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AGAINST NATURE? WHY ECOLOGISTS SHOULD NOT DIVERGE FROM NATURAL HISTORY

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ECOLOGY
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FORMAL HYPOTHESIS TESTING
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ABSTRACT. – A sort of dichotomy pervaded ecological studies in the last decades. On the one hand, an important part of ecologists had the diffuse perception that the observational approach of natural history had to fade away in favour of more formal experimental or modelling approaches. Others, on the other hand, had an increasing perception that these formal approaches were dismissing important cultural components of natural history that fed ecology since its very beginning. We provide here a reconstruction of ecological thinking from natural history arguing that the above mentioned schism between 'schools of thinking' should be reconciled. Modern ecology and natural history deserve reciprocal scientific respect and both seek understanding nature, its components at different hierarchical levels (from species to ecosystems and beyond) and the way it works. Ecology needs natural history to figure out meaningful scenarios, select relevant variables and conceive meaningful hypotheses based on sound knowledge of species up to ecosystems. Similarly, natural history needs more structured ecological thinking for selecting appropriate experimental and/or quantitative approaches to ultimately move from field insight to hypothesis testing.

INTRODUCTION

Ecology is deeply rooted in natural history. Christened by Ernst Haeckel (1866), ecology was already much of the central point of Charles Darwin's investigation during his voyage with the *Beagle* in the 1830s. Although his final achievement has been a theory of evolution, Darwin was an ecologist due to his central interest on the organisms in relation with their environment (i.e., the very definition of ecology according to Haeckel). Using mainly the classical tools of a natural historian, i.e. observations made in the field, Darwin was able to verbally anticipate still influential ecological hypotheses such as the relationship between biodiversity and ecosystem functioning. In a highly influential book published in 1927, Charles S. Elton (Elton 1927) advocated that the still young science of ecology had to be seen as a sort of formal neo-naturalism ("scientific natural history" in his own words – an oxymoron, if one accepts that history is not a science, at least a 'hard science' capable of predictions). Not many years later, the term 'ecosystem' was coined by Arthur Tansley to define "a particular category among the physical systems that make up the universe" (Tansley 1935). Elton's and Tansley's works thus sparked the so-called "physics envy" of ecologists, i.e. the effort to make a hard science of ecology (Egler 1986). Giant steps in this direction have been made during the 20th century by Alfred J. Lotka, Vito Volterra, Georgy Gause, Raymond Lindeman, Robert McArthur, Ramon Margalef & Eugene P., Howard T. & Elisabeth C. Odum, among many others (McIntosh 1985). In recent decades, the enhancement of computer calculation power, the development of statistical tools, related logics and pertinent softwares have allowed to run more and more sophisticated simulations and to analyse huge data sets using rigorous techniques (Green 1979, Underwood 1997). This was mostly done in the perspective of approximating the typical approach of hard sciences. In his last seminal book, Peters (1991) provocatively suggested that ecologists might be better off forgetting about explanation and instead aiming at mere statistical prediction. But what happened to natural history in the meanwhile? Apparently, it turned away from ecology, as it may appear from many ecological studies published in recent decades. A major scientific journal in the field, *The American Naturalist*, does not publish natural history papers anymore, giving place to models for evolution, biology and ecology (Ricklefs 2012). Journals explicitly having the word 'ecology' in their name are by far more numerous than those recalling 'natural history'. Wilcove & Eisner (2000) provocatively stated that natural history is a science on the brink of extinction.

This viewpoint paper aims at critically re-examining the scope of both natural history and ecology, providing a brief reconstruction of the evolution of ecological thinking from natural history, with special (but not exclusive) attention to the marine field, which we are more familiar with. We argue that a new deal is necessary between the two approaches, thereby allowing for a significant step forward in the understanding of nature.

Natural history

Natural history is the modern expression for the Latin *naturalis historia* of classical times (see e.g. Gaius Plinius Secundus, known as Pliny the Elder, who wrote the encyclopaedia named *Naturalis Historia* in 77 AD). It is essentially a body of knowledge about 'nature', in the broadest sense. Natural history began with Aristotle and developed during medieval and renaissance times (Morri *et al*. 1999), to culminate with Linnaeus and the 19th century European thinkers. Initially, natural history included geology, botany and zoology, but in its modern meaning it is the study of living organisms in their environment, leaning more towards descriptive rather than modelling or experimental methods (Bartholomew 1986, Bates 1990, Greene 2005).

