Species Distributions, Quantum Theory, and the Enhancement of Biodiversity Measures

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Abstract.—Species distributions are typically represented by records of their observed occurrence at a given spatial and temporal scale. Such records are inevitably incomplete and contingent on the spatial–temporal circumstances under which the observations were made. Moreover, organisms may respond differently to similar environmental conditions at different places or moments, so their distribution is, in principle, not completely predictable. We argue that this uncertainty exists, and warrants considering species distributions as analogous to coherent quantum objects, whose distributions are better described by a wavefunction rather than by a set of locations. We use this to extend the existing concept of "dark diversity", which incorporates into biodiversity metrics those species that could, but which have not yet been observed to, inhabit a region—thereby developing the idea of "potential biodiversity". We show how conceptualizing species' distributions in this way could help overcome important weaknesses in current biodiversity metrics, both in theory and by using a worked case study of mammal distributions in Spain over the last decade. We propose that considerable theoretical advances could eventually be gained through interdisciplinary collaboration between biogeographers and quantum physicists. [Biogeography; favorability; physics; predictability; probability; species occurrence; uncertainty; wavefunction.]

UNCERTAINTY IN SPECIES DISTRIBUTION MODELS

Biogeography is an essential part of systematic biology, constituting the study of the distribution of living beings in space and time, and the processes that drive that distribution (Lomolino et al. 2006). Species distribution data sets are composed of records of the observed occurrence of species at specific locations and times, which are a subset of the locations belonging to the distribution and vary with time. Biogeography thus has to deal with the problem of abstracting and representing a continuous and varying species distribution from an incomplete and fixed set of records (Hengeveld 1992). As is the case in other scientific fields, a biogeographer needs to conceptualize the observed distribution patterns and the inferred underlying processes through the use of models—either conceptual, mathematical, or cartographical. Here, we propose that analogies from quantum theory in physics may be helpful in interpreting and working with species distribution data and, thus, in the endeavor of modeling inherently uncertain species distributions from observations.

A model is a simplified representation of a real-world system, and can be used to explore how it works or to understand and predict its behavior. Models are typically conceptual, often consisting of ideas or hypotheses encapsulated into mathematical formulas. Statistical models are those based inductively on direct observation, measurement, and extensive data records; whereas "mechanistic" models are those derived deductively from an understanding of the behavior of a system's components. Both are valid, but of greater or lesser utility under different circumstances. All other things being equal, however, mechanistic models should be more "powerful", as they tell us about the underlying processes driving the observed patterns, and are more likely to work correctly when extrapolated beyond observed conditions (Bolker 2008).

Models are widely applied to social, biological, and ecological sciences, where the urgent need for improved mechanistic models has been recognized (Purves et al. 2013)—for example, for the study and prediction of species geographical distributions. An entire field has flourished around species distribution models (SDMs) and the related concepts of ecological niche models, habitat suitability models, or bioclimatic envelope models (Guisan and Zimmermann 2000; Peterson et al. 2011). Most such models use known or inferred relationships between species occurrence and environmental variables to explain or predict where the individuals belonging to a species should occur. SDMs are biogeographical models now widely used in macro-ecology, evolutionary biology, conservation and management, serving numerous important purposes (see e.g., Jiménez-Valverde and Lobo 2007, for a brief review). Their applications in systematics include the study of species distributions, the detection and location

of sympatry, parapatry and diversification areas, and the inference of hybrid zones and of splits between taxa (Swenson 2006; Martínez-Freiría et al. 2008, 2009; Gutiérrez-Rodríguez et al. 2016). We point out that biodiversity is hierarchical, and it is often relevant to study the geographic distribution and local richness of sub-specific (e.g., within-species lineages, haplotypes, genetic variants) or supra-specific entities (e.g., genera, families, clades in a phylogenetic tree). We generally refer to "species" throughout this article for simplicity, but models can be applied to any entity (taxonomic or not) whose distribution or diversity can be studied.

