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Ecological predictions: Disentangling corroboration and anticipation

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Abstract

In the current context of global change and a biodiversity crisis, there are increasing demands for greater predictive power in ecology, in both the scientific literature and at the science–policy interface. The implicit assumption is that this will increase knowledge and, in turn lead to better decision-making. However, the justification for this assumption remains uncertain, not least because the definition of ‘prediction’ is unclear. We propose that two types of prediction should be distinguished: *corroboratory-prediction* is linked to the validation of theories; and *anticipatory-prediction* is linked to the description of possible futures. We then discuss four families of obstacles to prediction, linked to the specific features of ecosystems: (i) they are historical entities, (ii) they are complex, (iii) their dynamics are stochastic, and (iv) they are influenced by socio-economic drivers. A naïve understanding of ecological science suggests that the two types of predictions are simply two phases in a sequence in which scientists first improve their knowledge of ecological systems via corroboratory-predictions, and then apply this knowledge in order to forecast future states of ecosystems via anticipatory-predictions in order to help policy makers taking decisions. This sequence is however not straightforward, partly because corroboration and anticipation are not affected by the obstacles to prediction in the same way. We thus invite to reconsider the role of ecological prediction as a tool in a deliberative model of decision-making rather than as external scientific information aimed at enlightening the political process. Doing so would be beneficial for both the policy-relevance of anticipatory-prediction and the theoretical-relevance of corroboratory-prediction.

1. Introduction

For the past two decades, ecologists have emphasized the challenge of making predictions in biodiversity sciences, calling explicitly for a more “predictive ecology” (Clark et al. 2001, Evans et al. 2012, Sutherland and Freckleton 2012, Petchey et al. 2015, Mouquet et al. 2015, Houlahan 2017). This search for increased predictive power can be linked to at least two factors.

First, recent technical and methodological advances have raised hope regarding potential progress in ecological knowledge. These include the increased amount of data provided by observational and experimental networks, greater computational power, new ecological models, and related statistical and optimization methodologies (Green et al. 2005, Luo et al. 2011).

Second, society’s demand for ecological predictions has grown alongside increasing awareness of the environmental crisis. In a world that is undergoing rapid changes, the scientific knowledge provided by ecological sciences is often thought of as a prerequisite to assess the possible impacts of human activities on ecosystems (e.g. climate change, land-use change, over-exploitation of natural resources, pollution), and to help policymakers and practitioners design environmental policies (Palmer et al. 2005).

However, the call for delivering predictions that could help defining and implementing public policies in conservation and climate change mitigation becomes controversial when it comes to the ways we should proceed. Some scientists seem to favor prediction as something that could be derived from the huge datasets we can now gather, and the biocomputing and statistical tool likely to exploit them, therefore announcing ‘the end of theory’ (Anderson 2008). Similarly, public policies and conservation measures could be handled in an evidence-based framework, analogous to strategies used in medicine: evaluating what works or does not work among environmental policies would allow to incrementally improve our action

(Sutherland et al. 2004). In these views, we should not spend too much time trying to devise an explanatory theory of what's going on in order to eventually predict successes and failures of various courses of action. Yet, many ecologists remain skeptical regarding the idea that better and more useful predictions could be attained without improving available theoretical frameworks or designing testable theories (Houlahan et al. 2017). As argued by Marquet et al. (2014), only better theories could allow to discriminate between correct and spurious predictions based on mere data gathering and mining (for analogous arguments in evolutionary biology, see (Servedio et al. 2014)).

In this paper, we contribute to frame this debate by arguing that 'prediction' may mean different things, and that those meanings are used indifferently, thus creating confusion. Although the term *prediction* is common to both conventional scientific discourse and everyday language, two senses can indeed be distinguished. First, it can refer to a step in the scientific process of understanding: hypotheses, models or theories are tested by comparing what is expected to occur (i.e. predicted) with what actually occurs. When expectations coincide with actual events, this lends support to the scientific understanding of how things work (Popper 1959). This support can be understood in various terms, for instance in Popperian terms of corroboration, in the context of inductive logics, or in probabilistic (e.g. Bayesian) framework. Second, it can refer to a description of a possible future: we seek to anticipate possible futures believing that such knowledge can stimulate beneficial action in the present, or help taking good decisions for the future (Bell 2010). The coexistence of – and confusions created by - these two meanings in biological science were early emphasized by Ernst Mayr: “The word prediction is being used in two entirely different senses. When the philosopher of science speaks of prediction, he means logical prediction, that is, conformance of individual observations with a theory or a scientific law. [...]. Theories are tested by the predictions

which they permit. Prediction, in daily usage, is an inference from the present to the future, it deals with a sequence of events, it is temporal prediction (Mayr 1982, p. 57).

These very distinct meanings, however, are not made explicit in the current rush to make predictions in ecological science, and this generates several sources of confusion. While it is likely that they closely interact, here we argue that predictions used to anticipate future events are unlike those used to validate theoretical hypotheses.

In the first section, we investigate the role of prediction in the history of ecology, and distinguish the two epistemological dimensions of prediction that underlie research, namely corroboratory-prediction and anticipatory-prediction. The second section examines obstacles to prediction in ecology, and how they affect the two types of prediction. In the third section, we describe the interactions between them and their articulation with environmental action.

2. Two epistemological dimensions of prediction

While the recent emphasis on predictive ecology may suggest that we are experiencing a new era in ecological research, the question of predictive power has been a theme that has run through the discipline since its early development.

2.1. Historical background

In his book that retraces the history of ecology, Robert P. McIntosh (1986) describes a turning point in the 1960s and 1970s. At this time, the development of theoretical ecology and model building led many ecologists to believe that the discipline would become a hard science, with a general theory and strong predictive power. McIntosh summarized this period as follows: “Hope was expressed for a unifying general theory that would allow ecologists to penetrate the veil of complexity which had traditionally obscured ecological communities and ecosystems. It might eliminate the descriptive, particularized ecology that, it was said, defied generalization, had low predictive capacity, and damned ecology, as a ‘soft’ science, to suffer

‘physics envy’” (McIntosh 1986). Many ecologists were inspired by the goal of building a general theory, mainly based on the idea of competition for limited resources that was thought to be able to explain and predict species distribution and community structure, a goal first proposed by G. Evelyn Hutchinson (1959), then significantly extended by Robert MacArthur and Richard Levins (MacArthur and Levins 1967), Edward O. Wilson (MacArthur and Wilson 1967), and Robert May (May 1973).

