Chapter 11
Biodiversity, Disparity and Evolvability

Alessandro Minelli

Abstract A key problem in conservation biology is how to measure biological diversity. Taxic diversity (the number of species in a community or in a local biota) is not necessarily the most important aspect, if what most matters is to evaluate how the loss of the different species may impact on the future of the surviving species and communities. Alternative approaches focus on functional diversity (a measure of the distribution of the species among the different 'jobs' in the ecosystem), others on morphological disparity, still others on phylogenetic diversity. There are three major reasons to prioritize the survival of species which provide the largest contributions to the overall phylogenetic diversity. First, evolutionarily isolated lineages are frequently characterized by unique traits. Second, conserving phylogenetically diverse sets of taxa is valuable because it conserves some sort of trait diversity, itself important in so far as it helps maintain ecosystem functioning, although a strict relationships between phylogenetic diversity and functional diversity cannot be taken for granted. Third, in this way we maximize the "evolutionary potential" depending on the *evolvability* of the survivors. This suggests an approach to conservation problems focussed on evolvability, robustness and phenotypic plasticity of developmental systems in the face of natural selection: in other terms, an approach based on evolutionary developmental biology.

Keywords Evolvability · Functional diversity · Morphological disparity · Phenotypic plasticity · Phylogenetic diversity

11.1 A Concern for Biodiversity: Evolution's Products at Risk

A key problem in conservation biology is how to measure the biological diversity at risk of loss, or already lost at the global scale or in a given area or habitat.

A. Minelli (✉)
Department of Biology, University of Padova, Padova, Italy
e-mail: alessandro.minelli@unipd.it

E. Casetta et al. (eds.), *From Assessing to Conserving Biodiversity*,
History, Philosophy and Theory of the Life Sciences 24,
https://doi.org/10.1007/978-3-030-10991-2_11

The origin of the concept of biodiversity from within ecology (Wilson 1988) explains why biological diversity is primarily described and measured in terms of the number of species in a community, or in a local biota. However, when describing the ongoing extinction of the Anthropocene, the total number of species involved is not necessarily the most important issue. What matters in the end is what has been lost or may be lost with them, and how this loss may impact on the future of both species and communities.

What we eventually prioritize is often heavily biased by our emotional preference for a few kinds of organisms and also for selected areas or habitats. Vertebrates are given much more attention than nematodes, big cats quite more than rodents. Whole biotas of particular sites are cause of special concern, for example those of remote oceanic islands like the Hawaii or the Galápagos. In other instances, individual species become the target of dedicated conservation efforts because of the peculiar role they play in the ecosystem, for example (in the case of bees and other insects) as pollinators or (in the case of corals) as builders of reefs on which the existence of many other marine species depends. Other reasons for identifying a species as worth of special conservation effort are less obvious and perhaps, *prima facie*, just academic or antiquarian – as for example, when we decide that a given species is worth of special conservation effort only because it is the only member or the last survivor of a peculiar evolutionary lineage.

11.1.1 Beyond Species Number

The latter example deserves closer scrutiny. Low species number is not necessarily a sign of scarce success of the whole lineage, or of impending risk of extinction: in several instances, it is a consequence of ecological marginality, that is, of adaptation to infrequent habitats, or to habitats confined to very small corners of the planet's surface. Ricklefs (2005) demonstrated that this is indeed the case for a number of tribes and even families of passerine birds. In this huge group (about 6000 extant species), one to five species belonging to each of these small subgroups are morphologically quite unusual and this correlates with their adaptation to marginal habitats. For example, these birds have unusually long legs and elongated bills facilitating feeding when the birds are perching or forage on hard substrates such as bark or rock. Within each of these small groups, genetic distances among the few extant species are generally large, indicating old divergence and, by inference, low speciation rate – opposite to the trend prevailing in species-rich, successful groups inhabiting more widely distributed habitats. The fact that these groups are still around in spite of a low speciation rate suggests that in these groups also the rate of extinction is lower than the average.

Clearly, estimates of biological diversity limited to counting species number in a community or in the fauna or flora of a given area fail to capture all the information we need to obtain a satisfactory assessment of possible criticalities and, as a consequence, to formulate sensible conservation measures that might be eventually adopted.

