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Ecosystemology: A new approach toward a taxonomy of ecosystems

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ABSTRACT

Over the last several years, the IUCN Red List approach for assessing the risk of extinction faced by species has been adapted into a Red List of Ecosystems methodology. This endeavor faces several important challenges, including how to define the types of ecosystems to which the Red List criteria are applied, and how to manage information on the geographic distribution of ecosystems in an open, transparent, and standardized manner linking mapping, typology, and field studies. We propose a fundamentally novel approach that differs from currently available ecosystem typologies in three important aspects by (1) offering a new way of conceptualizing types of ecosystems, (2) providing an explicit method for communicating the conceptualized ecosystems and how they are circumscribed, and (3) developing technical tools for managing the resulting conceptual model. Firstly, ecosystem types are defined by studying biogeoclimatic gradients using an approach that is both modular (in which combinations of ecological factors are studied at a given scale) and hierarchical (involving relative spatial and temporal scales in which local/site gradients are dependent on bioclimatic/regional gradients). This avoids the problem of classes that are not mutually exclusive and enables the classification of all types of ecosystems, including for example marshes on rocky outcrops in superhumid tropical montane areas. Secondly, the names of ecosystem species are linked to a nomenclatural type defined by a 'type site' or 'biotype', adopting a principle that makes clear a given author's notion of an ecosystem type even if the accompanying name and description are partial or imperfect, or when the ecosystem type is delimited too broadly according to the interpretation of another author. Ecosystem names are structured as a descriptive diagnosis based on a standardized set of characters and character states. This typological approach for facilitating the naming and comparison of ecosystem circumscriptions is thus truly taxonomic in nature. Thirdly, in order to facilitate the use and application of the conceptual approach presented here, we translate it into a practical tool by developing a smartphone-based system to collect data for observing and describing virtual ecosystem specimens in the field, along with the "Bio" database, which manages ecosystem data and also enables tracking synonymies using an open system that entails assigning *determinavits* to biotypes.

1. Introduction

The effort to conserve biodiversity involves a wide range of approaches, including several that incorporate the identification of threatened species according to the criteria established by the IUCN Red List (IUCN, 2017), recently extended to the notion of threatened ecosystems (Bland et al., 2015; Keith et al., 2013). Several international standards extensively used in both the public and private sectors, such as the HCV approach (High Conservation Values; Brown et al., 2013) developed by the Forest Stewardship Council (FSC), the Critical Habitat approach developed by the International Finance Corporation (IFC, 2012), and the Key Biodiversity Areas approach (KBA Standards and Appeals Committee, 2019), are partly framed in terms of ecosystems or habitats, but none of them propose a clear definition of these notions,

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whose interpretation is thus left to the discretion of users (KBA) or private companies (Critical Habitat), or must be developed at a national scale (HCV).

Although the overall approach used by these standards seems to be appropriate, raw data originating from basic field observations remain largely dominated by species occurrences, especially as documented by collected specimens, which generally lack details on the populations at each of the recorded sites and on the identity and characteristics of the ecosystems in which they were observed. Although several typologies have been proposed for ecosystems (such as Faber-Langendoen et al., 2014; Sayre et al., 2014), none of them has been accepted as an international standard. However, even if the global scientific community could agree on a single standard typology, "taxonomy" (including one of ecosystem types) is not just a list of accepted entities that is improved progressively with the publication of each new version. Taxonomy is also (from a cognitive and general point of view; Goldstone et al., 2018; Keller et al., 2003: p.106; Pavlinov, 2015; Rips et al., 2012), a 'language method' that enables naming and communicating in an explicit manner about conceptualized entities, which are themselves dynamic conceptual hypotheses. Today, after more than a century of effort, we still lack a taxonomy of ecosystems and, worst still, the lack of awareness of this gap remains unrecognized.

This situation is compounded by the absence of a database system capable of managing ecosystem taxonomic data as well as associated raw occurrence data, even though numerous biodiversity databases have been developed over the last four decades. These two issues may be related: the lack of a taxonomy of ecosystems may result, at least in part, from the difficulty of having to solve complex conceptual and technical issues simultaneously, which depend on one another. Indeed, to understand the notion of ecosystem fully and in depth, it is necessary to have a clear understanding of a large number of more elementary notions that contribute to defining the notion of ecosystem. It takes years for a botanist to assimilate the technical concepts and terminology required to develop a robust notion of species (i.e. to 'visualize' a species mentally), which largely involves basic notions about things we can see and touch (e.g. simple, opposite leaves, etc.). The same holds true for ecosystems. In fact, to understand things, the human brain needs to see or visualize a concept (Benedek and Lajos, 2014), which gradually becomes clearer over time, to name it (in order to store the concept), and finally to visualize its connections with other related concepts (so as to remember better where it is stored in the brain and to understand it more thoroughly; Dörfler et al., 2009; Dörfler, 2010). Thus, the dissection of the notion of ecosystem followed by its virtual representation in the form of an explicit database system is a key element for the full assimilation of the elementary concepts required for an improved understanding of ecosystems per se, through a series of recursive loops (Morin, 2006). The cognitive process by which we recognize discrete concepts within a continuum of perceptions, and then link those concepts to conceptually account for that continuum, is essential for a human understanding of nature. This bioecological formalism is not the language of nature (i.e. it is not written in nature). Rather, it is a human formalism designed to translate nature's language into something that we can learn, understand, and talk about.

In this paper, we present the results of an ontological study on the notion of ecosystem and on the conceptualization of a taxonomic method for defining and characterizing ecosystems in order to facilitate their study and improve their conservation. The conceptual system we develop is then presented in the form of a database, designed to meet the basic needs of naturalists making observations in the field (observations being the basis for any conceptualization). The approach and underlying logic used to develop the ideas presented below can be understood best by refraining from any pre-conceived notions or currently accepted paradigms. The thinking we propose is not built on any particular traditional discipline (taxonomy, phytosociology, biogeography, landscape ecology, climatology, geomorphology, bioinformatics, etc.), but rather draws on concepts, methods, and tools provided by these disciplines, each of which concerns the same reality seen from a different perspective. Refining each of these points of view (specialization) is important but can take a lifetime and will inevitably compete with the development of a more general, multidimensional vision. We therefore borrow from each discipline, mobilizing the aspects we have found to be useful for our own interpretation of reality, paying particular attention to resonances between them. Our approach is thus intended to be trans-disciplinary and naturalistic.

2. Principles of ecosystem conceptualization (typology)

In the IUCN guidelines for the Red Listing of Ecosystems (RLE: Bland et al., 2015; Keith et al., 2013; Rodriguez et al., 2015), the matter of ecosystem typology is left to user opinion (see also the critique by Boitani et al., 2015), although they recommended the typology proposed by the IUCN (2016) and promised to develop (in a future version of the guidelines) a consolidated typology based on a physio-eco-floristic approach directly derived from the Yangambi classification (Aubréville, 1965; Keay, 1959; Trochain, 1957), UNESCO (Mueller-Dombois, 1984; UNESCO, 1973), TNC (Grossman et al., 1998), and especially from NatureServe (Faber-Langendoen et al., 2016, 2014), all of which are fundamental to the subject of ecosystem typology. These works summarize half a century of improvements and adjustments, and they provide a detailed description of the various 'ecosystem characters' that have been recognized, which serve as a language base. Nevertheless, 'vegetation' and 'ecosystem' are not synonymous, as explained below (see Section 3). All complex systems (living or not) develop and evolve through time and can represent spatial scales from small to large. It is therefore essential to further improve the integration of primary and secondary dynamics of vegetation (which we assimilate to the notions of evolution and development), as well as levels of spatial scale (and we detail below how we propose to do so). Although the new ecosystem typology promised by the IUCN has now been partly published (Keith et al., 2020; Keith et al., 2021; Murray et al., 2020), it does not address the main issues that we discuss below and it does not represent a profound shift from the earlier studies mentioned above. A detailed discussion of those typologies and their issues is provided in Senterre et al. (2020, pp. 103–124).

The approach we develop below aims to integrate studies derived from the Yangambi classification into a modular-hierarchical system (such as in Di Gregorio, 2005; Sayre et al. 2013, 2014; see also Meunier et al., 2010) based on relative scales of space and time (Senterre and Wagner, 2014). It is systemic rather than systematic, i.e. it aims to represent natural systems rather than an organized classification system. We attempt to eliminate descriptions focused on external appearances (a bureaucracy of appearances: Klein, 2018) and instead focus on the most intimate nature of ecosystems as they are, i.e. at their own scales of space and time (rather than ours). This approach was first defined and applied by Senterre and Wagner (2014) for the Seychelles, and a simplified explanation was proposed by Senterre (2014) and Senterre et al. (2017) for Liberia and the Republic of Congo, respectively. More recently, the method was applied to the evaluation of an Ecosystem Red List for Mont Nimba (in Guinea) by Senterre et al. (2019a), and then extended to most of West Africa (Senterre et al., 2020), where the complete taxonomic formalism proposed here is implemented.

2.1. Relative spatial scales

The regional ecosystem scale adopted here is based on the life zone concept (Holdridge, 1967). Life zones are defined by climatic seasonality, wetness, and temperature, and are thus linked to latitude, continentality, and altitude (Bailey, 2009), as well as to more localized climatic effects such as those of mass elevation (MEE: Van Steenis, 1961; Baiping and Yonghui, 2016) and Foehn (Elvidge and Renfrew, 2016). Examples include White's Hygrophilous coastal evergreen rain forest (White, 1983: 76, 1986) and what he referred to as Drier peripheral semi-evergreen rain forest, and Montane rain forest. Moreover, the montane belt, for example, itself varies according to latitude and continentality (Rivas-Martínez et al., 2011, p. 4; Schnell, 1952, 1979, p. 175; Senterre et al., 2019a; Stadel, 1991) and therefore cannot be recognized as a single life zone. Rather, it is preferable to integrate in a more systematic way the regional ecosystem factors of latitude and continentality on the one hand, and altitudinal belts on the other. Thus, in the tropics, doing so makes it conceptually possible to recognize superhumid montane zones as well as perhumid and humid montane zones (corresponding to the evergreen to semi-deciduous forest zones of the lowland). Regional ecosystems therefore comprise all the existing combinations of the gradients mentioned above, where each continuous gradient is simplified (rendered discrete) into classes such as those defined in the systems derived from Yangambi, i.e. bio-ecologically meaningful classes (modeling as best as possible the observed correlations between biotic and abiotic components).

The ecosystem stand scale (based on the concept of "stand": Flahault and Schröter, 1910; Whittaker, 1962) is the most widely used in vegetation studies (often more or less obscurely mixed with entities of regional scale). It is defined by 'local' factors (at a human scale, i.e. in a given site that we are capable of observing directly) such as topographic-edaphic wetness or other limiting factors (hydromorphy, salinity, etc.) and 'influencing' factors at the same scale (e.g. lithology: Kruckeberg, 2002; Dürr et al., 2005; Sayre et al., 2013).

Both the regional and the stand ecosystem scales can be more or less spatially stretched or contracted. For example, the continentality gradient (Fig. 1b) and a ridge-valley gradient (Fig. 1d) are both stretched at their own scale compared to the contraction ("telescoping", see also Senterre et al., 2009) observed in association with e.g. the Foehn effect (Fig. 1a) or on an inselberg's saxicolous fringe (Fig. 1c) (at regional and stand scale, respectively). Therefore, the concept of a 'relative scale' of space clearly provides a more general model for the conceptualization of ecosystems. By contrast, the consideration of a wet ravine as being of a distinct spatial scale (lower scale) compared to the mesic vegetation surrounding it (e.g. Bailey, 2009: "microecosystem"; see also Senterre and Wagner, 2014: 9) is not useful because, even though a ravine may occupy a much smaller absolute scale of space (a few meters wide vs. hundreds or thousands of meters for the surrounding mesic vegetation), both the ravine and its mesic surroundings represent the same relative scale of space (the stand scale).