At the same time, there were calls for the development of applied ecology that would formulate recommendations for policymakers. This required a way to anticipate the dynamics of ecosystems, or the effects of a specific policy on them. Ecology was, in the 1960s, thrust into the limelight by the widespread perception of an environmental crisis. Biodiversity decline was dramatically brought home to the general public and policymakers (Carson 1962, Dasmann 1968, Ehrenfeld 1973) and ecology was seized on as an established discipline with the ability to address environmental concerns. The initiation of the International Biological Program in 1966 is one example of the call for ecology to deliver applicable knowledge to tackle environmental issues (Hagen 1992).

The aim to design ecological science as a hard science and to deliver robust evaluations of the future state of nature both inherit from this historical background and are embodied in two facets of ecological predictions.

2. 2. Prediction as a step towards explanation: corroboratory-prediction

Scientific theories contain universal or general propositions regarding the system in question; they generally encompass a set of models, or rules to build models, as representations of the properties and dynamics of target systems. Models can then be expressed as hypotheses within a formal framework (van Fraassen 1980, Giere 2004). All models imply predictions that, in turn, can be corroborated by observations. We name this kind of prediction *corroboratory*

tory-prediction, meaning that, by matching hypothesis-derived predictions, observations corroborate hypotheses.

This use of prediction is not necessarily deterministic. For instance, hypotheses that are based on probabilities are often framed in terms of probability distributions. In this case, the frequency of observations found in datasets can be compared to predictions, in order to corroborate (or not) hypotheses. This approach is found in many areas of ecology, where mathematical models are developed in order to make predictions, and data (observations) are compared with these predictions. Even approaches to hypothesis testing much more distant from the Popperian falsificationism, such as Bayesian frameworks, rely upon the basic strategy of deriving predictions, comparing them to the data, and then making claims about the validity, power, or reliability of the theory.

Predictions in this sense are not only about assessing a theory as a set of claims, but also about finding the best theories among several of them. Recently reflecting on the indispensable role of theory in ecology, Marquet and colleagues (2014) characterized the key role of predictions in theory testing as follows: “The best theories are those that explain or unify the greatest number of phenomena and generate the most predictions on the basis of the fewest assumptions and free parameters.” Hence, the efficiency of a theory is a trade-off between the small number of free parameters and assumptions, and the richness of predictions.

Three features of corroboratory-predictions deserve attention: namely their relation to time, observations and validity (Table 1). First, it should be noted that this meaning of prediction is time-neutral. More precisely, predictions often specify what is expected if we do such-and-such a thing, or if we observe certain phenomenon. They state what would happen as a consequence of either observations or experiments; however, they do not specify the timing, relative to the present, of these consequences. For instance, when it comes to assessing the value

of two models, one generally favors - e.g. in accordance with Akaike Information Criterion - the best trade-off between goodness of fit and simplicity (namely, the fewest parameters possible), since too many parameters make the model oversensitive to noise (Foster and Sober 1994). Hence, the capacity of predicting the next data point is taken into account while assessing models; but whether this data point is closer or further in time does not play any epistemological role. More generally, whether the prediction concerns the result of a future experiment, such as the increase in bacteria strains after thousands of rounds of controlled evolution (Lenski and Travisano 1994), or past observations - e.g. when we compare two models of paleontological data such as the diversification of invertebrates marine clades (e.g. Huang et al. 2015) - makes no difference to the value of the prediction as a corroboratory tool. According to Mayr “Darwin's theory of common descent, for instance, permitted Haeckel the prediction that "missing links" between apes and humans would be found in the fossil record” (Mayr, 1982).

Second, corroboratory-predictions are inseparable from observations. The quality of the prediction depends on being able to observe whether what is predicted actually happens or not. Consequently, predictions that cannot be empirically attested in any manner (for instance because humans change their behavior to avoid predicted outcome) cannot be considered as appropriate corroboratory-prediction. While in the experimental sciences observations related to predictions often require experiments, this is not necessarily the case. Sometimes, prediction testing can rely upon the observation of existing data so that there is no need for any further field observations or experimental results, instead the analysis draws upon a database. For instance, the French Breeding Bird Survey is a long-term campaign to monitor common bird populations. This exercise has made it possible to test many hypotheses about the res-

ponse of bird communities to climate change (Devictor et al. 2008) or the relation between functional and phylogenetic diversity (Calba et al. 2014).

Third, as mentioned earlier, the *raison-d'être* of corroboratory-prediction is to assess the validity of a model, in order to increase confidence in a hypothesis or general theory. When predictions match observations, the hypothesis or theory is corroborated. This, in turn, suggests that the model is accurate. On the other hand, when observations differ from predictions, hypotheses must be reformulated, theories revised, or models modified (Popper 1959).

Overall, corroboratory-prediction has mostly an epistemological role, and can be understood as a necessary component of knowledge building. The central goal of corroboration is to comfort or to improve our understanding of the world and its critical feature is reproducibility (Houlahan et al. 2017).

2. 3. Prediction as a step towards anticipation: anticipatory-prediction

Predictions may be made about what the world could look like in the future, either given present conditions or if different courses of action are followed. For instance, the models developed by the Intergovernmental Panel on Climate Change (IPCC) are not designed to corroborate a specific hypothesis or theory of climate sciences, instead they forecast what could occur in the future given certain assumptions.