Indeed, a number of metrics of biological diversity have been proposed (summarized in Erwin 2008) other than those that measure just *taxic diversity*, i.e. the number of species or of lower (e.g., subspecies) or higher (e.g., genera or families) classificatory units. Some alternative approaches focus instead on *functional diversity* (a measure of the distribution of the species among the different 'jobs' in the ecosystem), others on *morphological disparity*, still others on *phylogenetic diversity*. All these approaches (which should be intended as complementary rather than alternative, although their usefulness is likely to be uneven in different instances) result in estimates of biodiversity to which all species in the community or biota contribute, although not necessarily to the same extent. In the next paragraphs I will briefly comment on these metrics, before moving to a less conventional approach to conservation problems, largely based on intrinsic properties of the individual species.

11.1.2 Disparity vs. Diversity

In terms of species number, birds are more diverse than mammals (some 10,000 vs. ca. 5600 extant species worldwide), but are instead quite more uniform in terms of morphology, reproductive biology and developmental schedules. Even including less conventional kinds such as the flightless penguins and ratites (ostrich and relatives), the range of bird structural types is much narrower than the range of structural types of mammals, which include humans and whales, bats and giraffes, moles and armadillos. All birds are oviparous, whereas in mammals there are a handful of oviparous species alongside a vast majority of viviparous species. Among the latter, some, like kangaroos, are borne at a developmental stage that deserves be called a larva, whereas others develop in their mother's wombs up to a much more advanced stage and are often capable to feed for themselves in the very day in which they are born. In technical terms, the *disparity* of mammals is much higher than the disparity of birds.

The choice of characters we can consider to evaluate a group's disparity is arbitrary, but morphological traits are usually given priority, often exclusive (Foote 1997; McGhee 1999; Wills 2001; Erwin 2007), because these aspects are the most readily accessible to quantification. As noted by Gerber et al. (2008), the concept of morphological disparity (Gould 1989, 1991; Foote 1997) has proved to be an invaluable source of information, both in palaeontology (e.g., Foote 1993, 1995, 1997; Wills et al. 1994; Dommergues et al. 1996; Roy and Foote 1997) and in the study of extant organisms (e.g., Ricklefs and Miles 1994; Ricklefs 2005).

In some lineages, the level of disparity goes together with the success as measured in terms of species diversity. Examples are some huge animal and plant genera among whose representatives disparate body plans or life styles have evolved in a relatively short time. Examples include *Megaselia* (a genus of phorid flies of which 1559 species have been described, but these are probably a minor subset of those existing on Earth, and their morphological and ecological disparity are enormous); among the flowering plants, genera combining high diversity and high disparity include *Euphorbia* (2150 species, ranging from tiny herbs to quite large trees, and also including a number of succulents) and *Lobelia* (417 species, among which are small herbaceous plants alongside woody giants). However, there are also many large animal and plant genera within which the morphological differences are minor (low disparity), and vice versa (Minelli 2016). An example of low diversity combined with high disparity is the phylum Ctenophora, with 165 species described thus far, classified in 27 families, ten of which include only one species each.

11.1.3 Functional Diversity

By measuring disparity rather than simply counting species, we move a step in the direction of acknowledging the different functional roles the individual species play in respect to their biotic and abiotic environment. This aspects has been addressed in a more direct way by a number of approaches to biodiversity which try to capture the so-called *functional diversity*, the component of diversity that influences ecosystem dynamics, stability, productivity, nutrient balance, and other aspect of ecosystem functioning (Tilman 2001) through targeted descriptors and the calculation of corresponding indices (e.g., Mason et al. 2005; Bremner 2008; Villéger et al. 2008; Laliberté and Legendre 2010; Schleuter et al. 2010; Mouillot et al. 2013; Gagic et al. 2015; Gusmao-Junior and Lana 2015). Estimates of functional diversity are based, for example, on the number and kinds of trophic groups (e.g., primary producers, primary consumers, predators, parasites) and the number and relative abundance of species belonging to each group.

11.1.4 Phylogeny vs. Function

Phylogeny, and evolution at large, feature prominently in assessments of biological diversity and disparity, but it is not always obvious why. Of course, evolution is responsible both for the origin of the species whose number is the most popular measure of biodiversity, and for their structural and functional disparity, the two aspects mirroring the two main facets of evolutionary process – the splitting of lineages (cladogenesis) and the steady changes accumulating along each lineage (anagenesis), respectively. However, the frequent focus on phylogenetic diversity as an estimate of biodiversity and a criterion for ranking species to establish conservation priorities (Buckley 2016), deserves some explanation.

Several algorithms have been proposed to calculate phylogenetic diversity, based on the cladistic relations among the taxa (more often species, but also infraspecific units) (e.g., Vanewright et al. 1991; Faith 1992; Crozier 1997; Moritz 2002; Tucker et al. 2017).