Traditionally, two major 'cultural components' of natural history are taxonomy and field observations, both being rather little valued in modern ecology. Readers of ecological journals, in fact, are seldom allowed to know the list of species found in the communities or ecosystems dealt with. Not too long ago this information was considered as the best descriptor of ecosystems (Botkin *et al*. 1979). On the contrary, in many modern ecological studies species have become mere taxonomic units that are a means to an end: that end being to show results on tables or diagrams that do not refer back to the natural history of the species causing such results. Recognizing species is a primary component of a naturalist expertise, while ecologists are seldom fully trained in botany or zoology. Ecological papers are hardly ever rejected by international journals because of poor or incorrect species lists, whereas a negative verdict is expected when the sampling design or data treatment look as well inaccurate.

The importance of field observations to decipher nature in a meaningful way and to better understand the way it works is basic to every ecological study, a message clearly flagged by Dayton & Dayton (2011) since the title of their seminal article "*Observations in nature: the keystone to understanding natural systems*". Through experiential learning in the field, ecologists may increase their knowledge about nature. Without this 'cultural' component, in addition, an ecologist investing only on formal aspects seriously risks to have an aseptic perception of nature, without that sense of wonder that is the fuel for any scientist (Dayton & Sala 2001).

Ecology

Haeckel himself (1866) defined ecology as the study of the relationship between organisms *and* their environment (compare with the above definition of natural history as the study of organisms *in* their environment), and most ecological textbooks underline that an organism's environment includes both the other living beings and the physical components of the habitat. Through the course of the 20th century, other definitions of ecology have been proposed to reflect growth of the discipline, to found new specialities, or to mark out disciplinary territory. A definition, which is perhaps the most commonly repeated, considers ecology to be the study of the distribution and abundance of organisms (Andrewartha and Birch 1954). Today, the scope of ecology covers a wide array of interacting levels of organization and spatial scales. Traditionally, ecology has been divided in three subdisciplines:

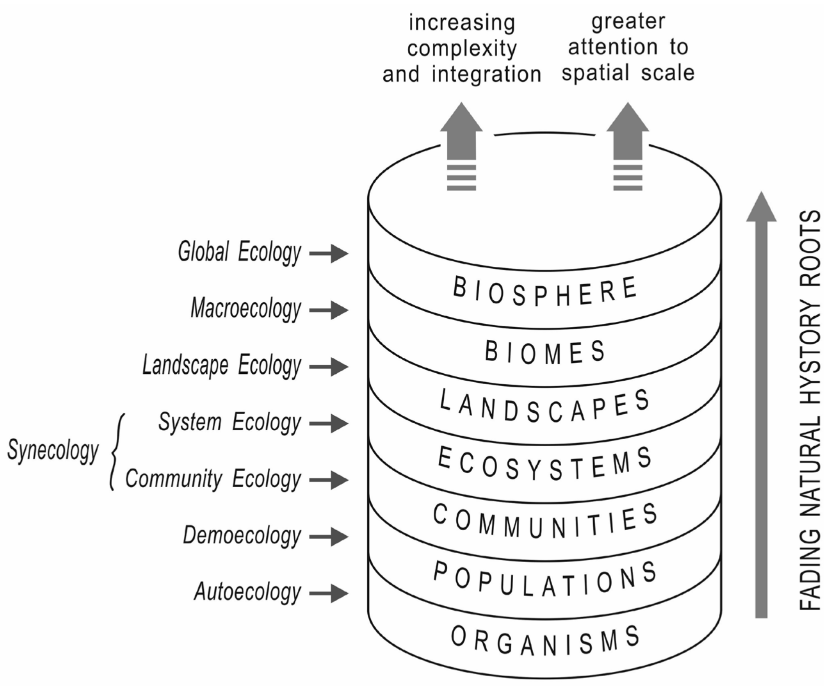

Fig. 1 - The multilayered pie of ecology, showing the progressive estrangement of ecology from natural history as scale, integration and complexity increase.