SDMs are also often categorized as being either mechanistic or statistical models (Guisan and Zimmermann 2000). Mechanistic SDMs are based on hypothetical cause–effect relationships and, consequently, require knowledge about species' life histories: they use variables that, according to existing theory or to experimental results, have a direct effect on a species' survival. They result from a "bottom-up" reductionist understanding of distributions, which lacks the complementary "top-down" holistic understanding typical of biogeography. While they are generally considered more ecologically meaningful (Bolker 2008), mechanistic SDMs are impractical or even unfeasible for most species and geographical regions: we cannot perform physiological experiments or gather sufficient ecological knowledge but for very few species or populations of interest (Guisan and Zimmermann 2000). Developers of mechanistic SDMs are also susceptible to being misled by unusual patterns in the data (Bolker 2008), and these models usually perform less well than statistical SDMs at predicting species occurrence (Hilborn and Mangel 1997; Guisan and Zimmermann 2000). Statistical models, on the other hand, are based on observed correlations between a species distribution and variables that do not necessarily have a direct effect on the individuals, but may be related to broad-scale patterns of the species distribution and help to predict where the species is most likely to occur (Hilborn and Mangel 1997; Guisan and Zimmermann 2000). Overall, both reductionist and holistic views may be seen as contributing to the observed pattern. However, one element that mechanistic and statistical models usually share is a deterministic view of ecosystems—that is, it is assumed that truly intrinsic uncertainty (as opposed to a lack of knowledge on the part of the observer) does not actually exist in ecological systems (Regan et al. 2002).

Deterministic versus Nondeterministic SDMs

Conversely, we argue that SDMs might perform poorly not only due to our incomplete knowledge as to what governs species occurrence, or to a lack of ability to compute all the relevant interactions between different biotic and abiotic factors within an ecosystem, but also because biological systems fundamentally do *not* work in an entirely deterministic and predictable way. A deterministic system is one in which every event

is involved in a fixed cause–effect relationship. So, in principle, if everything is known about the initial state of the system and the processes that drive it, any future state of the system can be accurately predicted. A non-deterministic system is one in which even complete knowledge about the system does not enable the future state of the system to be predicted with certainty. That is, the system is characterized by a certain level of intrinsic uncertainty, or "inherent randomness" as labeled by Regan et al. (2002).

Contemporary physics holds that the physical universe is essentially non-deterministic (Davies and Betts 1994). As mentioned, ecologists often assume that this intrinsic non-determinism does not apply to organisms (Regan et al. 2002). However, there is emerging evidence that organisms rely upon quantum phenomena for a variety of biological and ecological processes (Ball 2011; Rodríguez et al. 2015a, 2015b). Since biological organisms possess a degree of autonomy from the environment, and in relying upon quantum processes may respond inconsistently to the same environmental conditions, then it should perhaps be assumed that individual organisms behave, to at least some extent, unpredictably.

In turn, this implies that a degree of inherent non-determinism may be inevitable in species distributions. Classical determinism is consequently not the most adequate framework for conceptualizing SDMs, and a framework that incorporates uncertainty is more appropriate, both conceptually and practically. In fact, recent literature has proposed the use of tools from quantum theory in modeling and understanding ecological dynamics (Bull 2015; Rodríguez et al. 2015a, 2015b). Building upon these proposals, and given that quantum theory provides a well-developed framework for modeling nondeterministic systems, we explore in this article the idea of building SDMs using concepts found in quantum theory.

SDMs as Analogous to Quantum Particle Wavefunctions

In quantum mechanics, any object (such as a particle) is characterized by its "wavefunction". Until the object is directly observed (i.e., measured), it cannot be said to have a definite location in space or time, but instead can be considered to have a probability of existing at a number of locations simultaneously, as described by the wavefunction. Coherent quantum objects interact based upon their wavefunctions rather than directly upon their probabilities of occurrence. It is the squared amplitude of the positional wavefunction at a given location that gives the probability of the object being observed to occur at that point in space. Once the object is actually physically observed, the wavefunction "collapses" in a process that is not yet fully understood, and the object can then temporarily only be found in that known single location (in quantum theory, the object has become "decoherent"; Zurek 1991). Over time, if not measured

again, the object becomes coherent, and its exact location is again uncertain.

Under our premise that the organisms composing a species do not move and distribute in an entirely deterministic manner, it cannot be known with certainty where they will occur: their geographical distribution can be better thought of as a spatial probability of occurrence that derives from a related underlying driving function. In this way, the geographical distribution could be modeled analogously to a particle's probability of occurrence in quantum mechanics. In fact, there is a precedent for this in the literature: the favorability function (Real et al. 2006), which represents potential for observation and may therefore be considered analogous to a wavefunction. The favorability function removes the effect of prevalence (i.e., the proportion of observed presences) from probabilities obtained using any mathematical method, thus enabling direct quantitative comparisons between predictions for different species. The idea of favorability was included in Laplace's (1825) definition of probability as the ratio of the number of *favorable* cases for the occurrence of an event to the whole number of possible cases. If all cases were totally favorable or unfavorable, then this ratio would depend only on the prevalence of the event. However, different cases may differ in favorability, and favorability may take continuous values that can be constrained to range asymptotically between 0 and 1. If this continuous and gradual value is applied to the status of a location as favorable or unfavorable for the occurrence of a species, then a quality of the locations emerges which is termed favorability. Thus, the probability of a species occurring under certain conditions combines the general prevalence of the species and the local favorability for that species occurring under those particular conditions. If probability is a function of favorability and prevalence, then favorability is also a function of probability and prevalence. Favorability for the occurrence of a species can be obtained with the formula:

