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Humboldt's enigma viewed through the lens of ecosystem theory. Explanation by simple principles.

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ABSTRACT

The observation that mountain regions generally display higher diversity than tropical regions has recently been presented as a puzzle or "enigma", since it seems to contradict the normal belief that the highest diversity on Earth occurs in the rain forest ecosystems around the equator. The observation seems to be well supported by data gathered for several animal and plant communities, and thus deserves further attention, including investigation of how it arises. However, re-interpretation of the enigma in the light of ecosystem theory serves to resolve the problem, explaining the increased diversity as the result of the presence of a larger set of thermodynamic and thermo-chemical variables, which vary in quantity, quality, time, and space, together with the forcing functions usually present. This permits a more intensive exploitation of the gradients in an oscillating environment as formulated for instance in the intermediate disturbance hypothesis combined with the niche construction concept. Put simply, mountain regions offer an environment with a greater and more variable set of gradients, in terms of both quantity and quality, than occur in the more stable environments found in relatively flat areas. This gives an extra stimulus to speciation processes, resulting in the elevated diversity observed.

1. Introduction

Discussions about the conservation of biodiversity on Earth have received increasing attention from politicians, managers, and scientists over the latest decades, and several reasons can be suggested for this. First, it has become increasingly clear that human activities are impacting our fellow passengers on the planet, and results in an increasing numbers of species extinctions. This leads to many concerns, reflecting numerous aspects of this potentially critical issue: these include practical, rational, aesthetic, and ethical standpoints, and a variety of attitudes to the question of why we should attempt to preserve biodiversity. Secondly, we tend to believe that avoidance of anthropogenic destruction together management concentrated on preservation or mitigation of damage to biodiversity are a crucial issues which may help to safeguard the function of our own biosphere (Vernadsky, 1998 (annotated edition 1998)), including its ecological integrity (Müller 2005; Haase et al. 2018), ecosystem health (a metaphor from Aldo Leopold (Rapport, 1998)) and ultimately the concept of sustainability developed in the Rio report (WCED, 1987) and elaborated further through the SDG's. (UN, 2015).

Furthermore, the rationale for protecting biodiversity and mitigating and remediating damaged ecosystems is related to political concepts such as resilience and ecosystem services. Based on an intuitive understanding and in spite of the lack of clear definitions, diversity and biodiversity have therefore become popular indicators of ecosystem state (Marques, 2001).

Traditionally, areas of maximum diversity have been believed to occur in the tropical rain forests around the equator, and statements to this effect may be found in many university textbooks on ecology (Begon et al., 2005; Krebs, 2007; Molles and Sher, 2018). The reasons are assumed to be simple since a high level of solar radiation coupled to generally higher temperatures speeds up all processes in the biophysical environment. Other things being equal, this in turn leads on the one hand to a higher capture of energy (exergy) from the sun, and on the other hand, to a faster rate of biochemical and bio-geochemical processes. Both factors are assumed to promote increased biodiversity by increasing the rate of evolution and species formation. When coupled to time as a factor, long periods of stability in certain regions leads to areas with even higher biodiversity levels, referred to as hot-spots (Myers, 1988, 1990), as for instance in the tropical rain forests of the Amazonas

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or at coral reefs. It should be mentioned that the concept of hotspots implies a high number of endemic species that at the same time are considered to be under threat from human activities.

Additionally, such evolutionary exuberance has been assisted by a high spatio-temporal variability in living conditions. However, this does not seem to be the full story about biodiversity. When taking a look of maps of high diversity regions in the world (e.g. Myers et al., 2000; Hobohm, 2003) one must notice that also areas outside the equatorial regions exist which have been identified as hotspots. Observation of the areas indicate that other factors than temperature and insolation may infer increased levels of biodiversity, such as elevated supply of nutrients, exchange with adjacent areas – in both cases valid to coastal plain ecosystems, and geologically disruptive periods with interim stable periods which allows for adaptation and speciation to take place.

In a couple of recent papers, some prominent researchers have discussed what they refer to as "Humboldt's Enigma", which arises from observations disproving the usual belief that biodiversity is highest in the tropics by establishing that even higher diversities are in fact found in mountain regions (Rahbek et al., 2019b). In an adjoining paper (Rahbek et al., 2019a), the authors attempt to explain this as a consequence of geological and evolutionary processes.

