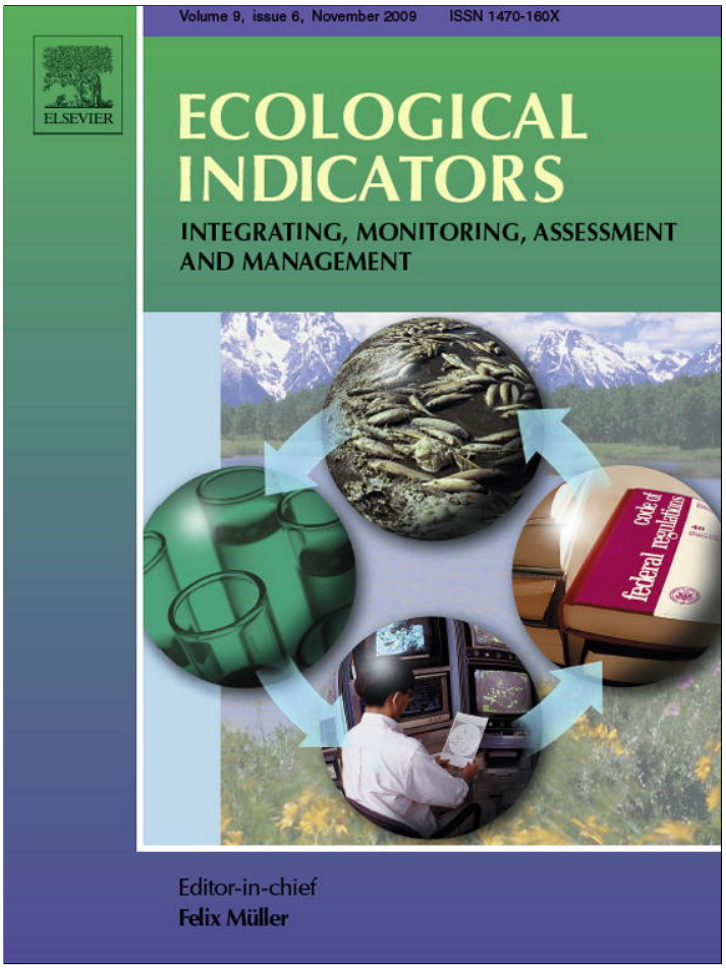

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A flexible multi-scale approach for standardised recording of plant species richness patterns

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ABSTRACT

A sound monitoring of appropriate biodiversity indicators is necessary in order to assess the progress towards the internationally agreed target of halting the loss of biodiversity by 2010. However, existing monitoring schemes often do not address species richness as a key component of biodiversity directly or do so with insufficient methods. I provide an overview and assessment of the large variety of different sampling approaches for small-scale plant species richness. Major shortcomings of many of these are (i) non-uniform plot sizes or shapes; (ii) analysis of only one spatial scale despite the scale dependence of nearly all biodiversity parameters; (iii) lack of replication of smaller subplots; and (iv) exclusion of bryophytes and lichens despite their often large contribution to total plant diversity. Based on this review, I propose a new standardised sampling approach for plant diversity patterns at small scales that is applicable for a multitude of purposes and in any biome. In its basic variant, species composition is recorded on nested squares of 0.01 m^2, 0.1 m^2, 1 m^2, 10 m^2, and 100 m^2, with all smaller subplots being replicated at least 3-fold and evenly spaced within the next larger plot. Not only terricolous vascular plants, but also bryophytes, lichens, macro-algae as well as non-terricolous taxa should be recorded with the any-part system, i.e. those plants are counted within a plot whose superficial parts reach over it. This approach can be used to assess plant diversity patterns (i) of individual plots of interest, (ii) along environmental gradients, (iii) within specific vegetation types, or (iv) for landscape sectors. In the latter case, the series of nested plots must be placed randomly or systematically, but irrespective of plot homogeneity. The proposed approach allows the calculation of many meaningful biodiversity indicators, while being well compatible with a range of other sampling schemes, but avoiding their shortcomings. As this approach is not very time-consuming in its basic variant, but can easily be extended for specific purposes, I suggest its use for any kind of biodiversity studies and particularly for monitoring.

1. Introduction

Biodiversity is seriously threatened by anthropogenic global change (Sala et al., 2000). At the 2002 World Summit on Sustainable Development in Johannesburg, 190 nations agreed on "... achieving by 2010 a significant reduction in the current rate of biodiversity loss at the global, national, and regional level ..." (Balmford et al., 2005a, b; EEA, 2007). Biodiversity may be lost due to many different processes, such as climate change, intensification of agriculture on productive sites, abandonment of agriculture on marginal sites, direct habitat loss, habitat fragmentation, and nitrogen deposition (e.g. Sala et al., 2000). Various measures have been taken to counteract these negative tendencies, for example, by establishment of nature reserves, 'agri-environment schemes', or organic farming. However, it is largely unknown whether and how these numerous presumably negative and positive factors actually influence biodiversity. Moreover, 'biodiversity' is not a single, easy-to-measure figure, but a multi-facetted phenomenon, ranging from genes, over species to ecosystems, including both the number of different 'entities', their composition and spatial variability, and behaving differently for different taxa and at different spatial scales (e.g. Heywood and Watson, 1995; van der Maarel, 1997).

For species diversity as the central dimension of biodiversity, global patterns are well documented and reasonably understood for vascular plants and vertebrates, but only at large spatial scales (10,000 km^2 and more) (Gaston, 2000; Mutke and Barthlott, 2005). In well-surveyed regions as some parts of Europe, for vascular plants and bryophytes data of good quality are available down to the scale of quadrants of topographic map sheets (approximately 30 km^2) (e.g. Benkert et al., 1996; Meinunger and Schröder, 2007). For smaller scales, such as 1 m^2 or 1000 m^2, it is presently even in central Europe impossible to answer seemingly trivial questions such as "What is the mean species density?" or "Which are the

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most frequent taxa?" However, these are the scales on which species interact with each other and with their changing environment; thus, processes at these small scales ultimately produce the well-known global patterns.