2.2. Relative time scales

Secondary series of vegetation (which develop after disturbance), from pioneer to mature, can represent very different absolute time scales from one type of ecosystem to another (such as in a forest ecosystem vs. a meadow). Therefore, and by analogy with the discussion above on spatial scale, the use of 'relative' time scales provides a more general model for the definition and study of types of ecosystems. We define two relative time scales, developmental and evolutionary, these being the two components of the dynamics of any complex system (see e.g. Salthe, 1985, 2005, 2010). The ecosystem developmental scale corresponds to secondary series (pioneer to mature, followed by senescent), whereas the ecosystem evolutionary scale corresponds to primary series (progressive climax due to climate changes, erosion/stabilization of soils, swamp aggradation, etc.). In practice, this conceptual approach simply means that "secondary forests", for example, are regarded as a developmental stage and not as a kind of ecosystem per se. By contrast, disturbances responsible for climax shifts (disclimax) or climax retrogressions and progressions (Clements, 1936; Peltzer et al., 2010; Senterre and Wagner, 2014) contribute to the definition of different types of ecosystems (e.g. pyrophilic disclimax savannas: forest formations converted into 'stable' savannas by the persistence of fires, whether of natural and/or of human origin; see detailed explanation in Senterre et al., 2019a: III.1.2).

2.3. The modular-hierarchical approach

Once the concept of relative spatial scales, as described above (for the regional and stand scales), has been understood along with the notion that secondary series involve variations of developmental stages (not distinct types of ecosystems), the confusion between 'levels of

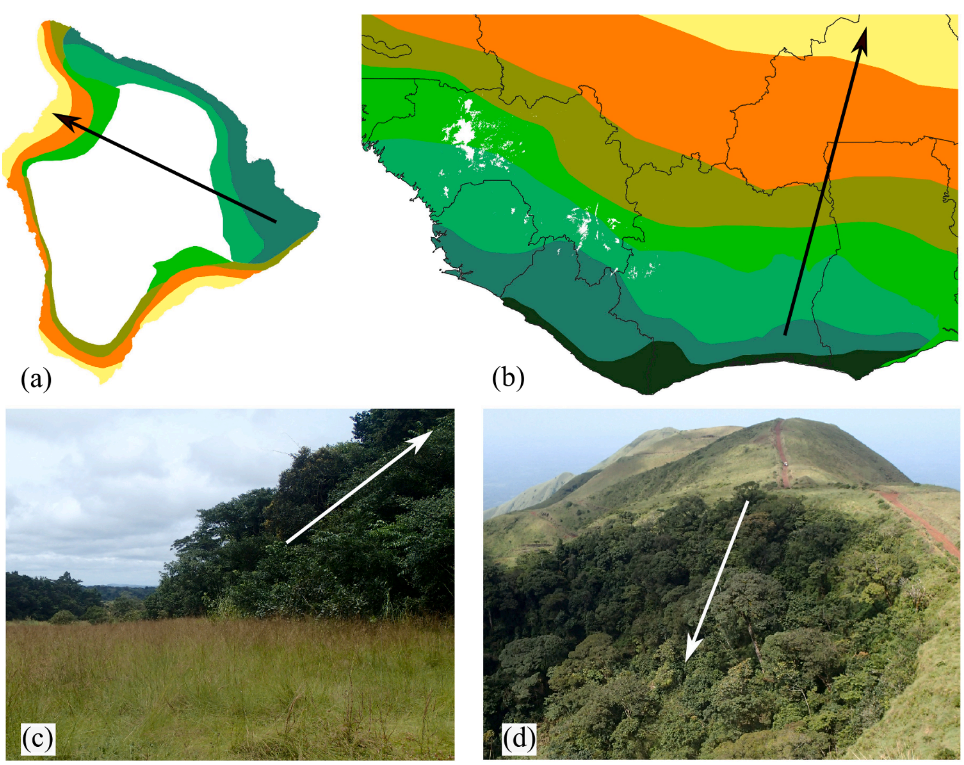


Fig. 1. Contraction and stretching of gradients. At the regional scale, a transition is observed from a lowland mesic vegetation type of 'perhumid rainforest' (green, windward) to lowland mesic herb savannas (yellow, leeward) within (a) ca. 100 km in Hawai`i (Mueller-Dombois, 1984) vs. (b) ca. 1000 km in West Africa (Senterre et al., 2019a). At the stand scale, a transition is observed from a 'dwarf forest' to a 'high forest' within just a few meters (from the saxicolous fringe of an ironstone outcrop, or bowal, to the nearby mesic forest) vs. several tens of meters (from an over-drained steep slope of a ridge to the bottom of a ravine) (photos from Mont Nimba, Guinea).

organization' and 'levels of classification' (Rowe, 1961; Senterre and Wagner, 2014) becomes clearer. Pragmatically, this implies that the use of vegetation physiognomy (both current and polyclimax) as a higher level of ecosystem typology must be discarded, and also that scale levels should be applied separately, thus creating a typology of regional ecosystems on the one hand, and of stand scale ecosystems on the other. The combination of these two typologies then provides definitions for stand scale ecosystem types that integrate their regional context. At each level (regional and stand scale), each ecosystem type is conceptualized based on the combination of ecosystem characters defined at its particular scale (Annex 1), without any hierarchical level (i.e. modular component).

Furthermore, the types of ecosystems recognized above can be defined as 'ecosystem genera' (or 'generic ecosystems', or 'eco-genera'), i.e. entities that are ecologically explicit and that can be generalized independently of (bio)geography, and therefore independently of the country and biogeographic hypothesis. It should be noted that the concept of ecosystem genus, as defined here, explicitly excludes any biotic connotations, such as species or associations of species. Within an ecosystem genus, one can then define 'ecosystem species' (or 'specific ecosystems', or 'eco-species') by considering only biotic characters. The consideration of biotic characters at the lower levels of a typology is an aspect shared with all those derived from the Yangambi classification, with one difference: in our case, intergenerational biotic variability (from one generation to another or from one individual stand to another, i.e. not related to evolutionary discontinuities or centers of endemism) is not taken into consideration for the distinction of different types of specific ecosystems (see Senterre and Wagner, 2014: 18-19) but rather for the description of individual stands (Fig. 2). Our concept of a specific ecosystem or ecosystem species therefore integrates aspects related to secondary dynamics (or "sigmetum" in landscape phytosociology: Bioret et al., 2019; Choisnet et al., 2019; Géhu, 2006; Rivas-Martinez, 2005) and inter-individual stochastic variability ("facies", "variants", "sub-associations": Duvigneaud, 1946; Katembo et al., 2020), and it is ecologically more precise than Sayre's "Ecological Land Units" (ELU, Sayre et al., 2013, 2014). Moreover, in all typologies derived from the Yangambi classification, biotic characters are not restricted to the ultimate level of the hierarchy but rather are spread over 2 to 5 levels, mixed with abiotic characters (Faber-Langendoen et al., 2014, p. 544; Fig. 2), which is symptomatic of an influence from classical phytosociology (Alliances and Classes) and does not provide a suitable integration of biotic and abiotic characters because of confusion between levels of classification (resemblance) and of organization (interdependency).

In practice, the recognition of specific ecosystems can thus be accomplished by combining three elements (Fig. 2): (1) the type of life zone, (2) the type of stand, and (3) the biogeographic entity, as mapped by Olson and Dinerstein (2002) or White (1979), or as identified with more recent/detailed data on species endemism for a given generic ecosystem (e.g. among freshwater ecosystems: Abell et al., 2008; Dodds et al., 2019, 2015; Lebrun and Gilbert, 1954, pp. 44–45; Saenger et al., 2019; Senterre, 2005, pp. 67, 287; Troupin, 1966). This modular-hierarchical approach, unlike those derived from the Yangambi classification, makes it possible to classify any type of environment (such as lowland marshes, montane marshes of superhumid climate, or montane marshes on ironstone in perhumid climate: Box 1) because the hierarchical component is based on mutually exclusive entities, defined by relative spatial scales. Furthermore, the levels of hierarchy are conceived based on natural concepts, each representing a biological reality, and not according to an organization that is intended to be practical but which will inevitably depend on a given opinion of the priority of some ecosystem characters relative to others. The notion of trying to identify a useful or meaningful hierarchy of stand scale gradients (starting with coastal, then hydromorphy, soils, and finally topography, etc.) must be abandoned. There are no linear solutions (i.e. a hierarchy of classes) to a complex, multi-dimensional problem (i.e. the multiple combinations of stand scale factors that can have more or less influence, depending on the context). Historical attempts to develop a typology (i.e. the numerous variations of the Yangambi classification) represent a response to the need for some kind of storage system and for identification tools (keys), rather than the conceptualization of natural entities (systems).

2.4. *Field observation methods*

In the field, the conceptual approach described above involves the exploration of the principal environmental gradients and their individual study by observation at different levels of intensity for a particular gradient, all other gradients being kept constant as much as possible (see Haeussler, 2011). The same principle is then applied for each of the main gradients within a study area, e.g. regional climate, soil depth (saxicolous), or hydromorphy. For the study of temporal gradients (dynamics), the principle of space-for-time substitution is used (Pickett, 1989; Sternberg et al., 2011), which involves identifying ecologically homologous stands differing only in their dynamics (development stage, rejuvenation, history of disturbances, etc.). This principle was used by Schnell (1952: 358), for example, when he described the recent bowalization of some previously forested stands in the foothills of Mont Nimba. This observation method is very similar to that developed in geosymphytosociology (Choisnet et al., 2019), except for its more precise description of abiotic characters and an interpretation of biotic data according to combinations of entangled ecological groups rather than to discrete biotic entities (Duvigneaud, 1946; Senterre et al., 2020, p.11).

2.5. *Conceptualization vs. quantitative description of spatio-temporal processes*

Conceptualization is a fundamental element of comprehension and communication (Benedek and Lajos, 2014). Without it we would not have been able to write these sentences, and dialogue would merely be a continuum of meaningless sounds. Yet dialogue contains a continuum of non-verbal expressions that are essential for a clear understanding of the meaning of words. The rendering of our environment into discrete concepts, while artificial, nevertheless works because it is complemented by an attempt to understand the context of those concepts, i.e. their edges and their connections with other concepts. This is what enables understanding continua like those typically found in complex ecological systems. Seen this way, recent developments in landscape ecology (e.g. Cushman et al., 2010; MacFadyen et al., 2016), which examine quantitative ecosystem modeling based on continuous gradients that are not subdivided into discrete classes, are not fundamentally incompatible with the conceptualization proposed here (see Cushman et al., 2010, p.94) but rather are complementary to them. The quantitative gradient approach of landscape ecology is to our ecosystem approach what phylogeny and functional ecology are to species taxonomy. The first approach provides understanding and a way to refer to elements of nature, and the second one quantitatively deepens our understanding of the spatio-temporal patterns and processes of those elements (including ecosystem quality and environmental heterogeneity), ultimately leading to conceptual adjustments and improvements of the elements themselves. Neither of these approaches is dominant or more general than the other; each deals with a fundamentally different aspect of complex cognitive understanding.