The present paper aims to demonstrate that it is possible to reduce the problem to a point where the enigma vanishes. In fact, it becomes difficult to see why biodiversity levels in mountain regions should not be even higher. Thus, this paper is intended on the one hand to demonstrate the powers of modern ecosystem theory in resolving a complex problem of this type, and on the other hand to establish a number of testable hypotheses or conundrums by applying ecosystem theory to the phenomena observed and demonstrated in the unique dataset presented by Rahbek and coworkers (Rahbek et al., 2019a,b). So, what are the efficient causes of these seemingly unexpected observations? Efficient cause is here used in an Aristotelian sense, but we are convinced that this property is developed in a dialectic interaction with material and formal causes shaped by adaptive processes. The possible existence of final cause(s) will not be discussed here.

2. Getting to the crux by simplifying

Takin into consideration the complex of possible causes behind an elevated biodiversity, we find that the ideal situation would be to find as simple a solution to the problem as possible. So the first thing to do is to apply the principle of Ockam's razor. This principle is named after the Franciscan friar, a theologist and philosopher, who stated that solutions to problems should aim at simplicity and include as few elements as possible. This at least is the interpretation used in this paper; some modern elaborations of the principle state that the simplest solution also must be the "right" one, which in our experience is not necessarily the case.

So, if we apply Occam's razor and rethink the observations of Rahbek and coworkers in the light of Modern Ecosystem Theory (Jørgensen, 1992, 1997; Jørgensen et al., 2007; Nielsen et al., 2019), the essential reasons for and underlying (material and formal) causes of the problem described as "Humboldt's Enigma" can in fact be reduced to a few explanatory principles, as follows:

1) Mountain regions consist primarily of slopes, where gravity and weathering processes create increased gradients of bio-geochemical processes, resulting in increased physico-chemical impacts on abiotic ecosystem processes and living conditions;
2) This increased set of gradients – both in terms of quantity and quality - provides greater opportunities in the ecosystem in the form of available energies that can be exploited in a number of processes;
3) These processes result in an enhanced role for variation as a creative force, and thus in higher amounts of variation due to the greater availability of energy which can be exploited by means of speciation - as observed for instance in disturbed aquatic areas;
4) The innate capacity of organisms to exploit the opportunities offered by the environment and interact with it permits them actively to take part in shaping their environment further, for instance by niche construction.

As stated in the introduction, the purpose of this paper is to point out that these simple principles can provide a central explanation of the general evolution in ecosystems. In combination, they operate as a set of sufficient factors that promote increases in biodiversity. As some of these factors are very prevalent in mountainous regions, these principles thus take the enigma out of the problem. In fact, it follows logically that biodiversity can be expected to be higher, given such conditions. These points will be further elaborated and explained in the following.

2.1. *Gradients and exploitable energies*

Since the works of Lotka (1922a, 1925) and Schrödinger (1944), it has been clear that the existence of biological systems is founded on gradients of free energy imposed on the systems by their surroundings. The gradients are based on various energy forms: radiative (light and heat), or chemical (water and nutrients) as powers that are entirely physical in character such as gravity, which are likely to be of particular importance to the findings of this paper. The fact that ecosystems are open to such energy flows allows them to grow and develop.

In general, the above-mentioned energies need to be available in the form of gradients: for instance, as differences in chemical potentials between systems – normally as higher concentrations on the outside compared to the inside for chemicals or nutrients that are necessary for growth. Growth is correlated with accumulation processes along a spatial axis and thus with gradient development (see Müller, 2005; Müller 1998). This is valid not only for autotrophs, but also for heterotrophs, since the availability of any kind of food in the form of biomass is equal to (bio-)chemical energy and can be seen as a gradient directed into the next link in the trophic network. Examples of such a conceptualization of ecosystems may be found among the input-output type of models used in network descriptions of ecosystems. Here the model is transformed into a Markovian matrix and flows are often proportional to tensions between component state variables delivered by either predated species (output) or predating species (input) or both. The 'tensions' are often estimated from and expressed through the respective relative biomass or normalized unit concentration of the elements either measured as energy, biomass or major bio-geochemical elements of which living systems are composed (CHNOPS, cf. Morowitz, 1968). In the case of mountains, the intensity of the gradients is increased.

