Behavioral Diversity (Ethodiversity): A Neglected Level in the Study of Biodiversity

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The concept of biodiversity embraces a multifaceted and hierarchical analysis of the complexity of life, with implications in many areas of science, philosophy, ethics, politics, and even religion. Three levels are included in the commonly accepted definitions: genetical, species, and ecosystem diversity, going from the intraspecific level to the landscape. Here, I argue that a fourth level, never included in biodiversity studies, is of prominent relevance: ethological diversity or “ethodiversity.” There is a growing number of studies describing alternative behaviors, behavioral plasticity, learning, and even personality, as characteristics of animal populations or individuals. Ethodiversity is also relevant in unraveling cryptic biodiversity, such as species that differ in their behavior but are otherwise undistinguishable. Maintaining ethodiversity is therefore essential in conservation, and cannot be achieved simply by focusing on genetic diversity. Behavior has profound ecological consequences, particularly in species interactions, and is a crucial element in the adaptability of animals to new environments. Ethodiversity is important at the intraspecific, inter-population, and species level and has practical relevance in several fields, like captive breeding, eco-novelties, and popular science. Finally, I expect ethodiversity to show a latitudinal cline, with more diverse and elaborate behaviors per species in the tropical regions, given the increase in interactions near the equator.

Keywords: biological diversity, ethodiversity, behavioral diversity, behavior, concept, cultural significant units, Ethology

INTRODUCTION

The variety of life has been a fascinating theme for human curiosity, probably since our emergence as a species, as is clear from the prehistoric art. We are part of the diversity of life, and we depend on it for all our needs. This self-evident statement encompasses much more complex ideas that seem at first sight (Takacs, 1996). During the second half of the twentieth century, the study of biological diversity was mainly an ecological endeavor, with the species as the basic unit of biotic interactions. Many indexes were proposed to grasp species diversity inside and among ecosystems (Magurran, 1988). The concepts of alpha, beta, and gamma diversity refer in fact to species diversity (Whittaker, 1972), although they can be easily expanded to other levels of biological diversity.

The word “biodiversity” appeared in the scientific literature as the title of a book edited by Wilson and Peter (1988). Walter G. Rosen, who proposed the term, says “It was easy to do: all you do is take the ‘logical’ out of ‘biological’” and ironizes: “To take the logical out of something that’s supposed to be science is a bit of a contradiction in terms, right?” (Takacs, 1996). The term
was coined at the interplay between science and politics (Maclaurin and Sterelny, 2008), with the clear purpose to contribute to biodiversity conservation (Takacs, 1996). In this sense, the word was instrumental and readily adopted by important organizations with a great social and political impact, like WWF (Adams, 2004).

Given the widespread use and the success of the concept of biodiversity, it is surprising that behavioral diversity is rarely considered in the literature on biodiversity. Caro and Sherman (2012) explicitly argued to consider behavioral diversity as part of biodiversity, although they restricted their definition of behavioral diversity to the population and species level. Inter-population divergences in behavior have been considered part of biodiversity (Stone et al., 2012), but it is clear that other levels are also of relevance: “personality differences are an important, yet up to now largely neglected, dimension of biodiversity” (Wolf and Weissing, 2012). The aims of this essay are to highlight the importance of behavioral diversification in the origin and maintenance of biodiversity at all its levels, and the implications of behavioral diversity in Conservation Biology. To effectively preserve biodiversity we need an explicit assessment of all its components, which means overcoming counting genes, species or ecosystems. Ethological components underpin many aspects of the mechanisms that result in species formation and thus in the generation of biodiversity. I propose the term “ethodiversity” for this concept.

**Biodiversity as a Meta-concept**

Takacs (1996) interviewed a group of 23 prominent biologists in 1992, asking them for a definition of biodiversity and obtained an array of different answers. Van Dyke (2008) lists 14 definitions compiled from the literature. Entire books are dedicated to defining and describing this concept (Lévêque and Mounolou, 2003; Gaston and Spicer, 2004; Maclaurin and Sterelny, 2008). Even if these definitions are as diverse as the concept that they try to delineate, most share the idea that biodiversity is a hierarchical concept with three main levels: intraspecific genetic variability, differences between species and between ecosystems.