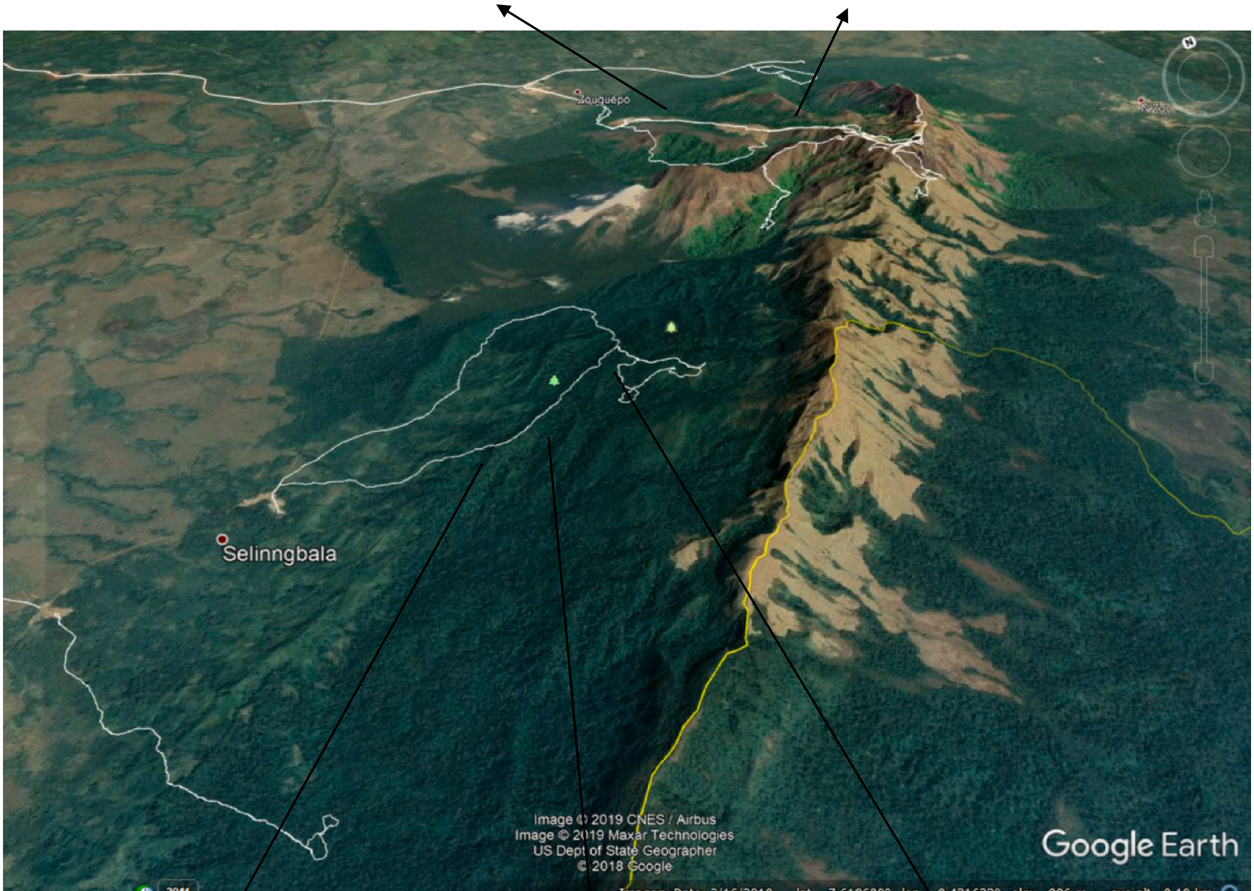
For landscape ecologists, it is also important to note that the concept of "habitat" in Clementsian ecology (and more generally in botany) is not "organism specific" (Cushman et al., 2010, p. 93), i.e. habitats are not defined as being related to any particular species (a notion that instead corresponds to species autecology or species habitat-use). Although many authors have drawn attention to common misconceptions regarding key terms such as habitat (as well as biotope, ecotope, niche, etc.; see Senterre and Wagner, 2014), the misuse of these words is too deeply rooted to be eliminated, and the comparatively young field of landscape ecology has in some cases overlooked its own roots, for

Box 1

Example of ecosystem species recognized and named using the proposed approach: the Mounts Nimba (Guinea), a site with numerous life zones. A few synonyms are included, mostly from the detailed work of Schnell (1952), in which species names used to designate types of ecosystems emphasize the idea that plant communities are better seen as entanglements of ecological groups rather than as discrete entities. To understand the pragmatic implications of the method proposed in this paper, we recommend that the reader consult our exhaustive ecosystemology case study (Senterre et al., 2019a, 2020), which includes comparisons and synonymies with various typology systems.

West African Mesic forest of the Submontane tropical humid moist seasonal semi-deciduous rainforest zone (Senterre et al., 2019a: 47).
= *Forêts mésophiles submontagnardes à Parinari excelsa et Carapa procera* (Schnell, 1952: 371).

West African Mesic forest of the Lowland tropical humid moist seasonal semi-deciduous rainforest zone (Senterre et al., 2019a: 43).
= *Forêt mésophile de l'étage inférieur à Chrysophyllum perpulchrum et Triplochiton scleroxylon* (Schnell, 1952: 371).



West African mesic forest of the Lowland tropical perhumid moist evergreen rainforest zone (Senterre et al., 2019a: 35).
= *Forêt ombrophile de l'étage inférieur à Tarrietia utilis et Lophira procera* (Schnell, 1952: 365).
= *Guinea Moist evergreen forest* (Hawthorne et al., 2010: 10, 31, 39).

West African Mesic forest of the Submontane tropical perhumid moist evergreen rainforest zone (Senterre et al., 2019a: 38).
= *Forêt ombrophile à Lophira procera et Parinari excelsa* (Schnell, 1952: 369).

West African Ravine forest of the Lowland tropical humid moist seasonal semi-deciduous rainforest zone (Senterre et al., 2019a: 44).
= *Forêt mésophile vallicole à Chidlovia sanguinea* (Schnell, 1952: 371).

example by introducing new words, such as patch, for old concepts, such as stand. It is just this kind of misconception that led Cushman et al. (2010, p.94) to regard rendering gradient ecology into discrete classes as being inconsistent with basic ecological theories. In the approach proposed here, ecosystems are defined based on our knowledge of life and its relations to abiotic factors, even in situations where life no longer exists or has not yet developed (as exemplified by the Jezero crater and the Mars 2020 Perseverance Rover project). This is what we mean by a non-species-centric conception of ecosystems. The biotic components of those ecosystems are not ignored or downgraded either (see Fig. 2),

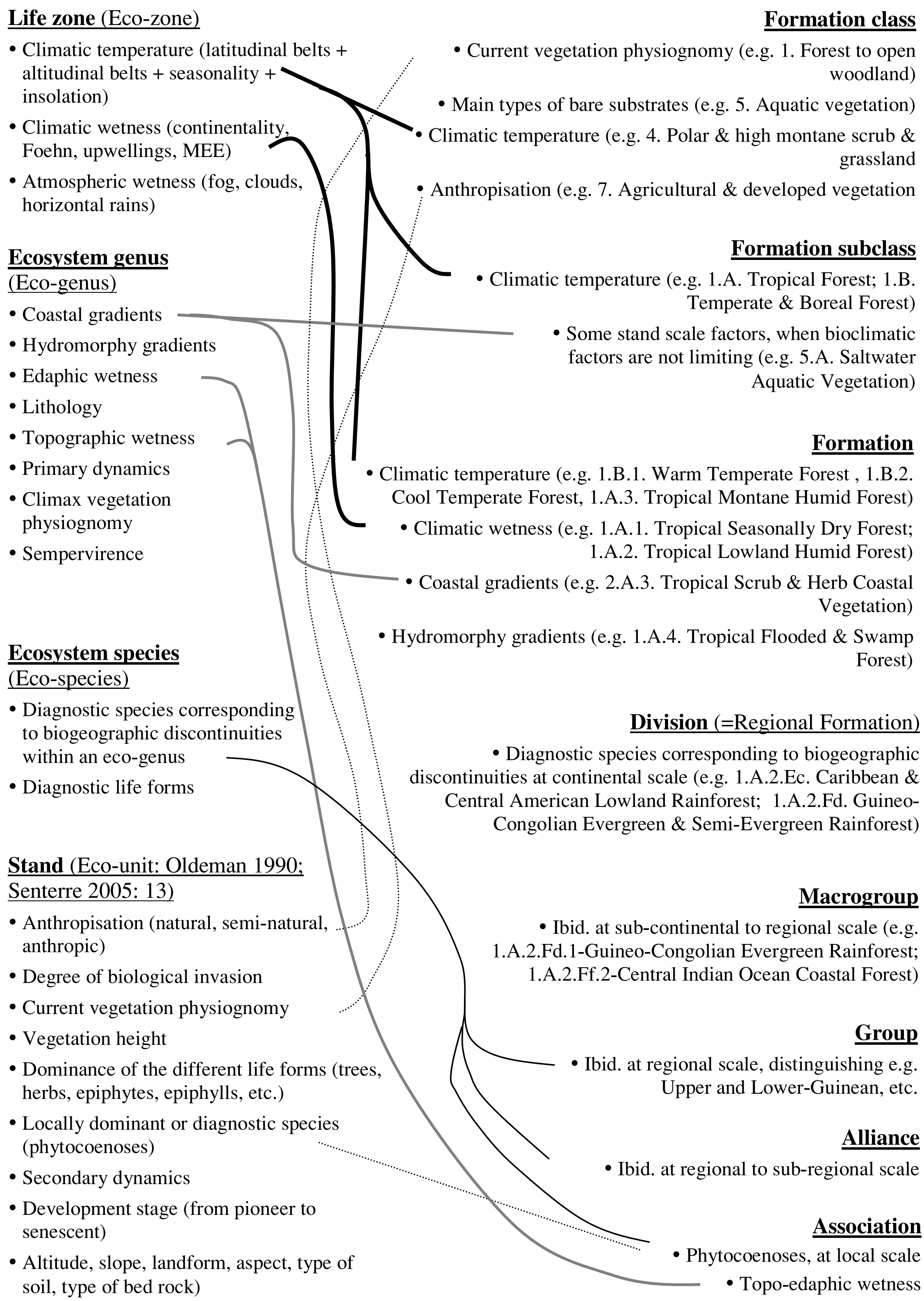


Fig. 2. Representation (on the left) of the hierarchical levels and their corresponding combinations of characters (see details in Annex 1) as defined in the current approach. For comparison, the hierarchical levels and their corresponding characters according to the Yangambi-UNESCO classification (as adapted by Faber-Langendoen et al., 2016, 2014, Oldeman, 1990) are summarized (on the right) and correspondences with our approach are indicated with lines.

simply reducing ecosystems to environmental heterogeneity, but rather are reorganized and integrated into the concepts of ecosystem species and individual stands. Seen this way, rendering continuous gradients into discrete classes is fully consistent with the conceptualization of non-species-centric ecosystem types or habitat-types. Moreover, the study of species habitat-uses (habitats, in the sense used by landscape ecologists) can be studied separately, preferably using quantitative gradient approaches, or even an approach in which they are rendered discrete, such as in the concept of ecological groups (and ecological substitutions).

3. Principles of a taxonomic nomenclature of ecosystems

In order to study and properly understand a concept, it must be named (Goldstone et al., 2018; Rips et al., 2012). Furthermore, for a name to emerge, the concept it represents must also be sufficiently understood. This is in reality a complex process, often long and convoluted, involving minor revolutions (Kuhn, 1996) followed by reversals. The emergence of the word "ecosystem" (Tansley, 1935) was undeniably such a revolution. It materialized into both a simple word and a more comprehensive concept that was already represented in the notions of habitat (see discussion and definitions in Senterre and Wagner, 2014) and climax (Clements, 1936, 1904). But the recognition of this concept, which extended well beyond living things[1], did not bring about substantial change in traditional species-centric methodologies. Even now, ecosystems are conceived of and named predominantly based on the species that characterize them. It is therefore necessary to propose a term that expresses the need to study ecosystems using a systems approach, one that better reflects this need than "systems ecology". It was this need for a highly trans-disciplinary systems approach (in many ways similar to the one we propose here) that led Arnold Schultz to introduce the word "ecosystemology" in the 1960s (Schultz, 2009). This term was also coined (apparently independently and with the same intention) by Rowe (1996). Although ecosystemology has not received the level of attention it deserves, at least not beyond the USA, it is unquestionably worthy of support and our aim is to strengthen it by adding a nomenclatural component.