There are limits, both upper and lower, to the energy inputs on which the existence of stable ecosystems depends. This can be illustrated by analogy with a classical example from physics – that of the emergence of structures known as Benard Cells as the result of an application of a thermal gradient to a liquid enclosed between two fixed boundaries. When a heat source is applied to the one side, usually the lower, of the experimental setup, the heat is transferred through the liquid to the upper side of the system. If the heat applied is weak, no structure arises and transport of heat occurs by conduction only. When the heat source is strong enough, visible cells arise in which laminar transport occurs, bringing the heat up from the lower side. When cooled, the process reverses, removing the thermal gradient by convection at a faster rate than that of simple diffusion. At even higher heat inputs, the regular structures break down, resulting in a turbulent and disorganized pattern. In other words, the system is constrained by the strength of the gradient: if too weak, no structure will emerge, and if too strong the structure is impossible to maintain and disrupts. Only within a restricted range of exergy inputs is the emergence of self-organized structure possible. Transferring this analogy to biology, the structure has a "window of viability", and we assume that an analogous situation also applies in the case of mountain slopes. Thus, use the "window of viability" concept here is in accordance with early usage by Schneider and Kay (pers. Comm.) rather than its later use together with “window of vitality” in network theory.

A mountain slope by its nature provides gradients that offer variations in e.g. light regimes, physico-geological conditions such as the movement of water, chemical inputs (both in quantity and quality), as well as thermal conditions. We may see mountain slopes as providing series of edges or ecotones – the two concepts are being used as synonymous (e.g. Harris, 1988, Baker et al. 2002. The series may dissolve into almost continuous conditions where states are practically and empirically inseparable due to time-space scale interactions.

Many of these gradients are gravity-driven, leading to downward fluxes of precipitated water carrying dissolved nutrients and particles. The absence of such gradients in ecosystems with low or no slope will – over time – restrict them to developing diversity solely on the basis of the internal cycling of nutrients. At the same time, interpreting mountainous regions as landscapes of cones also implies variations in other gradients. The orientation of slopes relative to the points of the compass leads to quite different patterns of insolation (radiative energy) and heat inputs, even at similar altitudes. Both will vary locally with orientation and altitude, contributing to increased diversity.

Statement: The greater the quantity and variety of resources offered by the prevailing conditions – within the limits of the window of viability - the greater the number of possibilities for forming and testing new species. This leads to increased biodiversity.

2.2. Thermodynamic function and energy utilization

All living systems at any level of the biological hierarchy are constrained by the supply of available energy. They carry out their respective activities based on at least one of three basic types of energy (Brillouin, 1956), namely 1) high quality energy in the form of short wave radiation as delivered from the sun, 2) chemical energies (mainly of intermediate quality) provided by geological agencies recruiting various nutrients from the earth’s crust, and 3) heat energy: the rate of processes is regulated to a certain extent by external solar heat (e.g. heterotherms) or by internal heat originating in metabolism (homeotherms).

2.2.1. Light

High value energy in the form of solar radiation plays a fundamentally important role by providing the energy input to the autotrophic compartments. In this sense, the energy flow in ecosystems is clearly bottom-up regulated: all internal energy flows are consequences of the input to the primary producers. Both spatio-temporal, local surplus together with variation present important constraints to the development of increased biodiversity.

A clear difference between ecosystems must exist between latitudes, since the availability of light varies on differing time-scales. In the tropics, the variation is daily, with equal hours of light and dark each day, whereas within the polar circle autotrophs are faced with conditions varying on an annual cycle, varying from continuous daylight at midsummer to continuous darkness at midwinter.

2.2.2. Heat

Variations in insolation lead to differing patterns of thermal inputs, which tend to be almost constant around the equator and increasingly variable at increasing distances from there.

The energies are normally exchanged between the levels of hierarchies. The relationship between two subsequent levels (usually focal level and the level above or below is that of a physical embeddedness – the lower levels being physically included in the level above. This is the case up to the level of organisms – after which this issue is determined by the modeler, i.e. must be seen as a construction made by the observer of the system. This is often the case of ecosystems, from the population level and upwards. In the latter case this adds a layer of subjectivity to the energetic balances in the models (Nielsen, 2009; Nielsen and Müller, 2009; Nielsen and Ulanowicz, 2000).

2.2.3. Nutrients - in the widest sense

In all circumstances, autotrophs need to take up nutrients: from soils in terrestrial systems, or dissolved nutrients (often soil-derived) in freshwater systems, on their way to the oceans. In these systems the amount and composition of nutrients is largely determined by erosion processes. In aquatic systems, nutrient availability is highly affected by the rate of water flow, ranging from facilitation of diffusion right up to degradation by turbulent water movements. In terrestrial systems, nutrient uptake will be highly dependent on oscillations in temperature and resulting weathering of the ground, and last but not least, the movement of the resulting nutrients to other systems through gradients, which are plentiful in mountainous regions.