$$F = \frac{\frac{P}{(1-P)}}{\frac{n_1}{n_0} + \frac{P}{(1-P)}}, \qquad (1)$$

where F is the favorability for species occurrence, P is the probability value obtained according to any modeling method that yields probability of occurrence, and n_1 and n_0 are the numbers of modeled presences and absences, respectively.

Although both probability and favorability range from 0 to 1, they differ in a fundamental aspect. Probability of a species occurrence in a location is affected both by the overall prevalence of the species and by the degree to which the conditions of that specific location make the occurrence of the species more or less likely. Favorability is precisely this second part. If a given location is favorable, then P at that location is higher than can be attributed to the general prevalence of the species alone. Conversely, a high probability of occurrence can arise in conditions of low favorability if overall prevalence is high. P and F represent different philosophical concepts, logical systems (crisp and fuzzy logic, respectively), and mathematical domains—and yield different, although many times complementary, outcomes. The favorability function describes local favorability for species occurrence in all localities in a manner that is independent of the prevalence of the species, and is the fundamental driver of the species distribution from which observed distribution data derive. We therefore consider it as being analogous to a particle wavefunction.

To make a second analogy between favorability and wavefunctions, Acevedo and Real (2012) showed that it is the interaction between favorabilities, rather than between occurrence probabilities, that enables the combination of SDMs when several species are involved. Likewise, the interaction between quantum objects is based on their wavefunctions rather than on the respective probabilities of the objects being observed to occur.

As a third analogy, and deriving from Equation (1), the probability of a species being observed to occur at a specific location is a function of the favorability at that location:

$$P = n_1 F / (n_0 + F(n_1 - n_0)), \qquad (2)$$

where P is the probability of occurrence, F the favorability for occurrence, n_1 the number of presence records, and n_0 the number of absence records. Note that, for any species that we know to have existed (i.e., that has been observed at least once), n_1 is at least one and so F is always greater than zero (Real et al. 2006), so P is also always greater than zero. This idea—that a species always has a non-zero probability of being observed, no matter how small—is actually rather a good reflection of reality. Even highly charismatic species thought to be extinct have been known to re-appear in their home range some time later (e.g., Fitzpatrick et al. 2005).

This view also reflects species distributions better than a static understanding of observations. No map of observed distribution can claim to completely represent a species' distribution, but only a series of observations resulting from the true distribution of the species (Barbosa et al. 2013b). First, a species distribution is dynamic rather than static: even for sedentary organisms such as plants or corals, the geographical distribution changes with time over multiple spatial scales. Differences between mobile and sedentary organisms in this regard are quantitative rather than qualitative. A species distribution range is an expression of its continuous (and changing) range of responses to varying environmental conditions (Hengeveld 1992). Second, and consequently, at any given point in time, a species covers a set of locations simultaneously with differing intensity, while the exact place where we find each individual depends on the exact moment when we observe it. Even if the species distribution records are gathered along a period of several years, as is often the case (e.g., Palomo and Gisbert 2002), the recorded
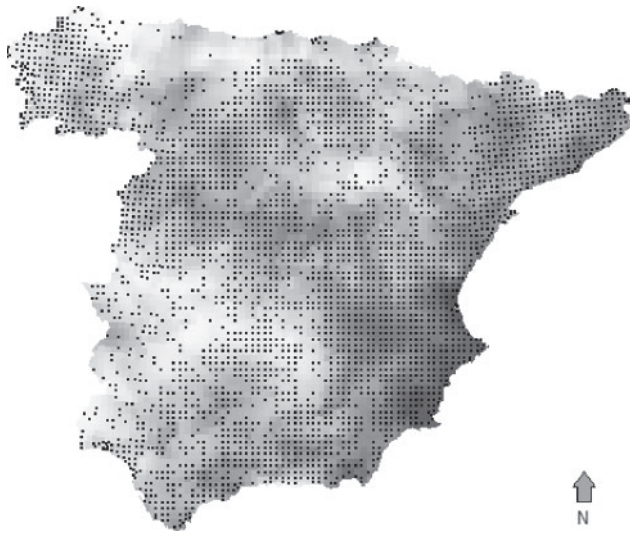
FIGURE 1. Distribution records (black dots) of the European rabbit (*Oryctolagus cuniculus*) on UTM 10 km × 10 km squares of mainland Spain (Palomo and Gisbert 2002), and environmental favorability (increasing from white to black) based on a distribution model (Real et al. 2009). Occurrence records are analogous to a classical view of the species distribution, while favorability is analogous to a quantum mechanical (wavefunction) view of the species distribution.

