

A STRATEGY FOR MEASURING BIODIVERSITY

GONZALO HALFFTER* & MATTHIAS RÖS

Instituto de Ecología, A.C., Red de Ecoetología.

Carretera Antigua a Coatepec 351, El Haya, 91070, Xalapa, México

*Author for correspondence: <gonzalo.halffter@inecol.edu.mx>

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ABSTRACT. Several recent studies insist that multiplying the indices used to measure biological diversity (or rather, characteristics, related to it) makes no contribution to comparative studies, or to our understanding of the importance and characteristics of the changes caused by anthropic disturbance. In this study we propose a program that we call strategy, in order to measure biodiversity for the purpose of comparison. Although we bring together ideas that have been published (some, in very recent dates), the proposal as a whole, that is as a strategy, is new. We discuss in detail and substantiate using the literature, each of the aspects and recommendations of the strategy: 1) The use of the landscape as the spatio-temporal unit; 2) The application of the criterion of continuous landscapes, instead of the binary vision of the landscape divided into patches within a matrix; 3) The use of “windows” for sampling and analyzing the landscape, particularly when dealing with variegated landscapes, but also for other types of landscape; 4) The use of indicator groups as a means of measuring species richness and individual frequency, in spite of the limitations we discuss; 5) The expression of the results in terms of true diversities based on the concepts introduced by Lou Jost. We conclude with some suggestions (a sample) about the kind of questions for which the strategy is useful. The cases presented imply comparisons and reflect our interest in obtaining a real, testable measure of how human actions affect biological diversity under different ecological conditions.

Key words: biodiversity measures, alpha diversity, beta diversity, gamma diversity.

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RESUMEN. Con verdadera insistencia varios trabajos recientes señalan que la multiplicación de índices para medir la diversidad biológica (más bien características relacionadas con la misma), no contribuye a facilitar los estudios comparativos, ni la comprensión de la importancia y características de los cambios provocados por las perturbaciones antrópicas. En este trabajo proponemos un programa (al que hemos denominado estrategia) para medir con fines comparativos la biodiversidad. Aunque recogemos ideas ya publicadas (algunas de ellas en fechas muy recientes), la propuesta como conjunto, es decir como estrategia, es nueva. Discutimos en detalle y con suficiente apoyo bibliográfico, cada uno de los aspectos (o recomendaciones) de la estrategia: 1) Por qué utilizar como unidad de espacio-tiempo el paisaje; 2) Por qué seguimos el criterio de paisajes continuos, en lugar de la visión binaria del paisaje dividido en

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parches y matriz; 3) Por qué utilizar “ventanas” para el muestreo y análisis del paisaje especialmente cuando se trata de paisajes variegados pero también en otros tipos de paisaje; 4) Por qué usar grupos indicadores como medio para medir la riqueza de especies y la frecuencia de individuos, a pesar de las limitaciones que señalamos en el texto; 5) y por qué expresar los resultados en términos de diversidades verdaderas según los conceptos introducidos por Lou Jost. Terminamos nuestro artículo con algunas sugerencias (una muestra) de para tratar que cuestiones la estrategia puede ser útil. Los casos planteados implican comparaciones y corresponden a nuestra inquietud por aproximarnos a una medida real y comprobable de cómo las acciones humanas afectan a la diversidad en distintas condiciones ecológicas.

Palabras clave: medir biodiversidad, diversidad alfa, diversidad beta, diversidad gama.

INTRODUCTION

Currently, one of the fundamental themes in biology is that of biodiversity; that is, the measure and meaning of the different levels of organization in which life manifests – from genes to ecosystems. There is growing concern, and one that is widely justified if not always well evaluated, that human activities are causing the massive, irreparable loss of biodiversity. When we say not well evaluated we refer to those calculations and speculations that extrapolate the species losses that occur at the local level or in small areas to landscapes, regions and even for generalized conclusions. These extrapolations have been criticized both methodologically (Haila 2002; He & Hubbell 2011; Rahbek & Colwell 2011), and because of the lack of evidence in field studies (Wright 2005; Wright & Muller-Landau 2006a, b; Quintero & Halffter 2009). This situation leads us to want to measure with some degree of certainty the biodiversity that we have, and that which is being lost. However, even though different indices have been proposed over the last 40 years —variegated hundreds of them according to Magurran and McGill, (2011)— that measure different aspects of biodiversity, it is not possible to say that there is any general consensus about their use. In part, this is because biological diversity is a very broad topic, with different facets, within which very different questions can be posed. As Magurran and McGill (2011a) have indicated, measuring biodiversity is not as easy as it appears at first blush. “The reason for this difficulty is that biological diversity is a multifaceted concept that can be defined and documented in different ways.”

