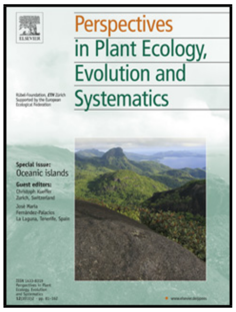

Title: A conceptual framework for the analysis of vascular epiphyte assemblages

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Highlights

- A framework is proposed to study patterns & dynamics of epiphyte assemblages (VEAs)
- VEAs offer unique research opportunities due to their inherent structural hierarchy
- To promote standardization, the coresampling unit should be the host individual
- The host individual can be connected to lower & higher ecological & spatial scales
- Data sharing is highlighted as essential for comparative meta-studies

Title: **A conceptual framework for the analysis of vascular epiphyte assemblages**

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Abstract

Despite their ecological importance, particularly in tropical rainforests, vascular epiphytes are amongst the least studied plant groups. Theoretical knowledge about the composition, structure and dynamics of epiphyte assemblages is strikingly scarce; in contrast to soil-rooted plants~~,~~ for which major insights have been gained in the last decades. These insights cannot be simply transferred to epiphytes, because structurally-dependent vascular epiphytes are fundamentally different in several aspects from non-structurally-dependent plants, as well as from other epiphyte types (e.g. mosses). Apart from the difficulty of accessing the canopy, we largely attribute the lack of development in the field to terminological issues and the lack of standardized sampling, both of which stem from the lack of a conceptual framework. We develop such a framework for future studies and illustrate the potential of this suggested approach. Our analysis is based on a review of studies of vascular epiphyte assemblages that have data on abundance, since diversity comprises two aspects: species richness and relative abundance. We found 62 studies of very idiosyncratic character over the last 30 years, of which 18% included a temporal component ranging from 4 months to 8 years. Surprisingly, over 80% of the studies collected data at the tree level, but few analysed the data at that level (34%) and none has made their data available for meta-analyses. We argue that this represents a problem in the development of the field and we urge researchers to make this wealth of data available. We suggest explicitly using the host individual as the sampling unit when studying vascular epiphyte assemblages. Moreover, the ecological scales (zone, tree and stand scales) i.e. relating to the three-dimensional nature of vascular epiphytes assemblages (VEAs), can be used to scale up or down from the host individual. The importance of scaling, and availability of data at the tree level, was assessed by comparing diversity patterns of vascular epiphytes at the tree and stand scales, which revealed clear and consistently different patterns. More general questions on the diversity patterns of vascular epiphytes could be answered if the wealth of data already collected were made accessible and if future sampling were to be standardized.

Introduction

Vascular epiphytes comprise about 9% of vascular plant species globally (Zotz, 2013a). They are a main diversity component in the tropics (Kitching 2006), providing ecological services related to hydrology and nutrient cycling (e.g. water interception, water and nutrient retention, Jarvis 2000; Stanton et al. 2014; Bruijnzeel et al. 2011). Also, they contribute to diversity through their interactions with other biota (Benzing, 1983; Yanoviak et al., 2007). In montane forests they may account for a substantial portion of green biomass (e.g. Tanner 1980). In spite of all this, they are amongst the least studied biodiversity components in the tropics (Kitching 2006).

In tropical "plant" communities, biodiversity research has mainly focused on trees. Although major insights have been gained into the mechanisms governing the composition, structure and dynamics of tropical tree communities (Condit et al., 1995; Feeley et al., 2011; Volkov et al., 2003), other life forms have been largely ignored in this regard. This is particularly obvious for functionally important and hyper-diverse groups such as lianas (Schnitzer and Carson, 2000) or epiphytes, for which there is "little theory" on the mechanisms behind their diversity in tropical forests (Kitching 2006). This neglect could be largely ignored, if conclusions from studies with trees were transferable to vascular epiphytes. However, this is arguably not the case. For example, while the structure and dynamics of tree communities are strongly influenced by biotic interactions (e.g. competition or pathogen/herbivore pressure), these processes seem to have hardly any influence on epiphyte communities (Zotz and Hietz, 2001). Moreover, since epiphytes are structurally dependent plants which use the three-dimensional matrix of colonizable substrate supplied by trees, their dynamics are affected by exogenous heterogeneity (Rees et al., 2001), not only caused by the host dynamics (Hietz, 1997), but also by climate and topography (Rees et al., 2001). Hence, the processes shaping epiphyte assemblages are expected to be inherently different from those of trees (Watkins et al., 2006). Available results from studies with non-vascular epiphytes (i.e. mosses or lichens, Ellis 2012) may also be of limited applicability to vascular epiphytes. For example, lichens and mosses in temperate forests behave as “patch-tracking” meta-populations (Snäll et al., 2005), which implies that local extinctions usually occur due to patch turnover (i.e. tree falls, Löbel et al. 2006). In contrast, the few data available for vascular epiphytes suggest very different dynamics, in which extinctions are frequent in the absence of tree or branch fall (Laube and Zotz, 2007).

It is often argued that progress in epiphyte research has been rather slow because of logistical problems accessing the forest canopy (e.g. Flores-Palacios & García-Franco 2001). While partly true, we argue that terminological issues and the lack of standardized sampling play at least an equally important role. These issues are common in canopy ecology and can be found in all stages of research (e.g. sampling and data analysis), hindering future meta-analyses dependent on consistency of approach. First, terminological issues range from the misuse or ambiguous use of established terminology to the lack of established definitions for commonly used terms in canopy ecology. For instance, one of the most commonly misused terms in epiphyte research is “canopy”. Moffett (2000) compiled a set of definitions of terms in canopy research, but subsequent studies still confuse “canopy” with “crown” (e.g. Kluge & Kessler 2011; Watkins et al. 2006; Zytynska et al. 2011); although the latter is defined as the aboveground parts of a tree or shrub, particularly its topmost limbs and leaves (Moffett, 2000), i.e. is a part of the canopy. This trivial example illustrates a deeply rooted issue that is widespread across epiphyte research. Another clear example of the lack of established definitions for commonly used terminology is the term “epiphyte”, since there are still arguments about the delimitation of vascular epiphytes from other structurally dependent plants with divergent ecologies such as hemiepiphytes, parasites, or climbing plants (e.g. Zotz 2013a, 2013b). These issues are connected and contribute to a vicious circle. For instance, when a definition of epiphyte is not provided, it is likely to find epiphytes, hemiepiphytes and nomadic vines (*sensu* Zotz 2013b; Zotz 2013a) and sometimes even mistletoes lumped into the same category and analyzed together. This makes it difficult to obtain records on the incidence of epiphytism or hemiepiphytism, urgently needed for a better understanding of their taxonomical occurrence and biogeography. Furthermore, it prevents us from differentiating whether these ecologically different life forms may show different spatiotemporal patterns. Second, standardized sampling has still to be adopted across the field. Understandably, different objectives may require different sampling strategies, but it is possible to direct sampling towards standardized data collection. This lack of standardization is not due to a scarcity of methodological tools, since issues of data collection in vascular epiphyte assemblages have received considerable attention in the last decades (e.g. quantification of abundance and sampling effort, Wolf et al. 2009; Zotz & Bader 2011).

We argue that the mentioned problems most likely derive from the lack of a conceptual framework to assess vascular epiphyte diversity, which combines terminology and methodological tools already in use. Therefore, we propose such a framework to advance our understanding of vascular epiphyte diversity. While there has been a previous attempt to develop an analytical framework by Burns & Zotz (2010), their approach was solely focused on the topology of the host-epiphyte network. Thus, its conceptualization is analysis-based and may be less useful to explore other aspects of the ecology of vascular epiphytes (e.g. colonization-extinction dynamics and directional changes in species composition, Feeley et al., 2011).

To that aim, we review and summarize studies on vascular epiphyte assemblages, and unify terminology by formalizing concepts implicitly used. We formalize the vascular epiphyte assemblage (VEA) as the unit of study to address vascular epiphyte diversity, with the host individual being the most “natural” sampling unit. We identify biologically relevant ecological scales along gradients of environmental heterogeneity, which are formalized as “zone”, “tree” and “stand” based assemblages (ZBA, TBA and SBA). Furthermore, we briefly illustrate the importance of scaling and the potential of this framework. We argue that exploring extrinsic factors of VEAs, using interacting spatial scales (Ellis, 2012), should allow real progress in the understanding of the mechanisms behind epiphyte diversity.

The conceptual framework: *a proposal for standardization*

For over 100 years ecologists have been taking into account the two aspects of diversity: species richness or the number of species in a sample and the relative species abundance or the disparity in abundance (commonness and rarity, Bell 2000; Hubbell 2001). Species abundance data make it possible to answer questions related to demographics (i. e. mortality or growth), as well as to track populations or assemblages and their changes as a response to their environment or disturbance. For vascular epiphytes, species lists are available for a substantial number of localities (e.g. Sugden & Robins 1979; ter Steege & Cornelissen 1989). More recently, the study of species richness patterns has come into focus (Cardelús et al. 2006; Krömer et al. 2005). Although useful in several contexts (e.g. in the analysis of diversity changes along elevational gradients, or in a conservation context, by comparing epiphyte species richness in disturbed vs. undisturbed forest, Wolf & Flamenco-S 2003, Köster et al. 2009), their potential to help us understand the spatiotemporal changes in assemblage structure is limited. Therefore, we focus on studies considering both aspects of diversity (richness and abundance), to go beyond the description of the spatial and temporal variation in assemblage composition, and to push forward the understanding of the mechanisms and factors affecting vascular epiphyte diversity.