All in all, the increase in complexity in ecosystems has been argued to be a result of a generalized optimization of the use of available resources (Jørgensen, 1988, Jørgensen and Mejer, 1979,1981, Kay, 2000, Kay and Schneider, 1994, 1995, Lotka, 1922b, Mejer and Jørgensen, 1979, Odum and Pinkerton, 1955, Schneider and Kay, 1994a, b, Skene, 2017). By their nature, mountainous regions are home to physical forces that increase one or more of the three types of gradients: light, heat and nutrients. i. e. there are one or more increased gradients to be explored.

Essentially, the quantity and quality of the available energies are important factors that shape and change biodiversity. A mountain slope provides a huge complex of local gradients, offering variations in light regimes, physico-geological conditions, water movements, chemical inputs, and thermal conditions. Hypothetically, the higher the quantitative value and qualitative differences in resources offered by the prevailing conditions, the greater the number of opportunities to form and test new species, and this will lead to increasing biodiversity. The observations seem to confirm this.

To summarize, the increased gradients both in terms of variations in quantity and quality offer greater numbers of possibilities for improved utilization of the thermodynamic and chemical energies available to the system, which takes us beyond the role of inputs of solar radiation and thermal conditions. This can potentially be exploited for speciation to an extent that is not available to the more two-dimensional systems with only minor variations in altitude.

Statement: All living systems need a supply of energy, which may be available in different forms: solar radiation, chemical energy and heat. Organisms from different levels in the ecosystem network may exploit any of these energies at various levels of efficiency dependent on their trophic position. The amount and quality of available energies are in themselves important factors helping to shape and increase biodiversity.

2.3. The creative powers of disturbance

When compared to conditions in more stable environments, several authors have observed that more or less regular disturbances lead to an increase in biodiversity. This is known as the intermediate disturbance hypothesis (IDH). As with the gradients the disturbances must be neither too weak nor too strong but at a suitable intermediate level, hence the name of the hypothesis.

The concept poses an interesting parallel to the pulsing principle of H.T. Odum (Odum and Pinkerton, 1955), who considered pulsing (oscillations) to be a major reason for the increased exploitation and conversion of bio-geochemical resources in ecosystems. The principle is important in relation to eco-technology or ecological engineering, and pulsing is considered important in causing an elevated biodiversity of coastal lagoons and various types of wetland systems (Odum et al., 1995).

In general, the patterns in disturbances or pulsing are expressed as variations in natural physical patterns through time but may also sometimes be the result of anthropogenic factors affecting the ecosystem under consideration. Although the hypothesis has been criticized, e.g

Fox (2013) it is also strongly defended and has been found to be valid in several types of ecosystems (Connell, 1978; Jørgensen and Padiśak, 1996) including tropical forests, coral reefs and lakes. It has also been found to lead to the coexistence patterns and patchy dynamics that underlie the increased biodiversity (Johst and Huth, 2005; Shea et al., 2004, Roxburgh et al., 2004).

Disturbances have been found to stimulate speciation processes. This must be seen as a time-dependent factor induced by the variation in the gradients over time. Meanwhile, it seems clear that disturbances at a moderate level are necessary both for creation of structures and promotion of evolutionary processes. However, when too high they become too destructive for a properly functional system to be established. This will be described in the following.

Gravity, erosion and weathering also create physico-geological disturbances in mountain ecosystems. The disturbances are here assumed to vary with the gradient, from very strong in steep localities, weaker in less steep areas, reaching a lower limit approximating to flat lowland systems, for instance in plateau areas of mountain regions. The situation resembles that in the physical demonstration experiment of Benard Cells, where the significant gradients need to exceed a certain level to build up structure, which then breaks down when the gradient becomes too strong (Schneider and Kay, 1995).

In general, the patterns of disturbance or pulsing are the result of variations in natural physical patterns over time, but they can also result from anthropogenic factors affecting the ecosystem under consideration. As described above, the hypothesis has been found to be valid in various ecosystems, and the observations from mountainous regions only seem to stress the importance of disturbances in shaping the evolution and development of ecosystems in these areas. Disturbances are also found to lead to the formation of additional coexistence patterns and patchy dynamics that in turn underlie increased diversity. Hypothetically, stable patterns of oscillation in the gradients' spatiotemporal conditions will stimulate biodiversity even more.

Statement: Temporal variation patterns in gradients serve to stimulate biodiversity even more. The outcome will depend on a match between the time scale of the disturbances and the lifetime of the various organisms involved.