As in any other research proposal, a study of biodiversity must start with three premises: What question(s) do we want to answer or address? On what spatio-temporal scale do we wish to work, and which group of organisms and analytical method do we want to use? What are the ultimate aims of our study?

For the strategy that we have come up with, our initial premise is to study the richness of species and their individual abundance at the three levels of diversity: alpha, beta and gamma. Regarding how to do this, we offer the reader a discussion for each of our decisions: the spatio-temporal units selected, the indicator groups used, the concept of the continuous landscape, the use of windows as spatial sampling units and the expression of the results in terms of true diversity *sensu* Jost (Jost 2006; Jost

2007). The latter three aspects are rather recent, and we discuss these in greater depth. What can the results obtained be used for? Clearly, for comparative studies between different landscapes, or between landscapes with little modification and those with differing degrees of anthropization, for monitoring programs, the comparison of protected areas, the evaluation of anthropic changes, etc. We conclude by exploring possible uses.

We use the term strategy to express our proposal, which in part picks up on earlier proposals (Halffter 1998), is conceived of as a whole for which each of the elements meshes together and which meets a clear need in this field of research: "A strategy is required to address concrete issues and achieve defined objectives. In order for the strategy to be useful it must produce results that are comparable; results that allow us to draw general conclusions and to generate models." (Halffter 1998).

SPATIO-TEMPORAL UNIT OF STUDY

Both the methods used for measuring biodiversity and the results obtained change according to the spatio-temporal scale employed. The results obtained on one scale are not automatically transferable to another. This is why once we determine the concrete aspect of biodiversity that we wish to study; it is of prime importance to select the appropriate scale. For studies outlined in this strategy the most convenient scale, though not the only one, is the landscape.

In ecology, the term landscape refers to a unit of space with geographic limits and defined climate and geomorphological characteristics. Internally, a landscape may exhibit varying degrees of heterogeneity as it is comprised of different communities, *i.e.* different groups of interacting plants and animals. The landscape, just like its geographic, abiotic and biological components, has a history. It is precisely at the landscape level where the interactions between the history of the land and the biogeographic history of the biota can be most clearly appreciated. Similarly, it is at the landscape level where we are best able to see the effects of human actions (Noss 1983; Franklin 1993; Chown & McGeoch 2011). As explored in below, the concept of landscape that we propose is that of the continuous landscape, as introduced by McIntyre and Barrett (1992).

The landscape should not be considered a closed unit. Over short periods of time it may even receive species from other landscapes, contiguous or separate. However, landscapes are characterized by great homeostasis. They tend to conserve their species composition through mechanisms of exchange between communities, and the resilience of the species of the original communities that can adapt to new conditions (see, for example, Rös *et al.*, 2012).

LANDSCAPE STRUCTURE

Starting in the 1970s, and under the influence of the concepts of island biogeography of MacArthur and Wilson (1967), terrestrial landscapes with some degree of human modification were considered binary, with patches (*i.e.* different sized remnants of the natural communities) and a matrix (*i.e.* agroecosystems or secondary formations). The matrix was considered hostile to the species surviving in the patches—a vision clearly derived from island biogeography which cast the matrix as a hostile sea—although a few authors began to examine the capacity of the matrix to allow for the exchange of individuals between patches.

In the 1990s, it was understood that this clearly simplistic interpretation did not explain what was found in the vast majority of landscapes that had undergone some degree of modification (see the excellent synthesis of the evolution of these ideas regarding the landscape in Manning *et al.*, 2004). One very important reaction is the introduction of the concepts of the variegated landscape and that of the continuous landscape (McIntyre & Barrett 1992; Feinsinger 1994; Nepstad *et al.* 1996; McIntyre & Hobbs 1999; Manning *et al.* 2004; Rös *et al.* 2012). For the biota, all landscapes are continuous in space and time, and what varies between different landscapes is the proportion occupied by natural communities and by those resulting from alteration. Depending on these proportions, landscapes can be considered as intact, variegated, fragmented and relictual (McIntyre & Barrett 1992; McIntyre & Hobbs 1999; Manning *et al.* 2004; Rös *et al.* 2012). The categories form a continuum that reflects the magnitude of human intervention.