Study unit: the vascular epiphyte assemblage (VEA)

A thorough search (Table 1, details of the search) of studies providing both species richness and abundance data yielded only 62 studies in the last 30 years (Table 1). In most cases, the unit of study is not consistently named or defined. An “assemblage” may either be 1) a set of species or 2) a set of species and their abundance. Moreover, “assemblage” is used interchangeably with "community". Since epiphytes seem not to fulfil the concept of "community", which demands interaction among species (Benzing, 1990; Ricklefs, 2008), we prefer the term "assemblage". Thus, we define a "vascular epiphyte assemblage" (VEA) as a set of vascular epiphyte species (n>1) with or without information on their abundance (e. g. number of individuals, Fig. 2.1.a); which should be clearly specified in the methodology. We encourage the collection of abundance data and in this review we focus entirely on this type of research. Because of its broad application, the "number of individuals" (following the "stand" concept, Sanford 1968) can be used as a preferred measure of abundance; although we do not discourage the use of biomass (Wolf et al., 2009), especially in longitudinal research (where repeated measures of the same individual are taken in a span of time, e.g. growth rate). Ideally, both measures are provided, since the number of individuals can be obtained while assessing biomass (Benavides et al., 2006). Moreover, the use of both measures could be complementary since species abundance distribution may vary according to the measure of abundance (Magurran & Henderson, 2010). Furthermore, a VEA is a non-dimensional unit of study, which can be limited by any spatial, temporal or ecological scale and in contrast to the definition of an "epiphyte community" by Johansson (1974), the concept of VEA does not exclude natural systems with a very low number of epiphyte species (Vergara-Torres et al., 2010).

Sampling unit: host individual

The majority of methodological protocols explicitly recommend sampling of entire trees as the most representative approach (e.g. Gradstein et al. 2003; Wolf et al. 2009) and possibly as a result, the large majority (81%) of the studies compiled in Table 1 sampled entire tree individuals. We argue that the shared host individual is the most natural and spatially explicit reference of a VEA, given that they act as islands and provide a unique set of microhabitats, as a result of ~~intra~~ intra-and inter-specific variability within the forest. Therefore, the **host individual** ought to be formalized as the standard **sampling unit** of VEAs (Fig. 2.1.b). Whenever possible, entire trees should be sampled and registering the most basic characteristics of the hosts is recommended (e.g. host species, diameter at breast height and height; for more details see Wolf et al., 2009).

Ecological scales: Zone, tree and stand assemblages

The three-dimensional distribution of vascular epiphytes comprises various gradients of environmental heterogeneity (Stein et al., 2014) and offers several scaling possibilities. As the scales partition this environmental heterogeneity, interacting or confounding effects among the ecological factors determining scales are prone to arise, highlighting the interacting nature of the scales (Ellis, 2012). The use of interacting scales and its progressive, yet informal, establishment has come along with the development of the field. Scale can be defined from a strictly spatial point of view or in an ecological sense (Gurevitch et al., 2006). The latter is usually implicitly done in vascular epiphyte research. In the compiled publications (Table 1), the used ecological scales are diverse (Fig. 1): 1) zones of the tree; either branches, the crown or the trunk (i.e. Hietz & Hietz-Seifert 1995; Irume et al. 2013; Mehltreter et al. 2005). 2) the tree individual (Irume et al., 2013; Nieder et al., 2000) and 3) the stand. These ecological scales are defined by different external factors (see below) or organizational scales, for example in studies of host specificity the stand scale is self-evident and used implicitly, given that the distribution of VEAs on different host species is compared (e.g. Vergara-Torres et al. 2010). We formalize these interacting ecological scales as the "zone based assemblage" (**ZBA**)[1], which is part of a "tree based assemblage" (**TBA**), which in turn can be scaled up to a "stand based assemblage" (**SBA**), i.e. the sum of any number of tree-based assemblages (Fig 2.1.c). To simplify the usage of the terms, they can be referred to as "**zone, tree,** and **stand** scales". Naturally, the term "tree" does not preclude the study of other hosts (i.e. shrubs, cacti, or lianas).

An advantage of clearly-defined ecological scales is the potential for the *a posteriori* use of data for integrated analyses, provided that the host individual is used as sampling unit and relevant ecological data have been collected. For example, if one were to scale up to SBAs delimited by host species, data on the host identity should be available. Conversely, if one were to scale down to particular ZBAs, such as trunks, data on the size (e.g. dbh/height) of the trunks are important. We argue that sampling units should be established by their ecological meaning and not merely by convenience, therefore the recommendation of adopting the host individual as the standard sampling unit. Using the proposed ecological scales (i.e. ZBA or SBA) as *a posteriori* scaling tools and not merely as haphazard sampling units will prevent us from producing more idiosyncratic studies with little utility for synthesis. This is true for sampling limited to the ZBA scale without accompanying ecological data, as for sampling at the SBA scale without information on the hosts.– Otherwise, comparisons are only possible between corresponding studies (e.g. Affeld et al. 2008), for which the spatial or ecological scale is known (Cardelús, 2007). Otherwise, comparisons among studies of diverse spatial or ecological scales (Fig. 1) are ambiguous to impossible (Krömer et al., 2013). Findings of studies focusing on

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[1] ZBA: zone based assemblage, TBA: tree based assemblage and SBA: stand based assemblage

zones of a tree cannot be generalized to all co-occurring epiphytes, since species numbers and dynamics are bound to vary with position in a tree. For instance, the only two studies of dynamics of ZBAs in montane rainforest focused on the inner crowns and trunks of trees and indicated mostly low annual mortality rates of vascular epiphytes (2 and 7% on branches within the crown to 10% on trunks; Hietz 1997; Werner 2011); while three other studies, all in the lowlands, focusing on entire trees showed consistently higher mortality rates (> 50% mortality rates after 3 - 4 years; Schmit-Neuerburg, 2002, Mendieta and Zotz *unpublished data*). Whether this reflects a genuine difference across tree zones or forest types, or whether this is only a sampling artefact due to the comparison of branches in the inner crown, tree lower trunks and entire host tree individuals, is an open question. Moreover, mortality rates varied across taxa and size classes in assemblages (Hietz, 1997; Werner, 2011) and in studies explicitly focussing on populations of different taxa (Orchidaceae and Bromeliaceae, Hietz et al. 2002; Winkler et al. 2007; Winkler et al. 2009)). Therefore, differences in composition and structure of assemblages are confounded by ecological scale (Küper et al., 2004).

The use of different ecological scales to assess the diversity patterns and dynamics of vascular epiphytes is key to their understanding, because patterns, processes, and the effect of ecological drivers on biodiversity are scale-dependent (Chase and Knight, 2013; Levin, 1992). The ecological scales (zone, tree and stand scales) can be used to explore the patterns and dynamics of VEAs independently or from a multi-scale perspective. The latter requires that an ecological aspect is evaluated simultaneously at different scales (Wiens, 1989). This type of research is critical to complement more conventional studies (Levin, 1992), given that epiphytes are structurally dependent and distributed three-dimensionally across various gradients of environmental heterogeneity. Multi-scale research is rather common in non-vascular epiphytes (e.g. Jüriado et al. 2008; Belinchón et al. 2009; Mota de Oliveira et al. 2009), but rare with vascular epiphytes. Among the compiled studies on VEAs only 16% may be considered at least in part of multi-scale nature. These studies addressed the spatial effect on demographic processes of TBAs and a SBA (Winkler et al., 2009), temporal changes in the structure of TBAs and SBAs (Laube and Zotz, 2007, 2006a) and by using different organizational levels to delimit single and multiple stands, they assessed the structural patterns of VEAs (Burns and Zotz, 2010), or their compositional differences (Larrea and Werner, 2010). This small number of studies already reflects the diversity of patterns and processes in which scaling may be applied.

Characterization of the external factors of VEAs

Vascular epiphytes are associated with a suite of external factors arguably influencing the patterns and dynamics of VEAs. Among those we consider: ***architecture***, ***bark characteristics***, ***growth rate and size/age*** of the host; which are associated with ***host identity***. Also important are ***disturbance*** and ***climate*** (Sarmento Cabral et al., 2015; Wagner et al., 2015). Although the former factors are intrinsic host characteristics and the latter are exogenous factors which also affect the host, from the vascular epiphyte point of view, all these factors and their variation create exogenous heterogeneity (Rees et al., 2001).