autoecology, or the ecology of individual organisms and single species; demoecology, or the ecology of populations; and synecology, or the ecology of communities and ecosystems (Begon *et al.* 1986). Following Odum (1971), the central focus of modern ecology is said to be the ecosystem, composed of both living and non-living components. It may appear, therefore, that ecology has rediscovered what natural history had apparently lost: the inclusion of both life and earth sciences. However, modern ecology has not run again into natural history. The growing environmental problems since the last decades of the 20th century forced ecology to expand, also towards applied issues, its spatial scale and levels of integration, giving birth to those emerging fields that range from landscape ecology to macroecology and global ecology (Fig. 1). These ecologies seem to be more and more distant from natural history. While autoecology takes usually into account the natural history of the species dealt with, from demoecology and synecology onward ecologists are pushed to know more about physics, economics and engineering than to deepen the knowledge on habitats and organisms on which they are working. Mechanistic models and sophisticated statistical techniques are more part of the ecologists' tools than the observational approaches typical of the natural historians.

How 'modern' ecology could improve our understanding of the world with respect to more traditional natural history

In an early seminal study, the Italian naturalist Lucia Rossi was the first to provide quantitative data on the marine communities of a Mediterranean Sea subtidal rocky reef thanks to underwater photography (Bianchi & Morri 2000). Watching the photographs, Rossi (1965) estimated the substrate cover by the individual species of the sessile biota. By eye, she recognised eight communities and said they were mainly distinguished by substrate depth and slope. We recently have had the chance to handle the same original data, using a more 'modern' approach: so we considered *depth* and *slope* as two orthogonal axes to plot the eight communities on a sort of ordination plane; then, we analysed Rossi's original biotic data using Bray-Curtis dissimilarity and distance-based redundancy analysis (Legendre & Anderson 1999). Depth and slope formally resulted as major explanatory variables in our analysis. After rotating and scaling, the two ordinations almost overlapped, indicating that an experienced naturalist by eye may have a quite similar discriminating capacity as a quantitative ecologist using more rigorous formal procedures and softwares (Fig. 2).

Understanding mechanisms generating observed patterns was the main goal of natural history and is one relevant goal, in more general terms, of ecology (with this latter that should basically involve the observational component of natural history). However, while more traditional natural historians tend to discern mechanisms from patterns, ecological approaches aim at testing mechanistic predictions or comparing the output of mechanistic models with the observed patterns. Predictions or explanatory mechanisms feeding ecologists often derive from general theory relying on inductive reasoning inspired by natural history (Ricklefs 2012). Whatever the approach, naturalists and modern ecologists have the essence of their goal in common: they use observed patterns and hypothesized mechanisms for understanding ecosystem functioning. From this perspective, their disagreement (that sometimes may take place) is mainly a matter of the preferred technique as confirmed by numerous common conclusions achieved by the two approaches. Examples of common achievements, obtained from different starting points and approaches include: the relationship between biodiversity and ecosystem functioning, already intuited by Darwin; the existence of the phase (or regime) shift, described by successional naturalists as a *relay* (Dansereau 1954) and later formally defined by Holling (1973) applying the catastrophe-theory to ecological systems; the recent definition of key-stone communities, earlier defined by Boero & Bonsdorff (2007) when referring to the crucial role of the meiobenthic community for the planktonic one, and later formally defined applying meta-community models (Mouquet *et al.* 2013).

Our feeling is that using robust formal approaches and appropriate designs to make reliable conclusions of ecological studies is absolutely important (Hurlbert 2004). However, natural history is necessary to make ecologists aware of the trap of testing hypotheses that are formally perfect but trivial (Dayton 2003). While the differences in skills between modern ecologists and naturalists may actually be a powerful enrichment to the understanding of nature, the apparent schism between the two disciplines is stepped up by the methodological implications of their approaches on published literature. Rejection of papers due to poor design and statistics, especially when outcomes are straightforward, or rejection due to the triviality of assumptions, in spite of the use of sophisticated design and analysis, usually upset the authors. Referees and authors are naturalists or ecologists coming from the same 'world' and in this atmosphere everyone tends to simply name the opponents as 'fundamentalists' (quantitative ecologists) or 'storytellers' (natural historians). There could be the risk that advocates of logical designs and model assumptions are *a priori* accused of neglecting observable facts in favour of abstruse rationales, whereas advocates of the need of re-evaluating natural history could be blamed for just telling stories.