distribution is merely a snapshot of the locations of the organisms at the moments when they were observed (e.g., the black dots in Fig. 1). Different locations would be obtained if observations were made at different moments. It could thus be argued that, conceptually, a species is present with differing intensity over the whole area covered by the home range of its constituent individuals, as the whole area holds a non-negligible degree of favorability for the species presence (e.g., the gray areas in Fig. 1).

In quantum theory, an experimental observation implies the interaction between a means of taking measurement (e.g., a photon that is bounced off an elementary particle) and the particle being observed, which alters the trajectory of the particle itself. As a result, any observation affects the properties that are being observed. Analogously, we can conceptualize the observation of species distributions in the field as producing a "change" in the perceived current distribution of that species. When we observe, we are detected by animals that, as a result, change course or move somewhere else, we move propagules when touching organisms for identification, or we modify the environment to make the localities physically reachable, so fundamentally altering the distribution we are observing. Note: we are not claiming here that observing an individual organism physically changes its state in the manner of Schrödinger's cat, but rather making an analogy.

This analogy with quantum theory allows us to go further: it could be said that there is some, albeit often negligible, degree of favorability beyond the home range for *any* species. This would mean that there is, in principle, a small but non-zero probability of observing a species anywhere outside what is considered to be their range. In fact, one could argue that the probability of an individual (at any life stage) of any one species being found anywhere within the global biosphere is never exactly zero. Again, we would contend that this reflects reality—certainly in relation to biological phenomena such as propagule dispersal and vagrancy (e.g., Gilroy and Lees 2003).

So, the distribution of any species may be better described, rather than by observed occurrence records, by a favorability model such as the one represented in gray scale in Fig. 1, which indicates how likely the species is to be found at each locality (based on how favorable the conditions are for it being there) each time that we observe. Favorability is analogous to the "wavefunction" for each species, which describes the dynamic behavior of the distribution. As in quantum mechanics, favorability potentially provides "complete information" about a species (complete information about a particle's location meaning not only where it is, but the wavefunction that describes everywhere it could be, and how likely it is to be there). Similarly, the complete information about a species distribution is not where it has been observed, but the locations where it has a greater or lesser potential to be observed. The favorability for the species occurrence at different locations is thus closer to the true species distribution, as it represents the "complete information" about the species potential presence, provided that the model has succeeded in capturing the relevant correlates of the species distribution.

Favorability may be derived from either a statistical or mechanistic model, depending on how the probability values are obtained. However, if we take into account that, in quantum mechanics, probabilities can be described only as a statistical distribution and only when the experiment or observation is repeated many times, the difference between mechanistic and statistical SDMs gets blurred, and statistical models may approximate to (quantum) mechanistic models given sufficient numbers of observations.

However, some differences between species distributions and quantum wavefunctions are also patent, as the species is composed of many individuals while the particle is one, and the macroscopic and microscopic domains, respectively, of the phenomena involved render them different. In addition, and contrary to wave functions, favorability for occurrence depends on the specific environmental conditions and the history of the species. This is why the favorability function should not be of the kind applied customarily to quantum subatomic particles, but related to the probability of species occurrence, more in line with the concepts used is species distribution modeling or, more generally, in biogeography.

A Note: Quantum Phenomena in Living Things

Note, importantly, that the previous arguments do not require that living organisms themselves be treated

as quantum objects; indeed, no organism has been observed to demonstrate quantum behavior as a whole object (Romero-Isart et al. 2010; Bull and Gordon 2015; Li and Yin 2015; although see Rodríguez et al. 2015b). However, quantum phenomena are important in various biological and ecological processes (Ball 2011), including photosynthesis (Engel et al. 2007; Mohseni et al. 2008; Sarovar et al. 2010), magneto-reception (Ahmad et al. 2007; Gegear et al. 2008; Keary et al. 2009; Gauger et al. 2011), animal behavior (Aerts et al. 2014; Holland 2014), natural selection (Lloyd 2009), ecology and evolution (Rodríguez et al. 2015a, 2015b and references therein). It is thus not entirely surprising that larger-scale relationships between species distributions and the environment might also be understood within a framework that is analogous to quantum physics. In any case, here we are arguing for using the quantum analogy as a heuristic concept with the consequent heuristic tools (*sensu* Bull 2015). We do not provide the homolog mathematical tools to quantum-mechanically deal with species distributions, but rather propose that such a framework could apply and improve the way in which SDMs are built and evaluated in future work.

