1	Ecophysics reload – exploring applications of theoretical physics in
2	macroecology
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15	Abstract
16	Physics and ecology focus on different domains of nature and have developed under distinct
17	scientific paradigms. Still, both share critical features, such as dealing with systems of
18	irreducible complexity and inherent uncertainty at a fundamental level. Physics has embraced
19	such complexity earlier and has devised robustanalytical approaches todescribe general
20	principles of its systems, a path that ecosystem ecology has tracked, but organism-based ecology
21	has only started to.Here, we outlineapproaches from physics – from classical to quantum
22	mechanics - to address ecological questions that deal with emergent patterns of biodiversity,
23	such as species' distribution, niche, and trait variation, whichare of particular interest
24	tocommunity ecology, biogeography, and macroecology. These approaches can be further
25	extended, which would provide hese fields with a rationale common to other
26	scientificfields within and outside ecology.
27	Key words: dark diversity; emergent patterns; maximum entropy; species distribution; trait
28	distribution, ecological uncertainty

29 1. Introduction

Physics and ecology deal with different subsets of natural systems. Ecological systems gather 30 information from the environment and evolve, thus requiring the integration of historical 31 contingencies and evolutionary laws that are expendable in physics (Hopfield, 1994). However, 32 physics and ecology share several commonalities. Both disciplines deal with systems of 33 interacting components that can behave probabilistically in some relevant scale, and that give rise 34 to complex outcomes(Solé and Bascompte, 2006). Physics has though a longer, ubiquitous, and 35 successful history of development of analytical approaches and models to describe such systems. 36 Conversely, the strategies of ecology for explaining its subjects arevaried. Ecology emerged 37 from the combination of different lines of investigation, including plant physiology, plant 38 geography, animal biology, natural history, pest control, and others (McIntosh, 1985). From the 39 1960s onwards, a'modern ecology' was already recognisable, but it comprised two 40 dominantparadigmsthat persisted ever since:an ecosystem-based and an organism-based ecology. 41 42 Ecosystem ecology, which McIntosh (1985)referred to as "management-oriented ecological engineering", developed upon physical grounds, notably allowing for the laws of 43 thermodynamics (Odum and Pinkerton, 1955; Odum, 1969). Ecosystemswereincreasingly 44 described in terms of storage and transfer of energy and mass, efficiency, stability, and entropy 45 (Odum, 1971; Gallucci, 1973), thus theory in ecosystem ecology has been closer to the 46 physics'rationale and formalism (Solé and Bascompte, 2006; Rodríguez et al. 2019 and 47 references therein). 48 On the other hand, organism-based ecology –including population and community ecology 49 - has been primarily committed to explaining patterns of biodiversity, with emphasis on its 50 measurements, drivers, and evolutionary basis (MacArthur, 1965; Magurran, 1988; Lawton 1999). 51

52 Explanations norganism-based ecology have been far from homogeneous; they include

53 historical explanations, verbal descriptions, phenomenological models, mechanistic models, and

54 law-like mathematical models (see Pickett et al., 2010). Although organism-based ecology

follows on pursuing general principles(Lawton, 1999), its dominant thinking has praised the 55 description of variability over the regularity of ecological phenomena (Mayr, 1996; Hansson, 56 2003). This rationale differs from that adopted in physics, mainly statistical mechanics, and in 57 ecosystem ecology, which accepts an inherently haphazard behaviour of individual entities that 58 in turn convey to intelligible and predictable outcomes.Organism-based ecology delayed in 59 perceiving and describing this probabilistic nature of biodiversity patterns (Hubbell, 2001). 60 Still, physics' rationale is neither absent nor new tosome organism-based fields of 61 ecology.For instance, Porter and Gates (1969) established the physical foundations of exchange 62 of energy between animals and the environment. Subsequently, North American physicist James 63 P. Wesley proposed some physical applications to selected problems in ecology, including 64 ecosystems, populations and behaviour (Wesley, 1974). In his book, he coined the term 65 'ecophysics'. Later, Brown and Maurer (1989) introducedmacroecology, a research programthat 66 could address general principles of biodiversity through adopting probabilistic perspective of 67 68 biodiversity patterns, analogous to what statistical mechanics did in physics (Marquet, 2017). Macroecologyfostered ideas that include, for example, a critical role of scaling in ecological 69 patterns (Brown and West, 2000), ametabolic basis for several ecological patterns (Brown et al., 70 2004; Burger et al., 2019), and the description of statistical distributions of organisms in terms of 71 maximum information entropy (Harte, 2011). Despite all these applications and claims for a 72 73 further approximation between biodiversity research and physics (see Marquet et al., 2014; Marquet, 2017; Currie, 2019), the universe of approaches to address biodiversity patterns through 74 75 probabilistic models inspired in physics has only been scratched. The present paper is a synopsis of what we discussed in the symposium 'Applications of 76 Theoretical Physics in Ecology', during the International Society for Ecological 77 ModellingConference, at Salzburg, Austria, in October 2019. Here, we showcasea few 78 approaches and models brought in from different branches of physics – from classical- to 79 quantum mechanics – that can aid organism-based ecology, especially community ecology, 80