It has been said that naturalists tend to pursue the detail, while modern ecologists seek for general patterns (Mitchell 2000). However, ecologists themselves formulated the idiosyncratic theory, according to which the functional role of biodiversity depends on the natural history of each individual ecosystem (Emmerson *et al.* 2001, Pueyo *et*

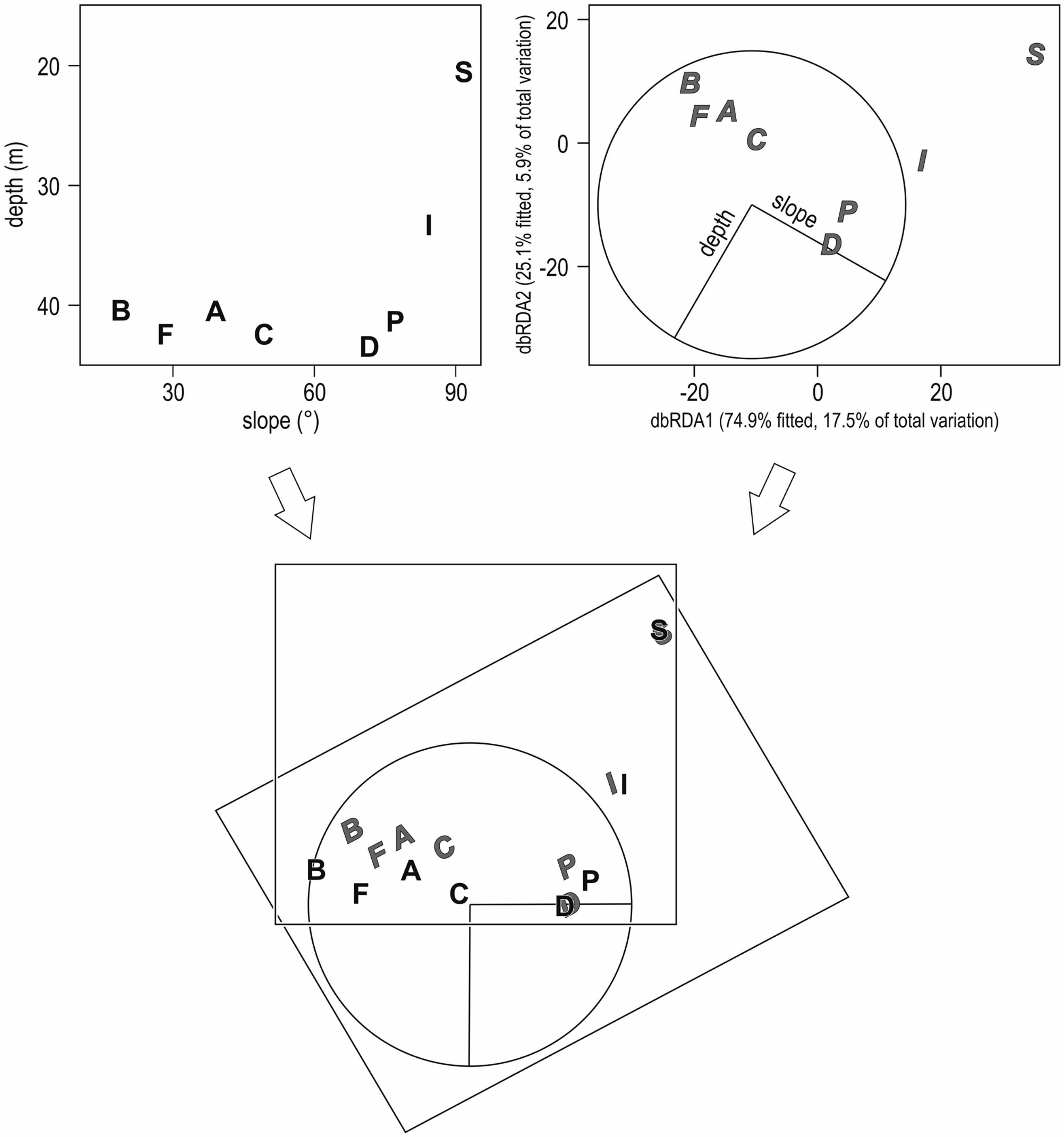

Fig. 2 - Determinants of the quali-quantitive composition of eight subtidal rocky reef communities (capital letters) studied by Rossi (1965) according to her 'naturalist' eye, who recognised depth and slope as major factors (upper-left panel), and to a modern 'ecological' approach (distance-based redundancy analysis), where depth and slope have been added as explanatory variables (upper right panel). After rotating and scaling, the two ordinations showed almost perfect agreement (lower panel).