Dark Diversity and the Geometric Mean of Favorabilities

We next provide one example of how treating species distributions using favorability values may result in an improvement on existing biodiversity metrics. Indices based on favorability, linked above to quantum theory, serve to illustrate the potential usefulness of our proposals, showing them to be not only philosophical, but also practical.

"Biodiversity" is the "sum total of all biotic variation from the level of genes to ecosystems" (Purvis and Hector 2000) and is a fundamental concept in ecology and evolution. However, there is no one universally agreed unit or conceptual framework that can satisfactorily express the total biodiversity contained within a system (Purvis and Hector 2000). The subject of effective biodiversity metrics is one of intense research interest (Buckland et al. 2005). The majority of current metrics are based on the variability observed within a volume of space.

Potential Biodiversity

As mentioned, the use of SDMs based on a favorability function is loosely analogous to the use of wavefunctions to model particles in quantum mechanics, and yields non-zero probabilities of species appearance even outside their home range (e.g., vagrants). A recent development in the biodiversity literature that is related to this notion is the concept of "dark diversity". The original proposal was that conservation scientists consider not only the observed local diversity of an ecological community, but also the set of absent species "that can potentially inhabit those particular ecological conditions", the latter set constituting the

"dark diversity" of the community (Pärtel et al. 2011). This concept was further developed (Mokany and Paini 2011) with the suggestion that the contribution of each species i to a region's biodiversity should be weighted by the species' probability P_{ij} of inhabiting the location j. The dark diversity would then be calculated from the ratio of the summed probabilities of species not present in the community in question, and all species present in the wider region $= \sum P_{ij}(\text{not in})/\sum P_{ij}$ (all). This metric thus goes beyond a measure of the presence/absence of species, and considers those species that are not present but have the potential to be. Emerging research has explored whether dark diversity can be measured in practice (Lewis et al. 2016). By calculating dark diversity for a set of points across a given region, one would obtain a "dark SDM", which might be just as important for conservation as an SDM based on known occurrences.

Dark diversity, *sensu* Pärtel et al. (2011), essentially captures the set of species that for some reason have not been observed to occur in what otherwise might be considered a favorable location for those species. Species can be absent, for example, from a favorable patch within a metapopulation due to a local (possibly temporary) extinction (Levins 1969), but this unoccupied favorable patch may play a key role in the survival of the whole metapopulation (Hanski and Simberloff 1997). Considering all the areas that are favorable for different species is necessary when using models to define important areas for conservation (Estrada et al. 2008), or when combining models of ecologically interacting species (Real et al. 2009; Acevedo et al. 2010).

In keeping with the perspective expressed throughout this article, these concepts can be taken a step further. Instead of making a distinction between observed diversity and dark diversity, *all* species can be understood in terms of the probability that they will be found in each region, whether or not they have been observed. This probability can be treated as a function of the favorability of the region for each species and other factors, and the summed favorabilities may be considered the "potential biodiversity" of the region. Individuals representing any species would then not be assumed to be inside a region or otherwise; rather, they would be treated as having some relative likelihood of occurring within the region.

One result of treating species this way would be that metrics originally developed to measure dark diversity—that is, species potentially but not actually present in a region—(Mokany and Paini 2011) could be applied to biodiversity as a whole. That is, the biodiversity of a volume of space would be a composite favorability function for the different species that might occur there, rather than a measure of the observed set of species: that is, analogous to a quantum mechanical treatment of particles in a volume of space. In practice, it is already becoming common in ecology and biogeography to work with probability functions of species presence rather than observed distributions or abundances (Guisan and Zimmermann 2000; Jiménez-Valverde and Lobo 2007; Guarino et al. 2012), as this is,

for example, a better way of dealing with source-sink and metapopulation dynamics (Pulliam 1988; Muñoz et al. 2005). Estrada et al. (2008, 2011) and Fa et al. (2014) used the accumulated favorability for a group of species as a surrogate of biodiversity to identify priority areas for conservation, and Fa et al. (2015) used the same notion to relate the sustainability of bushmeat hunting with human nutrition in Central Africa.