Following the work of Vane-Wright et al. (1991), Faith (1992) and later authors (summarized in Mazel et al. 2017), there are three major reasons to prioritize the survival of species representing species-poor lineages only distantly related to the others in the sample and thus providing the largest contributions to the overall phylogenetic diversity.

First, in this way we conserve the greatest amount of evolutionary history (Vane-Wright et al. 1991), an ill-defined concept at the core of which, however, there is a sensible notion: evolutionarily isolated lineages, often represented by only one or very few extant species, are frequently characterized by unique traits, such as the two continuously growing leaves of *Welwitschia* or the egg-laying habit of the monotremes, strongly contrasting with the viviparity of all other mammals (Rosauer and Mooers 2013).

Second, conserving phylogenetically diverse sets of taxa is valuable because it conserves some sort of trait diversity (e.g., Mazel et al. 2017) This is the most popular among the arguments advocated in favour of using phylogenetic diversity as a basis on which to determine priorities for conservation. Trait diversity is considered important in so far as it helps maintain ecosystem functioning (e.g., Cadotte et al. 2008; Best et al. 2013; Winter et al. 2013; Gross et al. 2017).

Unfortunately, a strict relationships between phylogenetic diversity and functional diversity cannot be taken for granted. Through an elegant set of mathematical simulations, Mazel et al. (2017) were able to demonstrate that basing on estimates of phylogenetic diversity a strategy for conserving functional diversity is not necessarily a good strategy: the relationships between these two aspects of diversity depend on the shape of the tree depicting the phylogenetic relationships among the species involved and also on the model according to which their traits evolve across the generations. Therefore, generalizations are unwarranted. Still worse, Mazel et al. (2017) found that under plausible scenarios of evolution and ecology, prioritizing species conservation based on phylogenetic diversity can actually lead to levels of functional diversity lower than those obtained by conservation priorities determined by a random listing of the same species.

The third reason often advocated to explain why conservation priorities should be based on phylogenetic diversity is that in this way we maximize the “evolutionary potential” of the surviving biota (Faith 1992; Forest et al. 2007). As explained in a later section of this article, this vague term acquires a precise meaning and content when approached from the point of view of evolutionary developmental biology.

11.1.5 Antiquarian Sensibility

We value some human artefacts because of their current usefulness or at least because of the aesthetic pleasure we obtain by looking at them; but we also value other artefacts, even if devoid of any practical use and aesthetic qualities, simply because of their age. Museums are full of nondescript pieces of metal, bone or stone, witnesses of the human presence in particular sites at particular and often remote times, and of the cultural evolution of our ancestors. Similarly, a plant or animal lineage is often regarded as one of singular conservation value just because of the very long time since it split away from its closest living relatives. Monotremes (of which the platypus and the echidnas are the only living representatives) are an obvious example: the last common ancestor they share with the other living mammals lived between 162.9 and 191.1 million years ago (dos Reis et al. 2012). This circumstance, together with the strong unbalance in species richness (5 species only in the monotremes, compared to more than thousand times as many in the sister branch–the Theria, that is marsupials plus placentals) provides a good argument for regarding the platypus and the echidnas as a group of mammals we should not risk to bring to extinction. Another example is the tuatara, a reptile quite similar to a large lizard, but anatomically peculiar enough to deserve being placed in a distinct order, the Rhynchocephalia, of which it is the only survivor, confined to about 30 small islands off the North Island of New Zealand. This group separated from the Squamata (lizards, snakes and allies) about 228 million years ago or earlier (Hipsley et al. 2009).

Sometimes we realize too late the amount of history that is cancelled with the extinction of the last survivor(s) of a plant or animal group. This happened for example with the nesophontids, small mammals of which eight different species inhabited Cuba, Hispaniola, Puerto Rico and the Cayman Islands until their recent extinction, probably caused by the introduction of black rats by European sailors ca. 500 years ago. The nesophontids are classified with the insectivores and their closest relatives are the solenodontids, also confined in the Caribbean area. The two living species of the latter family, however, are poor substitutes for the loss of the nesophontids, not simply because they are themselves on the verge of extinction, but especially because the split between the two families (Nesophontidae and Solenodontidae) is very old, more than 50 million years (Brace et al. 2016) – longer, for example, than the age of the split between the New Worlds monkeys (the platyrrhines) and the Old World monkeys, including apes and humans (the catarrhines), and broadly the same age as the split between the ruminants and the lineage including hippos, whales and dolphins (O'Leary et al. 2013).