al. 2007). A second distinction is that modern ecologists include humans among the drivers of ecosystem structure and functioning, while pure naturalists are interested in the behaviour of pristine ecosystems, without any human influence. However, since many decades we live in the Anthropocene (Steffen *et al.* 2007) and intact ecosystems do not exist anymore, the human footprint extending to the whole biosphere (Jackson & Sala 2001, Stachowitsch 2003). Natural history observations are instrumental also to conservation ecology and ecosystem-wide management, which, at the very end, aim at getting knowledge in order to balance human uses and conservation (Bianchi *et al.* 2012). Recent quantitative conservation tools developed by ecologists rely on experts' (i.e. naturalists) opinion (Halpern *et al.* 2008, Parravicini *et al.* 2012). Similarly, life-history traits of species are receiving increasing attention by ecologists as an important way to understand ecosystem functioning (Belmaker *et al*. 2013, Mouillot *et al*. 2013) and knowledge of species traits indeed is one of the main jobs of naturalists. From this perspective, there is a major point to stress that could allow for a re-evaluation of the role for natural history observations in a world continuously changing under the influence of natural dynamics and human impacts. Observations of species to communities' distribution patterns in space and time at multiple scales, changes of breeding periods, occurrence, intensity and frequency of disease and catastrophic events etc. can represent crucial information to better interpret ongoing changes and adopt proper management measures. However, quite often such crucial pieces of information are not brought together into easily accessible sources, as it should be (Boero 2013). Besides the more traditional scientific publications, perhaps observations and natural history could be even more valued by means of other tools, like websites and other easily accessible online and continuously updatable sources (see e.g. www.marinespecies.org or www.marlin.ac.uk/species.php).

Need and time for reconciliation and synthesis

Natural history and ecology are far from being mutually exclusive. Ecology still needs natural history, or we may better say that the latter is part of the former. Ecologists should recognize that their discipline has an inevitable and intrinsic historical component that prevents it from being a completely hard science (Boero 2010): shifting the name from 'natural history' to 'natural science' is not mere semantics. Ecologists tend to use a mechanistic approach in their search for general explanations (Parravicini *et al*. 2010). On the contrary, the naturalistic approach is observational and intuitive, which may enable scientists to construct appropriate general frameworks where to run experiments at scales large enough in space and time to grasp biological, physical and climate interactions shaping communities and ecosystems (Levin *et al*. 2011). Basic knowledge of habitats and species obtained by field observations, and the study of their interactions by running experiments are synergistic to help understanding ecological processes as well as assessing anthropogenic impacts.

In many cases, ecological theory has been tested with elegant statistical designs but including only a handful of species in mesocosms or in simplified ecosystems (Zak *et al*. 2003), whereas natural environments are actually characterized by thousands of interacting species. Small- or meso-scale experiments, however elegant they may be, always carry the risk not to catch up with this broader perspective if they are not founded on solid natural history. Similarly, models help in understanding mechanisms behind observed patterns, but their results may not automatically and always apply to real-world ecosystems. On the other hand, field observation itself may seldom allow disentangling mechanisms from patterns, given the high number of confounding variables found in the real world. Natural history knowledge should serve modern ecology; it may help being aware of the degree to which conclusions drawn from models and experiments can be reliable when applied to complex natural systems, or of the scales, in space and time, at which conclusions can be extended. From the other perspective, natural history alone can be limitative in terms of conclusive inference on patterns and causal processes. Models and experiments should be always commensurate to the ecological questions addressed (Underwood 1997), as paradigms cannot be built out of ignorance (Dyson 2012).

One important point is that the quality of 'output data' (even if they are in the form of aesthetically pleasant analyses) is strictly dependent on the 'input data' whose quality, in terms of correct species classification, may need the help of naturalists to avoid the so-called GIGO: garbage in, garbage out (Boero 2003). Just as an example, two similar species of marine tubeworms, *Hydroides elegans* and *H. norvegica*, had been confused with each other for long (Bianchi 1981): as the former is typical of polluted waters and the latter of clean waters, the ecologist would draw misleading conclusions about the environmental quality from the abundance of one of the two, whenever the two species are not properly classified.

