Perspectives in Plant Ecology, Evolution and Systematics 17 (2015) 510–521

Contents lists available at ScienceDirect

Perspectives in Plant Ecology, Evolution and Systematics

journal homepage: www.elsevier.com/locate/ppees

Review

A conceptual framework for the analysis of vascular epiphyte assemblages

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ARTICLE INFO

Article history:
Received 7 October 2014
Received in revised form 8 September 2015
Accepted 18 September 2015
Available online 21 September 2015

Keywords:
Assemblage
Ecological scales
Host individual
Environmental heterogeneity
Diversity
Vascular epiphytes

ABSTRACT

Despite their ecological importance, particularly in tropical rainforests, vascular epiphytes are among 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 analyzed 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.

Contents

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http://dx.doi.org/10.1016/j.ppees.2015.09.003
1433-8319/

1. 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 among 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 and 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 and 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,b). 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, 2013a,b) 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 and 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 and 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.

2. 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