When exploring possible futures, prediction encompasses several other concepts that include forecasting, projections, foresight or scenarios (Coreau et al., 2009). Very few anticipatory-predictions aim at describing what will necessarily happen; rather they try to imagine possible futures, acknowledging the great uncertainties inherent in the exercise (Thuiller 2004). Most anticipatory-predictions are either projections of past trends (regardless of the probability that they will continue into the future), forecasts (i.e. the best projection or prediction based on a particular model, the typical example being weather forecasts), or an explora-

tion of possible futures given certain parameters we can call a scenarios set (i.e. analyses of the consequences of different climate trajectories on biodiversity). Scenarios are indeed plausible descriptions of alternative futures, based on a coherent and consistent set of assumptions about key relationships and driving forces. They are increasingly found in the ecological literature, notably since the publication of the *Millennium Ecosystem Assessment* (2005).

The fundamental differences between corroboratory-prediction and anticipatory-prediction are based on the three features mentioned above: time, observations and validity (Table 1).

Anticipatory-predictions have an explicit relationship to time: they are mostly future-oriented. What characterizes them is the fact that they cannot be compared with tangible, present or past, facts. They address possible events and objects in the future, and may have the status of counterfactuals such as: “If we were maintaining the same level of greenhouse gases emission for the coming 30 years, then the climate would be such and such”. This is manifest with many anticipatory predictions concerning climate change or biodiversity loss: once they are formulated, they often trigger a set of actions and decisions intended to avoid their outcome. Moreover, unlike corroboratory predictions they are not governed by a requisite of reproducibility, since they often concern a single future result of a specific state of the world and human activity, which will not be reiterated twice.

Anticipatory-predictions also differ from corroboratory-predictions in their much looser link to observations. They are not constrained by currently-available data, and their quality does not necessarily depend on what actually happens – in fact many anticipatory-predictions cannot be verified in the short-term. They can define an unwanted state of the world, such as the worst-case scenarios discussed by the IPCC or the report *Limits to Growth* from the Club of Rome. They can also define a desirable state of the world as some of the “branch point scenarios” (Gallopín et al., 1997). In this case, far from describing what would occur with the

highest probability according to the current state of knowledge, the theory underlying the prediction can be used to change the forecasted trajectory of the system. Necessarily, such predictions are unlikely to be confirmed. More, they are not designed to be confirmed and the fact that they actually happen or not in the future has in most cases no importance whatsoever. That makes their logical status different from the status of corroboratory predictions.

Finally, anticipatory-predictions use established theory to develop robust expectations. Consequently, they are often a second step in a modeling process where the aim is to extend to more distant futures what has been corroborated by past or present observations (corroboratory-predictions). If there is no theory or causal relationship that can explain a phenomenon, anticipatory-predictions can make explicit assumptions about missing knowledge, provided that they do not contradict established knowledge. Hence they use and apply rather than test and challenge existing theories and models.

The fact that a given anticipatory-prediction does not match subsequent observations does not necessarily invalidate a theory or model, since the conditions in which the data are observed may be very different to hypothetical assumptions. The aim of an anticipatory-prediction is often to guide action in the present, and therefore to influence the future itself. Ultimately, the quality of an anticipatory-prediction does not rely on its ability to corroborate a hypothesis or test a particular model, but on its usefulness for decision-making. For instance, Tittensor et al. (2014) have proposed a baseline built upon scenario analysis against which to measure progress toward international biodiversity targets. In doing so, they acknowledged that such a framework is necessarily incomplete (e.g. in terms of data, scale and taxonomic coverage) and rests on strong and unchecked assumptions (e.g. ecological processes remaining constant into the future).

Overall, anticipatory-prediction has mostly a pragmatic role, and can be understood as a necessary component to decision-making, rather than an epistemic tool. It is indeed not meant to be testable. The central goal of anticipation is not to understand the world, but to inform policy and management, that is to say, to help changing the world by undertaking the appropriate actions regarding specific goals. Hence, its key feature is relevance for policy-making (Sutherland 2006).

As a consequence of this distinction between corroboratory and anticipatory prediction, one must keep in mind that the call for more predictive ecology can mean two very different things: we may want more predictions, so that we will be in better position to forge ‘efficient theories’ (Houlahan et al. 2017, Marquet et al. 2014); or we may want more predictions in order to make more educated decisions regarding environment and climate change (Sutherland and Freckleton 2012). The kinds of predictions that are wanted in those two contexts are different as well as their link with ecological knowledge.

3. Obstacles to predictions in ecology

Despite the numerous calls for a more predictive ecology, it is widely admitted that formulating ecological predictions is a difficult task. Michael Dietze (2007) developed a formal framework to quantify and to weight diverse sources of uncertainty on predictability¹. Here, even before taking for granted the predictability of dynamic ecological systems, we qualitatively explore four families of obstacles to prediction, linked to the specific features of ecosystems: (i) they are historical entities, (ii) they are complex, (iii) their dynamics are stochastic, and (iv) they are influenced by socio-economic drivers. In the following, we show

¹ Dietze(2017) was published while the first version of the present paper was completed. While both papers concur on certain characteristic features of predictive ecology, its focus is the uncertainties of prediction, whereas our paper first and foremost addresses the dual nature of ecological prediction, and only then considers the obstacles and uncertainties of predictions in the perspective of this duality.

how these four features affect corroboratory-predictions and anticipatory-predictions differently.

3.1 Ecosystems as historical entities: contingency and evolution

In the 1960s and 1970s, Robert MacArthur and his supporters put forward the idea that ecologists should develop theories that eliminate historical details, and instead focus on the study of the equilibrium through the use of mathematical tools (McIntosh 1986, Kingsland 1995). They emphasized the difference between ‘science’ and ‘natural history’, arguing that natural history involved little more than endless fact collecting. This desire to increase the robustness of theoretical ecology by eliminating its historical dimension was described as an “eclipse of history” by Sharon Kingsland (Kingsland 1995). However, this approach downplays two central features of ecological processes: the importance of contingent events, and the evolutionary history of organisms.