2.4. Niche construction and competitive exclusion

Solar radiation is often claimed to be sufficiently abundant and, in general, not limiting. This is to a certain extent true when one considers that the process of carbon uptake by autotrophs is generally constrained by the efficiency of photosynthesis. This means that the general, dominant determinator is to be found among the biogeochemical gradients where the limits are set by Liebig's law of the most valued oxidant (Liebig, 1842) – the compound with highest free energy - thereby linking back to the competitive exclusion principle (CEP). In other words, increased variation in quality gradients in particulars at the same time increases the number of elements which may be competed for and thus increases the role of CEP in determining evolutionary patterns.

Competitive exclusion serves to expand the variational pattern in a spatial dimension where coexistence is allowed but where the patterns are also arranged following a sequence whereby the existence of organisms follows the optimal exhaustion of available energies, from the highest free energies to the successively lower-value substrates.

The conditions discussed in sections 2.1-2.3 add to the complexity of the ecosystem by enhancing the importance of the interactions, both on temporal and spatial scales. This will in fact result in higher diversity – probably due to the introduction of more fine-grained mosaics than would otherwise exist. It also seems to favor the coexistence of organisms with shorter lifetimes, such as microorganisms (Lowery and Ursell, 2019). Mathematical studies show that coexistence at a steady state may be possible and that the CEP is apparently violated (Wang and Liu, 2020). This may in turn be explained by coexistence made possible by combining organisms living on differing temporal and spatial scales (Kalmykov and Kalmykov, 2013) in oscillating or even stochastically varying environments (Hening and Nguyen, 2020).

The Niche Construction principle, presented by Odling-Smee (2013) allows an organism to produce feedback that affects and shapes its own environment in accordance with particular needs. All of the processes discussed above increase the importance of Niche Construction (NC) activities and competitive exclusion (CE) processes, which in turn will contribute to additional upsurges in diversity. The increased set of gradients both in terms of quantity and quality served to increase and the strengthen the role and interaction between both NC and CE.

Statement: The available energies discussed in sections 2.1 - 2.3 allow for a spatial organization leading to an even greater increase in biodiversity. More intensive interaction between organisms and the prevailing environmental conditions serves to increase competition and create even more possibilities.

3. Inferences for further testing

The simplified analysis presented above leads to a series of questions and tentative conclusions. Verification of these would be an important step in further strengthening the basis of ecosystem theory. Here we list an unprioritized set of issues that deserve further attention.

- Is there an optimum slope and range of disturbances - analogous to Benard Cells? The slope is important in creating gradients and forming the thermodynamic regime, but the physical conditions may also be too extreme. So is there a lower limit – for instance determined by the angle of slope – below which there is no difference between mountain regions and lowlands and is there an upper limit above which physical conditions do not allow any increase in biodiversity? It is assumed that the plotting biodiversity as a function of angle would result in a bell-shaped curve which is probably skewed or truncated when the angle gets too high.
- Is there a systematic variation for the same altitudes with respect to compass orientation? How does this vary at the same latitude? Would it be possible to further discriminate the roles of insolation and thermal conditions respectively – for instance by considering the angle towards the sun relative to the altitude?
- Is there a fundamental difference between plants and animals, with increased disturbance arising because animals can move? The capacity of animals to flee and avoid unfavorable conditions is possibly reflected in the data but could also just lead to the conclusion that there is greater variation over time. Plants do not have this possibility to the same extent and will probably have a set of preferred conditions where their environment offers less disturbance relative to the environments of animals.
- Do steeper slopes favor species with shorter reaction times? In principle, this applies both to plants and animals. In accordance with allometric principles, for instance, we could expect that the greater the disturbance, the smaller the species size in both classes. Does disturbance favor a shift towards microorganisms?
- Does the exhaustion of chemical gradients at lower altitudes lead to a more important role for Niche Construction and Competitive Exclusion? Following a combination of the above statements, the occurrence of a localized maximum of biodiversity under intermediate regimes should also lead to more rapid and efficient exploitation – and consequent exhaustion - of the gradients. This could possibly lead to a subsequent fall in biodiversity, potentially falling even lower than in more stable regions in lowlands, where organisms have specialized in internal recycling.

Some of these questions have been partially answered while others merit increased attention and investigation, perhaps based on the extraordinary data set provided in the two papers by Rahbek et al. (2019a,b).

As final conclusion, we believe that this paper demonstrates the powers of modern ecosystem theory and shows that it can be helpful in understanding practical problems. In the case discussed here, the really new is the simultaneous use of only a few principles demonstrates such a high explanatory power in this context. It appears that even a very condensed version of the simple principles derived from ecosystem theory can simplify apparent problems to a degree where subtle speculations are no longer needed.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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