External factors

The effect of some of these factors on VEAs has already been studied (e.g. Aguirre et al. 2010; Cardelús 2007; Goode & Allen 2008; Hietz & Hietz-Seifert 1995; Zotz 2007a; Zotz & Vollrath 2003), but their scale-dependence has seldom been addressed (for indirect or implicit examples see: Benavides et al. 2005; Benavides et al. 2011; Hietz & Hietz-Seifert 1995; Irume et al. 2013; Zimmerman & Olmsted 1992). We argue that by using the host individual as a standard sampling unit, the variation of the external factors, their effect on vascular epiphyte diversity and the scale dependence of this effect can be evaluated; scaling up from the zone to the stand scale (Fig. 2). Figure 3 outlines a framework which comprises the ecological scales (zone, tree and stand scales) distributed across gradients of environmental heterogeneity. At each ecological scale, natural organizational levels may be used to delimit the assemblages, as well as ecological or structural schemes delimited by the external factors. For example, at the zone scale, assemblages may be delimited by levels of organization pertaining to the host individual, such as: branch, trunk and crown, or by schemes based on extrinsic factors: such as the vertical zonation of the tropical forest (e.g. understorey vs. crown) , structural groups (Zotz, 2007a) or leaf phenology (Einzmann et al., 2014). At the stand scale in the same fashion, for example at the host population level, the host species identity (Wagner et al., 2015) may be used to delimit a stand, while at the "community" level and others of larger scale: ecological succession, forest age, forest type and altitude may be used to define a stand.

The way that **climate** affects VEAs varies from the effect of microclimate at the zone scale, which can be evaluated by, e.g., comparing the inner and the outer crown or crowns with different microclimate (Cardelús, 2007), over the tree scale, where differences across the vertical gradient can be assessed using the tree individual, to the effect of climate at the stand scale, via the effect of elevation or other geographical gradients (Küper et al., 2004). Similarly, the effect of **disturbance** varies across ecological scales, from the zone scale, as instability of the substrate e.g. flaking bark (Zotz et al., 2005), to the tree scale, as branch fall events (Rosenberger and Williams, 1999; Sarmento Cabral et al., 2015), to the effect of large-scale catastrophic events such as hurricanes (Goode and Allen, 2008) at the stand scale (Fig. 3). For example, to test the intermediate disturbance hypothesis (Connell 1978) in epiphytes, the interacting ecological scales along ecological gradients noted here would provide an optimal set up. Likewise, the effect of substrate **age** or **size** on VEAs can be studied across an ecological gradient, evaluating the effect of ontogenetic changes at each ecological scale (Fig. 3).

Finally, host **architecture**, **bark characteristics** (physical and chemical) and host **growth rate** are all bound to **host identity** and in the same way, their effect across ecological gradients (Fig. 3) can be studied independently or in combination at each ecological scale or across scales. For example, the effect of **architecture** can be scaled up from the zone scale to the tree and stand scale by assessing e.g. the effect of different branching patterns among crowns, differences of VEAs in trees of different habits (Aguirre et al., 2010) and e.g. differences among VEAs of different forest types (Benavides et al. 2011), respectively.

Importance of scaling in the analysis of VEAs

In the assessment of biodiversity (here we focus on "species diversity") and its spatial and temporal variation the use of a multi-scale approach is crucial (Levin, 1992). Diversity, which has two aspects; the number of species and the disparity in abundance (Bell, 2000), varies across spatiotemporal scales. Recent studies have found clear differences in species richness patterns between epiphytic and non-epiphytic groups (e.g. Kluge and Kessler, 2007). Still, the effect of scaling on vascular epiphyte diversity has seldom been addressed (for species richness see Krömer et al., 2005; Küper et al., 2004). However, temporal changes in the composition and structure of vascular epiphyte assemblages have been studied separately at two ecological scales (tree and stand scales). Changes at the tree scale suggested that, on average, TBAs became more similar to each other over time (i.e. increase of among TBA similarity, measured with the Chao-Sørensen index), with only one of the studies reporting a *significant* difference. In contrast, at the stand scale vascular epiphyte assemblages seem to be quiet stable in time (Laube and Zotz, 2007, 2006a). Here, we consider stability as the persistence and evenness in abundance of species and maintenance of the numbers of species in an assemblage (May and McLean, 2007). Thus, temporal changes in diversity may vary according to ecological or spatial scale.

To detect possible differences in diversity across scales, we calculated and compared similarities using the stand and tree scales, for different scenarios and datasets. To be able to compare the aspects of diversity across scales, we make use of the "Hill numbers" in the construction of multi-assemblage similarity profiles. Diversity profiles are a unifying tool for the analysis of diversity (Gotelli and Chao, 2013; Jost et al., 2010) and the "Hill numbers" are arguably the most adequate way to quantify biological diversity (Ellison, 2010). We used multi-assemblage similarity profiles, which reflect the average percentage of species overlap among assemblages (Chao et al. 2012; Jost et al. 2010), obtained with the overlap measure (C_{qN}). This measure assesses compositional differentiation and similarity and it ranges from 0, when assemblages are completely distinct, to 1, when they are identical. This measure (C_{qN}) is a normalization of the between-group or “beta” component of the “Hill numbers”, where q is a parameter that determines the measure’s sensitivity to species relative abundances and N is the number of assemblages being compared. The measure includes a continuum of multi-assemblage generalizations of known similarity indexes, differing in their sensitivity to relative species abundances (when q=0, this is equivalent to the classic two-assemblage Sorensen index where species abundances do not count at all, when q=1, equivalent to the Horn overlap index where species are weighed in proportion to their frequency and when q=2, equivalent to the Morisita-Horn similarity index where abundant species weight more than rare species, Gotelli & Chao 2013). The “Hill numbers” provide a unified framework for measuring biodiversity, being recently extended to include genetic and functional diversity (Chao et al., 2012).

First, to assess how the effect of forest alteration on epiphyte diversity varies across scales, we re-analysed data from Larrea & Werner (2010) and second, to assess the scale dependence of temporal changes in diversity we used partially published datasets (Laube & Zotz, 2006a, Mendieta-Leiva and Zotz, *unpublished data*); in both cases using the tree (TBA) and stand (SBA) scales.

In the first study, the authors evaluated differences of VEAs on the tree species *Erythrina edulis* distributed across a land-use gradient; unmanaged forest, managed forest and isolated remnant trees (IRTs)[2], for details see Larrea & Werner (2010). The expectation of the study was

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[2] IRT: isolated remnant tree

a stronger response to massive alteration of the original vegetation (IRTs stand) than to moderate disturbance (managed forest stand). Their findings, however, supported this hypothesis for neither species richness nor abundance. Nevertheless, the number of species of particular taxa differed significantly between the unmanaged forest and IRTs, and significant compositional differences were detected based on pair-wise comparisons of TBAs (Larrea and Werner, 2010). We constructed multi-assemblage similarity profiles at both the tree and stand scales (Fig. 4B and A, respectively), i.e. we compared SBAs, defined by land use type and TBAs, within each stand per land use type. The profiles (Fig. 4) showed that when comparing land use types at the stand scale, assemblages of the different land use types had a rather high similarity (80%) in terms of species richness and structure (Fig. 4A). Using the tree scale revealed a somewhat different picture. Among-tree similarity decreased from the managed forest to IRTs to the unmanaged forest, suggesting significant differences in mean similarity between unmanaged and managed TBAs (confidence intervals did not overlap, Fig. 4B). This result contradicts the conclusion of Larrea & Werner (2010), indicating that moderate disturbance (managed forest) rather than massive alteration of the vegetation (IRTs), had the strongest effect on the floristic composition of VEAs (Fig. 4). In summary, the illustrated example showcases distinct outcomes at both scales. For instance, at the stand level, the land use type stands differed very little in any aspect of diversity; while at the tree scale, among-tree similarity revealed a difference between the unmanaged and managed assemblages for all orders of diversity (species richness to dominance). Surprisingly, the measure of similarity in terms of species richness (q=0), showed no difference between the stand and tree scale (i.e. mean similarity is comparable at both scales, Fig. 4A and B, q=0).

Second, to assess the scale-dependence of ecological heterogeneity and temporal changes in diversity, we used two data sets of concurrent and congruent quantitative data. The first set of two large censuses, spanned 10 years (2002 – 2012) and will be referred to as “FOREST” (compare Zotz & Schultz 2008). This census includes 264 tree individuals, comprising 77 species within 35 families. The second set consists of a series of short-span censuses carried out about every other year for 11 years (1999-2010) on 30 individuals of the host tree species *Socratea exorrhiza*, from now on referred to as “SOCRATEA” (compare Laube & Zotz 2006a). Abundance values are based on the TBAs included in this paper, those which had abundance data at each census. Thus, data may sometimes differ from those found in Laube & Zotz (2006a) and Zotz & Schultz (2008b). We compared the relative compositional similarity in time, according to dataset and scales, by calculating similarity between censuses (stand scale, Fig. 5A) and within and among censuses (tree scale, Fig. 5B). The profiles of the censuses with different temporal grains at both scales (stand and tree scale) showed that indeed the stand scale generally depicts a fairly stable structure of VEAs in time (FOREST and SOCRATEA: Fig. 5A). In contrast, at the tree scale the patterns of similarity in time differed between stands (Fig. 5B). At the stand scale, changes in both censuses (SOCRATEA and FOREST) were rather similar in time, in spite of their varying temporal grains and characteristics (Mendieta-Leiva and Zotz, *unpublished data*). Average percentage overlap of species in time was relatively high, between 80 - 92% for species richness, and for typical and dominant species in both stands (Fig. 5A); indicating a relatively stable structure of vascular epiphyte assemblages in time at this scale. Using the tree scale, we found differences in among-TBA similarity between stands, although in general there was a trend of increased compositional similarity with time (q=0 and 1, Fig. 5 B). Compositional similarity was considerably higher in the FOREST than in the SOCRATEA stand (*q*=0, Fig. 5B). In the FOREST, the profiles crossed (*q*≈1.5, Fig. 5B), indicating that after 10 years among-tree similarity increased in terms of species ~~richness~~ composition (by ca. 2%, between *q*=0 and 1), but decreased in terms of very abundant species (by 1% at *q*=2). In SOCRATEA, trees became increasingly similar in all aspects of diversity (species ~~richness~~composition, typical and very abundant species).