In a notorious paper entitled “Are there general laws in ecology?”, John H. Lawton argues that at the scale of the community, contingency is pervasive and, therefore, ecology is a “mess” characterized by “a large number of case histories and very little other than weak, fuzzy generalizations” (Lawton 1999). The paper sparked controversies, and indeed there are many ways to argue that ecology gives rise to laws (Mikkelsen 2003, Weber 1999), for instance. Moreover, even hypothetico-deductive view of science might lead to less skepticism with respect to ecology since many mechanisms have already been identified and we are struggling to even better understand their proper combined effects (McGill and Nekola 2010). Vellend (2016) intended to construe ecology in a way parallel to the modern synthesis of evolution, by identifying key basic processes (competition, speciation immigration and drift, parallel to selection, mutation, migration and drift) whose combinations yield distinct models likely to make testable predictions and account for communities dynamics.

More generally, Marquet et al. (2014) or Servedio et al. (2015) argued that varieties of hypothetico-deductive methods, which rely on general hypotheses corroborating predictions, are likely to capture counterfactual-supporting generalities in ecosystems, and therefore actually operate a distinction between the ‘noise’ constituted by the idiosyncratic cases and the ‘signal’ constituted by the regular effect of the variables correctly captured and properly parameterized in the model. But even if the argument of Lawton was overstretched, the claim that corroboratory-predictions and the possibility to capture either laws or wide-ranging generalities are challenged by the degree of contingency in ecosystems remains valid.

It must be noted that in our context, contingency does not negate causal determinism, but it can mean two things: (a) Sometimes an event is said to be contingent because it lies at the intersection of multiple, independent causal chains. Here, ‘independent’ indicates that events are remote enough in the system to be studied by independent theories. In turn, theories are said to be independent when the variations studied by one theory can, in principle, be modeled without considering variations modeled by another. An example of such contingent event is the asteroid collision that contributed significantly to the K–T extinction: this mass extinction was caused by an event that had nothing to do with the ecology of dinosaurs; and, reciprocally, asteroid cycles are independent of the biosphere ecology.

(b) ‘Contingent’ is often used in the sense of ‘contingent upon’; and ‘A is contingent upon B’ often means A causally depends upon B. However this meaning is very wide, since everything is contingent in a world ruled by causal laws or relations. Talking of contingency here becomes interesting in the case of some specific ways for A to depend upon B, namely, when A is highly dependent on a fine-grained specification of the initial conditions B - because we have only a coarse-grained knowledge of B, the determination of A appears as random. An example is community assembly, which is contingent when the immigration history is a de-

terminant of the present composition (Fukami 2010). Here, the species composition of the community is a function of the order in which species arrived. Several studies (e.g. Almany 2004) of coral reef fish communities have shown that the present structure of the community depends on ‘priority effects’, in which early-arriving species affect, either negatively or positively, the population growth of later arrivals.

In the first sense (a), predictions (either for corroboration or anticipation) are not in principle difficult to state, but this contingency means that incorrect predictions are due to events and forces not included in the field of the theory one is aiming to test. Those contingent events are by definition rare, otherwise the independence between causal chains would not make sense; hence it means that predictions are still possible for a significant lapse of time, as in the case of Gould’s example (Gould, 1989), for which the only inaccurate predictions are very long term predictions, articulated at the geological scale. This may precisely raise an issue for anticipatory predictions. Granted time is not a relevant feature of corroboratory predictions; thereby they can still be formulated and used to corroborate theories, even though contingency precludes prediction in the long run. However, long run is often what matters for forecasting; therefore such contingency would preclude anticipatory predictions while allowing corroboratory predictions.

The second sense (b), akin to high sensitivity to initial conditions, is more opposed to the very possibility of making corroboratory predictions. Suppose for instance that hypothesis H1 predicts the value A1 for variable A on the basis of the value B1 of variable B, but that we cannot access to fine-grain enough determination of B in observations: then the fact that A1 is not observed is not exclusive of H1 being correct, since it could be the case that the state of B was not exactly B1 but B'1. One may instead in such cases design qualitative predictions, as it can be the case in some areas of physics: a model predicts few distinct varieties of behaviors -

simulations being often the only way to design those predictions - , and one tests whether those happen and in which range of values of the variables.

For anticipatory predictions, the situation is different since we assume a hypothesis or a model or model set according to which H is correct. Then, if the states of the world as we know them are not enough finely discriminated to allow us to implement the two scenarios S1 and S2, based on H, that predict very distinct future states B1 and B2, the anticipatory prediction cannot provide a benchmark to adjust our action.

Ecology also has to address evolutionary history. Although researchers work within the general framework of evolutionary theory, it is often assumed for modeling purpose that the slow rate of macroevolutionary change renders an evolutionary perspective irrelevant when studying processes at the community or ecosystem scales. Nevertheless, evolutionary biology has produced compelling evidence that strong selection pressures and fast evolution are commonplace (Agrawal et al. 2007, Carroll et al. 2007, Cavender-Bares et al. 2009). The idea of an “eco-evolutionary feedback loop” (Kokko and López-Sepulcre 2007) is pervasive; it links macroevolutionary change to ecosystem succession, while at the same time it affects macroevolutionary change by shaping the organism’s environment. Although modeling of this feedback is in its early stages (Hendry 2016), its existence attests to the fact that ecology cannot understate the historical character of its systems.

According to MacArthur and his followers, ecology should be able to overlook historicity in order to formulate appropriate corroboratory-predictions. The typical controlled experiment isolates one or two causal mechanisms that contribute to unknown contingent events (Hobbie et al. 2006). Evolutionary hypotheses can even be tested using models of micro-evolutionary history tested against historical data, as has been done for the neutral theory of evolution (Kreitman 2000). At larger scale, some ecological patterns or processes such as species-areas

relationships can be explained by generalizations focusing on the structural and functional dimensions of ecological entities rather than their historicity (Mikkelsen 2003). Therefore, even if it may be difficult to find support for corroboratory-predictions using evolutionary systems, it is possible to disentangle causal chains or formulate *ex post* explanations. From the anticipatory-prediction perspective, the historical character of ecological systems represents a different kind of obstacle. True contingency – in the senses of (a) or (b) – directly impairs the ability to formulate reliable predictions of future states of ecological systems. However, if the main objective is to inform decision-making, anticipatory-predictions may, to some extent, overcome the problem of contingency by examining different events in different scenarios and comparing the results. Rather than one prediction of a probable future, we obtain a set of possible scenarios, given the uncertainty they will occur and the desirability of the outcome.