The first half of the 20th century was clearly the golden age of ecosystemology, marked by an active search for conceptual and nomenclatural methods through the study of analogies with species taxonomy. The first nomenclatural system created was that of Braun-Blanquet (Braun-Blanquet, 1932; van der Maarel, 1975), in which ecosystems were confused with plant communities and were named with a Latinized binomial or polynomial based on the species considered to be characteristic (e.g. "*Loudetietum arundinaceae*" for an 'ecosystem' characterized by *Loudetia arundinacea*). An ecosystem is, however, much more than just the 'vegetation' (i.e. its physiognomy, whether a forest, savanna, etc.) that can be observed at a given stage of development, and the plant communities that apparently characterize a type of ecosystem at a given moment, which change through time. A phytosociological nomenclature is therefore not adequate for naming ecosystems, and indeed it has been strongly rejected, and as a consequence, the search for an explicit language method (i.e. an essential element toward a taxonomy of ecosystems) was abandoned in ecosystemology. Phytosociological nomenclature was thus "the straw that broke the camel's back", which was already overloaded by attempts to develop the concept of ecosystem using phrases and expressions that carried an excessive organicism or deterministic connotation (Bergandi, 1999; Eliot, 2011, 2007; Kirchhoff, 2020). An ecosystem, after all, is not truly an "organism" (and note that an organism itself is not always truly an organism: Koskella et al., 2017).

Nevertheless, one way or another, continuum or not, we still need names for ecosystems and most importantly we need a scientific nomenclature that is explicit, open, and dynamic, just like the taxonomic nomenclature of species. Braun-Blanquet was therefore on the right track when he imagined a system based on the principle of the nomenclatural type. But such a type could not be restricted to a "type relevé" (a reference or 'type' inventory of species, mostly plants, sometimes accompanied by an ecological description). Indeed, the type of an ecosystem must represent the concept to which it refers, i.e. a system (whether living or not). Monod (1968) shared this view and named such a type, applied to ecosystemology, as a "biotype".

Unfortunately, these ideas were proposed before their time, prior to the advent of bioinformatics and the internet, which are indispensable for materializing and managing a taxonomy of ecosystems. Starting in the 1970s, the concept of ecosystem became much more widely used, so much so that its complex nature (and especially the unanswered fundamental questions surrounding it) have become largely overlooked and taken for granted. To our knowledge, Monod (1968) was the last person to plead for a taxonomy of ecosystems and the first to consider this from a systems approach. We concur with his basic principles of such an ecosystem taxonomy, which we translate into the concepts developed below.

Specifically, a taxonomy of ecosystems should be based on the following principles:

1. A particular kind of ecosystem should be named using a complete 'biogeoclimatic diagnosis', including regional and stand scale characters/gradients (e.g. "West African Mesic forest of the Montane tropical humid moist seasonal semi-deciduous rainforest zone": Senterre et al., 2019a, 2020; Box 2).
2. A diagnosis should be built on a combination of characters and character states defined according to a standardized ontology (Annex 1), translated into several languages (e.g. the 'altitudinal belt' character, containing the character states 'lowland', 'submontane', 'montane', etc.[2]).
3. For a given kind of ecosystem, a name should be associated with a 'type stand', or "biotype", which is a reference geographical object observed at a particular point in time (t) and in an explicit location, ideally accompanied by geographic coordinates. The type stand should be documented based on field observation of as many ecosystem characters as possible, according to a standardized ontology, i.e. it should be a 'virtual ecosystem specimen'. If no biotype can be established that is geographically explicit (e.g. for names derived from the literature) or if the biotype has been destroyed or transformed, a neobiotype should be designated.
4. Data related to virtual ecosystem specimens (biotypes and others) should be published or deposited and stored in a manner accessible to all, enabling consultation of the various interpretations of identification by different authors (i.e. their "determinavit", a term that we define by analogy to its use for specimens in species taxonomy). The place of deposit should be an international repository of virtual ecosystem specimens, in the form of a single, standardized database.
5. No name or language should be imposed on users, nor should the taxonomic system be required to have one and only one 'accepted' name for a specific ecosystem conceptualized at a given point in time. A name created by an author is typified by its biotype, and an ecosystem species circumscription is defined by the individual stands (potentially including two or more biotypes for several published names) considered to belong to the same ecosystem species, identified as such by a determinavit. If several biotypes are included within

[1] Ecosystems are generally defined as the combination of biotic and abiotic components, plus all of the interactions between these components. One can go a step further and say that the notion of ecosystem does not necessarily need to include a biotic component, in which case, if life on Earth were to disappear instantaneously, ecosystems would still exist (coastal, montane, etc.).

[2] One should avoid common ontological mistakes such as "lowland – upland" for states of the altitudinal belt character, "upland" being a character state related to soil hydromorphy (wetland – upland) rather than to altitudinal belts. One should also avoid confusion between 'descriptive' terms and biogeoecological terms, e.g. "mountain" and "montane" ("de montagne" and "montagnard", in French); and for the same reason, terms such as "of middle elevation" – "of high elevation" – "of very high elevation", etc., should be avoided, especially if equivalent and often more precise biogeoecological terms are available (i.e. terms defined by the modelling of ecological gradients, based on observed correlations between abiotic and biotic changes).

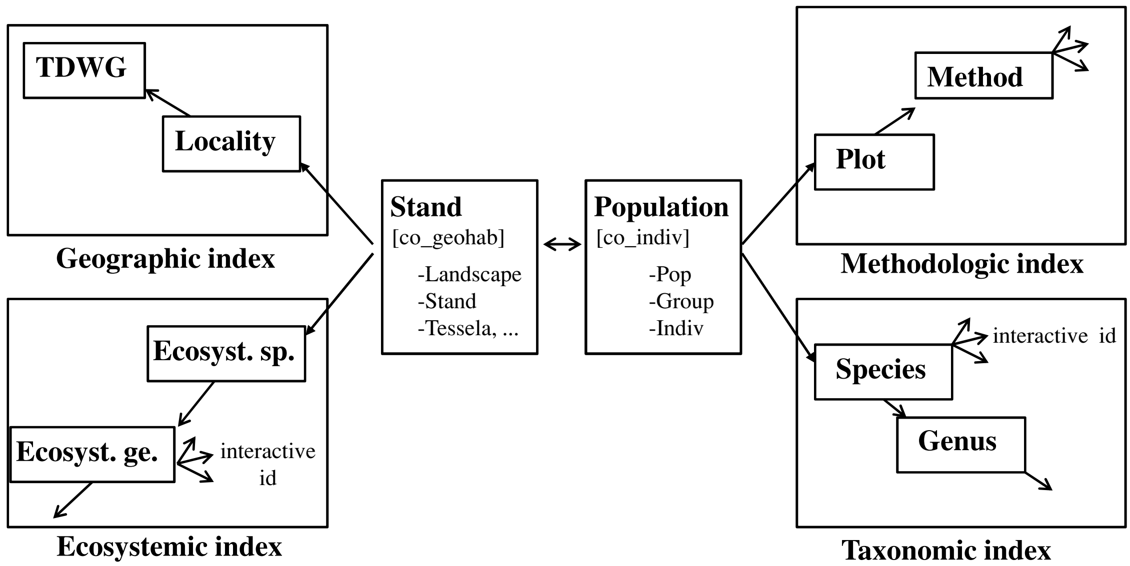


Fig. 3. Schematic representation of the Data Model of the Bio database. Individual Stand data are linked to the ecosystem index via a table of ecosystem *determinavit* (Fig. 4). Similarly, data on individual population records are linked to the taxonomic index via a *determinavit* table.

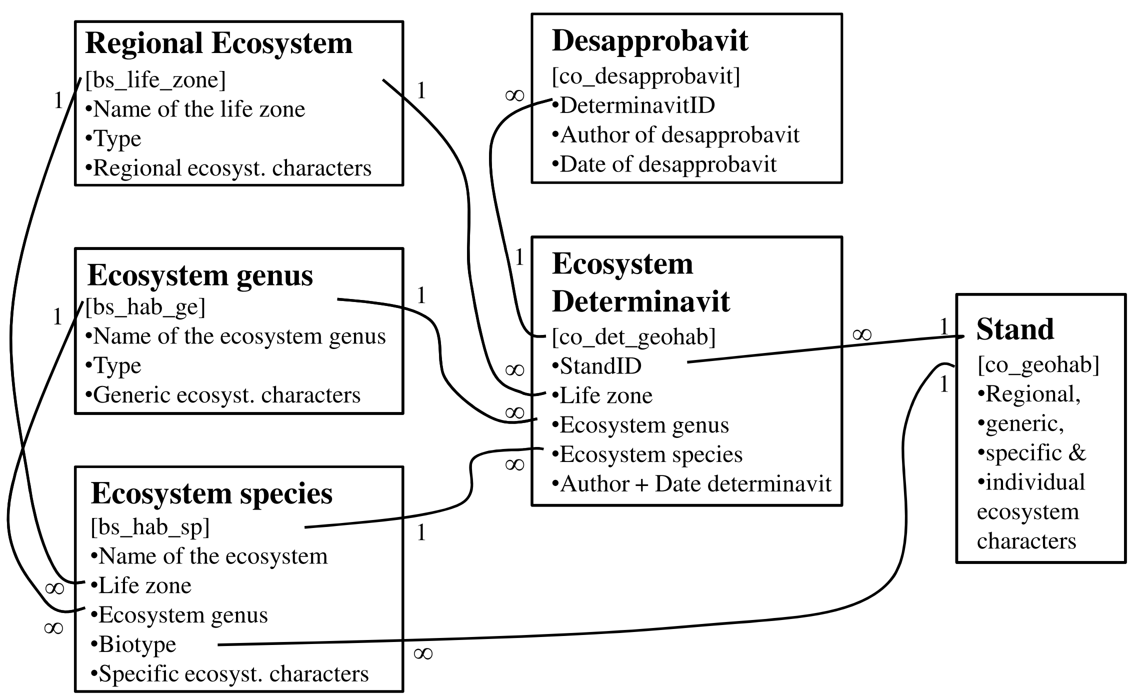


Fig. 4. Detailed view of the Bio data model clarifying how we propose to deal with ecosystem taxonomic data and ecosystem synonymies. The characters of regional, generic, specific ecosystems and individual stands are detailed Annex 1.

an ecosystem species, the species can be designated equally by any of those names, as long as it is clearly referenced by its author and biotype. The other names thus become synonyms of the designated name.

6. Because the names of ecosystem species are diagnoses (i.e. polynomials), an improved understanding of the ecosystem species or the discovery of new ecosystem species might require updates to previously-published diagnosis (thus generating a homotypic synonym). Thus, one of the core principles of species taxonomy, namely the principle of priority (under which the oldest name has priority over all those published more recently), does not apply to ecosystem taxonomy.

While it would remain possible to create names using a phytosociological style or syntax (e.g. "Forest of species *x*"), this should be avoided when describing new ecosystem species, although it will remain necessary to integrate previously published names. The main reason for avoiding the publication of such names is that similar groupings of species can occur in distinct types of ecosystems (Gleason, 1926, p. 11), for example due to ecological substitutions/equivalences (e.g. between montane mesic forests and lowland ravine forests: Senterre, 2005). It is therefore preferable to name ecosystems in a way that emphasizes their true nature, e.g. 'montane mesic' vs. 'lowland ravine' (Box 1). Names using a phytosociological formulation (such as "Forest of species *x*") can instead be used as 'local names', which are more or less explicit locally or nationally.