biogeography and macroecology, in pursuing generalisations about emergent patterns of
biodiversity. These approaches deal with biodiversity patterns that emerge from complex
organismal dynamics, to which a thoroughly reductionist approach appears to be ineffective. In
doing so, we intend to encourage the expansion of these approaches and the development of
others, and to fuel further debate about the integration of organism-based ecology and physics.

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87 2. Macroscopic approximation of biophysical forcing

Like macroecology, classical physics provides a coarse but often satisfactory description of 88 complex dynamics, provided that they are analysed at the appropriate scale. In classical 89 mechanics, fields such as fluid dynamics treat the matter as continuous quantities despite their 90 91 discrete, atomic nature. Under some force, although individual particles move haphazardly, the entire fluid assumes an average trajectory that can be deduced by general principles. This 92 macroscopic approximation suffices to characterise the behaviour of these systems at the scale of 93 94 typical objects. This behaviour is mainly expressed by differential equations that relate the change of a quantity relative to some dimension of reference (e.g., time or position). In formal 95 physical description through differential equation, the variation of the focal quantity can be 96 assessed relative to the reference dimension or other variables of the equation through its partial 97 derivatives (Hutter and Jöhnk, 2004). 98

99 If we think of a particular trait of a species (e.g., body size) as a macroscopic state subject to an external force such as an environmental constraint, we could also view the geographic 100 101 variation – or the evolution – of this trait as a response to that constrant similar to how physics treats the change of a quantity along a reference dimension. This reasoning was recently applied 102 to the variation of body size of anurans as a response to potential evapotranspiration (Gouveia et 103 al., 2019). The authors derived a set of partial differential equations for the change (i.e., thought 104 as sensitivity) of evaporative water loss relative to two features that control the water loss: body 105 size and total resistance (a physiological attribute related to the anurans' skin). These functions 106

followed from a well-known equation that describes the loss of water out of the animal's body –
equivalent to Darcy's law of diffusion (Porter and Gates, 1969) – and they provide testable
predictions about the variation of size and resistance across environmental gradients at the
macroscale.

In addition to finding empirical support, Gouveia et al. (2019) provided a theoretical 111 112 benchmark for analysing water balance and body size variation among anurans at the macroscale. A critical point of this approach is that it requires a first principle – such as the 113 diffusion equation – from which to derive the theoretical predictions of the macroecological 114 pattern. It is also critical that these predictions are taken as theoretical expectations of particular 115 processes, which may or may not find empirical support. Because ecological and evolutionary 116 patterns are multifactorial, the observed patterns will always be subject to multiple competing 117 forces. However, as we become capable of formulating clear-cut hypotheses from underlying 118 principles, we will be able to balance the conflicting evidence – which abounds in ecology – 119 120 given the theory, not irrespective of it.

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122 3. The maximum entropy formalism to scale up individual-microclimate interactions

Ecologists are increasingly challenged to predict the responses of organisms to environmental 123 change. This task requires models to predict the value of key traits involved in organismal 124 125 sensitivity and theirpotential to cope with changes in climatic conditions (Huey et al., 2012; Urban et al., 2016). Advances in biophysical modelling now enable predictions of key traits such 126 127 as body temperature, water balance, and metabolic rate of individuals from microclimatic information (Kearney and Porter, 2017). These predictions are critical to model the repertoire of 128 microclimates that many organisms exploit to maintain homeostasis under changing conditions. 129 However, animal behaviour has many degrees of freedom, which poses a fundamental 130 obstacle to mechanistic modelling. For example, the animals' potential to explore the thermal 131 heterogeneity of their habitat results from multiple deterministic (e.g., selection of 132

microclimates) and stochastic processes (e.g., predator avoidance). Capturing these rules with
mechanistic models is difficult, especially when dealing with large ensembles of organisms such
as populations or communities, to which the range of responses increases exponentially with the
number of individuals.