When comparing both systems (Fig. 4 and 5), the need for a multi-scale approach in the analysis of epiphyte diversity becomes obvious. The stand scale seems to show VEAs as stably structured, independently of the grain of the spatial scale (e.g. number of TBAs) or length of the temporal scale, while the use of the tree scale reflects changes according to the organizational level or extrinsic factor used to delimit the assemblage. Clearly, stand and tree scales represent different facets of the spatio-temporal patterns of VEAs. As the choice of a scale may affect the results and comparability of analysis (Rahbek, 2004), it is important to understand the effect of ecological scales on the spatio-temporal patterns of VEAs.

This degree of ~~consistence~~ consistency in the species composition and structure of VEAs at the stand scale has been observed in this and other forests (Mendieta-Leiva and Zotz, *unpublished data*). Here we show that the relatively small temporal variation shown by VEAs at the stand scale is not a sampling artifact due to short intervals between censuses, but instead a general characteristic of VEAs at this scale. This finding is highly relevant to identifying differences at larger spatial scales. These differences across scales indicate the importance of using several scales in the analysis of vascular epiphyte diversity.

Discussion

There are plenty of species lists of vascular epiphytes for a considerable number of locations and, to a lesser extent, publications specifying local or regional diversity. Recently, the floristic turnover across ecological gradients has received more attention (Cardelús et al. 2006; Kluge & Kessler 2011; Kreft et al. 2004; Krömer et al. 2005; Krömer et al. 2013; Küper et al. 2004). Unfortunately, these studies focus only on one aspect of diversity, ignoring species abundances. Data on species abundance provide information on commonness and rarity and demographics (i. e. mortality or growth). The ecological importance and validity of this type of data is indisputable. Admittedly, the collection of such data is labour intensive, along with the use of the host individual as sampling unit, but the establishment of 50 ha forest plots and other long-term vegetation monitoring (Rees et al., 2001) were equally arduous; nonetheless, those efforts have proven invaluable for our understanding of soil-rooted plant diversity. Moreover, the fact that 62 studies with epiphytes in the last 30 years have collected abundance data shows the feasibility of our approach. In addition, 81% of the studies compiled in Table 1 have already collected data at the tree level. While this is a very positive indication of advancement towards standardization, data have also to be analysed at this level or at least made available for *post-hoc* and meta-analyses.

Compared to most other plant types, scaling in vascular epiphytes is more intuitive, biologically meaningful and not merely pragmatic, because in the former the sampling grain is mostly defined by the feasibility of transect or plot size. For vascular epiphytes, we can take advantage of their dependence on a host and their three-dimensional distribution patterns. For instance, vascular epiphytes are known to be non-randomly distributed (Burns and Zotz, 2010) and vertical segregation is commonly reported (Krömer et al., 2006; Zotz, 2007a). Recently, their spatial segregation along the "horizontal" axis of the forest has received more attention (e.g. Burns & Zotz 2010; Sáyago et al. 2013). Studies addressing this ecological dimension often refer to it as host specificity (Wagner et al., 2015). In these studies, for example, the use of the stand scale is self-evident. In summary, VEAs can be scaled up or down to ZBAs, TBAs and SBAs by means of organizational scales and extrinsic factors. These ecological scales may be used in combination (multi-scale approach) when assessing e.g. spatiotemporal patterns of diversity or to evaluate the scale dependency in the effect of extrinsic factors on diversity. According to the question, research can scale up or down from the zone to the stand scale and otherwise (Fig. 2).

The inherent three-dimensional distribution of vascular epiphytes has been rarely used as a naturally structured framework, except for a typical subdivision of the host tree into so-called Johansson zones (JZ, Johansson, 1974). This scheme sections the host tree, making use of natural "zones" of environmental conditions and it has frequently been applied to capture the vertical stratification of VEAs (e.g. ter Steege & Cornelissen 1989).Although it became a common tool in the study of VEAs, it is of limited use for our understanding of patterns and dynamics. The scheme is not comparable across studies, as it is hard to apply equally to all trees within a forest or to different forest types (Bøgh, 1992; Zotz, 2007b). Additionally, its biological meaning may be doubtful, because the vertical stratification of epiphytes may be rather shaped by microclimatic gradients of the entire vegetation and not the individual tree (Zotz, 2007b). Moreover, it focuses on already established assemblages of large trees and excludes hosts with unusual architecture (e.g. palm trees). We do not disapprove of the use of Johansson zones in the context of our framework, but recommend a more thought-out application. Johansson (1974) conceived of these zones 40 years ago for large trees. Without information on the relative position of a tree in the vegetation, assigning epiphytes to the outer crown may actually result in misleading comparisons of epiphyte distributions, when including, e.g. epiphytes on understory, mid-story and emergent trees. Here, simply using height above ground may provide more insights into underlying mechanisms of distributional differences (e.g. Petter et al., 2015). Similarly, varying abundances in different zones have often led to claims of preferences for particular zones, ignoring that the relative surface area per zone differs within and among host species (Krömer et al., 2006). Irrespective of how zones are delimited, additional measurements should be taken into consideration as a minimum requirement for later comparisons: a proxy of host size or age, host species, habit (*sensu* Zotz, 2013b), and substrate diameter (Wagner et al., 2015; Wolf et al., 2009). For example, ZBAs delimited by crowns or trunks can be compared using surface area or size as covariable. The other two scales (tree and stand scales) are more intuitive in their use and especially the latter is commonly used for analyses in epiphyte research. Stands have been delimited according to: spatial proximity of tree individuals, soil characteristics and elevation (Benavides et al. 2011; Burns & Zotz 2010; Kluge & Kessler 2011; Laube & Zotz 2006b; Laube & Zotz 2007)~~,~~. ~~this~~ This small number of examples reflects already a wide array of possible organizational scales.

Using available data from different studies for a cross-scale effort may be further impeded by the idiosyncratic character of the many epiphyte studies (Krömer et al., 2005). However, data accessibility is noticeably the most problematic aspect. The compiled studies (Table 1) provide aggregated data only as species lists and their abundance, irrespective of scale (e.g. Irume et al. 2013), or in some cases according to host species (e.g. Brown 1990; Laube & Zotz 2006b). Within the studies which collected data at the tree level a majority (75%) provided summarized data but not a single one provided their data at the tree level. Hence, this wealth of information cannot be accessed, although it could potentially help us to reveal macro-ecological patterns of

VEAs. We urge researchers to make past and future data available (e.g. as electronic supplements); for this purpose we make our own datasets from published studies from the lowlands of Panama available upon request (Zotz and Schultz, 2008b; Zotz et al., 1999).

Clearly defined VEAs would maximize gain in the pursuit of individual project goals, and provide the conceptual clarity for concurrent or subsequent comparisons across studies. Researchers would better fulfil the aims of their epiphyte studies by dividing or grouping VEAs for analytical purposes, as well as for a multi-scale approach (e.g. Laube & Zotz 2006a) using predefined ecological scales (Fig. 2.1.c) and secondly but more importantly, for the advancement of the field as a whole, they would produce comparable datasets. Certainly, the kind of analyses to be carried out are dependent on the specific question, although we are confident that several aspects related to the diversity of VEAs may be answered if standardized data were available, taking into account ~~the~~ appropriate considerations. This is supported by the fact that most of the compiled studies have collected data at the tree scale and still addressed a wide array of ecological aspects. Among these considerations, we suggest: 1. Unambiguous use of terminology, for example, habit differentiation between epiphyte, hemiepiphyte and nomadic vine (e.g. Boelter et al 2014), 2. Explicit specification of the unit of analyses, whether a VEA comprises abundance data or not, 3. Collection of supplementary ecological data, including host identity and a proxy of size (dbh, crown size, height and/or trunk or bark surface). Whenever spatial replication were possible, data on the geographic distance of host individuals as well as general characteristics of the forest stands may be helpful. Provided that intensive sampling is possible, data on the location of epiphyte individuals in relation the host individual, i.e. height and substrate diameter may be collected.