Some ecologists have suggested that if history matters, then ecologists should provide historical narratives rather than mathematical models (Mayr 1982, Cronon 1992), or that ecology should follow a case study method (Shrader-Frechette and McCoy 1993). By compiling heterogeneous elements from various perspectives into one coherent, plausible narrative, *scenarios* can capture some of the contingency of ecological systems (Allen et al. 2005). They have proven useful in attempts to address contingency in complex systems, and in assessing the coherence and quality of futures studies (Zellmer et al. 2006). Therefore, the main challenge of historicity arises when the aim of anticipatory-prediction is to describe what the future will be, based on formalized, quantitative projections. On the other hand, when the aim is to inform decision by providing a range of possible future scenarios, narratives can be developed that can overcome those challenges.

In short, the impacts of contingency on corroboratory and anticipatory predictions are different. Corroboratory-predictions can overcome contingency when predictions are formulated

based on one or a few dependent causal chains in a system in which all other parameters are controlled. Anticipatory-predictions have to address the numerous surprises that can change the expected dynamics of ecological systems (Doak et al. 2008). Nonetheless, the issue can sometimes be overcome, for instance by switching from the search for a description of what the future should be (or even the probability that it will occur), to a search for a set of possible scenarios based on an understanding of the diversity and unpredictability of ecological futures.

3.2. Ecosystem complexity: emergent properties and interactions between scales

Ecologists often characterize the phenomena they study as immensely complex (Levin 2005). However, this adjective encompasses two properties: complexity as complicatedness and complexity *per se*. Complicatedness is a matter of degree, and is a function of the number of relationships between ecological entities (see also Allen et al. 2017 on complicatedness and complexity). On the other hand, complexity *per se* relates to the nature of such relationships. A system is complicated when it is a tangle of many causal relationships. A system is complex when new features emerge from the combination of its sub-components that cannot be expected based on knowledge of these components (Simon 1962).

The complicatedness of ecological systems is an obstacle to prediction. Darwin's metaphor of an "entangled bank" is often used to describe the multiple and various interactions between species (Montoya et al. 2006, Barker et al. 2014). Variation exists at every level of organization, and ecological entities can interact with each other via several processes (e.g. predation, competition, mutualism, facilitation, and parasitism) and their environment (e.g. abiotic fluctuation or disturbance). Ecological networks are one attempt at a tractable simplification of this complicatedness (Pimm 1984). It is evaluated by a diversity of indicators, such as species richness (i.e. number of species); connectance (i.e. the ratio between actual and possible inter-

species interactions); interaction strength (i.e. the effect of one species' density on the growth rate of another species), and evenness (i.e. variance in species' abundance distribution) (Pimm 1984, Montoya et al. 2006).

The second aspect of complexity is related to the hierarchical organization of ecological systems. Simon (1962) defined complex systems as those in which “the whole is more than the sum of the parts, not in an ultimate, metaphysical sense but in the important pragmatic sense that, given the properties of the parts and the laws of their interaction, it is not a trivial matter to infer the properties of the whole.” Simon claimed that systems where quasi-independence is found (hence called modules) – in other words, where some subparts or levels encompass far more internal than external interactions – are much more mathematically tractable than others. This is because we could model the system by characterizing a single module as one entity instead of a large set of interactions, so that the complexity of the system (as measured by the number of interacting entities) significantly decreases. Fewer equations are therefore required to capture the behavior of the system, which generally makes the mathematics more tractable.

In a quasi-independent system, there are at least several modules; those can also hierarchically be organized, which determines a higher degree of complexity. Actually, ecologists must deal with levels of organization that range from the gene to the whole biosphere. An important consequence of hierarchical complexity is that as components or subsets are combined to produce larger wholes, new properties emerge that were not observable at the lower level. Accordingly, an emergent property of an ecological level or unit cannot be trivially deduced from the study of the components of another level or unit (Anderson 1972). In the case of ecological communities, limits on the similarity of competing species (MacArthur and Levins

1967), or the stability of a food web faced with a disturbance (Worm and Duffy 2003) are examples of emergent properties.

However, while emergent properties may impede predictions because emergence per se means a certain kind of unpredictability, it may happen that the emergent level is in itself easier to mathematically describe and then support predictions, than the basic level. ‘Computational emergence’ as characterized by Bedau (2007) constitutes a concept of emergence supposed to be observer-independent, and formally identifiable; it is defined by “the incompressibility of the computation of a final state (macrolevel) from an initial state (microlevel)”, entailing that the latter is reachable only by simulation. This concept has been applied by Grantham (2007) to biogeographical ranges. It answers the strong objections that have been addressed by philosophers, since Kim (1999), to the usual combinatorial concept of emergence (according to which emergence means that the whole's properties differ from the sum of the parts' properties); however, it makes many things emergent and faces a risk of triviality. But among computationally emergent properties or states, some of them include the occurring of regular dependences between macrostates, and those dependences in turn allow predictions, notwithstanding the unpredictability of the final states in terms of the theory of the microstates (Huneman 2008). Hence, among systems that meet the criteria of computational emergence understood as a philosophically satisfying concept of emergence, many impede predictive capacity but some of them foster it.