The Geometric Mean of Favorabilities

One application of measuring the biodiversity of a region or volume of space is to monitor trends for the purposes of conservation. A key metric in modern conservation is the geometric mean of species abundances, but this metric has two important limitations (Buckland et al. 2011; see below). The metric devised for dark diversity can be extended for all species in a region to form what is essentially a geometric mean of probabilities rather than abundances, and thus overcome these limitations. While a probabilistic treatment of species does not equate to a quantum mechanical treatment of species—since the probability of occurrence is only related to, and not equivalent to, a quantum wavefunction—the favorability for occurrence does. Therefore, we propose the use of a geometric mean of favorabilities as a general biodiversity metric.

In Mokany and Paini (2011) the quantity $\sum P_{ij}$(all) is defined: that is, the combination of probabilities that each species i will be in the region j. We adapt this definition by first specifying the finite series $\sum_{i=1}^{N} F_{iV}(t)$, where $F_{iV}(t)$ is the favorability for the presence of species i in a volume of space V at time t, and there are a total of N species for which volume V has any degree of favorability at that time. If this sum were normalized to a value between 0 and 1, it would be comparable for different volumes of space; this could be achieved by including a factor $(1/N)$, that is, $(1/N)*\sum_{i=1}^{N} F_{iV}(t)$, a value which is the arithmetic mean of species' favorabilities. If the natural logarithm of favorabilities is taken and the sum is placed in the exponential, then this becomes a geometric mean of favorabilities (Buckland et al. 2005):

$$B_V(t) = \exp\{(1/N)*\sum_{i=1}^{N} \ln[F_{iV}(t)]\}. \quad (3)$$

In order to consider a change in this quantity with time, it is necessary to calculate the change in the favorability function summed across all species. For a period $t_1 - t_2$, this could be expressed as the increment in the geometric mean of favorabilities:

$$\Delta B_V(t_1 - t_2) = \exp\{(1/N)*\sum_{i=1}^{N} \ln[F_{iV}(t_1)/F_{iV}(t_2)]\}. \quad (4)$$

The geometric mean of relative species abundances is increasingly used to examine trends in biodiversity and has numerous advantages over other metrics (Buckland et al. 2011). However, abundance records are available only for restricted regions and species pools. More importantly, this measure has the major limitations that: (i) it cannot be calculated if any of the relative abundance estimates is zero; and (ii) it is too highly sensitive to species that are recorded so rarely as to be characterized by dramatic changes in observed abundance (Buckland et al. 2011). Crucially, by applying the geometric mean to favorabilities (Equation (3)) as opposed to observed abundances, based on the conceptual treatment we have discussed through this article, these two limitations are overcome. In the case of limitation (i): there is never in principle a favorability of zero for a species to be observed in a region, however unlikely it may be. In the case of limitation (ii): the *favorability* for the occurrence of a rarely recorded species is likely to change far more gradually over space or time than its *observed abundance*, say, during annual surveys, as abundance is positively related with favorability (e.g., Real et al. 2009; Guarino et al. 2012), but with a triangular fit with increased abundance range at higher favorability values (Muñoz et al. 2015). In addition, unlike abundance, favorability can be obtained for any species with reasonably good data on its occurrence and the relevant environmental parameters.

A Worked Case Study with Known Species

As a case study, we analyzed the distributions of 63 terrestrial non-flying mammals of Spain at two different times, based on an atlas from the beginning of the century (Palomo and Gisbert 2002) and on the current database of the Spanish Ministry of Agriculture, Food and the Environment (downloaded 26 July 2015 from http://www.magrama.gob.es/es/biodiversidad/temas/inventarios-nacionales/inventario-especies-terrestres/inventario-nacional-de-biodiversidad/bdn-ieet-default.aspx). Environmental favorability for each species was obtained with methods and variables described previously (Barbosa et al. 2009; Real et al. 2009; Barbosa and Real 2010), using the same set of predictors for both distribution data sets. Analyses were performed with package *fuzzySim* (Barbosa 2015), under the R statistical environment (R Core Team 2014). We calculated the geometric mean of favorabilities (Equation (3)) and its increment (Equation (4)) with the R functions provided in Online Appendix 1, available on Dryad at http://dx.doi.org/10.5061/dryad.gn6qb.