Clearly, there is no single, “correct” scale for describing a system (Levin, 1992), nor a single organizational framework, much less for organisms with a patchy distribution (Talley, 2007) such as vascular epiphytes. Currently, we are not able to distinguish between the ecological scales at which mechanisms generating diversity are inhibited or promoted, and those scales in which stochasticity is dominant (Kitching 2006; Levin 1992). Therefore, the biological relevance of the ecological and organizational scales should be tested, using a multi-scale approach (e.g. Belinchón et al. 2009). Alternatively, the use of different frameworks may be more rewarding (e.g. Talley 2007). This can be executed with the outlined framework by combining the corresponding organizational and hierarchical scales, given its integrative character. For example, as indicated by Talley (2007), approaches such as the patch, gradient and hierarchical frameworks may be combined to identify patterns and underlying processes, as well as scale dependent-processes and interactions among scales. In vascular epiphyte assemblages, analysis combining these approaches to assess e.g. the variation in the distribution of VEAs, would identify tree individuals as patches (Laube and Zotz, 2007), branch classes (Zotz, 2007a) or host dbh classes as gradients, and crowns or trunks (ZBAs) of SBAs delimited by host tree species, as a hierarchical system.

Final remarks

A considerable amount of work has gone into the compilation of local epiphyte inventories. We argue that in these studies data have not been collected, and reported, in the most useful way, leading to an odd situation that in spite of 62 published community studies, we still do not have sufficient data for meta-analyses to search for general patterns in the community structure and dynamics of vascular epiphytes.

The future development of the entire field largely depends on standardization in the use of concepts, of sampling and of data availability, to produce comparable research. Therefore, throughout the text we have formalized terms already in use within the proposed framework and suggested a simple change that could lead to the standardization of sampling and analysis, which is using the host individual as the standard sampling unit when assessing vascular epiphyte assemblages. One cannot overemphasize the importance of making data available. Importantly, these could also be unpublished data sets from previous papers, we take the first step and hope for other researchers to join this initiative.

In conclusion, we have summarized research efforts on the patterns and dynamics of vascular epiphytes in the last decades. In an effort to advance research, we suggest the use of a standard sampling unit and discuss the use of ecological and organizational scales; taking advantage of the inherent three-dimensional distribution of vascular epiphytes.

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531 **Footnote table**

1	VEA: vascular epiphyte assemblage
2	ZBA: zone based assemblage, TBA: tree based assemblage and SBA: stand based assemblage
3	IRT: isolated remnant tree

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Figure 1 Summary of all studies dealing with vascular epiphyte assemblages across spatiotemporal scales (compare Table 1). The horizontal axis represents the temporal scale in years and the vertical axis represents different ecological scales, i.e. along ecological gradients of spatial complexity. The ecological scales comprise: 1. ZBA: when studies analyzed assemblies delimited by a zone of the host (i.e. a vertical and horizontal line indicates studies focused on the trunk and the crown, respectively). 2. TBA: studies which analyzed assemblies at the host scale (i.e. among TBA similarity or the vertical gradient), 3. SBA: studies delimiting assemblages as stands for analyses. These may use plots as sampling units and may involve more than one stand, grouped according to particular organizational scales, i.e. physical factors (e.g. altitude) or biological levels of organization (e.g. host tree species). We depict each study according to scale used in analyses. Each symbol represents a study. Closed symbols indicate studies with a temporal component, open symbols those without. On the left side, the bars distributed across more than one scale indicate one or more studies using more than one scale in analyses (i.e. all of them, SBA and TBA or SBA and ZBA); these studies used different scales to address different ecological aspects of vascular epiphytes. Those studies, which used a multi-scale approach, i.e. they assessed the same question at more than one scale are noted with a thicker border.

Figure 2 Schematic~~s~~ diagrams illustrating the concept of vascular epiphyte assemblage, the proposed sampling unit and interacting spatial scales. Additionally, an example of how to explore the dynamics of VEAs and the use of organizational levels is shown. Tree species are indicated by different crown shapes, different symbols represent different epiphyte species. Given the dimensionality of vascular epiphytes the shared host tree (1.b) is the most intuitive and spatially explicit reference of a vascular epiphyte assemblage (VEA 1.a). A VEA (1.a) is comprised of m individuals of n species. Interacting spatial scales (1.c) are the zone, tree and stand. The interacting spatial scales are dubbed “zone based assemblage” (ZBA), "tree based assemblage" (TBA) and the "stand based assemblage" (SBA). (2) Example of an analytical~~sis~~ roadmap: Dynamics of VEAs may be analyzed across scales. (a) Changes in time at the stand level as the sum of all TBAs may be compared with (b) changes in time at the tree level (i.e. species turnover in each TBA in time, blue dotted lines). To detect directionality in the changes of the SBA, differences in among-TBA dissimilarity over time should be assessed (blue continuous line). (3) An example of how to use organizational levels (see text).

Figure 3 Possible analytical framework of VEAs. In the left column the external factors of the patterns and dynamics of VEAs are shown. The other columns depict examples of how the effect of each external factor may be assessed according to ecological scale. The ecological scales are distributed across an ecological gradient and range from ZBA (zone based assemblage), TBA (tree based assemblage) to the SBA (stand based assemblage).We elaborate on examples of how to address the effect of external factor on the patterns and dynamics of VEAs in the text.

Figure 4 Diversity aspects across ecological scales, scenario 1: Effect of forest alteration on epiphyte diversity. Multiple-assemblage similarity profiles (C*q*N) portraying average percentage species overlap of land use types at different scales and their confidence intervals (shaded polygons). The x-axis shows the orders of *q* (sensitivity parameter) and y-axis the values of the overlap measure (C*q*N). The sensitivity parameter (*q*) weights the importance of abundance. Similarity profiles of land use types **A**. at the stand scale, compares the three land use types. **B**. at the tree scale depicts among-TBA similarity of VEAs defined by land-use in a montane forest as defined by Larrea & Werner (2010): unmanaged forest, managed forest and isolated remnant trees (IRT).

Figure 5 Diversity aspects across ecological scales, scenario 2: Scale dependence of temporal changes. Multiple-assemblage similarity profiles (C*q*N) portraying average percentage species overlap of datasets at different spatiotemporal scales and their confidence intervals (shaded polygons). The x-axis shows the orders of *q* (sensitivity parameter) and y-axis the values of overlap measure (C*q*N). The sensitivity parameter (*q*) weights the importance of abundance. Similarity profiles of censuses **A**. at the stand scale, the comparison comprises two and five censuses (FOREST and SOCRATEA, respectively, upper lines). **B**. at the tree scale. Each line represents a census, line type indicates the dataset (FOREST: entire lines and SOCRATEA: dotted lines) and colour intensity (from grey to dark) indicates the temporal sequence of the censuses.