Ecological systems are hierarchized into levels, some of them being emergent, and they also span across several spatial- and timescales. The diversity of organizational scales is central to ecological complexity. While some scales are nested, and interact closely (e.g. population and community dynamics), others seem incommensurable both in space and time (e.g. gene and biome) and, in practice, are studied separately. However, as Levin (1992) argued in

an influential paper: “there is no single natural scale at which ecological phenomena should be studied. [...] Applied challenges, such as the prediction of the ecological causes and consequences of global climate change, require the interfacing of phenomena that occur on very different scales of space, time, and ecological organization.” The significance of this statement is that when scales are decoupled, the causal variables that are relevant to phenomena at one scale must only pertain to this scale. For instance, one can see the contingency of the K-T extinction due to an asteroid as a sign of the decoupling between astronomical timescales and the time scales of evolution: if they were not decoupled, astronomical events would affect evolutionary history all the time (not only when extraordinary events such as an asteroid collision occur), and astronomical forces, entities and phenomena should thereby be integrated within evolutionary theory. Or, imagining that macroevolutionary scale and community or functional ecology scale were coupled, then the interactions supposed to underlie the community structure and the ecosystem functioning change at the same time as those structure and functioning are constituted. In order to make predictions, this in turn requires a more sophisticated mathematical apparatus than when macroevolution is timescale decoupled, in a way that the extant clades and families can be considered as invariant. But the risk is that those predictions are for this reason intractable, and cannot deliver meaningful information to reliably base actions.

In other words, when restricted to a given ecological level, with delineated spatial and temporal scales, ecological corroboratory and anticipatory predictions can be relevant. When scales are coupled, however; it becomes very difficult to make any prediction, in any sense of the term.

But this difficulty for prediction in systems with coupled timescales seems to vanish when one considers that modeling a system as open means considering the interactions between

subsystems at distinct spatial (and possibly temporal) scales. In this respect, Mikkelsen (2007) described the case of nutrient enriching experiment and showed that, in some cases, it's precisely when one sees a system as open, and therefore couples its dynamics with the timescales of other dynamics, that the modeling can capture what happens more accurately.

Along those lines, a very general example of the predictive possibilities opened by scale coupling is the coupling between a focal community and a metacommunity: As pointed out by Ricklefs (2008), it is by considering the whole system of the community and the metacommunity that the dynamics of the community can be explained. The same kinds of interactions are occurring at the two scales - call this 'interaction homogeneity' -, so that the modeling of the coupled system does not require integrating heterogeneous mathematical equations. However, the above-mentioned cases of coupling that prevent prediction were different, because there is no such homogeneity of interactions.

Summarizing, complexity (in the sense of intertwined levels of organization and trans-level causation), and timescale coupling can therefore be two limits to both corroboratory and anticipatory predictions. When conditions of uncoupling and quasi-independence (in the sense of Simon (1962)) are met, there is scope for corroboratory-predictability: but predictability may also occur thanks to some sort of emergence processes (when regularities are identifiable at the emergent level) and scale coupling with interaction homogeneity.. This is confirmed by recent attempts to provide a mechanistic approach to scaling-up, and theories that address scale transition, self-organization and predictions of catastrophic shifts (Denny and Benedetti-Cecchi 2012). Similarly, over time, refinements to scenario-based hypotheses have led to greater attention being given to complex socio-ecological phenomena. For instance, the *Millennium Ecosystem Assessment* integrates demographic and economic parameters into its sce-

narios in order to couple different scales of interaction, going from biophysical processes to social dynamics.

Anticipatory predictions here face a specific issue. When one intends to formulate anticipations on the basis of assumed general theories of a set of complex ecosystems, she faces the risk of identically handling systems in which predictions are precluded by scale coupling, and systems where in the contrary predictions are allowed by scale coupling. Only with a theory which explains in which category the system belongs, could she be authorized to design anticipation about this system. Therefore complexity, emergence and scale hierarchy required for anticipatory predictions to be grounded on some specific explanatory theory of the system.

3.3. Ecosystem stochasticity: nonlinear dynamics and chaos

Throughout most of the discipline's history, ecologists have been influenced by the assumption that ecological systems can be described as equilibrium states, a notion quickly popularized as "the balance of nature" (Egerton 1973). This term usually implies that undisturbed nature is ordered and harmonious, and that deviations from an equilibrium state are caused by external perturbations, most often human. This led early researchers to study ecological systems in the same way as Newtonian mechanics. However, it quickly became apparent that ecology had to address problems related to processes, whose rates depended nonlinearly on the state of the system and for which "equilibria" could not be clearly defined and was rarely observed in the field (Worster 1990). Moreover, advances in computing power and availability in the 1970s led to the discovery that such nonlinearities could cause spontaneous oscillations. Even the *logistic map*, one of the simplest ecological models, used to describe density-dependent population growth with discrete generations, can give rise to remarkably complex dynamics, including cycles and chaos (May 1976).

Some ecological mechanisms may lead to nonlinear response to gradual changes in an external parameter: so-called *catastrophic shifts* (Scheffer et al. 2001). An example is drylands where a gradual fall in mean annual rainfall can lead to a gradual decrease in vegetation cover. This continues until an annual rainfall threshold is reached, at which point the entire ecosystem can suddenly collapse into a desert (Kéfi et al. 2007). A characteristic of catastrophic shifts is that they are unannounced and difficult to reverse once they occur: for a desert to return to a dryland, mean annual rainfall must increase to levels that are significantly higher than those at which the collapse occurred, a phenomenon known as *hysteresis*. Because of the ecological and economic consequences of such shifts, a number of indicators have been proposed that aim to predict their approach. Many of these *early warning signals*, have been proposed in the theoretical literature (Scheffer et al. 2009, Dakos et al. 2012, Kéfi et al. 2014), and they are based on the very general phenomenon of *critical slowing down*, characterized by the slowing down of a system's response to perturbations as it approaches a catastrophic shift.

The successful detection of these early warning signals in a number of controlled experiments (e.g. Drake and Griffen 2010, Carpenter et al. 2011, Dai et al. 2012) suggests that they are a promising research avenue. However, other studies have argued that they may be too general to be useful to generate reliable anticipatory predictions in real systems (see e.g. the discussion in (Kéfi et al. 2013, Boettiger and Hastings 2013)). Until now, all such indicators have been identified *a posteriori* in experimental systems, and it remains to be seen whether they can anticipate an upcoming shift in real-world ecosystems. Moreover, although the development of early warning signals may be a way to improve our knowledge about the forthcoming trajectories of ecosystems, they say nothing about underlying mechanisms, and therefore have little explanatory power. Hence stochasticity contributes to create a gap between

corroborative predictions and anticipatory predictions. But an even more intricate source of unpredictability lies in the human dimensions of ecological systems.