Both the sum and the geometric mean of favorabilities were greater than 0 at all locations, and varied more gradually in space than recorded species richness (Figs. 2 and 3). In addition, these measures showed different overall patterns, with species richness showing more spatially irregular "peaks", not all of which are matched by similar peaks in favorability (e.g., at protected areas such as Picos de Europa, in central-northern, and Sierra de Gredos, in central-western Spain, Fig. 2). Many such peaks are likely to reflect survey bias, a methodological artifact known to widely affect biodiversity records (e.g., Barbosa et al. 2013a). In our study, species
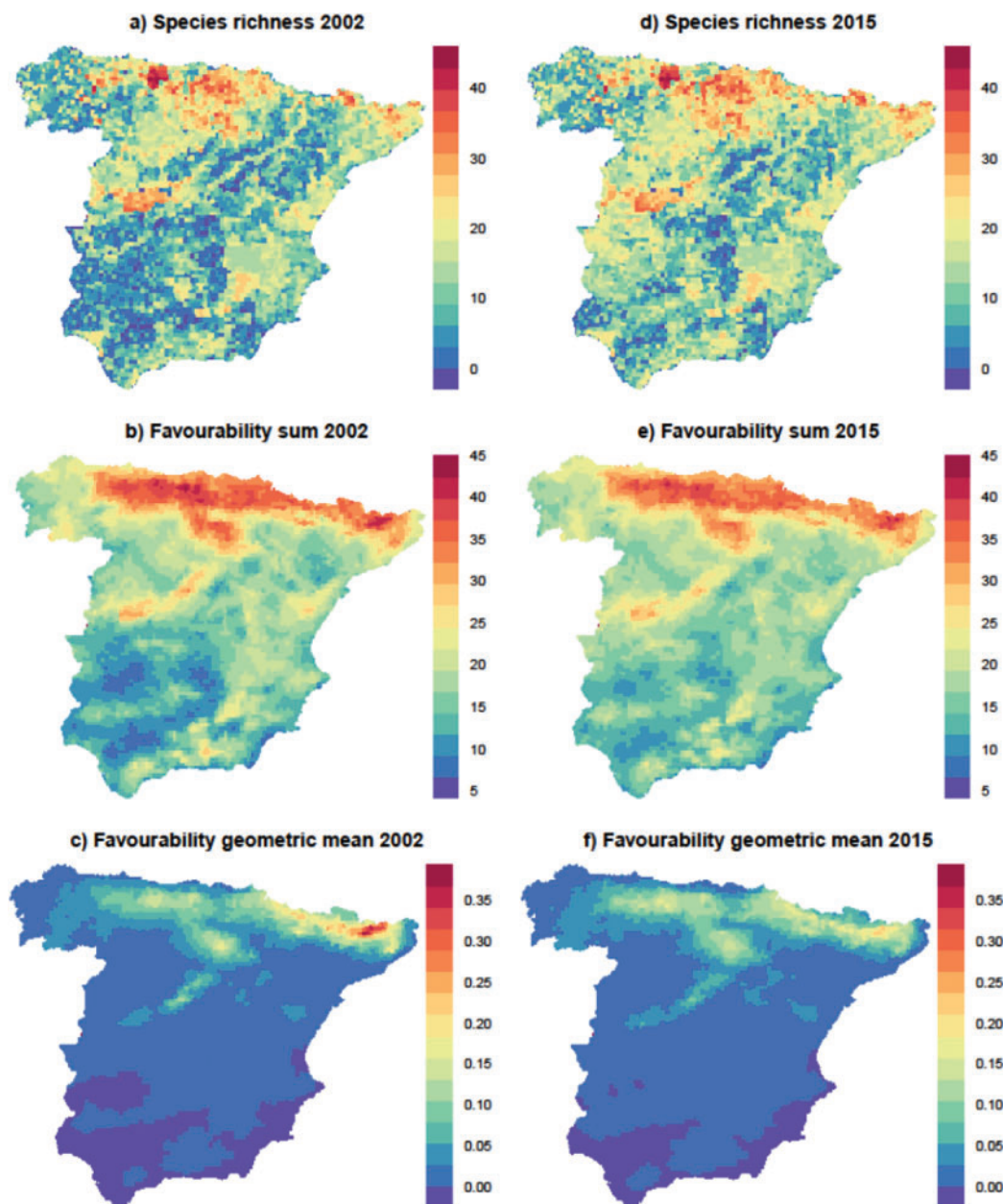
FIGURE 2.   Species richness, and the sum and geometric mean of favorabilities, for Spanish terrestrial mammals recorded in the distribution atlas of Palomo and Gisbert (2002) and in the national database of 2015. North is up, and grid squares measure 10 km^2.