To analyze changes in species richness and frequency, the figure of the continuous landscape is doubtless superior to that of dividing the landscape into patches (original habitat) and its surrounding matrix (not original habitat). Our proposal gives greater importance to the spatial structure of the landscape, that is to its composition in communities and the spatial distribution (topology) of them, as one of the most important elements in the configuration of diversity, especially that of beta diversity. The nature of the matrix and the difficulties that may or may not impede the movement of different organisms or propagules between the fragments directly affects the connectivity of the landscape and species dispersal, and, as a consequence their richness and frequency (Ricketts 2001; Bender & Fahrig 2005; Numa *et al.* 2009 with an extensive bibliography).

On using the continuous landscape concept changes several things: 1) the idea of a uniform or binary physical and biological space is replaced by one of environmental heterogeneity; 2) the assumptions of communities in equilibrium, are replaced by ideas of spatial and temporal changes owing to processes that are not in equilibrium; 3) the search for regularities in the biological world is replaced by the acceptance of the spatial and temporal specificity of ecological processes (for a thorough discussion, see Haila, 2002). The heterogeneous and dynamic world generated by this new

vision of the landscape is much more suitable for explaining the processes that determine species richness and individual abundance, than more rigid and mechanistic schemes that are based mainly on competition and island biogeography.

HOW SHOULD THE LANDSCAPE BE STUDIED?

To return to the initial question of how the landscape should be studied, a historical analysis reveals that according to Whittaker (1960, 1972), for years the measures of alpha and beta diversity referred to types of vegetation or to comparisons between types of vegetation. However, with the growing fragmentation and modification of landscapes, reference to only vegetation types gives an incomplete idea of the heterogeneity and structure of the actual landscape. In most cases, mainly in tropical landscapes, there are a multitude of different types of land use and vegetation. To analyze this type of situation, we propose the landscape be sampled using a certain number of “windows” (Rös *et al.* 2012). These windows are equivalent spaces, randomly situated or placed to maximize representativeness, throughout the landscape (Fig. 1). They are sampling units that reflect the heterogeneity of the landscape, which is spatially unequal. In the study of the impact of humankind on landscapes it is of less importance to know what type of use is favorable or damaging for the communities of plants and animals than it is to know the overall impact of all types of use together and natural vegetation types on them. This set of effects is best studied using windows. The values of diversity obtained in each window are treated as alpha diversity. One comparison between windows will reveal the different degrees of heterogeneity in the



Figure 1. Sampling design using windows in a landscape where natural and human actions cause a mosaic of different vegetation types (in this case four vegetation types, increasing modification from dark to light colors). The windows (black frames) serve as representative samples of the landscape. This example shows a disturbance gradient between windows where the original vegetation (dark gray) persists in each window to different extents, just as the modified ones. The sampling design within windows depends on the group of organisms studied; there are options for random, proportional or equal sampling in each vegetation type.

vegetation or in use by humans and their effect on species turnover (beta diversity). If we cross the results of the analysis based on vegetation types with those obtained using the windows we will have a more complete view of the landscape's diversity and how it responds to environmental variables and human activities (Lindenmayer *et al.* 2002; Rös *et al.* 2012). Another important topic is that of the search for thresholds in terms of the area of favorable vs. not favorable types of vegetation (McIntyre *et al.* 2000), which are generally specific for each landscape (Lindenmayer & Hobbs 2007). Although it is difficult to extrapolate the results from one scale (windows) to the other (landscape), windows give a much better idea of possible thresholds in a landscape than any other type of sampling design. Windows also make it possible to repeat sampling and analysis in the same site, independently of whether the area covered by the different types of vegetation has changed. This estimate is especially recommended for landscapes with a variegated structure where, at the outset, it is difficult to differentiate between the types of vegetation (Rös *et al.* 2012). Finally, windows offer the possibility of comparing this heterogeneity among landscapes with, for example, differing degrees of human intervention. Windows have been used, without necessarily using the term and applications that we mention, by Lindenmayer *et al.* (2003), Arroyo-Rodríguez *et al.* (2009), Numa *et al.* (2009), Rös *et al.* (2012), and Arriaga *et al.* (2012), and other authors.

WHAT TYPE OF UNITS SHOULD BE USED TO MEASURE BIODIVERSITY?

It is evident that for the problems that we wish to deal with the type of biological unit that should be used is the species. Magurran and McGill (2011b) discuss the reasons that species richness and related measures are the “iconic” unit of measure for biological diversity.