3.4. The cultural dynamics of ecosystems: human causalities and reflexivity

As the scientific community seeks to predict the behavior of ecological systems, the boundaries between natural and social sciences are blurring, or at least overlapping. It is generally accepted that the transformation of ecological systems largely depends on socio-economic drivers. Ecology is broadening its scope from supposedly ‘natural’, to human-dominated systems (Vitousek et al. 1997). Currently, most ecosystems are better described as socio-ecosystems, whose properties are directly affected by human activities (both biotic and abiotic components), which only partially respect the rules or laws that describe the behavior of natural systems. For instance, in the case of global warming, future climate impact scenarios are, in part, based on estimates of human population growth and energy consumption. Both of these variables are a function of human choices and behaviors that are influenced by a variety of needs and goals. This creates a deep layer of uncertainty – not only are there multiple causal chains, but also contingencies and complexity have psychological, political, economic, and technical origins. Moreover, modeling those eco-social systems requires considering that the main drivers are not constant, as shown about land-use change at the landscape level by Oliver et al. (2015). Hence, a simple extrapolation of past trends to the future is often a poor way to forecast socio-ecosystem’s dynamics.

The problem is amplified by the numerous interactions and cross-causalities between social and ecological phenomena. For instance, the future of the human population depends upon the future of ecological systems (Millennium Ecosystem Assessment 2005) as the latter determines the availability of vital resources. Reciprocally, human demography has a significant impact on the state of ecosystems, as the growth of the human population and the conse-

quent requirement for more space and resources may accelerate the destruction of natural habitats.

More fundamentally, the focus on human affairs in anticipatory-predictions concerning socio-ecosystems highlights a specific challenge that is due to the retroactive effect of predictions themselves. Human beings are reflexive agents. A stone or a bird will not change its behavior following a prediction of its future. However, ecological anticipatory-predictions could change the course of human affairs – moreover, their express intention is often to improve predicted outcomes. In climate scenarios for instance, catastrophic predictions can be used to raise the awareness of individuals and policymakers, in order to make them change their practices. Depending of the content of scenarios, of the chosen key parameters and of the targeted audience, the ability of anticipatory-predictions to have an impact on socio-ecosystems and the nature and extent of this impact can vary a lot..

The so-called *Pressure State Response* model makes this interactive loop explicit. The model identifies human activities (Pressure) that influence the quality and quantity of natural resources in the environment (State). This, in turn, provokes a societal response to these changes in the form of environmental, economic and sectorial policies (Response). Human reflexivity is therefore embedded in a strategic model of problem solving that is itself built upon a network of heterogeneous actors.

Once addressing socio-ecological systems rather than strictly ecological systems, the call for a more predictive ecology is generally associated to anticipation rather than corroboration of theories. For environmental policy-making, risk-assessment, biodiversity management, some information about the future states of ecosystems is needed. These future states depend on the evolution of different drivers of change, such as climate, resource use, land cover, but also on the possible existence of new drivers, such a technological innovation or new envi-

ronmental policies. Whereas already corroborated knowledge can help to anticipate the effect of the evolution of certain drivers on the system under study, the interaction between these drivers and, even more critically, the possibility that radically new drivers may affect the system, cannot hardly rely on already tested and repeatable results. It is thus necessary to integrate qualitative hypothesis, expert knowledge and storyline scenarios to produce a range of possible outcomes. As argued by Oliver et al. (2015), the issue then is not to choose between reductionist quantitative predictions based on corroborated hypothesis and systemic qualitative predictions that are not testable, but rather to find a compromise between them both in order to develop models that will be progressively fine-tuned while time passes and more data become available.

4. Prediction in practice

A simple way to understand the link between predictions and decision-making would be to follow a straightforward sequence running from theory to practice: corroboratory predictions improve ecological knowledge about the driving forces and causal relationships in a given ecosystem (Dietze 2017). This knowledge is mobilized to formulate simple anticipatory-predictions about future states, or the consequences of different courses of action. Policymakers could then make the best decision.

However, this framework (scientists propose, policymakers decide) is misleading for several reasons. First, better knowledge does not always lead to better decisions. Public action requires that decision-makers are willing to engage into it and that appropriate means and resources are available and well organised. (Guillet and Mermet 2013). A reliance on knowledge alone is therefore insufficient.

Moreover, the idea that action must be based on corroborated theory is itself questionable. For example, Don Driscoll and David Lindenmayer (2009) examined the applicability of the-

ories (assembly rules, metacommunity, metapopulation) and found that they had no or very little anticipatory value, even though corroboratory predictions are built-in the theory since they were used for its validation. In the same vein, authors have argued that the need for answers to pressing environmental problems cannot wait for the corroboratory-predictive power of theories to be improved (Carpenter 2002, Peterson et al. 2003). To conflate the corroborative part and the anticipative part of scientific activity may delay action in a way that is not aligned with the urgency of ecological issues.

Is it reasonable, then, to argue that policymakers should rely on anticipatory-predictions, even when they are not based on strongly corroborated knowledge? For instance, in the domain of ecosystem dynamics, the frequency of false positives, questioned the reliability of generic early warning signals as forecasting tools (Section 3.3) so that “ecologists should resist the lure of general rules” (Boettiger and Hastings 2013). These authors insist that those signals are significant for forecasting only when some theoretical approach to the specific system under study is available and backs them up. Hence, they warn against an indiscriminate trust in anticipatory predictions that intend to generally bypass the establishment of a strongly corroborated theory. An indiscriminate reliance on too conservative signals may indeed weaken credibility of science in the future. However in some cases, like this one, only the elaboration of new specific theories will allow robust forecasting, as has been shown in 3.3 regarding scale coupling and emergence, and this may take long to be acquired.