Ford (2000) classifies scientific concepts into three categories: natural, functional, and integrative. Natural concepts refer to phenomena that can be easily described and grasped by our senses, like a tree or a stone. Functional concepts describe the properties of natural concepts or relate two or more natural concepts. Predatory behavior is an example of a functional concept. Integrative concepts are theoretical constructions about nature, based on the relationship between natural and functional concepts, and usually refer to a hierarchical system. The forest is an example of an integrative concept (Cordero-Rivera, 2012).

The concept of biodiversity is clearly a combination of many points of view to describe the complexity of life. It encompasses ecological, genetic, and taxonomic hierarchies, including social, philosophical, ethical, and religious aspects. Therefore, biodiversity is a meta-concept, an integration of several already integrative concepts. Consider the usual definitions that include genetic and ecological diversity. These belong to two partially overlapping hierarchies, from genes within populations, to species in communities, to ecosystems in different biomes. Other aspects of biodiversity, seldom addressed in biodiversity inventories include phylogenetic diversity, diversity of ecological functions (functional diversity), and ethological (behavioral) diversity. Ethodiversity is defined as the variability of behavioral traits in the biological hierarchy, including the individual level (for example personality), the population level (for instance alternative reproductive strategies), and the ecosystem level (like contrasting behavioral patterns between species). If behavior is defined as the response of biological entities to the environment (see Levitis et al., 2009, for a discussion of the concept), this term can also be applied not only to individuals or species, but also to communities. There is therefore also an ethological hierarchy embedded in the concept of biodiversity.

**Ethodiversity is not equivalent to functional diversity**

Species diversity alone is not a good descriptor of community complexity. This has led to the use of functional diversity as a measure of species interactions and relative importance in the community, because this property is expected to influence ecosystem stability, productivity, dynamics, nutrient cycling, and so on (Tilman et al., 2014). Species perform different functions in a community when they use contrasting ways to obtain their food or resources, even if they belong to the same trophic level, like plants able to fix atmospheric nitrogen and those unable to perform this task. For this reason, studies of functional diversity select only a few traits, those that are considered of relevance for community structure (Petchey and Gaston, 2002), and usually ignore behavior or the diversity of processes in which these traits are functional.

For example, consider the spiders of the family Deinopidae (Figure 1). They are functionally equivalent to other orb-web spiders, but they use a unique and specialized way of capturing their prey: they construct a web and maintain it open with their legs, instead of constructing a web fixed to the substratum. Then, sit and wait and use a backward strike to capture aerial prey and a forward strike to capture walking prey (Getty and Coyle, 1996). Their presence in a community increases ethological diversity of the spider functional group, but does not affect functional diversity.

The interactions between plants and their pollinators is a system where functional diversity has been intensively studied (Fenster et al., 2004). The extinction of pollinators has profound consequences in the community, even with cascading effects between birds and plants (Anderson et al., 2011). Insect pollinators have been shown to belong to several functional groups, reflecting somehow their taxonomic identity (Fenster et al., 2004). Plants are considered to select between alternative pollinator functional groups due to the form of the flower. This has led to the repeated “discovery” by pollinators of the robbery strategy, i.e., obtaining nectar through a hole made in the corolla. The ecological consequences of such behavior for the plant might be negative, because robbers get the prize without contributing to pollination. Several species of birds, bees, and ants have been
found acting as nectar robbers, and irrespective of their impacts on plants as cheaters or mutualists (Irwin et al., 2010), they contribute to the ethological diversity of pollinator functional groups, without increasing functional diversity.

**SOURCES OF ETHODIVERSITY**

In classic ethology, the first step to study animal behavior was the construction of an “ethogram,” considered the complete description of behavioral repertory of an animal (Alcock, 2003). This approach is rarely used recently, probably because it is considered too descriptive, and very difficult to standardize (Schleidt et al., 1984).

Recent research on individual variation in other fields of Ecology has highlighted the relevance of variation across individuals in community ecology (Bolnick et al., 2011). Ethologists and Behavioral Ecologists have described a surprising variety of behaviors, and found many ecological correlates that allow predicting behavioral patterns (Alcock, 1993). Many studies have found high phenotypic plasticity in behavior (Cordero Rivera and Andrés, 2002), alternative strategies in males (Cade, 1980) and females (Sirot et al., 2003), or animal personalities (Briffa and Weiss, 2010). Animal culture is relevant in conservation planning of small populations (Ryan, 2006). So, how is this variation maintained?