Figure 1

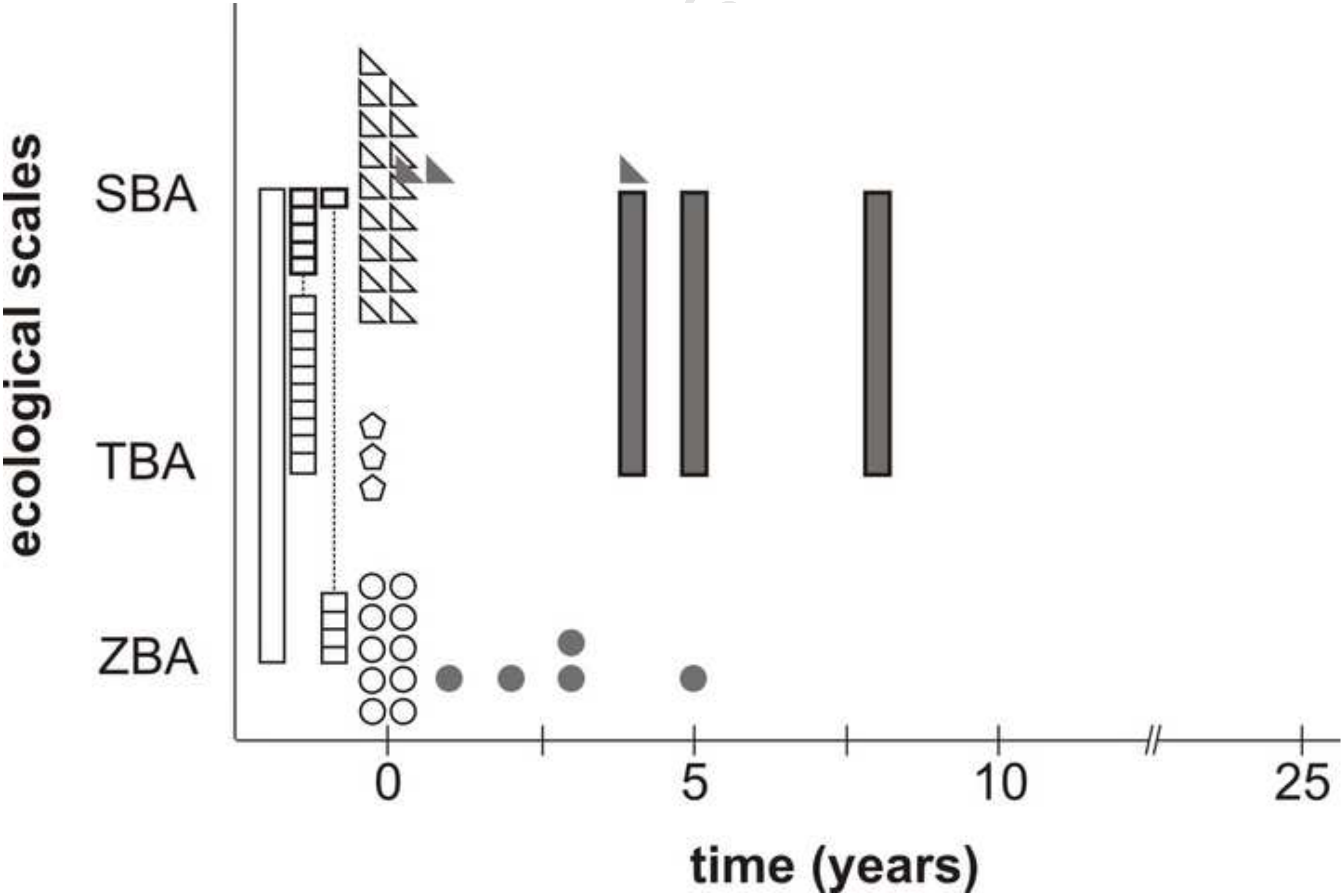

Figure 2

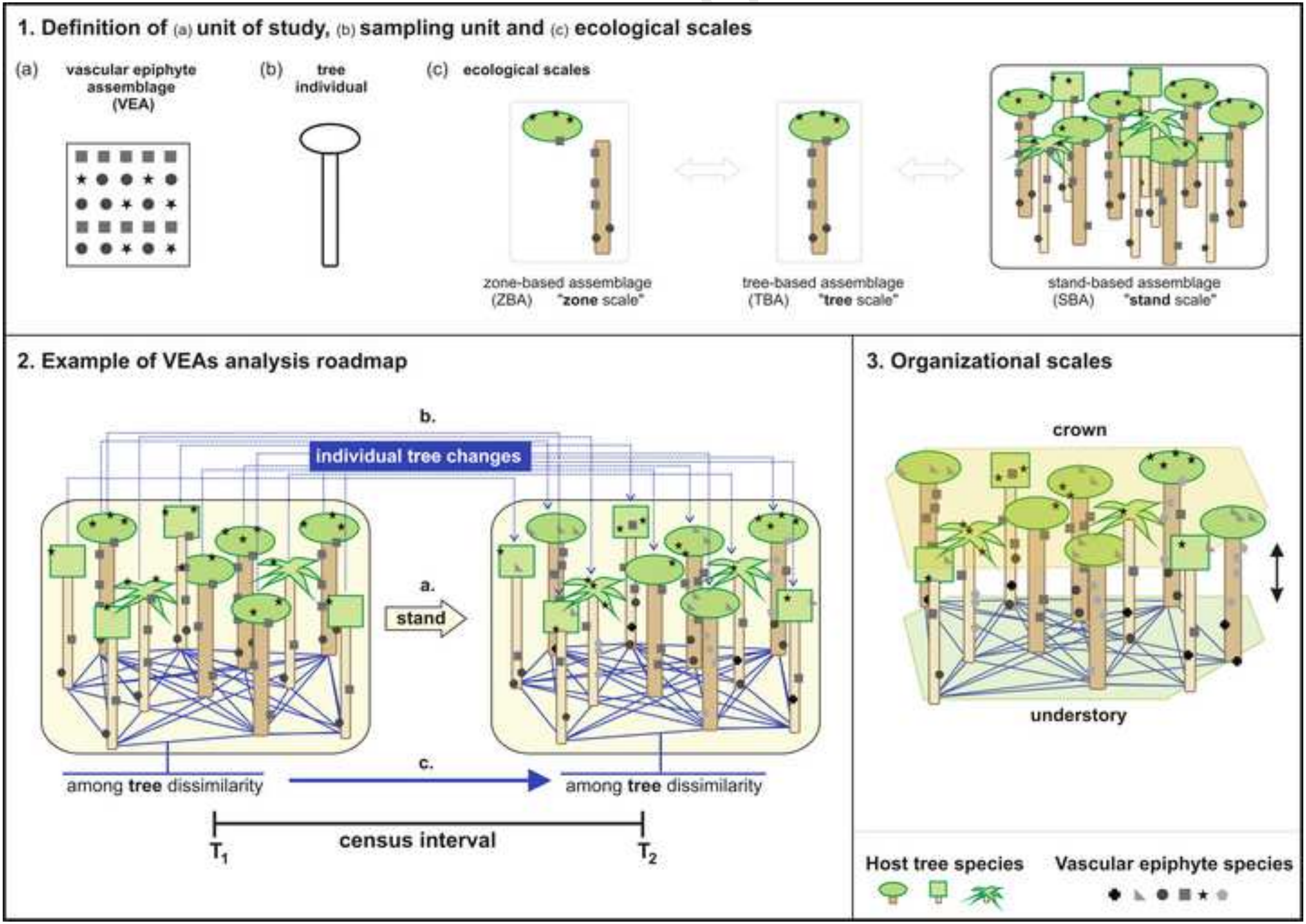
1. Definition of (a) unit of study, (b) sampling unit and (c) ecological scales
(a) vascular epiphyte assemblage (VEA)
(b) tree individual
(c) ecological scales
zone-based assemblage (ZBA) "zone scale"
tree-based assemblage (TBA) "tree scale"
stand-based assemblage (SBA) "stand scale"
2. Example of VEAs analysis roadmap
b.
individual tree changes
a.
stand
c.
among tree dissimilarity
among tree dissimilarity
T_1
census interval
T_2
3. Organizational scales
crown
understory
Host tree species
Vascular epiphyte species

Figure 3

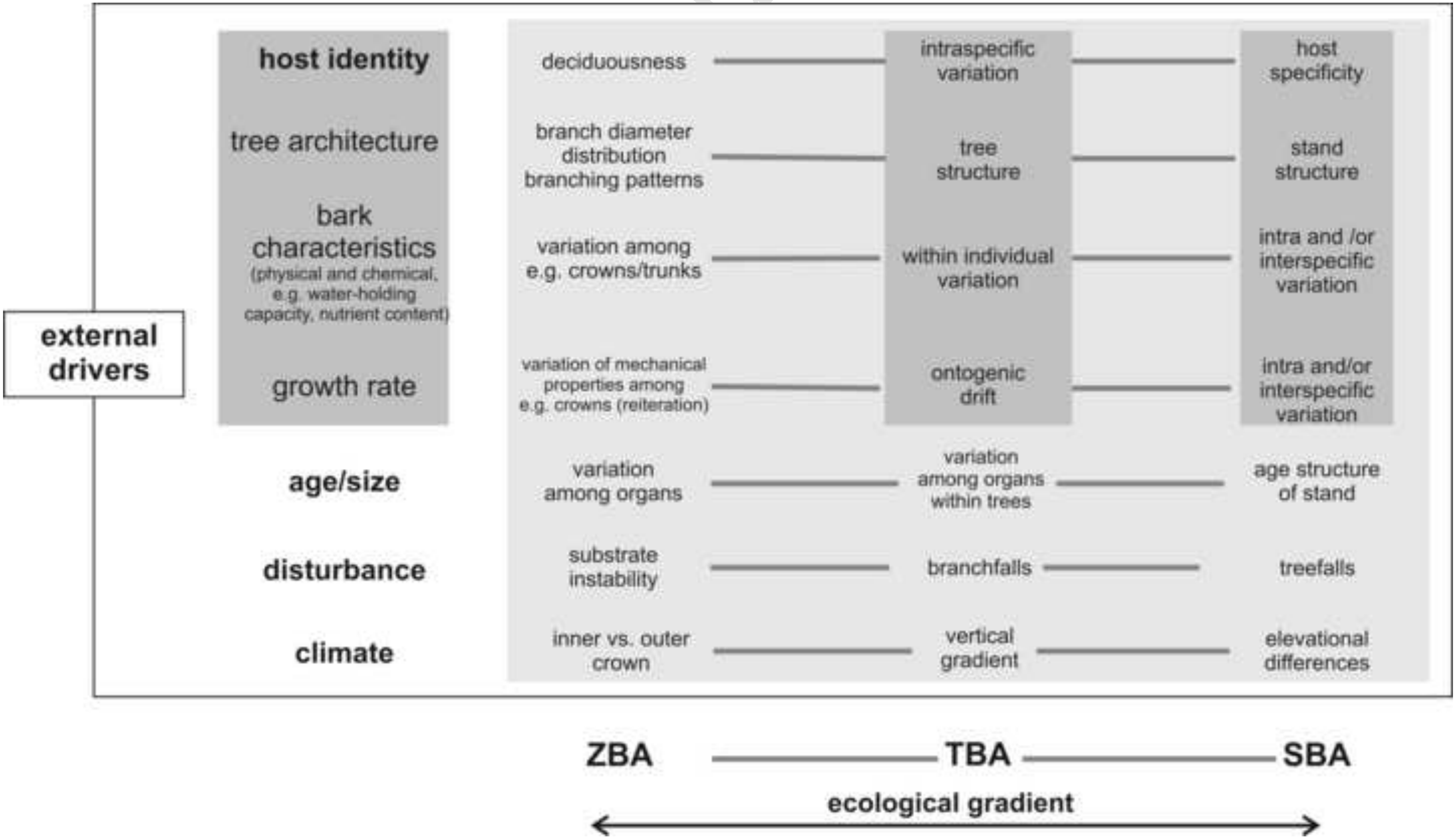
external drivers
host identity
tree architecture
bark characteristics (physical and chemical, e.g. water-holding capacity, nutrient content)
growth rate
age/size
disturbance
climate
deciduousness
intraspecific variation
host specificity
branch diameter distribution branching patterns
tree structure
stand structure
variation among e.g. crowns/trunks
within individual variation
intra and /or interspecific variation
variation of mechanical properties among e.g. crowns (reiteration)
ontogenic drift
intra and/or interspecific variation
variation among organs
variation among organs within trees
age structure of stand
substrate instability
branchfalls
treefalls
inner vs. outer crown
vertical gradient
elevational differences
ZBA
TBA
SBA
ecological gradient

