beyond traits. *Evolutionary Applications* 5:183–191.
- Palumbi, S. R. 2001. Humans as the world's greatest evolutionary force. *Science* 293:1786–1790.
- Piazzon, M., A. R. Larrinaga, and L. Santamaría. 2011. Are nested networks more robust to disturbance? A test using epiphyte-tree, commensalistic networks. *PLoS ONE* 6:e19637. doi: 10.1371/journal.pone.0019637.
- Pimm, S. L., L. Dollar, and O. L. Bass Jr. 2006. The genetic rescue of the Florida panther. *Animal Conservation* 9:115–122.
- Rapport, D. J., R. Constanza, and A. J. McMichael. 1998. Assessing ecosystem health. *Trends in Ecology and Evolution* 13:397–402.
- Sala, O. E., F. S. Chapin III, J. J. Armesto *et al.* 2000. Global biodiversity scenarios for the year 2100. *Science* 287:1770–1774.
- Salducci, M. D., J.-F. Martin, N. Pech, R. Chappaz, C. Costedoat, and A. Gilles. 2004. Deciphering the evolutionary biology of freshwater fish using multiple approaches – insights for the biological conservation of the Vairone (*Leuciscus souffia souffia*). *Conservation Genetics* 5:63–77.
- Seastedt, T. R., R. J. Hobbs, and K. N. Suding. 2008. Management of novel ecosystems: are novel approaches required? *Frontiers in Ecology and the Environment* 6:547–553.
- Secretariat of the Convention on Biological Diversity. 2010. *Global Biodiversity Outlook 3*. Montréal, QC, Canada.
- Shine, R. 2012. Invasive species as drivers of evolutionary change: cane toads in tropical Australia. *Evolutionary Applications* 5:107–116.
- Sipilä, T. 2003. Conservation biology of Saimaa ringed seal (*Phoca hispida saimensis*) with reference to other European seal populations. PhD Thesis, University of Helsinki, Finland. <https://helda.helsinki.fi/bitstream/handle/10138/22401/conserva.pdf?sequence=2> (accessed on 16 January 2012).
- Stewart, J. R. 2009. The evolutionary consequence of the individualistic response to climate change. *Journal of Evolutionary Biology* 22:2363–2375.
- Stockwell, C. A., A. P. Hendry, and M. T. Kinnison. 2003. Contemporary evolution meets conservation biology. *Trends in Ecology and Evolution* 18:94–101.
- Stockwell, C. A., M. T. Kinnison, and A. P. Hendry. 2006. Evolutionary restoration ecology. In D. A. Falk, M. A. Palmer, and J. B. Zedler, eds. *Foundations of Restoration Ecology*, pp. 113–138. Island Press, Washington, DC.
- Stralberg, D., D. Jongsomjit, C. A. Howell *et al.* 2009. Re-shuffling of species with climate disruption: a no-analog future for California birds? *PLoS ONE* 4:e6825. doi: 10.1371/journal.pone.0006825.
- Swain, D. P., A. F. Sinclair, and J. M. Hanson. 2007. Evolutionary response to size-selective mortality in an exploited fish population. *Proceedings of the Royal Society, Series B: Biological Sciences* 274:1015–1022.
- Taberlet, P., J.-J. Camarra, S. Griffin, E. Uhrès, O. Hanotte, L. P. Waits, C. Dubois-Paganon *et al.* 1997. Noninvasive genetic tracking of the endangered Pyrenean brown bear population. *Molecular Ecology* 6:869–876.
- Tallmon, D. A., G. Luikart, and R. S. Waples. 2004. The alluring simplicity and complex reality of genetic rescue. *Trends in Ecology and Evolution* 19:489–496.
- Thompson, J. N. 1998. Rapid evolution as an ecological process. *Trends in Ecology and Evolution* 13:329–332.
- Thompson, J. N. 2005. *The Geographic Mosaic of Coevolution*. The University of Chicago Press, Chicago.
- Thompson, J. N. 2009. The coevolving web of life. *American Naturalist* 173:125–150.
- Urban, M. C., L. De Meester, M. Vellend, R. Stoks, and J. Vano-verbek. 2012. A crucial step towards realism: responses to climate change from an evolving metacommunity perspective. *Evolutionary Applications* 5:154–167.
- Van Dyck, H. 2012. Changing organisms in rapidly changing anthropogenic landscapes: the significance of the “Umwelt”-concept and functional habitat for animal conservation. *Evolutionary Applications* 5:144–153.
- Williams, J. W., and S. T. Jackson. 2007. Novel climates, no-analog communities, and ecological surprises. *Frontiers in Ecology and the Environment* 5:475–482. doi: 10.1890/070037.
- Wilson, S. C., G. Mo, and T. Sipilä. 2001. Legal protection for seals in small populations in European Community and Mediterranean coastal waters. *Mammalia* 65:335–348.
- Wood, T. E., N. Takebayashi, M. S. Barker, I. Mayrose, P. B. Greenspoon, and L. H. Rieseberg. 2009. The frequency of polyploid speciation in vascular plants. *Proceedings of the National Academy of Sciences* 106:13875–13879.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Summary description of the Convention on Biological Diversity.

Appendix S2. Overview of EU biodiversity policy.

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