A promising alternative is to study statistical tendencies of these ensembles and identify 137 138 regularities that provide macroscopic indicators of their response to environmental changes. The maximum entropy formalism is a powerful inferential method that provides the most probable 139 representation of a system composed of multiple entities (for other applications in ecology, see 140 Harte, 2011; Phillips et al., 2006; Pueyo et al., 2007). If we think of organisms living in 141 heterogeneous landscapes as one such system, the maximum entropyapproach allows 142 143 transcending the individual physiology and behaviour into statistical tendencies of a population. Rubalcaba et al. (2019) applied this approach to model the influence of microclimatic 144 heterogeneity on populations of thermoregulating lizards. By simulating populations as large 145 146 systems of particles moving in a heterogeneous thermal landscape, they derived the most probable distribution of individuals among microenvironments and the probability distribution of 147 body temperatures that characterises the population at any time. Under the maximum entropy 148 principle, the most probable distribution is the one that maximises Shannon's information 149 entropy while satisfying a set of constraints such as average values of some moment functions. 150 151 Rubalcaba et al. (2019) propose that, in a population of thermoregulating ectotherms, the mean of the distribution of body temperatures approaches their preferred body temperature. Deviations 152 153 from the mean may occur because individuals move away from their preferred microenvironment, e.g., for foraging, breeding or evading predators. Their work predicted 154 daytime distributions of body temperature of desert lizards accurately and, more critically, it 155 provided a macroscopic indicator of the constraint imposed by the thermal environment on 156 animal activity. Although this representation does not capture the full complexity of the system's 157 mechanisms, it integrates and scales up information into macroscopic behaviours, which 158

159 constitutes a fundamental step to reliably project the impacts of climate change across broad160 spatiotemporal scales.

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162 **4. Seeing the forest for the** *quantum* **trees**

Describing community patterns has proven a formidable task, especially if one tries to combine 163 164 the several deterministic (e.g., competition, ammensalism, commensalism) and stochastic (e.g., dispersal, ecological drift and random extinction) processes involved (Chesson, 2000). An 165 example of such complex patterns is the size distribution of trees (height – H, and diameter at 166 breast height – DBH) in a forest stand. Without interactions among trees (neutralism) and with 167 their growth resulting from homogeneous external factors (e.g., climate) plus random noise, the 168 169 density distribution function of their H and DBH would be described by a Gaussian function. However, neither Gaussian nor beta, gamma, lognormal, Weibull or Johnson's functions 170 describe these patterns always well (Cao, 2004; Gorgoso-Varela et al., 2016; Fonseca et al., 171

172 2009; Pretzsch, 2009).

An analogous problem in physics is to describe the energy levels of the atomic nuclei of heavy atoms, which results from a large number of interactions between their components.Attempts to write down – let alone to solve – Schrödinger's equations for such systems have failed. Alternatively, Wigner (1951) proposed to consider the eigenvalues of random matrices consisting of 0 and 1 to describe the energy levels of such nuclei. The density distribution function of the eigenvalues of a random matrix can be described by Wigner's Semicircle Law (Dyson, 1962; Mehta, 2004):

$$f(s) = A \cdot \frac{\pi s}{2B} \cdot \exp\left(-\frac{\pi s^2}{4B^2}\right)$$
 Equation 1

181 where *s* is a distance between energy levels, and A and B are constants. By introducing y = 1/H182 and z = 1/DBH as ecological analogues of the energy *s* for trees of different ages with different 183 values of H and DBH, and introducing normalised indices (where w = y, z), then the H and DBH

density distribution functions for sample plots can be described with high accuracy by equation 184 (1) (Fig. 1). 185



Fig. 1. Density distribution function for 1/height of an inventory with more than 5000 187 188 trees of different species (pine, birch, larch) and various ages (from 20 to 90 years) at Eastern Siberia (Valley of the Angara River). The dashed line (2) stands for data and 1 for the model. 189 190

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The agreement of the density distribution function for s with the distribution of the 191 eigenvalues of random matrices may suggest, for the forest ecosystem, i) an analogous of the 192 Hamiltonian system of physics, which describes the interaction of multiple moving objects; and 193 ii) the application of an extreme principle to the description of ecosystems; not the principle of 194 minimum energy, but the principle of minimum probability of mortality of the ecosystems' 195 components. All density distribution functions of forest stands have long tails by normalised 196 inventory indicators, suggesting the presence of younger (i.e., smaller) trees of different species 197 and ages that accounts for 5 to 10% of the community. A possible explanation for this effect may 198 parallel a model of weakly non-ideal condensed Bose gas (Bogolyubov, 2007), with the 199 community consisting of a two-level system: establishedtrees and growing trees. In a condensed 200 201 ideal Bose gas, all bosons must be at the lower energy level according to the principle of minimum energy in a stationary state. However, the total interaction energy of all particles in the 202 8

system will be less when a small proportion of the bosons are at the upper energy level, ratherthan when all bosons are at a lower level (Bogolyubov, 2007).