11.2 Conserving Evolutionary Processes

As noted by Buckley (2016), "by conserving genetic or phylogenetic diversity, we are facilitating the ability of lineages to adapt to future environmental changes." Since the early times of what eventually became conservation biology, far-seeing scientists have remarked that strategies for the long-term survival of wild species must take into account the continuing evolution of populations: as a consequence, policies should be based on adequate understanding of the population-genetics principles of conservation (Frankel 1974) about which quite little was known at the time. Twenty years later, progress in this direction was still insufficient, witness the plea of Smith et al. (1993, p. 164) who stressed that "If we are to conserve biodiversity the ecological and evolutionary mechanisms generating genetic diversity and the isolating mechanisms critical for speciation must also be preserved." Things have not changed much in the following years, and Moritz (2002) still lamented that "Less progress has been made on how to prioritize habitats, species, or populations in relation to persistence, that is, ensuring that the processes that sustain current and future diversity are protected."

Some authors (e.g., Gillson 2015) have remarked the paradox of conservation: we seek to preserve systems that are incessantly in flux, because of a number of processes running at different spatial and temporal scale, partly driven by extrinsic factors such as climate change and human disturbancy, partly expressing the organisms' evolutionary dynamics that would be innatural to contrast, if ever it would prove possible. Thus, if we can try to contrast the current biodiversity crisis by limiting the human impact on the environment, and even try to reduce, at least in some areas, the disruptive effect of rapid climate change, we may better help the survival of living species and lineages by devising conservation policies based on a sound understanding of *evolvability*.

11.3 Evo-Devo: Evolvability, Robustness, Plasticity

What is evolvability? Unfortunately, this is one of those technical terms for which too many definitions have been proposed (Pigliucci 2008; Brookfield 2009; Minelli 2017). Most of these, however, agree on regarding evolvability as the ability of populations to generate heritable phenotypic variation (Brigandt 2007; Kirschner and Gerhart 1998; G. P. Wagner and Altenberg 1996), but some are quite more specific, e.g. in focussing on the capacity to evolve new adaptations (Bedau and Packard 1992). Eventually, I prefer the definition proposed by Masel and Trotter (2010, p. 406), according to which evolvability is "the capacity of a population to produce heritable phenotypic variation of a kind that is not unconditionally deleterious. This definition includes both evolution from standing variation and the ability of the population to produce new variants."

According to Hendrikse et al. (2007), focussing on evolvability is the most characteristic feature of the research programme of *evolutionary developmental biology* (also called evo-devo). This young branch of the life sciences has much to offer to conservation (Campbell et al. 2017). Up to now, conservation efforts based on the preservation of genetic variation have followed the approach to intraspecific diversity characteristic of population genetics. But this is too limiting: as remarked long ago by Waddington (1957), the expression of genetic variation is structured by development. And this is exactly where evo-devo operates, in a systematic effort to unravel the complex relationships between genotype and phenotype (the so-called genotype→phenotype map; cf. Alberch 1991; Wagner and Altenberg 1996; Pigliucci 2001; West-Eberhard 2003; Draghi and Wagner 2008).

Indeed, to understand evolvability, we must acknowledge that the path leading from genotype to phenotype is complex and not necessarily predictable (Minelli

2017). On the one hand, due to environmental influences but also to stochastic impredictability, different phenotypes can be produced by developing organisms that share identical genotypes; reciprocally, identical phenotypes can be produced by developmental systems with different genotypes. Elaborating upon Waddington's insight, students of evo-devo have demonstrated that the expression of genetic variation is largely dependent on the structure and *robustness* of the developing system (Hansen 2006; Kirschner and Gerhart 1998; Wagner 2005; Wagner and Altenberg 1996).

Together with evolvability, robustness plays a central role in evolutionary developmental biology. The robustness of a phenotypic trait can be operationally defined as the absence of variation in the face of environmental or genetic perturbations (Félix and Barkoulas 2015). According to some authors, robustness constrains and contrasts evolvability, with negative effects on biodiversity: the rationale is that, if mutations and environmental changes have little effect, there is not much variation on which selection can act. Others (e.g., Kitano 2004; Wagner 2008; Masel and Trotter 2010; Melzer and Theißen 2016; Theißen and Melzer 2016) regard this view as simplistic and even contend that robustness may promote evolvability, i.e. the ability to produce heritable phenotypic variation (Pigliucci 2008). To explain how, we must first distinguish between two aspects of robustness, genetic vs. developmental.

Genetic robustness is "robustness to perturbations both in the form of new mutations and in the form of the creation of new combinations of existing alleles by recombination" (Masel and Trotter 2010, p. 407), without visible effects on the phenotype. In this way, in the absence of exposure to novel selective challenges, populations accumulate genetic diversity on the base of which they gain easier access to a greater range of novel genotypes, some of which may eventually prove to be advantageous (A. Wagner 2005, 2008, 2011).