There does not seem to be a general solution to this problem - namely, whether anticipatory predictions (such as early warning signal detection) should elaborate on a proper theory of the target system to be reliable. The patience required to elaborate targeted theories backing up anticipatory predictions should reasonably be proportionate to the measure of the risk at stake. Risk of urgent ecological disaster would for instance justify relying on anticipatory predic-

tions based on no theories, and the cost of false positives would be highly superseded by the cost of an undetected signal (namely an ecological catastrophe). However very often the measure of the risk itself is an issue: what is the value of the loss of a whole family of birds, for instance? Therefore, the reliability of predictions themselves cannot be taken wholly independently from political and ethical controversies - e.g. between an ecosystem services approach (Colyvan et al. 2010) vs claims for intrinsic value of nature (Vucetich et al. 2015), etc.

The success of IPCC scenarios at moving climate issues to the top of the international environmental agenda may be one reason why anticipatory-predictions have become so popular among ecologists. They may, however, be less well-suited to the technocratic model of decision-making because they are more adapted to exploring a set of possible options (i.e. imagining a plurality of possible future biodiversity scenarios) rather than developing a single scientific solution (i.e. modeling the consequences of a unique policy option on biodiversity). They are consistent with a more deliberative model of decision-making, where actions are negotiated by stakeholders with different opinions, who all draw upon a diversity of anticipatory predictions.

5. Conclusion

Policymakers, science–policy interfaces, funding agencies and scientists themselves are all calling for greater predictive power in ecology, in order to help society tackle global challenges to ecosystem services provisioning and biodiversity conservation. The implicit, underlying logic is that better science will mechanically lead to better decisions. However, actual action depends on more than just science.

In the context of ecology, the notion of prediction has two sometimes overlapping but not equivalent meanings: one refers to the corroboratory role and the other to the anticipatory of predictions. Conflating them leads to cross talk, misunderstandings and misplaced expecta-

tions as, for instance, the latter does not imply the requirements for testability and reproducibility that characterizes the former, and this paper has shown that there are several obstacles which distinctively affect the two types of predictions.

A naïve understanding of ecological science suggests that the two types of predictions are simply two phases in a sequence in which scientists first improve their knowledge of ecological systems via corroboratory-predictions, and then apply this knowledge in order to forecast future state of ecosystems via anticipatory-predictions. The reality is more challenging. In the case of corroboratory-predictions, the obstacles may be overcome by reducing the complexity of the system, for instance by controlling experimental parameters. However, although this may improve predictability, it does not really improve decision-making since in real-life contexts, conditions cannot be controlled and many parameters remain unknown. So many uncertainties lead to the development of future scenarios and narratives describing a range of numerous possible futures.

Although such anticipatory predictions remain relevant to policymaking and biodiversity management, they do not have the same epistemic status as corroborated knowledge. Their reliability cannot be measured only on theoretical grounds, but should also be measured against the degree of emergency of the events at stake. For instance, if astronomers predict that a meteorite will hit a specific region in the next 30 days, this knowledge can be considered as a fact and action can be taken to evacuate the population. But the anticipatory predictions at play in ecological scenarios are different. Not only are there numerous, complex uncertainties, but also they rely upon different kinds of hypotheses. Some of these are very robust, others are less substantial, and all can be positively or negatively affected by what is at stake. Although we do not seek to dismiss the scientific validity or relevance of predictive ecology in decision-making, it should be viewed in an appropriate context; not so much as an adjunct to

the debate, but as an integral part of the deliberation process itself and, where necessary, the democratic process.

Failing to distinguish these two forms of prediction may be problematic and counter effective for both scientists and policy makers.

From the decision-making perspective, the confusion between corroboration and anticipation may lead policy makers to put unrealistic expectations on scientific expertise, waiting for corroborated knowledge to inform on the futures like reading in a crystal bowl. Even if scientists are generally aware of the uncertainties of ecological anticipations, they may fail to communicate consistently about them or purposely feed these unrealistic expectations, for instance because they fear that uncertain anticipations would discredit their scientific knowledge or preclude or delay action against climate change (Patt and Weber 2013).

Furthermore, this confusion between the two types of predictions may divert scientists from working on the most appropriate tools to help decision making while formulating anticipatory-predictions (Sutherland and Freckleton 2012): models or scenarios focusing on the proper scale (one does not need to know each and every inter-specific interaction to relate habitat destruction to biodiversity decline); models or scenarios integrating parameters relevant for action (it is more useful to know the relationship between pollutant discharge and eutrophication than just acidity and eutrophication); models or scenarios that are open to deliberation, into the scientific community but also outside the scientific community. Anticipation could thus become part of the political deliberative process itself and not only an external input.

From the purely theoretical perspective, facing the data deluge allowed by new technologies, ecologists should pursue the advancement of this young science by a continuing effort to formulate testable hypothesis and to produce reproducible results in order to develop corroboration.

rated theories (Marquet et al. 2014). This may need time and means for pure science and experimentation free from the pressure to deliver applicable outcomes.

The pressing need for anticipatory predictions should not mean that ecology is doomed to be a weak science. It is precisely by recognizing the difference between anticipatory and corroborative predictions that we allow ecologists to work at different time scales and recognize the value of slowly acquired corroborated knowledge that may in the future build up into a practical science, just as has happened into other areas of knowledge.

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Table 1: Main differences between corroboratory-prediction and anticipatory-prediction

	Corroboration	Anticipation
What is it ?	A step in knowledge building	An application of knowledge
What is it for ?	To understand the world	To transform the world
Key feature	Reproducibility	Relevance for policy-making
Relation to time	Time-neutral	Future-oriented
Relation to observation	Inseparable from observations. The <i>raison-d'être</i> of the prediction is to be corroborated by observation.	The prediction does not depend directly of its confirmation by future observations.
Relation to validity	The prediction tests the validity of theories or models.	The prediction assumes the validity of theories or models or explicitly assesses uncertainties and lack of knowledge.