Figure 4

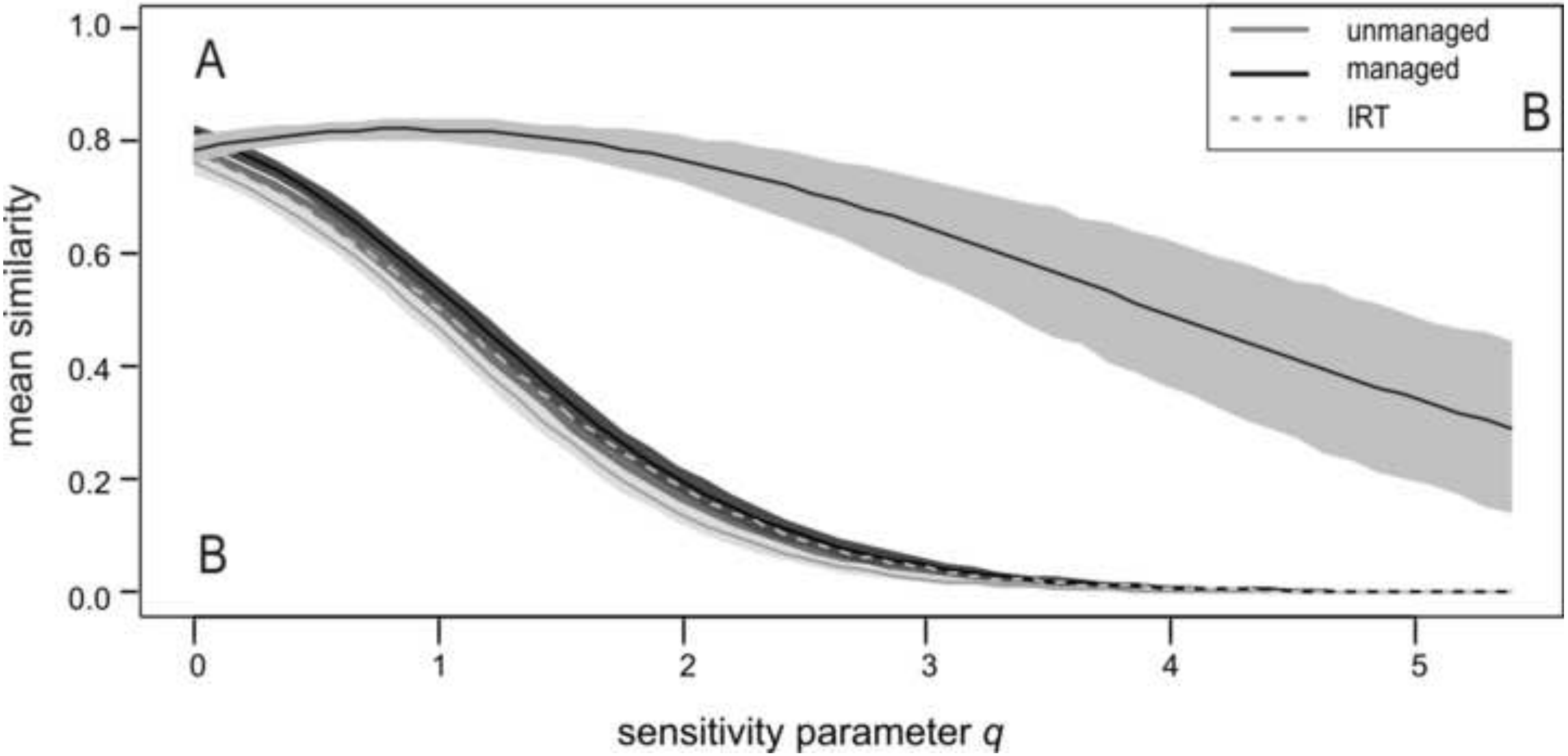
1.0
0.8
0.6
0.4
0.2
0.0
mean similarity
A
B
unmanaged
managed
IRT
B
0
1
2
3
4
5
sensitivity parameter q

Figure 5

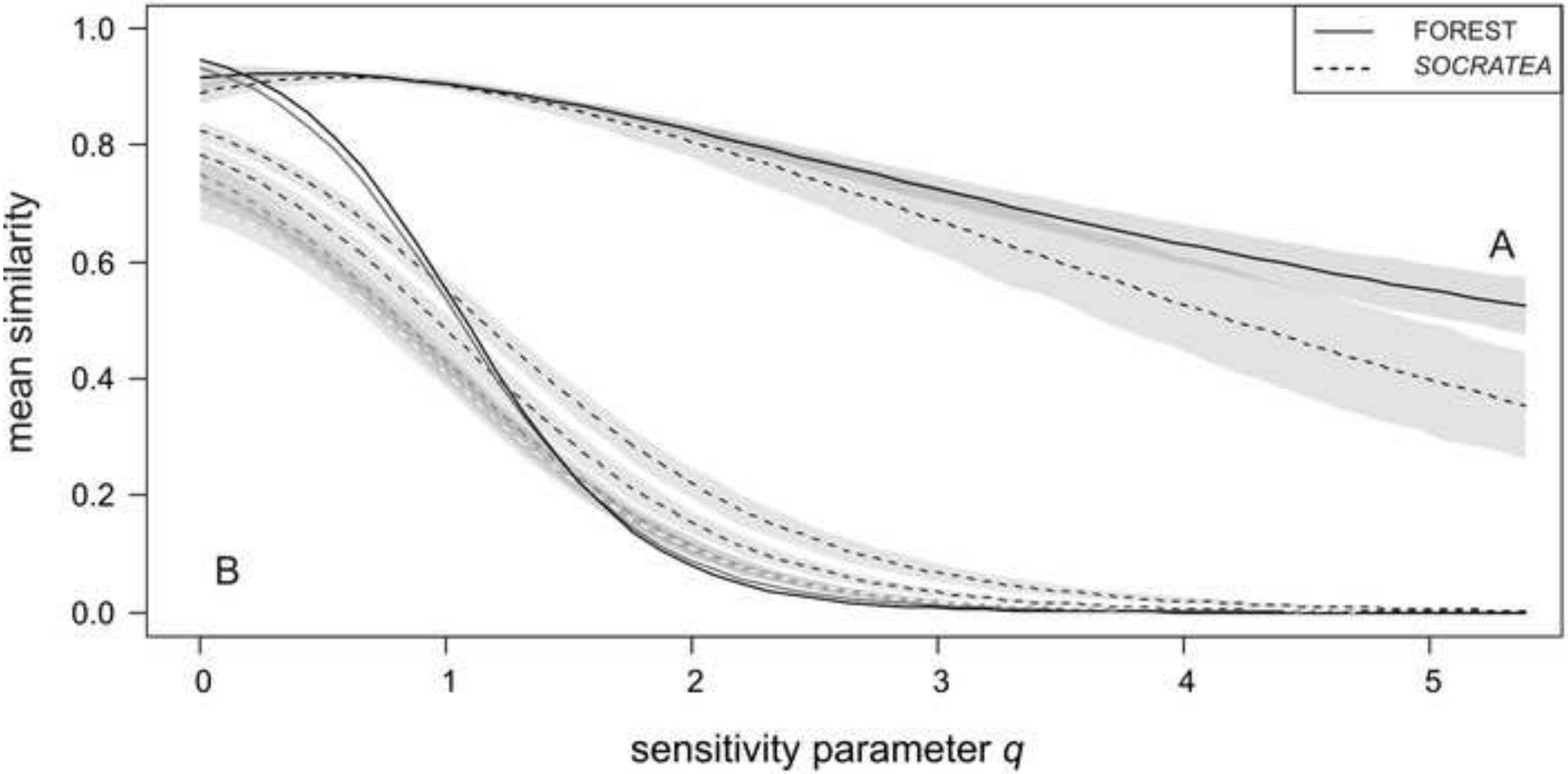
1.0
0.8
0.6
0.4
0.2
0.0
mean similarity
0
1
2
3
4
5
sensitivity parameter *q*
FOREST
SOCRATEA
A
B

Table 1 Compilation of studies on vascular epiphytes assemblages, defined as a set of > 1 species with information on abundance, within a specified spatial unit. An asterisk (*) next to the publication details that although the total abundance is not explicitly mentioned in the paper, is hypothetically available. SDC: indicates the minimum scale at which data has been collected and SDA: indicates the scales used in data analysis (compare Fig. 1 and 2);sSBA: single stand and mSBA: multiple stands. Time: indicates the length of the study in months (in studies with a temporal component), Species and individuals: the number of species and individuals and Scope: indicates studies including the entire assemblage found in a defined spatial scale (AS) and others, which focused on particular epiphytic taxa (TS). Based on the available data as described in the MM section of each study, we provide examples of analytical tools that could be potentiallyapplied, i.e. DP.: diversity profile(s), SP.: similarity profile(s) (space: across ecological scales and time: in time), Direct: Directionality of species composition (Feeley et al., 2011).