Considering trees as analogues of bosons, the interaction functions of trees may 205 characterise their mortality risks, and the total risk function, in turn, should be minimal in steady-206 state forest stands. If the proportion of growing (i.e., high-energy) trees in the stand is small, and 207 208 they do not interact with each other (as the bosons at the upper level in the Bogolyubov model), it can be shown that the total risk function in the stand with younger trees is less than in stands 209 without them (see Muller-Landau et al. 2006). Therefore, the existence of growing, younger trees 210 (e.g., due to weak disturbances) in the ecosystem reduces the total risk of tree mortality in the 211 community. 212

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5. Quantum theory and the intrinsic uncertainty in species distributions

On a macroecological and biogeographic perspective, a species' geographical distribution is 215 216 typically depicted as a set of localities or regions where the species has been observed to occur. However, such distribution is merely a collection of "snapshots" of the places where some 217 individuals were observed at particular moments. Species move (at varying rates), so their 218 distributions change constantly, and it is impossible to know where all individuals are or will be 219 at a specific time. While ecologists tend to classify "occurrence" localities as such, an occurrence 220 cantake a range of values: within each locality, a species can occur regularly or occasionally, 221 year-round or seasonally, throughout or at a corner. So, a species is neither present nor absent: it 222 is present to a certain degree in each place. What we observe may be either presence or absence 223 each time we visit each place, but the full distribution behind those observations is actually a 224 continuous state, which can only be determined by repeatedly visiting those places. 225

This reasoning leads us to set an analogy with quantum physics (Real et al., 2017), in which it is impossible to know the exact position of a particle except when we observe it. We can only know how probable it is to find a particle at each location, and that probability is obtained by repeating the observation many times. The complete information about a particle's spatial
distribution is not the set of its observed positions, but a wavefunction that describes all of its
possible positions and the probability of each one (Merali, 2012). The same applies to species
distributions: a species is everywhere to varying degrees, it is not possible to pinpoint where each
individual will be at any given moment, and the distribution is better described by a function
describing how likely the species is to be found at each place (Real et al., 2017).

Although living beings do not behave like quantum particles, they also show a degree of 235 intrinsic unpredictability which makes their momentary distributions not precisely predictable. 236 With inert macroscopic objects such as planets or bullets, if the initial positions and the forces 237 238 involved are known, we can determine with certainty where they will be at a given point in time. 239 With quantum particles, knowing their exact positions is physically impossible. Living organisms are somewhere in the middle of this spectrum: We can determine the drivers of their 240 distributions and predict their most likely – but not their exact – locations, as they have some 241 degree of freedom from external forces, and they can respond to the same conditions in different 242 ways. Real et al. (2017) thus argued that the response of living beings to the environment is not 243 entirely deterministic. 244

This is not to say that species distributions are utterly unpredictable – on the contrary, and 245 here the quantum analogy is also useful. According to Hawking & Mlodinow (2010), quantum 246 physics does not undermine the idea that nature is governed by laws, but brings about a new 247 form of determinism instead: "Given the state of a system at some time, the laws of nature 248 determine the probabilities of various futures and pasts rather than determining the future and 249 past with certainty". Likewise, species distributions are not random, though they are not 250 251 categorical either: they are probabilistic. Hawking &Mlodinow (2010) also pointed out that, despite the probabilistic nature of quantum mechanics, it provides quantitative predictions that 252 can be rigorously tested. This testable aspect of probabilistic predictions also applies to species 253 distributions (e.g. Areias-Guerreiro et al., 2016). Probabilistic species distributions provide 254

significant advantages (Karger et al., 2016), and they can be directly analysed even with indices

originally designed to work with categorical presences (Barbosa, 2015).