Kareiva (2000) wrote that, by focusing on tractable mini-questions for which results are rapid and easy to analyse, ecologists make themselves irrelevant. Mega-questions would logically require manipulations at appropriate scales that can be sometimes pragmatically or ethically unfeasible. Sometimes investigating the dynamics of natural systems may require a historical perspective (Guidetti & Micheli 2011). In these cases, observations (i.e. assessments of patterns sometimes sacrificing some precision and analytical elegance) may allow obtaining the relevant information.

A new subfield of ecology, called 'macroecology', developed in the last decades to combine observations and analytical rigour holistically at scales larger than those amenable to experimental ecology (Brown 1995). Since its inception, macroecology has largely been a terrestrial endeavour (Brown & Maurer 1989), but quite recently it also addressed the marine realm (Witman & Roy 2009). Similarly, landscape ecology, born to study large and heterogeneous systems difficult to tackle with experimental ecology, is now getting flanked by its younger sister 'seascape ecology' (Pittman *et al*. 2011).

Natural history knowledge may thus help ecologists whenever formally perfect experiments are hard to be done. Sometimes, for example, approaches such as 'space-for-time comparisons', even though not properly experimental, can provide crucial insights into the functioning of entire ecosystems (Jackson *et al*. 2001). Whenever 'perfect' experiments dealing with an entire ecosystem cannot be done to test the effects of multiple stressors (e.g. local impacts plus climate change), we can describe the ecosystem at sites along a gradient of human disturbance, from (nearly) unaltered to degraded, and see the way they change. Going along such a gradient is the 'spatial' proxy for a 'temporally' unfeasible sampling: degradation over time (Pandolfi *et al.* 2003, Parravicini *et al.* 2010). The 'space-per-time' approach is just an example. Gerrodette (2011) also recently questioned the absolute value of null hypothesis significance testing and demonstrates how alternative approaches can sometimes lead to better insight.

Replacing the intuitive capacity of the naturalist by the formalised methods of the ecologist may not always mean hugely improving our capacity to understand the world, as show by Rossi's (1965) example. For a significant step forward, we need integrating both disciplines. In this regard, promising virtuous examples include the growing interest by ecologists to Bayesian statistics, which allows the incorporation of ecosystem (or species) knowledge within analyses by means of informative priors (Ellison 2004) or the increasing employment of Structural Equation Models, whose model specification typically relies on the naturalistic knowledge of the system (Mitchell 1992). Similarly, population dynamic models, meta-population models and the quantitative assessment of species vulnerability for their management represent excellent examples of the modelling power when augmented with the knowledge of species life-history traits (Cheung *et al.* 2005, Bevacqua *et al.* 2007, Watson *et al.* 2011).

As the complexity of the body of knowledge has greatly grown since Rossi's times, finding today a scientist trained in both natural history and ecology is quite impossible. The integration of the two disciplines can today be done within teams putting ecologists and naturalists at work together, not by the individual scientist. However, academic curricula and post-doc recruitment are such that we are losing naturalists: older people getting retired are not replaced by younger colleagues. Ecologists may risk remaining without the deep knowledge of species and ecosystems that naturalists may have and provide. We advocate a change in research funding lines and in the criteria that drive editors to accept papers in the most relevant journals. There are no sound reasons why "natural history" should never be mentioned in, for instance, a grant application. It is just because the name recalls, to the minds of bureaucrats and of 'hard' scientists, a 19th century's image of net-wielding collectors and old-fashioned museum curators. Clearly, this oversimplified image is no longer true, and today naturalists are accurate scientists able to provide the basic knowledge that also more formal and quantitative ecologists need.

CONCLUSION

None of the existing methodological approaches in ecology, be they experimental, modelling or field observation, is necessarily universally superior (Brooke 2000). Natural history, in the context of ecological studies, is crucial to provide a proper background in which realistic scenarios can be envisaged and meaningful hypotheses be constructed, relevant variables selected and pertinent questions answered (Dayton & Sala 2001, Dayton 2003). Natural history and logical rigour are not in antithesis *a priori*, but this, notwithstanding the synthesis imagined by Elton nearly one century ago, has still to be fully achieved. Ecologists and naturalists should closely collaborate for finding the way to commensurate hypothetical-deductive formulations with natural history, if they want to realise a significant step forward. These two major approaches to environmental issues are the two sides of the same coin, and they deserve reciprocal intellectual respect and cooperative attitude.

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