Publication	Altitude (masl.)	SDC	SDA	Time	Species	Individuals	Scope	DP	SP space	SP time	Direct
Adhikari et al. (2012a)	1248-1728	TBA	SBAs		20	127	TS				
Adhikari et al. (2012b)	1248-1728	TBA	SBAs		20	127	TS				
Aguirre et al. (2010)	10	TBA	SBAs		11	345	AS	x	x		
Annaselvam and Parthasarathy (2001)	600-660	TBA	SBAs		26	3392	AS	x			
Arévalo and Betancur (2006)	250-350	TBA	SBAs		182	2016	AS	x	x		

Barthlott et al. (2001)*	2200-2700	TBA	SBAs		178/66	NA/1101	AS	x			
Benavides et al. (2005)	800	TBA	ZBAs,SBAs		213	6129	AS	x	x		
Benavides et al. (2011)	800	TBA	SBAs		236	5826	AS	x	x		
Bennett (1986)	<10	TBA	SBA	10	18	3789	TS				
Boelter, et al. (2014)	30-180	TBA	TBA,SBAs		122	21733	AS	x	x		
Bøgh (1992)	2900	TBA	ZBAs		104	3379	AS	x			
Brown (1990)*	900/1050	TBA	ZBAs,SBAs		47	NA	AS	x	x		
Burns and Zotz (2010)	130	TBA	TBA,SBAs		77	3709	AS	x			
Cardelus et al. (2007)	35-135	ZBA	ZBAs		53	2415	AS				
Carlsen (2000)	120	TBA	ZBAs		22	243	AS				
Cascante et al. (2006)	1050	TBA	SBAs		9	630	TS				
Goode and Allen (2008)[+]	<10	TBA	SBAs	4	22/18	3123/1429	AS	x	x	x	x
Gottsberger and Morawetz (1993)	50	TBA	SBA		7	118	AS	x			
Hietz (1997)	1300	ZBA	ZBAs	24	44	5124	AS				
Hietz et al. (2002)	1300	ZBA	ZBAs	60	7	946	TS				
HietzandHietz-Seifert (1995b)	1350	ZBA	ZBAs		39	1843	AS				

HietzandHietz-Seifert (1995a)*	720-2370	TBA	TBA,SBAs		22-53^{a}	(1*)	AS	x	x		
Hirata et al. (2009)	380-520	TBA	TBA,SBAs		21	578	TS				
Irume et al. (2013)	60-70	TBA	ZBAs,TBA,SBAs		164	3528	AS	x	x		
Isaza et al. (2004)	2900	TBA	TBA,SBAs		6	4395	TS				
Jácome et al. (2004)	200	TBA	TBA,SBAs		52	2957	TS				
Kluge and Kessler (2011)*	100-3400	TBA	ZBAs,SBAs		336	NA	TS				
Kreft et al. (2004)	230	TBA	SBA		146	8762	AS	x			
Larrea and Werner (2010)	2250	TBA	TBA,SBAs		115	760	AS	x			
Laube and Zotz (2006a)	130	TBA	TBA,SBA	60	65	763/899/957	AS	x		x	x
Laube and Zotz (2006b)	130	TBA	TBA,SBAs		39/47/22	354/496/227	AS	x			
Laube and Zotz (2007)	26	TBA	TBA,SBA	96	59/67	15000/23700^{b}	AS	x		x	x
Linares et al. (2009)	900-1100	TBA	SBAs		142	39735^{b}	AS	x	x		
Liu et al. (2010)	680-800	TBA	TBA,SBAs		27	769	AS	x			
Martinez-Melendez et al. (2008)	2500	TBA	TBA,SBAs		43	86387	AS	x			
Mehltreter et al. (2005)	1500-1600	ZBA	ZBAs		55	910	AS				
Nieder et al. (2000)	105	TBA	TBA,SBA		53	778	AS	x	x		

Pos and Sleegers (2010)	60	TBA	ZBAs		60	476	AS	x			
Quaresma and Jardim (2014)	<10	TBA	TBA,SBAs		11	477	AS	x	x		
Quaresma and Jardim (2012)	<10	TBA	SBA		8	1339	TS				
Reis and Fontoura (2009)	285-573	TBA	TBA		19	526	AS	x	x		
Rosenberger and Williams (1999)	1500	ZBA	ZBAs	12	35	379/408	AS				
Rudolph et al. (1998)	1780-2000	ZBA	ZBAs		81	2677	AS				
Ruiz et al. (2014)	1495	ZBA	ZBAs,SBAs		6	861	AS				
Sáyago et al. (2013)	500	TBA	SBAs		12	1304	TS				
Schmit-Neuerburg (2002)	105	TBA	SBA	48	62/80	980/1860	AS	x		x	x
Valdivia (1977)	100-160	TBA	TBA		153	13082	AS	x			
Vergara-Torres et al. (2010)	1495	TBA	SBAs		10	7501	AS	x	x		
Werneck and Do Espirito-Santo (2002)	1400	TBA	ZBAs,SBA		6	712	AS	x			
Werner, F. A. (2011)	2000	ZBA	ZBAs	36	NA	802	AS				
Wester et al. (2011)	550	TBA	SBA		147	8819	AS	x			
Winkler and Hietz (2001)	1350	ZBA	ZBAs	(2*)	3	1167	TS				
Winkler, M. et al. (2007)	1350	ZBA	ZBAs	36	5	1190	TS				

Winkler, M. et al. (2009)	1350	TBA	TBA,SBAs	48	3	NA	TS		
Zimmerman and Olmsted (1992)	<50	TBA	TBA,SBA		15	473	AS	x	x
Zotz (2007a)	130	TBA	ZBAs		45	11387	AS	x	
Zotz (2007b)	130	TBA	SBA		70	13099	AS	x	
Zotz et al. (1999)	26	TBA	TBA,SBA		68	15000	AS	x	
Zotz et al. (2014)	3300-3400	TBA	SBA		15	5322	AS	x	x
Zotz and Schultz (2008)	130	TBA	TBA,SBA		103	13099	AS	x	
Zotz and Vollrath (2003)	130	TBA	TBA		66	701	AS	x	
Zytynska et al. (2011)	300-600	ZBA	ZBAs		63	2142	TS		

We searched in Web of Science^{TM}the keywords: “vascular epiphyte”in combination with“assembly”, “community”, “structure”, “composition”and“diversity”, published until 2014. Publications in the specialized journal “Selbyana” were considered additionally, since the journal is not indexed in Web of Science^{TM}. We restricted our search to studies with data on assemblage structure (abundance, *sensustricto*: number of individuals), since other metrics such as cover, biomass or frequency (e.g. Acebey et al., 2010) would not be comparable and may be dependent on species-specific characteristics (e.g. Affeld et al. 2008, Muñoz et al. 2003).We included studies conducted in natural forest and in those studies comparing natural forest with disturbed areas, only data from natural forest areas is shown (whenever possible).Methodological studies were not included either(e.g. Burns, 2010; Wolf et al., 2009).We found a total of 318 studies, from these, 74% were excluded mostly because only a single aspect of diversity was considered (species composition or species richness). Within the remaining studies, although all contemplated the word "abundance" in their abstracts, many used currencies of abundance other than the number of individuals; thus weobtained a total of ~~55~~ 62studies. In some cases, more than one number of species or individuals is shown, these belong to different ecological scales or censuses. (1*) indicates that biomass was based on count data and (2*) that temporal data was provided by a previous study, the data consisted on the substrate's branch size of an additional set of individuals and their mortality. Based on these data the authors estimated age of fertility and average time to reach full size. Also, (a) indicates species per plot, (b) approximated values and NA, not available data. Finally a plus (+) sign next to the publication indicates that the sampling was spatially limited, the individuals or species distributed above 4 mwere not included.