There are two ways to estimate species diversity on the landscape level. The first is to try to take an inventory of all the species of extant organisms. The departure point for the second approach is accepting that it is impossible to do a complete inventory in the majority of landscapes, and select one or several indicators. An indicator group will give us a partial measure of richness and abundance; partial, because the data obtained can provide information about the group of organisms used, but cannot with validity be automatically extrapolated to other groups of organisms. If we use several groups of indicators at the same time, the information obtained from the extrapolation is more solid (Pineda *et al.* 2005; Barlow *et al.* 2007; Moreno *et al.* 2007). Some indicator groups are useful for some landscapes, but not others, so preliminary work is needed to determine which groups work well for the landscape to be studied. A given group of organisms should not be discarded just because it increases when there is disturbance instead of decreasing. The use of indicator groups has the advantage of making it possible to set concrete research objectives that are repeatable

under other conditions and in other locations, with reasonable times and costs. There are no reasons to not use them, as long as we are aware of their limitations.

Indicator groups (also called focal groups by some) have been used by Brown (1991), Halffter *et al.* (1992), Di Castri *et al.* (1992), Pearson and Cassola (1992), Kremen (1992), Halffter and Favila (1993), Prendergast *et al.* (1993), Kremen *et al.* (1993), and many other researchers since. Chown and Mc Geoch (2011) use the term “biodiversity indicator” with exactly the same meaning as we do, and distinguish it from “environmental indicator” and “ecological indicator”.

Halffter (1998) provides a series of conditions that a taxonomic group must meet in order to be useful as an indicator in the biodiversity studies that we propose: 1) The group must be rich in species and functionally important in the type of ecosystem being studied; 2) There must be sufficient information available on the natural history and taxonomy of the group; 3) The species of the group must be easy to catch by systems that can be standardized; 4) The collection of specimens during sampling must not put their conservation at risk; 5) Within a given ecosystem type, the indicator group should provide information not only about the intact or slightly disturbed communities, but also about communities that have different degrees of disturbance, including anthropic disturbances; 6) The spatio-temporal distribution of the group should be such that with a reasonable time investment in field work (weeks), there is sufficient data for the species accumulation curve to reach an asymptote.

HOW SHOULD LEVELS OF RICHNESS AND ABUNDANCE BE EXPRESSED?

As indicated by Maurer and McGill (2011) the plethora of indices complicates the essential task of comparison: “The most commonly used indices are used primarily because they have been used before, and not necessarily because they provide useful information”. If we express alpha, beta and gamma diversities only as the number of species (*i.e.* as species richness), there are no problems. But this only provides a partial view of the real situation since not all species are equal in their number of individuals or in their biomass. The measures that include abundance are called diversity indices (which is correct), but are not necessarily diversities. Many of them are entropies (Shannon, Renyi) or probabilities (Simpson, Gini-Simpson). Jost (2006) introduced the term “true diversity” to designate the sum of the different elements of an entity. For alpha and gamma, the different elements are species, and for beta diversity, communities.

BETA DIVERSITY

According to Ellison (2010), Jost’s (2007) proposal of using numbers equivalent in the partitioning of gamma into its components of alpha and beta is the most important

theoretical contribution in the measure of biodiversity since Whittaker introduced the concept of beta diversity in ecology. The proposal is presented in the partition theorem (Jost 2007; Jost *et al.* 2011) in which alpha and gamma are expressed in the effective number of species and beta in the effective number of communities. Gamma diversity is comprised of a multiplicative partition of alpha and beta. Alpha and beta are independent, the value of the first does not determine the value of the second; contrary to what occurs in many diversity indices and in additive partitioning (Baselga 2010). Beta diversity corresponds to the effective number of different communities on the landscape. It has a minimum value of one (no difference) and a maximum value equivalent to the number of sampling units, when these do not share any species.

In Figure 2 we give three different examples for beta diversity. A landscape where the sampling units do not share any species always has the highest beta diversity, and its value is equivalent to the number of sampling units in the three orders of beta with values of $q = 0$, $q = 1$ and $q = 2$ (Fig. 2 Landscape 1). The second example is of a landscape with two sampling units that share all of their species. The beta diversity of order $q = 0$ (species richness) indicates that there is only one effective community in the entire landscape. But species that are abundant in the first sampling unit are the