Given that behavior is a phenotypic trait, ethological diversity is maintained by the same mechanisms that maintain genetic diversity, and is also a by-product of ecological (ecosystem) diversity. However, some components of behavior escape this framework, like learning and cultural transmission of behaviors. On the other side, ethological differences may contribute or even predate speciation, and be the main process generating cryptic species, like crickets or birds only differentiable by male songs (Irwin et al., 2001; Mendelson and Shaw, 2005).

Whenever the environment is heterogeneous (in time or space) natural selection can be a strong force maintaining diversity, by means of the mechanisms of local adaptation. This frequently generates ethodiversity. American dippers constitute an example of ethodiversity in migratory strategies: some individuals are resident but others are altitudinal migrants (Gillis et al., 2008). Both strategies seem almost fixed, because only 2% of the monitored individuals switched strategy along their lives, but the individual’s strategy was not necessarily that of its parents. Fire salamanders (Salamandra salamandra) are nocturnal animals, active under humid mild climate (Figure 2a). Nevertheless, in two islands separated only by 12 km in the coast of NW Spain, they show contrasting behaviors, being nocturnal in one island but mainly diurnal in the other (Figure 2b), perhaps due to divergent predation regimes (Velo-Antón and Cordero-Rivera, 2011). In the same region, freshwater snakes (Natrix maura) go to seashore pools to capture marine fish (Galán, 2012), a behavior which has clear ecological consequences, but is rarely reported for the species. This last example might be due to learning (Pearce, 2008). Ethological innovations due to learning processes allow animals to change their response to ecological challenges very fast, unlike adaptation, which needs changes in gene pools (Supplementary Video 1; Supporting information; see also Rubenstein, 2016). Therefore, the usual inaspecific quantification of biodiversity, based on allelic diversity, does not capture the essence of inaspecific ethodiversity, particularly learning abilities, personalities, and culture.

**MEASURING ETHODIVERSITY**

As I discussed above, ethodiversity can be found at different levels of the biological hierarchy. It is clearly found at the individual level (plasticity, learning, personality). The existence of personalities in wild animals is an emergent topic of study (Briffa and Weiss, 2010), even in wild populations (Drent et al., 2003). This bridges with the newly revival of interest in the ecology of individual variation mentioned above (Bolnick et al., 2011).

As is typical of integrative concepts we cannot measure global ethodiversity, but only some surrogates (Ford, 2000). A further complication is the fact that behavioral variables are likely to be more plastic than other characters, and therefore scoring behavioral diversity might be limited by the ecological settings where behavior is observed. Currently several approaches have been developed to quantify genetic diversity at the individual and population level. These approaches tabulate genes and individuals, so that the frequency of each allele can be calculated from a particular sample, and diversity can then be estimated, and indexes of differentiation are derived, like FST-values (Nei, 1986).

In the case of ethodiversity, similar approaches may be fruitful. As an illustration Table S1 (Supporting information) shows a summary of reproductive behaviors in the Odonata, and alternative behaviors are listed, with examples of species for each alternative. To quantify ethodiversity in a group, for instance at the species level, one needs to study the reproductive behavior of a sample of individuals and record the frequency.
of each alternative behavior. Then, an index of diversity

PATTERNS IN ETHODIVERSITY

There is still little information about ethodiversity available
to characterize patterns. However, some predictable patterns
are expected. One is related to the latitudinal gradient in
biodiversity (Gaston, 2000). Ethodiversity is expected to be
related to biological complexity, and to be maximum in tropical
areas. An increase in species richness will obviously be positively
related to ethodiversity, simply because more species also mean,
generally, greater phylogenetic diversity. However, the increase in

β-diversity (e.g., morphological or genetic) in the tropics might
also enhance the diversity of ethological repertoires per species
and its variation across space. Therefore, the expectation is that
the “average species” will be more ethodiverse in tropical regions.
Human languages, a clear example of ethodiversity, are more
diverse precisely at biodiversity hot-spots (Gorenflo et al., 2012).
A study of song repertories in birds (Laiolo and Jovani, 2007)
could be useful to test this idea.