4. Materialization and practical implementation of our ecosystemologic approach

In the vast majority of biodiversity databases, "habitat-type" (a pragmatic variant of the holistic concept of ecosystem-type; Senterre and Wagner, 2014) is perceived as an attribute of observations made on species (Dauby et al., 2016: RAINBIO; Filer, 2010: BRAHMS; Missouri Botanical Garden 2021: TROPICOS; Yesson et al., 2007: GBIF) and consequently it is provided simply as a comment. By contrast, in phytosociology and for vegetation specialists, habitat-type is an attribute of a vegetation plot, which is primarily an inventory of species (Gillet, 2011: Phytobase; Gillison, 2002: VegClass; Hennekens and Schaminée, 2001: TURBOVEG; Peacock et al., 2007: RAINFOR; Peet et al., 2012: VegBank; Schmidt et al., 2012). Habitat is then often described using certain environmental characters, but neither in detail nor using a framework that integrates scales of space and time, such as the one we propose here. Moreover, this approach mixes methodological and ecosystemic aspects. However, a handful of databases focus explicitly on ecosystems (Di Gregorio, 2005: LCCS; Josse et al., 2003: Systems/LAC; NatureServe, 2017; Scott et al., 2014: Biotics5), among which Biotics5 (Biodiversity Tracking and Conservation System) seems to be the most advanced by far. This system is based on nearly 30 years of development, starting with Grossman et al. (1998), who published the first exhaustive synthesis of ecosystem characters, and continuing to Faber-Langendoen et al. (2014), whose approach appears to have been adopted in recent years as the predominant standard in the context of Red Listing of Ecosystems (Bland et al., 2015, p. 8; Ferrer-Paris et al., 2019, p. 2). Nevertheless, several major conceptual differences preclude the use of this system for implementing the approach we propose here. Below, we detail these differences and then describe the database we have developed to manage ecosystem data, which we have named "Bio" (Bio: Holistic Biodiversity Database on Species and Ecosystems).

4.1. Issues regarding the implementation of Biotics5 for a taxonomy of ecosystems

Firstly, Biotics5 is only accessible online and for a limited number of partners, mainly in the USA and Latin America. It is therefore not directly available to most potential users, and would in any case be problematic for those working in countries where internet access is poor or unreliable. Biotics5 would thus not be suitable as a global tool unless it were made universally accessible, and synchronization and offline functions were developed.

Secondly, the management of distribution data and the ecosystem taxonomy deployed in Biotics5 are based on a fundamentally phytosociological conceptualization, derived from the Yangambi classification, and are therefore based on a site's vegetation physiognomy and the grouping of "plant communities" into Associations, Alliances, macrogroups and formations (Fig. 2). Moreover, Biotics5 suffers from another result of having originated in the Yangambi classification, namely the distribution of several regional factors over multiple levels of hierarchy (altitudinal belts and regional climates), which makes it impossible to develop a comprehensive taxonomic conceptualization of life zones (as entities) and consequently to understand stand scale ecosystems and their dynamics. A direct consequence of this highly hierarchic, rigid approach, mixing levels of classification and levels of organization, is the simplification of life zones along both the climatic wetness gradient and the altitudinal gradient (see Annex 1A; Senterre et al., 2019a, 2020).

Thirdly, as for any typology derived from the Yangambi classification, the intention is to create a standard, globally acceptable typology by combining biogeography (i.e. a divisive approach) and phytosociology (an agglomerative approach). Biotics5 does not aim to create a taxonomic method to manage names and concepts that are seen as hypotheses in continuous evolution. Consequently, one of the most central ideas of phytosociology is overlooked, i.e. the nomenclatural type (see Faber-Langendoen et al., 2014, p. 6).

Finally, Biotics5 and the ecosystem typology accompanying it do not provide practical tools that facilitate the collection of ecosystem data in the field, and are only truly suited to a phytosociological approach, excluding methods such as rapid surveys. Yet it is essential to develop such tools in order to be able to collect 'virtual ecosystem specimens' (Senterre et al., 2019b) without having to conduct comprehensive floristic surveys, the 'relevé' being important but not indispensable.

4.2. The bio data model

The core part of Bio consists of two central tables (core tables): the Stand table ([co_geohab]) and the Populations table ([co_indiv]). The Stand table stores elementary observations on geography and ecology (in principle observations of a stand, although the scope could be more widely conceived or could even be purely geographical), whereas the Populations table contains data on species observations made at the level of local populations. Each table contains a field that defines the level of resolution of the observations (i.e. the conceptual extent). For example, in the Populations table, an elementary data record could be of a local population, a sub-group (cohort, etc.), or a single individual. These two central tables are related to four basic indexes (Fig. 3), although only the ecosystemic index will be discussed in detail in this paper.

The ecosystem index is essentially based on three tables with taxonomic content, viz. [bs_life_zone] for regional ecosystems, [bs_hab_ge] for generic ecosystems, and [bs_hab_sp] for specific ecosystems (Fig. 4). This is a direct result of the conceptualization of ecosystem species described above, i.e. integrating a generic element at the stand scale as well as a regional element. The numerous ecosystem characters (ontology of gradients) are judiciously distributed among these three hierarchic levels (Annex 1). By definition, a given ecosystem species (eco-species) belongs to a given generic ecosystem (ecosystem genus) and a given life zone, and is furthermore necessarily referenced by an element of the Stand table, i.e. a "virtual ecosystem type specimen" (or "biotype"). Another table ([co_det_geohab]) allows for the storage of 'ecosystem *determinavits*', which provide the means for verifying the identity of any virtual ecosystem specimen. If a *determinavit* (i.e. a reference to a name) is added to a biotype (also a reference to a name, by definition), a synonymy is established. Therefore, the grouping of all 'specimens' (including biotypes) considered to belong to a given ecosystem species is done simply by adding a *determinavit* of the preferred name to its own biotype (so as to confirm that name as being the one preferred at a given moment) and to the biotypes of all the other names considered to be synonyms. This method results from the Principle 6 proposed above in the Section 3.

Such a database system, openly accessible online, would make it possible to manage a global taxonomy of ecosystems using an open, objective, collaborative, and scientific approach. It should include a system for the management of *determinavits* from various users, similar to that found in iNaturalist, with an additional option for '*desapprobavit*', which would make it possible for a user to indicate that he/she/they do not agree with a given *determinavit*, in a way that would not invalidate the *determinavit* but would simply ignore it for that particular person's purposes. Another user would then have the option to take into consideration all *desapprobavit* (and could thus follow the most widely accepted opinion) or just his/her/their own opinion (thereby adopting just that person's own conception).

The table of virtual ecosystem specimens (or Stands: [co_geohab]) has been designed in an open and flexible way. Some of the records can be restricted to the most basic geographic data (country of occurrence), as was done for certain nomenclatural types of species collected by botanists in the 19th century. By contrast, other records might include an evaluation (conducted by the author while in the field) of a large number of ecosystem characters at any given level, i.e. characters of life zones or stands, biotic characters, and those describing the current state of the observed stand (development stage, current vegetation physiognomy/formation, degree of biological invasion, etc.). The [co_geohab] table can thus manage the observations of all ecosystem characters contained in the three tables [bs_life_zone], [bs_hab_ge], [bs_hab_sp], plus characters specific to individual stands. Such a large number of ecosystem and stand characters could quickly become overwhelming in the field, even for an expert with a thorough knowledge of the characters. But the robust foundation provided by our approach, based on raw field observations, is indispensable and cannot be compromised, because field observations are fundamental to any ecosystemic conceptualization.

To address this issue, we have developed an extension of the Bio database for smartphones using the Open Foris Collect Mobile application (Senterre et al., 2019b). This system, easily taken to the field and free, guides the naturalist in observing ecosystems through the detailed observation of a stand according to the standardized ontology of ecosystemic characters, taking advantage of inter-dependencies between characters to allow shortcuts (see for example Annex 1B: Frequency of hydromorphy). The smartphone application also facilitates the collection and management of some important information that is usually time consuming to manage using traditional methods, i.e. geographic coordinates and photographs of the stand. Moreover, it provides an easy option to record data on observed species, rapid biodiversity surveys (of species), or even extensive plant community inventories (relevés). Finally, smartphones have become excellent Global Navigation Satellite Systems over the last few years (GPS World Staff, 2018; Tomaštík et al., 2016) and can store large amounts of data that are then easily accessed in the field, including maps and detailed Geographic Information Systems (Nowak et al., 2020), resulting in improved exploration capacity and increased opportunities for discoveries.

4.3. Bio: technical developments and formats

In addition to managing taxonomic and raw occurrence data pertaining to ecosystems, the Bio database has several other interesting features such as: (1) a methodological index for the description of inventory methods according to a standardized framework (ranging from traditional species inventories to monitoring surveys of bird populations and rapid, plotless surveys; see Senterre et al., 2019b); (2) the management of species meta-data (synthetic data on species distribution, conservation status, etc.) distributed among three tables, which allows for the management of global and national statuses; and (3) the capability to define and capture raw data at three fundamental levels of resolution centered on the concept of local/stand-scale populations. Furthermore, Bio facilitates the use of images as well as shapefiles that record field exploration itineraries (i.e. data on existing trails and tracks, and even on routes followed when no observations were made), the collection of herbarium/museum specimens, and the description of habitat in the form of automatically generated text using standardized descriptions of observed ecosystem and stand characters.

These functions have been developed progressively since 2008, using an MS Access database designed by the first author, combined with QGIS (to visualize the data on maps using predefined coloring and legends), R (to evaluate range-size rarity, AOO, EOO: Dauby et al., 2017), and Open Foris Collect Mobile (to allow multiple teams to collect/record new data in parallel, using the 'Bio' standard). Between 2018 and 2020, a project funded by the Critical Ecosystem Partnership Fund (CEPF) resulted in an effort to convert the Bio database into a professional, standalone application developed with SQLite and PostgreSQL-PostGIS. This project is still ongoing and only covers the development of the interface and functionalities for species surveys, and thus does not yet include the development of the ecosystem index.

5. Conclusions

A model representing reality: While an ecosystem-type is nothing more than an artificial, human-conceived category to help model the reality of the environment as we see it, it is nevertheless essential in order to understand this reality better (every bit as much as a good dictionary). Species themselves, and in some cases even organisms (Jagers op Akkerhuis, 2010; Koskella et al., 2017; Krakauer et al., 2020), are also more or less artificial categories (Lamarck in Bonaparte, 1920, p. 11; Pante et al., 2015), yet the relevance of species taxonomy is widely accepted and highly integrated into conservation management and planning. The fact that it is sometimes difficult to recognize species or to decide on their taxonomic status does not in any way weaken the utility and importance of the taxonomic method; nature is what it is, a continuum comprising entities that are more or less well defined. It is likewise necessary to recognize the need for a taxonomy of ecosystems and the importance of addressing this need using a multi-dimensional, non-species-centric approach, as well as to accept that phytosociology is a useful component of field observation and description methods but is nevertheless of limited value for ecosystem conceptualization and nomenclature. We believe it is time to end repeated inter-disciplinary disagreements (Aronson et al., 2014; Carrión, 2010; Carrión and Fernández, 2009; Chiarucci et al., 2010; Eliot, 2011,2007; Larson, 2016; Loidi et al., 2010; Loidi and Fernández-González, 2012; Miller and Bestelmeyer, 2016; Mucina, 2010; Murcia et al., 2014), in particular between those who think that classifying is a need (related to ecological organicism) and those who hold that it is an artefact (continuum), a conflict that we regard as counter-productive and directly responsible for the reluctance to pursue the development of ecosystem taxonomy for fear of being subjected to virulent criticism (each side being unaware that the other represents a valid viewpoint).