richness was indeed strongly correlated with the number of records (including repeated species) per UTM cell, which are a proxy for survey effort (Barbosa et al. 2010; Fontaneto et al. 2012): Spearman's non-parametric correlation, Rho=0.93 in 2002, Rho=0.91 in 2015 ($P \ll 0.001$). Conversely, the geometric mean of favorabilities was visibly less correlated with survey effort (Fig. 2; Rho=0.42 in 2002, Rho=0.32 in 2015), suggesting that favorability could also help to minimize (albeit not completely eliminate) survey bias in biodiversity analyses. In a similar way, favorability may help to minimize other methodological artifacts such as errors in the location or identification of species records

(Barbosa 2015). The change in species richness from 2002 to 2015 was concentrated in the Spanish region of Extremadura in central-western Spain (Fig. 3a), probably due to the availability of new data from this particular region (Palomo and Gisbert 2002), while the increase in the geometric mean of favorabilities was more spread throughout the southern half of Spain (Fig. 3b).

CONCLUSION

An analogy means that a similarity exists in some respects between things that are otherwise dissimilar. Species distributions involve the presence of many

a) Species richness change

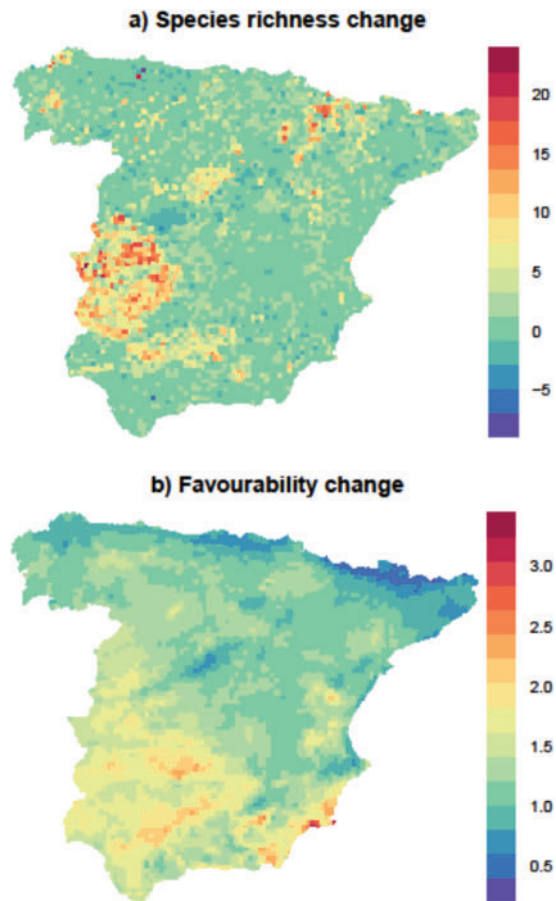

b) Favourability change

FIGURE 3.   Change in species richness (a) and in geometric mean of favorability (b) for Spanish terrestrial mammals in 2015 relative to those based on the distribution atlas of 2002. North is up, and grid squares measure 10 km².

individuals simultaneously in many and varying places, and it is the observer, when interacting with the species, who provides the specific spatial and temporal data to the observed distribution. This potentially justifies considering an individual belonging to a species as analogous to a quantum particle, and the favorability for species presence as reasonably analogous to the wave function of the particle.

The differences between species and particles are clearly important, making our comparison conceptual rather than actual, and the macroscopic and microscopic domains (respectively) of these two objects render them different. This is why the favorability function is not of the kind applied customarily to quantum subatomic particles, but related to the probability of species occurrence, more in line with the concepts and models used in biogeography. In our view, we are showing that using concepts derived from quantum mechanics is justified, reasonable and useful to approach species distribution modeling, while the actual formulae and models used should remain firmly rooted in biogeographical modeling.

Quantum physics and biogeography are two very different fields of science. However, we are at the early stages of a potential conversation between them and, although the analogies may not yet be perfect, there is reason to think that considering them may be useful, and may open up new ways of exploring and making sense of biodiversity data. We suggest that an integration of the two fields, with collaboration and methodological exchange between quantum physicists and biogeographical modelers, can significantly improve the understanding, prediction, and the evaluation of the prediction of species distributions and biodiversity trends, both of which are current pressing issues in ecology and biogeography. Quantum biogeography and its implications are not only interesting for theoretical advances in evolutionary and conservation biology, but may also provide more powerful tools for the study, management, and conservation of species in a rapidly changing and highly uncertain world.

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