A similar relationships between robustness and evolvability is found in the case of developmental robustness (also known as *canalization*, a term coined by Waddington (1942)) that is, the production of the same phenotype irrespective of genetic differences (and external perturbations). This also corresponds to the fact that populations harbour amounts of unexpressed genetic variation (*cryptic genetic variation*) that is not expressed in the phenotype unless revealed by environmental change or by modification in the overall genetic background (e.g., Badyaev 2005; Flatt 2005; Gibson and Dworkin 2004; Moczek 2007; Rieseberg et al. 2003; Schlichting 2008). This cryptic variation represents a standing potential for evolvability. Exposure to novel selective pressures can be dramatically accelerated by the human impact on the environment. In other terms, environmental change does not just alter the selective regime to which a population is exposed, but can also induce novel developmental responses even in the absence of genetic change. This property of the genotype→phenotype map is known as *phenotypic plasticity* (Fusco and Minelli 2010).

Phenotypic plasticity should not be regarded as an alternative to natural selection. On the one hand, the emergence of a novel phenotype by plasticity, following exposure to previously unexperienced environmental conditions creates a new target on which selection will operate; on the other, plasticity itself is subjected to selection, being favoured in fluctuating environments (Price et al. 2003; West-Eberhard 2003; Pfennig et al. 2010). As noted by Campbell et al. (2017), this is a situation likely experienced by a population introduced in a new area or living in habitats fragmented or otherwise damaged by man.

One might argue that phenotypic plasticity, although responsible for the emergence of new phenotypes, offers no warranty of their conservation, on the long term at least. But this would be a short-sighted perspective. An environmentally controlled phenotype can eventually fall under strict genetic control. The functional divide to be crossed is sometimes a very narrow one, as demonstrated by the control of wing development in the pea aphid, *Acyrtosiphum pisum*. In this little insect, some adults (males as well as females) are winged, while the others are wingless. In the male sex, the coexistence of these two alternative phenotypes is under genetic control, while in the females wing development is controlled by the exposure to different day-lengths in a critical phase of development. In technical terms, males exhibit genetic polymorphism for this trait, while females exhibit an environmentally controlled polyphenism, ie the outcome of phenotypic plasticity. This contrast, however, rests on minor mechanistic differences, because the developmental effect of day-length on wing development in the females is mediated by the gene product of the same gene whose alternative alleles are responsible for the wing polymorphism in the male (Braendle et al. 2005a, b). This circumstance suggests how easily a polyphenism can evolve into a genetic polymorphism, eventually allowing long-term conservation of phenotypes.

11.4 A Lesson from Past Mass Extinctions?

Irrespective of the different causes involved in these events, the mass extinctions of the past should be studied very carefully by researchers interested in conservation biology, but not so much to analyze the differential tribute paid by organisms belonging to different lineages, as to look for any possible explanation of the differential success of the survivors in the post-crisis recovery. Palaeobiologists have generally focussed on the ecological determinants of this process; that is, they have regarded the ecological space left empty by extinctions as the main determinant of the renewed occupation of morphospace. To some extent, the morphological disparity often expanded into dimensions other than those that were occupied prior to the mass extinction. However, no really new body plan emerged. This was, in a sense, a large-scale test demonstrating the developmental robustness of the main traits of body architecture of the survivors, the innovations being limited to secondary, evolutionarily plastic aspects (Erwin 2008).

Confronted with this (admittedly, only incompletely documented) evidence, it seems legitimate to rethink the evolutionary criteria in the light of which biodiversity and its ongoing loss are currently evaluated. It is hard to imagine a positive correlation between the phylogenetic relationships among the survivors and the possible outcome of their long-term evolution in a post-crisis recovery. Million years ago, by preferring to save a marsupial and a placental mammal rather than two placentals, because of the larger phylogenetic distance between the first two, we would not have been able to predict that at least two different subterranean lineages would have eventually evolved in any case: today there are indeed marsupial moles (*Notoryctes*) among the marsupials and moles (*Talpa*) and mole-rats (*Spalax*) among the placentals. More than because of the history of their lineage, survivors may be differentially important for the future of biodiversity as a function of their intrinsic qualities, particularly those expressed by the parameters on which evo-devo focuses – as said, robustness and evolvability.

Acknowledgements I am grateful to Elena Casetta and Davide Vecchi for their invitation to contribute to this volume and for their precious comments on a first draft text.

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