Relative scales of space and time: After more than a century of effort, no ecosystem classification system has yet been developed that is widely regarded as satisfactory and that consistently integrates all relevant scales, from global to local. Typologies derived from the Yangambi classification seem stuck in their original, overly-hierarchical paradigm, placing the current/observed vegetation physiognomy above everything else and then subdividing according to a hierarchy of limiting factors. But a given factor can be more or less limiting depending on the regional context and the kind of organisms observed. This results in hierarchies made up of classes that are never totally mutually exclusive. For example, how does one deal with 'montane swamps' in a system that recognizes 1.A.3. Tropical Montane Humid Forest and 1.A.4. Tropical Flooded & Swamp Forest (as defined by Faber-Langendoen et al., 2016)? We have attempted to solve this issue by developing a system in which the hierarchy is defined by natural entities, integrating relative scales of space and time. This approach allows for the conceptualization of stand scale ecosystem types that integrate their regional context, their dynamics, and their conservation state. Moreover, our approach appears to be supported by the theory of scale relativity (Auffray and Nottale, 2008; Nottale, 2010; Nottale and Auffray, 2008). Note that in our approach, the landscape scale (assemblages of ecological gradients, or geosigmetum in the language of landscape phytosociology/geosymphytosociology) is not recognized as a system at an intermediate relative scale between regions and stands (With, 2019), but rather is seen as way to describe landscapes (by simplification or aggregation) for the purpose of mapping (i.e. they are regarded as cartographic rather than ecosystemic entities).

Integration of humans into ecosystem classification: In our proposed system, humans are no longer considered separately from ecosystems, unlike in other approaches in which the anthropic factor is placed at the very top of the hierarchy (Fig. 2). Humans can, with or without help from nature, be the cause of semi-natural disclimaxes (which are autonomous after our disastrous impacts), secondary series, and sustained disclimaxes (forestry plantations, agriculture, cities, etc.). Although human impact can sometimes seem to dominate everything else, it is clear that our actions never fully cancel out the ecological context of a given site or area. A coastal garden is not the same as a montane garden, as anyone who grows plants knows intuitively. In our system, humans are merely one of several disturbance factors (all potentially responsible for primary or secondary series). The integration of humans is made possible because of the conceptualization of relative scales of space and time, which allows for the materialization of the stand and its secondary dynamics on the one hand, and the generic ecosystem and its primary dynamics on the other.

A tool to assist our brains: The complex process of 'solving' the puzzle of ecosystem taxonomy can be compared to trying to solve a puzzle whose pieces have been replaced by bits of paper describing them. It is therefore essential to find a way to represent and visualize the conceptual model of an ecosystem using virtual objects in a database, integrating ecosystem concepts and standardized ontologies of their characters (Annex 1). The Bio database has been developed specifically for this purpose, to provide a tool to manage ecosystem synonymies on the basis of *determinavits* added to the virtual ecosystem type specimens (or biotypes), nomenclatural types that are not based on phytosociological principles but rather integrate them. Furthermore, the Bio database includes a tool to assist the process of making field observations of virtual ecosystem specimens using Open Foris Collect Mobile (for Android smartphones). It is built on elementary characters of ecosystems and is therefore independent of any typology model. The installation files for Bio can be downloaded freely from ResearchGate.

Implications for invasion ecology: By dissecting geographic, ecological, and population characters, species autecology can be considered in a more holistic way. The database proposed here facilitates the observation and collection of information in the field, providing a data set in which traditional species identity and geographic information are complemented by data on the ecology and community structure and composition of the stand where the species is observed and on the state of its local population (developmental stage, human introduction or not, dominance and coverage). Because observations of a species occurrence are broken down according to criteria that contribute to various definitions of the concept of "invasive" (Senterre, 2009; Senterre et al., 2019b: p.5), the approach we have developed makes it possible to collect robust raw data for evaluating the invasive status of species and their potential impacts, depending on the recipient ecosystem types (as defined by Perkins et al., 2011) and independently of any definition of what "invasive" means, thereby reducing the risk of discrepancies between invasion theories and empirical studies due to inconsistent use of definitions (Richardson et al., 2000; Colautti and MacIsaac, 2004). Moreover, the word "habitat" has suffered from the same kind of misuse in invasion ecology (e.g. Barney and Whitlow, 2008; Catford et al., 2009) as in landscape ecology, as described in Section 2.5 above. Consequently, a clear understanding of ecosystem invasibility has been complicated by the fact that some have regarded this notion as an intrinsic emergent property of a given type of ecosystem, based on its community network (Hui et al., 2016), and related to 'ecosystem species', as defined here, whereas others have considered invasiveness as a relative, organism-specific relationship, based on ecological filtering (Perkins et al., 2011), and therefore related to what we refer to here as ecosystem genera. The degree of invasion of invaded sites (Guo et al., 2015) has also been partly confused with invasibility, and corresponds to our lower level of ecosystemic description, i.e. the individual stand (or ecosystem individual). Finally, the framework proposed here can also help better define types of recipient ecosystems and their state as a prerequisite for specialized studies in invasion ecology by better naming the subjects being studied, i.e. naming unambiguously the type of ecosystem in order to study its invasibility and/or degree of invasion (Kueffer and Daehler, 2009). Furthermore, and for the same reasons given above, our system can provide key data for a better understanding of species autecology, taking into consideration the principle of ecological substitutions/equivalences (Senterre, 2005: 222-227).

Implications for Red Listing of Ecosystems: Despite the lack of an international ecosystem taxonomy, the development of the Red List of Ecosystems (RLE) has been and continues to be an important undertaking. It is nevertheless essential to be cognizant of the impact that this significant methodological and nomenclatural gap can have on evaluations of ecosystem threat. If one assumes for a moment that there were no code of nomenclature for species taxonomy and that the same species were therefore being named differently by different people and in different countries without an explicit method to define synonymies and circumscriptions, it would only be possible to conduct an accurate evaluation of overall risk of extinction for locally endemic species. Moreover, if assessments were conducted on very broadly delimited species (which could be thought of as macro-species), as is sometimes done for ecosystems using the RLE approach (e.g. macro-groups; Fig. 2), this could lead to an evaluation of the threat status of, for example, 'Tree Euphorbiaceae of West Africa', i.e. an entity broadly conceived based on an aspect of physiognomy (tree) combined with knowledge of its true nature (Euphorbiaceae), but which is meaningless for biodiversity management and conservation. Consequently, the lack of a standardized ecosystem taxonomy and the use of macro-groups causes many types of ecosystems to be overlooked (because of aggregation) or for their threat level to be overestimated (in cases where ecosystems are considered to be geographically restricted simply because their presence in another country, under a different name, is not taken into consideration). The ecosystemology approach we propose, based on creative tools for both conceptualization and nomenclature, offers concrete solutions to overcome the lack of clear definitions of the notions of "habitats" and "ecosystems", as currently used in various international standards for identifying risks and defining conservation priorities (using HCVs, KBAs, and Critical Habitat). Moreover, it provides a robust and reproducible method for implementing Red Listing of Ecosystems based on verifiable and falsifiable ecosystem conceptualizations.

Perspectives for future development: Space limitations have precluded consideration in this paper of several aspects of our conceptual approach, which will be the subject of separate publications. For example, we have developed a comprehensive list of possible tropical ecosystem genera (ca. 150, a tentative attempt at an '*Ecosystema Naturae*'), which are arranged in two additional levels of hierarchy without taxonomic meaning, i.e. that do not represent taxonomic entities but rather define ecosystemic syndromes that can serve as a basis for facilitating the recognition and storage (classification) of known combinations of ecosystem characters, as observed in nature (see Senterre et al., 2020). Similarly, in another paper we will discuss the typification of names of ecosystem species, and we will propose solutions to deal with pro parte synonymies of specific ecosystem names using the concept of parabiotypes (see also Senterre et al., 2020). The conceptual approach presented here has been applied in part for an RLE assessment of Mont Nimba (Senterre et al., 2019a) and more fully for West Africa (Senterre et al., 2020), which will serve as an example for another publication that will include an interactive identification tool using XPer3. Finally, several other ecosystemology revisions currently being conducted in West Africa and the Indian Ocean will be published in the coming years.

Box 2
Example of a taxonomic description and synonymy of an ecosystem species, using a syntax analogous to that of plant species taxonomy (see Senterre et al. 2020 for additional examples of descriptions, correspondences with other typologies, and a more detailed explanation of the method for ecosystem taxonomic treatment.

Name: *West African Riparian forest of the Lowland tropical perhumid moist evergreen rainforest zone / Forêt ouest africaine ripicole de la zone des Forêts tropicales perhumides sempervirentes de plaine* (Senterre et al., 2019a: 37).

Biotype: Guinea: Massif du Mont Nimba, rivière Ya; 7.59207°N;

-8.46534°W; 611 m; *B. Senterre & E. Bidault BS61-77* (holo-, BIOID: BS61-20191011-1120-77).

Heterotypic synonyms:

River-side forest (Hawthorne et al., 2010: 10, 38). Type: Liberia: West Nimba, 500 m, banks of large rivers, *Stelecantha ziamaeanum* and *Strephonema pseudocola* are particularly frequent along rivers and in swampy parts of the landscape in the Liberian foothills, and much less so in Guinea; *W. Hawthorne s.n.* (holo-, BIOID: 20200813155845).

Galerie forestière (Diabaté et al., 2019: 16). Type: Liberia: Wologizi, Luyema, Placette 18, 8.05747°N, -9.71246°W, 393 m, Formation végétale de type édaphique le long des cours d'eau, fermée (85% à 95%) à des endroits et fortement ouvertes à d'autres endroits (45% à 65%). Quelques espèces caractéristiques sont: *Raphia hockerii, Uapaca* spp., *Cathormion altissimum, Pseudospondias microcarpa, Pterocarpus santalinoides*; M. *Diabaté s.n.* (lecto-, designated by Senterre et al., 2020, p.37, BIOID: 20200812094236).

River border forest of the evergreen forest zone (Voorhoeve, 1965: 21). Type: Liberia: riparian species are *Cathormion altissimum, Monopetalanthus pteridophyllus* (in the moist semi-deciduous zone replaced by *M. compactus*), *Plagiosiphon emarginatus* (a small tree with blunt spines on the bole), *Gluema ivorensis* and, locally gregarious, *Pandanus* sp.; *A.G. Voorhoeve s.n.* (holo-, BIOID: 20200807170321).

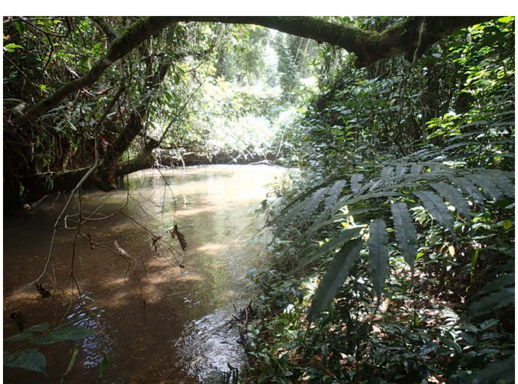
Other virtual ecosystemic specimens:

Liberia: North Lorma National Forest, Lawa River; 8.03166°N; -9.73583°W; 390 m; Riverine forest with abundant *Plagiosiphon emarginatus* mixed with many wet evergreen forest species such as *Achyrospermum oblongifolium, Costus deistelii, Cryptosepalum tetraphyllum, Mapania* spp., *Strephonema pseudocola* and *Triphyophyllum peltatum*, the latter mixed with many more widespread forest species; *C. Jongkind s.n.* (BIOID: 20200807175239, in Jongkind, 2007).