Sexual selection is a powerful force in evolution, which
has produced and maintains many of the most extraordinary
behaviors and morphological adaptations exhibited by animals
during mating (Eberhard, 1985; Andersson, 1994). I predict
that ethodiversity will be positively correlated with the intensity
of sexual selection. The birds of paradise unusual behavior
(Laman and Scholes, 2012) is probably the most clear example
of this.

Animal behavior is certainly a relevant issue in conservation
(Cassini, 1999; MacDonald, 2013). Several authors have reviewed
this topic (Curio, 1996; Caro, 1998; Gostling and Sutherland,
2000; Moore et al., 2008; Berger-Tal and Saltz, 2016), and
therefore I will not discuss it further. I will nevertheless
highlight the fact that captive breeding programs, particularly of
predatory animals, cannot be successful without an ethological
perspective, as the story of black-footed ferret recovery plan
clearly illustrates (Vargas et al., 1999). Maintaining ethological
diversity (and plasticity) is also crucial for the viability of re-
introduced animals (MacDonald, 2013), for the management of
small populations (Ryan, 2006) and in animal welfare (Grandin,
2003).

Ethodiversity is important in another field: popular science.
The social impact of science is one of the multiple approaches
to study its relevance, and animal behavior is clearly the most
popular and fascinating topic for most of the television programs
addressed to the great public. The interest of human society on
“what animals do” is an opportunity for conservation, and using
some animals and their diversity of behaviors might function as a
surrogate to protect their habitats (Laiolo and Jovani, 2007), in a similar way as the concept of “umbrella species” in Conservation Biology (Roberge and Aangelstam, 2004).

Ethodiversity is expected to be of great relevance in some ecological settings, one of which is related to the concept of naïveté and evolution on islands. I have already mentioned the example of the diurnal saltamanders, which illustrates the fact that islands are evolutionary laboratories. This has also deep consequences on biodiversity conservation. Extinctions have occurred at higher rates in islands than in continents, mostly due to the introduction of exotic predators and competitors (Nogales et al., 2004). Reduced behavioral diversity, and particularly the lack of strategies to cope with introduced predators, is behind the rapid extinction of many large flightless island arthropods, illustrated by the noteworthy example of Lord Howe “tree-lobster” Dryococelus australis rediscovery (Priddel et al., 2003). The naïveté of many animals, that do not recognize humans as predators, is also behind the rapid extinction of many island vertebrates (e.g., Holdaway and Jacomb, 2000). Behavioral diversity was suggested to be a relevant part of biological diversity precisely studying how domestic cats affected the behavior of lava lizards in the Galapagos (Stone et al., 2012). Super specialist predators, unable to change their behavior and feed on alternative prey, are also at high risk of extinction (e.g., Ferrer and Negro, 2004).

Conservation implications of the concept of ethodiversity might be also apparent at the ecosystem level. The consequences of species extinctions for ecological networks are at the center of applied ecology research, with much debate about the possible species redundancy and how this affects ecosystem function (e.g., Schwartz et al., 2000). Even if not explicitly recognized, much functional diversity is in fact ethological diversity: species are not only gene pools and a set of ecological attributes, they are divergent ethological entities. The loss of ecological interactions (Valiente-Banuet et al., 2015) is in many cases a loss of ethological diversity, which impairs ecological networks. For instance, human-induced defaunation affects large species more intensively, and this has cascading effects on plants when animals are the main seed dispersals (Pérez-Méndez et al., 2016), which is a behavioral attribute.

Despite the repeated claims advocating the relevance of animal behavior as basic for conservation science, the great potential of behavioral research to improve conservation practices is still far from being fulfilled (Angeloni et al., 2008). Future studies on biodiversity conservation must give more attention to animal behavior (or even plant behavior, van Loon, 2016). I hope that the term “ethodiversity,” due to its parallelism with “biodiversity,” might contribute to its acceptance by conservation biologists and therefore stimulate research on the conservation of behavior (Caro and Sherman, 2012).

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The author confirms being the sole contributor of this work and approved it for publication.

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SUPPLEMENTARY MATERIAL
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