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258	6. Dark matter and relativity theory applied to macroecological patterns
259	For Turnbull (2014), ecologists are often frustrated that their universe is "fuzzy and
260	unpredictable" because of strange entities, such as the niche. She also highlighted that physicists
261	have their strange entities, such as dark matter, but they seem to live with them much better than
262	ecologists do. Because galaxies and their clusters move with such speed that the gravity
263	generated by their observable matter could not keep them together, physicists were led to reason
264	that something invisible is at play, which they called dark matter. Although dark matter is
265	thought to constitute most of the universal matter, it can be detected only from its gravitational
266	effects (Caldwell and Kamionkowski, 2009). Turnbull (2014) suggested that niches are
267	ecology's dark matter. Ecologists do not know what they exactly are, but their presence is
268	universally felt. Ecological communities without niches, like galaxies without dark matter, would
269	collapse.

270 However, to take the analogy between niche and dark matter further, we need a definition of the niche more in line with the concepts used in physics. The most famous definition of niche 271 is Hutchinson's (1957) n-dimensional hypervolume of environmental conditions in which a 272 population can persist. This niche is a space defined by its position, boundaries, size, shape and 273 overlap, but it is too static to fit the dark matter analogy. By describing the "internal structure" of 274 Hutchinson's niche, Maguire (1973) considered niches as response functions of species to habitat 275 276 conditions, thus treating the niche as an interaction. Maguire (1973) even generalised that every physical, biological, and social system has a response function to each possible combination of 277 conditions of its environment, offering a unified framework for living beings and inert physical 278 objects. 279

Real et al. (2006) proposed to use favourability functions to quantify how a species 280 responds to the environmental conditions in each location, irrespective of its overall prevalence 281 over a broader region. Favourability functions may then stand as species response functions that 282 encapsulate Maguire's (1973) notion of the niche as an interaction. What, then, if we look at 283 species' responses to the environment in the same spatio-temporal context as physicists do in the 284 285 general relativity theory, the space-time? Olivero et al. (2017) did so by showing that a function of space and time described the trends in the distribution of Ebola outbreaks in Africa, which 286 was partially explained by deforestation events. The analogy between the attraction in space-time 287 of matter on other matter (gravity) and the attraction in space-time of environmental conditions 288 on living beings (niche) is tantalising and gives support to other approaches (see Ma, 2019). 289

290 The ecological niche, if defined as an interaction, plays for living beings the same role as matter does in the general relativity theory, being an attractor of species, and thus playing a 291 significant role in biodiversity patterns. The response function enables us to detect areas with 292 293 favourable conditions where the species has not been observed, which yields an analogue of dark matter: dark biodiversity. This notion fits, for instance, the ideas behind metapopulation theory 294 (Levins, 1969), in which populations occur across a set of suitable patches, some of which are 295 occupied and some are not. When applied to community ecology, this unobserved species pool 296 may entail the dark diversity of the community (Partel et al., 2011), i.e., the species that have 297 298 favourable conditions for occurring in a location but that, for diverse reasons, are absent there. This seemingly abstract idea of dark diversity can actually have important practical applications, 299 300 such as informing on biodiversity potential for current and future networks of natural reserves 301 (Estrada et al., 2018).

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303 7. Conclusions

Many approximations and models from theoretical physics in ecology already exist, especially in
ecosystem ecology (reviewedin Solé and Bascompte, 2006; Rodríguez et al. 2019), but also, and

to a lesser extent, in organism-based ecology (e.g., Porter and Gates, 1969; Wesley, 1974; Brown 306 et al., 2004, Burger et al. 2019). Fewer studies are committed to describing biodiversity patterns 307 through embracing their probabilistic nature (e.g., Hubbell, 2001; Harte, 2011; Karger et al., 308 2016). Here, we summarise some recent approaches, largely inspired by these, todeal with 309 biodiversity patterns that emerge from complex organismal dynamics. We show that these 310 311 approaches derived from physics can provide accurate descriptions of biodiversity patterns on a macroecological scale, despite theuncertain, probabilistic behaviour of the individual entities that 312 make up these systems. 313

Physicists have for long struggled to describe complex, inherently uncertainphenomena 314 that are beyond humans' observational capacity, having devised an ample analytical toolbox for 315 316 such purpose. If properly deployed, provided that limitations and assumptions are acknowledged, these macroscopic approaches from physics can provide ecology, particularly macroecology, 317 with a diversity of opportunities to improve its explanatory and inferential capacity. This 318 319 endeavour can also help to accelerate the integration between organism-based ecology and ecosystem ecology under common perspectives (Loreau et al., 2010), and ultimately to align 320 ecology withother sciences. 321

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