Sierra Leone: Gola East, site 4, Mahoi, 200 m away from the Mahoi river, on a small tributary; 7.3666°N; -11.2°W; The area was flat, low lying and probably partly flooded when the Mahoi was in spate during the rainy season; *A.G. Davies s.n.* (BIOID: 20200810184402, in Davies, 1987).

Description: The description is already largely included in the name (diagnosis), based on the standard ontology of ecosystem characters defined in Annex 1. The West African riparian forests of the lowland perhumid life zone are widespread in hilly landscapes, and appear within mountainous areas only for sites located downstream to a certain value of flow accumulation (which we calculated in the area of Mont Nimba, in Guinea). Their most visible abiotic characteristic is the presence of more or less extended alluvial plains on the river-side. Their biotic characteristics and variability is briefly shown through the synonymies provided above.

Illustration:



ANNEX 1. Ontology of (A) regional ecosystem characters, (B) generic ecosystem characters, (C) specific ecosystem characters and (D) characters of individual stands (observed at an instant 't').

A. *Regional ecosystem characters (characters of life zones)*

Climatic temperature: We follow the principles proposed by Holdridge (1967: see his Fig. 2, p.21). In the tropics, the recognition of the submontane belt is important as it contains its own endemic element (Senterre 2005). Nevertheless, it is lacking in most typologies derived from the Yangambi classification (see Faber-Langendoen et al. 2014, "1. A.2.Eg.873-Mesoamerican Submontane Humid Forest", nested within the formation "1.A.2 Tropical Lowland Humid Forest"). Beyond the tropical belt, other terms in addition to those proposed below exist (Rivas-Martínez et al., 2011, p. 17), but synonymies remain to be defined in order to retain the number of classes proposed here (28).

Code	T° zone	Latitudinal zone	English	French
10	1-Torrid	1-Tropical	Lowland tropical	Tropical de basse altitude
30	2-Hot	1-Tropical	Submontane tropical	Tropical submontagnard
20	2-Hot	2-Subtropical	Lowland subtropical	Subtropical de basse altitude
50	3-Warm	1-Tropical	Lower montane tropical	Tropical motagnard inférieur
60	3-Warm	2-Subtropical	Submontane subtropical	Subtropical submontagnard
40	3-Warm	3-Warm temperate	Lowland warm temperate	Tempéré chaud de basse altitude
80	4-Cool	1-Tropical	Upper montane tropical	Tropical montagnard supérieur
90	4-Cool	2-Subtropical	Lower montane subtropical	Subtropical montagnard inférieur
100	4-Cool	3-Warm temperate	Submontane warm temperate	Tempéré chaud submontagnard
70	4-Cool	4-Cool temperate	Lowland cool temperate	Tempéré froids de basse altitude
120	5-Cold	1-Tropical	Subalpine tropical	Tropical subalpin
130	5-Cold	2-Subtropical	Upper montane subtropical	Subtropical montagnard supérieur
140	5-Cold	3-Warm temperate	Lower montane warm temperate	Tempéré chaud montagnard inférieur
150	5-Cold	4-Cool temperate	Submontane cool temperate	Tempéré froids submontagnard
110	5-Cold	5-Boreal	Lowland boreal	Boréal de basse altitude
170	6-Subfrigid	1-Tropical	Alpine tropical	Tropical alpin
180	6-Subfrigid	2-Subtropical	Subalpine subtropical	Subtropical subalpin
190	6-Subfrigid	3-Warm temperate	Upper montane warm temperate	Tempéré chaud montagnard supérieur
200	6-Subfrigid	4-Cool temperate	Lower montane cool temperate	Tempéré froids montagnard inférieur
210	6-Subfrigid	5-Boreal	Submontane boreal	Boréal submontagnard
160	6-Subfrigid	6-Subpolar	Lowland subpolar	Subpolaire de basse altitude
230	7-Frigid	1-Tropical	Nival tropical	Tropical nival
240	7-Frigid	2-Subtropical	Alpine subtropical	Subtropical alpin
250	7-Frigid	3-Warm temperate	Subalpine warm temperate	Tempéré chaud subalpin
260	7-Frigid	4-Cool temperate	Upper montane cool temperate	Tempéré froids montagnard supérieur
270	7-Frigid	5-Boreal	Lower montane boreal	Boréal montagnard inférieur
280	7-Frigid	6-Subpolar	Submontane subpolar	Subpolaire submontagnard
220	7-Frigid	7-Polar	Lowland polar	Polaire de basse altitude

Climatic wetness: We follow the principles of Holdridge (1967). The simplification found in typologies derived from the Yangambi system is, to us, inappropriate (see detailed discussion in Senterre and Wagner, 2014: 23-24; Senterre et al., 2019a: 29, 31). Furthermore, we consider the higher level of detail proposed by Rivas-Martínez et al. (2011, p. 18: 17 classes) to be perfectly useful for descriptive purposes but not for the recognition of bioclimatic zones.

Code	English	French	Tropical example with a few synonymies
10	Superhumid	super humide	Wet rainforest; = Forêt hyperhumide littorale (White, 1983); Forêt ombrophile p.p. (Schnell, 1952)
20	Perhumid	perhumide	Moist rainforest; Forêt ombrophile p.p. (Schnell, 1952)
30	Humid	humide	Seasonal moist rainforest: Includes monsoon variations; = Forêts semi-décidues péri-guinéennes (White, 1983); = Forêts semi-décidues méridionales (Schnell, 1979); Forêt mésophile (Schnell, 1952)
40	Subhumid dry	sub-humide / sec	Seasonal dry rainforest; = Forêts semi-décidues septentrionales (Schnell, 1979)
50	semi-arid	semi-aride	Dry forest; = Forêt soudanienne xérophile (Schnell, 1952); Forêt tropophile (Lebrun and Gilbert, 1954)
60	Arid	aride	Dry woodlands and Thorn woodlands, pachycaule woodlands, etc.
70	Perarid	peraride	Dry scrub and steppes
80	Superarid	super aride	Desert

Atmospheric wetness and horizontal rain: Although this can be a geographically very local gradient, it still is a climatic factor, and is therefore regional, which interacts with other regional factors and contributes to the climatic influence on stand scale gradients.

Code	English	French	Definition
10	non-cloud	sans brumes	Without horizontal rains
20	Fog	à brumes	With some horizontal rains from a fog belt or oasis (Cereceda et al., 2008a, 2008b; Gioda et al., 1995)
30	Cloud	de nuages	With some horizontal rains from a cloud belt, e.g. tropical montane cloud forests (Bruijnzeel et al., 2011) and tropical lowland cloud forests (Gradstein et al., 2011)

B. Generic ecosystem characters (characters of ecosystem genera)

Coastal influence (coastal gradients): We distinguish between the words "coastal" and "littoral", the former corresponding to the proximity of the coast, and the latter being more related to the proximity of the oceanic source of climatic wetness (continentality).

Code	English	French	Definition
10	Offshore	de pleine mer	marine non-coastal
20	Nearshore	marin côtier	marine coastal
30	coastal frontshore spray zone	du front côtier	spray zone, without trees in life zones where (mono)climax is forest
40	coastal backshore spray zone	d'arrière-côte	spray zone and/or salt water influence, with trees in life zones where (mono) climax is forest
50	non-coastal	non côtier	terrestrial non-coastal ; no influence of coastal sprays and tides

Degree of exposure to sea spray, spring tides and storms (coastal gradients)

Code	English	French	Definition
10	highly exposed	très exposé	no lagoon, directly exposed to exceptional tides and storms
20	Exposed	exposé	no lagoon, not directly exposed
30	Sheltered	abritté	oceanward lagoon
40	highly sheltered	très abritté	atoll inner lagoon

(continued on next column)

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Degree of exposure to tides (coastal gradients)

Code	English	French	Definition
10	Subtidal	sub-tidal	coastal frontshore rarely exposed to air
20	Intertidal	inter-tidal	coastal frontshore exposed to air daily to monthly
30	Supratidal	supra-tidal	coastal frontshore, rarely affected by tide
40	tidal estuarine	estuarien à marée	estuary under tidal influence, with salt water
50	tidal freshwater	estuarien de l'intérieur	estuary under mixed tidal-freshwater influence
60	non-tidal	non-tidal	without influence of tides

Degree of hydromorphy

Code	English	French	Definition
10	aquatic wetland	aquatique	wetland, permanently aquatic
20	low water mark wetland	subaquatique	wetland, partly aquatic, saturated
30	high water mark wetland	hydromorphe	wetland, not always saturated/ flooded
40	extreme high water mark semi-wetland	innondable	wetland, occasionally saturated/ flooded
50	mesic upland	de terre ferme	upland, never flooded, except for disaster (the term 'upland' should not be confused as the opposite to 'lowland', but opposite to wetland)

Frequency of hydromorphy (applicable if the degree of hydromorphy is not equal to '50')

Code	English	French	Definition
10	Permanent	permanent	Stable
20	Seasonal	saisonier	Annual cycle
30	Tidal	tidal	Daily cycle
40	Occasional	occasionel	Irregularly

Salinity

Code	English	French	Definition
10	Hyperhaline	hyper-salin	> 35 ppt
20	Euhaline	salin	30 to 35 ppt
30	Brackish	d'eau saumâtre	0.5 to 29 ppt
40	Freshwater	d'eau douce	< 0.5 ppt

Type of water

Code	English	French	Definition
10	black water with tanins	eau noire à tanins	
20	brown eutrophic water	eau brune eutrophique	
30	anoxic water	eau désoxygénée	dissolved oxygen concentration of less than 0.5 milligrams per liter

Velocity of water

Code	English	French	Definition
10	Stagnant	stagnante	
20	non-stagnant low speed	courante	
30	non-stagnant high speed	rapide	Sometimes called "white water"

Soil depth (saxicolous character: edaphic wetness)

Code	English	French	Definition
10	bare rock	roche nue	e.g. inselberg rock
20	Subsaxicolous	subsaxicole	skeletic saxicolous soil, e.g. inselberg herbaceous/shrubby fringe
30	Saxicolous	saxicole	shallow saxicolous soil, e.g. inselberg saxicolous forest fringe
40	mesic / developed soil	sol profond	non-saxicolous, incl. rock boulders with large pockets of soil

Lithology (further simplified compared to Sayre et al. 2013, 2014)

Code	English	French	Definition
10	intrusive silicate	intrusive (e.g. granitique)	silicate (e.g. granitic)
20	effusive silicate	effusive (e.g. volcanique)	silicate (e.g. volcanic)
30	Phosphatic	phosphatique	phosphate
40	Carbonate	carbonaté	carbonate
50	Lateritic	latéritique	metallic (Fe, Al)
60	Ultramafic	ultramafique	metallic (Cu, Co, Ni, Ur)
70	gypsum evaporite	évaporite gypse	gypsum

3D rock structure

Code	English	French	Definition
10	deeply bouldery	blocs rocheux profonds	with deep wet dark clefts
20	deeply karstic	relief karstique profond	with deep wet dark clefts
30	Bouldery	blocs rocheux	more or less isolated or too small to generate a rock (sub)canopy
40	Karstic	relief karstique	dissected, more or less isolated or too small to generate a rock (sub)canopy
50	Rocky	substrat rocheux	more or less densely rocky
60	on rock sheet	dalle rocheuse	one massive rock sheet

Gross soil texture (as a limiting factor, not a descriptive one; edaphic wetness)