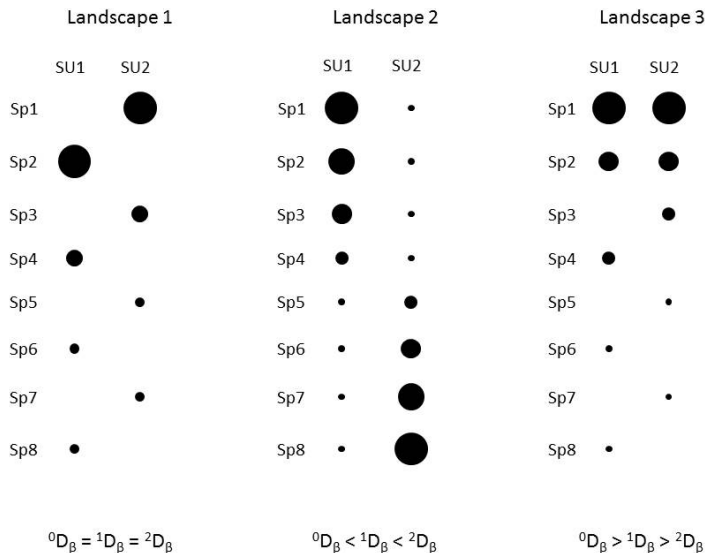


Figure 2. Beta diversity of $q=0, 1$ and 2 in three hypothetical landscapes. Relative species abundance values are shown as circles of different sizes for each sampling unit (SU). Large circles indicate higher abundances than small circles. The measure of abundance may be the number of individuals, biomass or something else.

most rare in the second sampling unit, and vice versa. Depending on the magnitude of the differences in abundances, beta diversities of the orders $q = 1$ and $q = 2$ are going to tend toward 2, indicating that the communities are very different (Fig. 2 Landscape 2). A contrasting case is that of a landscape where the two sampling units share very few species, but those that are shared are abundant (Figure 2 Landscape 3). In this case, the beta of richness ${}^0D_\beta$ is higher than ${}^1D_\beta$ and ${}^2D_\beta$. As such, we can calculate a profile of the beta diversities for any landscape. In contrast to alpha and gamma diversities, which decrease as q increases, and the abundance of its species is different, beta can decrease, increase or stay the same.

In the ecological literature there are many expressions for beta diversity and although all are measures of differentiation, they are also different concepts that should be clearly separated one from the other. True beta diversity is not the same as a measure of compositional similarity, and though one can be derived from the other, we must differentiate clearly between the concepts (Jost *et al.* 2011). Beta diversity tells us how many effective communities there are in a landscape while, for example, measure of compositional similarity measure how similar sampling units are to each other in terms of species composition and their relative abundances. Jost *et al.* (2011) demonstrate that concepts such as compositional similarity, overlap and others are mathematically related and can be derived from true beta diversity. This represents an important step toward a unified theory of species diversity.

WHAT QUESTIONS CAN THE STRATEGY BE USED TO ANSWER?

The strategy is intended to be used in those cases where we require comparable results from two or more sites or circumstances. Among these, as a tentative list, we offer the following:

- 1) When, in a region or for a landscape, we wish to compare the diversity and its structure (number and frequency of species, relative importance of alpha and beta diversity) in communities that are intact or almost intact and in communities with different degrees of anthropic disturbance. These studies require a measure of the effects of disturbance, though it is necessary to remember that this measure will always be dependent upon the indicator groups used, and that some of the groups of organisms may be more resistant than others to disturbances. We feel that it is of the utmost urgency to arrive at a solid vision of what is occurring with biodiversity and this can only be obtained through the interpretation of comparative analyses; for both species richness and individual abundance in landscapes that have been modified by humankind. Often, the area covered by this type of landscape is many times greater than the set of protected areas or of areas that might be protected, and so the survival of the majority of the species depends on their persistence in these landscapes (see Halffter, 2005).

2) The strategy is useful when we wish to compare two landscapes or two types of communities, as long as the environmental variables are broadly similar. For example, it would be useful for comparing tropical rainforests on two different continents, but not a rainforest with a desert; simply because it is very difficult to find an indicator group that works well for both types of ecosystems.

3) To see the effect of the topology of the landscape on biodiversity. For example, to compare landscapes with a similar biogeographical history and similar environmental conditions, but where one is intact, another has a variegated structure and a third is fragmented.

4) A line of research derived from the previous one would be the comparison of what happens when there are fragments of original vegetation that differ in size and shape. For the different fragments, this type of analysis could measure both the conservation of the original biota, as well as the degree of penetration of species from other communities.

5) To evaluate the conservation capacity of different protected areas within a given region.

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