Code	English	French	Definition
10	Sandy	sableux	sand
20	other (e.g. clay)	autre (e.g. argille)	non-sandy, no peat, no textural limiting factor
30	Peaty	tourbeux	e.g. distinguishing peat swamps from other swamps

Topographic wetness: a very important character, although generally overlooked

Code	English	French	Definition
10	basin/ depression	bassin/ dépression	basin/depression
20	Riparian	ripicole	riverine flood plain near large rivers
30	Ravine	de ravin	V-shaped landform on a slope, incl. ravine-like cliff / rocky slopes bottom
40	ravine-like	de pseudo-ravin	ravine-like cliff / rocky slopes bottom
50	mesic landforms	à topographie mésique	topographically mesic
60	overdrained landforms	à topographie sur-drainée	topographically dry
70	Cliff	falaise	incl. rock surfaces, vertical vegetation and steps in cliff

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Primary dynamics (primary series)

Code	English	French	Definition
10	without primary disturbance	sans dynamique primaire	either at (poly)climax or in secondary succession
20	Disclimax	disclimax	e.g. grazed meadows; pyrophilic or wind-pruned vegetation, etc.
30	progressive climax	progression primaire	e.g. post-fire shrublands on highly degraded soils
40	retrogressive climax	retrogression primaire	e.g. post-fire red/ferralitic soils under active erosion

Primary disturbance (primary series)

Code	English	French	Definition
10	Grazed	pâturée	Large herbivores
20	Ungrazed	dé-pâturée	
30	wind-pruned	rabougri par le vent	
40	post-fire (intense)	après feu intense	
50	Unburn	par suppression des feux	
60	on lava flow	sur coulée de lave	
70	flooded (dam)	inondé	
80	unflooded (drained)	exondé	
90	on volcanic ash	sur dépôts de cendres volcaniques	
100	on landslide down to bedrock	sur roche mise à nue par glissement de terrain	
110	on seabird guano deposit	sur dépôts de guano	
120	mined (soil removed)	après élimination du sol par des activités minières	
130	on reclaimed land	sur terrain construit sur la mer	

Vegetation physiognomy (plant formation sensu stricto, at stand scale and maturity, i.e. potential vegetation physiognomy): Although the climax physiognomy is often included in the names of life zones (and therefore has a meaning close to Clements's monoclimax: Clements, 1936), any physiognomy component must be removed from the conceptualization and nomenclature of life zones. For illustration, see USGS (1994).

Code	English	French	Definition (upper class)
10	Giant forest	forêt catédrale	Forest
20	Forest	forêt dense	Forest
30	Woodland	forêt claire	Forest
40	Sparse woodland	savanne boisée	Non-forest, mostly vegetated
50	Dwarf forest	forêt basse	Forest
60	Dwarf open forest	forêt basse ouverte	Forest
70	Shrubland	fourrés	Non-forest, mostly vegetated
80	Dwarf-shrubland	fourrés bas	Non-forest, mostly vegetated
90	Open-shrubland	fourrés clairs	Non-forest, mostly vegetated
100	Sparse shrubland	savanne arbustive	Non-forest, mostly vegetated
110	Herb savanna	savanne herbeuse	Non-forest, mostly vegetated
120		prairie	

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(*continued*)

Code	English	French	Definition (upper class)
	Herbaceous meadows		Non-forest, mostly vegetated
130	Steppic vegetation	steppe	Sparsely vegetated
140	Sparse vegetation	végétation éparse	Sparsely vegetated
150	Unvegetated	non végétalisé	Unvegetated

Sempervirence of the dominant stratum

Code	English	French	Definition
10	Sempervirent	sempervirent	Dominant stratum vegetation never loses leaves
20	sub-sempervirent	sub-sempervirent	Some elements of the dominant stratum vegetation loses leaves occasionally
30	semi-deciduous	semi-décidu	Some elements of the dominant stratum vegetation loses leaves seasonally
40	Deciduous	décidu	Most elements of the dominant stratum vegetation loses leaves seasonally
50	Ephemerous	éphémère	Dominant stratum vegetation can disappear during long periods of time

C. Specific ecosystem characters (characters of ecosystem species)

Diagnostic species with biogeographic value: Note that the idea of considering biogeography (biotic variations linked to geography) only after accounting for ecological determinism was presented by Senterre (2005: 67).

Dominance of life forms with indicator value

Code	English	French	Definition
10	with tree ferns	à fougères arborescentes	Abundance of tree ferns
20	with bamboos	à bambous	Presence of bamboos
30	with palms	à palmiers	Abundance of palm trees
40	with pachycaules	à plantes pachycaules	e.g. bottle trees, caudex
50	with cactiforms	à cactiformes	Presence of cactiforms
60	with termite mounds	à termitières	Presence of termite mounds

Dominance of some special leaf types (size and shape)

Code	English	French	Definition
10	needle leaved	aiguilles	e.g. Gymnosperms, Casuarina
20	Microphyllous	microphylles	Adapted to drought
30	Mesophyllous	mésophylles	Unlike the other categories
40	Megaphyllous	mégaphylles	e.g. palms, Musaceae, etc.

Dominance of some special leaf types (thickness and water content)

Code	English	French	Definition
10	Sclerophyllous	sclérophylles	Coriaceous
20	Papyraceous	papyracées	Thin and soft to more or less fleshy or leathery
30	Crassulous	crassulentes	Thick and containing water

Dominance of thorns

Code	English	French	Definition
10	Thorn	épineuses	Abundance of thorny plants
20	without thorns	non-épineuses	

D. Characters of ecosystem individuals (characters of a given stand)

Anthropization

Code	English	French	Definition
10	Natural	naturel	A stand which never had a direct influence of human impact, irrespective of its development stage (pioneer to mature). It includes 'sub-natural': i.e. more than just semi-natural having matured back to climax, e.g. where the human action is several centuries old (terra preta, palaeo-fires, palaeo-savannas)
20	semi-natural	semi-naturel	A managed or artificial stand where the human influence has stopped and which is progressively recovering toward a natural state.
30	Artificial	anthropisé	The human influence is maintained or repeated regularly so that the vegetation dynamics is stopped.

Secondary development stage: The term "climax" is here understood in a broad sense, analogous to the term "adult" (for an organism). The definition of "climax" used here does not include any biotic components, but rather indicates nothing more than a system that has reached a mature (adult) stage. This concept can be applied to a system at a regional scale (the monoclimax or climatic climax), although we use it here at the stand scale (polyclimax, or stand climax).

Code	English	French	Definition
10	Pioneer	pionier	physiognomy, structure and flora far from climax
20	early secondary	secondaire jeune	general physiognomy of the climax, but structure still more simple (e.g. unistratum); flora mostly short lived
30	late secondary	secondaire vieux	general physiognomy and structure of the climax; climax flora in the process of recovering
40	old growth	mature	dominated by climax species (long lived)

Secondary disturbance (secondary series)

Code	English	French	Definition
10	tree-fall gap	chablis	Size of a few meters or tens of meters; soil not affected
20	landslide (superficial)	glissement de terrain superficiel	Bed rock not exposed
30	Hurricane	ouragan	Soil not affected
40	post-fire (not intense)	feu	Soil not baked, washed away or compacted
50	invasive species controlled	élimination d'espèces invasives	Human action
60	sustainable extractions	extractions soutenables	Human action
70	native species planting	plantation d'espèces natives	Human action
80	selective logging	exploitation forestière à faible impact	Human action, low impact
90	clear cutting	exploitation forestière industrielle	Soil not affected
100	artisanal mining	activité minière artisanale	Small scale
110	Disease	maladie	Death of trees
120	animal disturbance	activités animales	e.g. mechanical disturbance by elephants

Degree of biological invasion

Code	English	French	Definition
10	Native	natif	purely or nearly purely native elements
20	mostly native	surtout natif	exotic elements are noticeable but remain dominated by natives
30	mixed natives-exotics	mélangé natif-exotique	natives and exotics are co-dominant
40	mostly exotic	surtout exotique	natives are present but clearly dominated
50	Exotic	exotique	no natives or nearly no natives are present

Characteristic species for a particular stand: Phytocoenoses, syntaxa and/or dominant species.

Observed vegetation physiognomy: Same classes as for the characters of potential vegetation physiognomy (see section B).

Descriptive ecological characters: Many descriptive characters could be included here, including exact landforms (Grossman et al., 1998: 96-100), slope (expressed in % or degrees, or according to visual semi-quantitative classes), soil type (Schultz, 2005, pp. 30–31), exact soil texture (Grossman et al., 1998: 104), geology of the bedrock (Grossman et al., 1998: 101), vegetation height (in meters), elevation, climatic parameters (Rivas-Martínez et al., 2011).

Abundance-Dominance coefficient of various life forms: Abundance-dominance of the main life forms that contribute to defining the physiognomy of the vegetation (trees, herbs, epiphytes, epiphylls, etc.). Any kind of semi-quantitative coefficient can be used. We recommend using the definitions proposed by van der Maarel (1979), to which we have added below the correspondence with two other common terminologies. Column "ab" provides a quantitative value of relative abundance based on the threshold values of the corresponding class; column "vdm" provides the corresponding coefficient according to van der Maarel; the "Upper class" column converts each class into a simplified 5-level abundance-dominance scale (which we call the ROFCA scale).

Code	abbrev	English	French	Upper class	Definition	Ab	Vdm
10	0	absent	absent	X		0	0
20	0.5	present nearby	présent aux alentours	R	out of the plot	0.5	0.5
30	1	very rare	très rare	R	1 individual	1	1
40	2	rare	rare	R	2 individuals	2	2
50	3	occasional	occasionnel	O	f = 5 %	3.5	3
60	4	almost frequent	assez fréquent	O	5< f = 10 %	7.5	4
70	5	frequent	fréquent	F	10< f = 15 %	12.5	5
80	6	very frequent	très fréquent	F	15< f = 25 %	20	6
90	7	common	commun	C	25< f = 50 %	37.5	7
100	8	abundant	abondant	A	50< f = 75 %	62.5	8
110	9	very abundant	très abondant	A	f > 75%	87.5	9
120	X	absent	absent	X	the presence has never been observed, although searched for	0	0
130	R	rare	rare	R	rarely seen, just a few individuals, difficult to find	1	1
140	O	occasional	occasionnel	O	quite rare but more than just a few individuals, not so difficult to find	3.5	3
150	F	frequent	fréquent	F	easily seen, but not found everywhere, uncommon, not dominant	12.5	5
160	C	common	commun	C	easily seen, almost everywhere (in the stand / habitat or / locality considered), slightly dominant	37.5	7
170	A	abundant	abondant	A	dominant species, representing more than 50 % of the individuals of the community	87.5	9

Type of human land use: see Faber-Langendoen et al. (2014), Di Gregorio (2005) and many other sources. Here we have only compiled the categories that seem to be the most essential.

Code	English	French	Definition, examples
10	protected area	aire protégée	Legally protected area
20	forestry	Foresterie	Production of timber
30	agro-forestry	agro-foresterie	
40	agriculture	Agriculture	
50	livestock	Élevage	
60	park	Parque	
70	garden	Jardin	
80	plant nursery	Pépinière	
90	cemetery	Cimetière	
100	houses	Habitation	Isolated houses or groups of houses
110	village	Village	Small sized, low density housing
120	urban	Urbain	Large size, high density housing
130	road	Route	Used by cars
140	trail	Sentier	Used for walking only
150	mining	Mine	

CRediT authorship contribution statement

Bruno Senterre: Conceptualization, Software, Writing – original draft, Writing – review & editing, Funding acquisition. **Porter P. Lowry:** Writing – review & editing, Funding acquisition. **Ehoarn Bidault:** Writing – review & editing. **Tariq Stévart:** Writing – review & editing, Funding acquisition.

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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