Nearly all aspects of biodiversity are scale-dependent, the species–area relationship (SAR) being only the most prominent one (Connor and McCoy, 2001; Crawley and Harral, 2001; Turner and Tjørve, 2005; Dengler, 2009). Regarding botanical diversity, spatial scale also affects co-occurrence patterns (e.g. Otýpková and Chytrý, 2006), species turnover along abiotic and land-use gradients (e.g. Reed et al., 1993; Spiegelberger et al., 2006), spatial patterns of diversity metrics (e.g. Kallimanis et al., 2008), species frequency distributions (reviewed in Dengler, 2003), as well as species constancies and thus vegetation classification (Dengler, 2003). Even species diversity patterns that are nearly universal at large scales may be reversed at small scales. Dengler and Löbel (2006) and Dengler and Boch (2008a), for example, found higher plant species richness at plot scale in the hemiboreal compared to the nemoral zone, contrasting to the usually assumed negative diversity trend towards the poles (e.g. Gaston and Spicer, 2004). Similarly, small-scale richness of vascular plants and bryophytes significantly increases in Switzerland from the colline to the montane to the subalpine belt (Koordinationsstelle Biodiversitätsmonitoring Schweiz, 2006), which deviates from the typical elevational decrease at larger scales (e.g. Gaston and Spicer, 2004).

A meaningful set of biodiversity indicators for monitoring is needed in order to assess progress towards the 2010 target of halting biodiversity loss (Balmford et al., 2005a, b; Dudley et al., 2005; see also Dröschmeister, 2000). Strangely, among the many proposed indicators within the framework of the Convention on Biological Diversity (CBD; see Balmford et al., 2005a; EEA, 2007) none addresses species richness directly and the majority even lack a straightforward relation to biodiversity. The coverage of protected areas or forests (two of the proposed indicators), for example, is not necessarily positively related to all components of biodiversity (see Dudley et al., 2005). Even recent biodiversity monitoring schemes that explicitly address plant species richness (e.g. Dröschmeister, 2001; Seidling, 2005) often neglect the scale dependency of biodiversity (by studying only one spatial scale) or the many methodological pitfalls involved in small-scale species richness sampling (for review, see Dengler, 2008).

With this article, I aim at providing an overview of existing major approaches for assessing species diversity and at evaluating their merits and shortcomings. As a result, I will present a new flexible multi-scale sampling approach. My focus is on botanical diversity, representing the one component of ecosystems that usually constitutes the major proportion of biomass, that shapes ecosystem functions and services, and that can be most easily assessed in a near-comprehensive manner (as compared to animals, fungi, and microbes).

2. Overview and evaluation of existing approaches

With the following review, I do not intend to list the multitude of published approaches comprehensively, but to discuss some major categories of widely used methodologies for recording local plant diversity patterns.

2.1. Phytosociological surveys

Phytosociological records, so-called relevés, presently probably constitute the largest proportion of available data on small-scale plant species richness. Numerous such relevés have been taken according to procedures described in phytosociological textbooks (e.g. Braun-Blanquet, 1964; Westhoff et al., 1973; Dierschke, 1994) in order to describe and classify vegetation, to analyse relationships between community composition and environment, and partly also to monitor vegetation changes. Worldwide, there are several million relevés, partly published, partly unpublished (Ewald, 2001; J. Schaminée and M. Chytrý, 2008, personal communication). In a recent survey, J. Schaminée and M. Chytrý (2008, personal communication) concluded that in Europe alone more than three million relevés exist. These relevés become increasingly available in large regional or national databases, e.g. approximately 460,000 in the Dutch database (Schaminée et al., 2006), 70,000 in the Czech database (Chytrý, 2007), and 50,000 in the largest German database, that of Mecklenburg-Vorpommern (Berg et al., 2004). These high numbers of relevés in combination with their good spatial (e.g. Berg and Dengler, 2004; Schaminée et al., 2006; Chytrý, 2007) and temporal coverage (phytosociological relevés have been taken in a basically similar way since nearly one century) constitute a great, yet largely unused potential for addressing ecological questions and for monitoring environmental change (Ewald, 2001; Dengler et al., 2008). Unfortunately, this potential power of past phytosociological data for biodiversity and other ecological research is diminished by several shortcomings: (i) phytosociological sampling procedures vary in many ways between researchers and are not always clearly documented in the studies (cf. Dengler, 2003); (ii) phytosociologists often place their plots subjectively according to the occurrence of assumed character species (see Glavač, 1996), leading to biases in species richness and species compositional data (e.g. Diekmann et al., 2007); (iii) in phytosociology, a very wide range of plot sizes has been suggested (e.g. Westhoff et al., 1973; Dierschke, 1994) and applied (see Chytrý and Otýpková, 2003), typically differing by a factor of 1000 within and 10,000 between vegetation classes; (iv) according to circumstantial evidence, relevés of larger plots are often rather incomplete (Chytrý, 2001; Dengler et al., 2006).

2.2. Whittaker plots and their modifications

In contrast to phytosociological relevés, 'Whittaker plots' have been specifically developed by R.H. Whittaker for sampling and comparing biodiversity patterns (Shmida, 1984; see Table 1). Whittaker plots together with their recent modifications are widely used in North America and in semiarid regions worldwide. In the original version (Shmida, 1984), a Whittaker plot consists of four different plot sizes, namely 1 m^2, 10 m^2, 100 m^2, and 1000 m^2, with the 10 m^2 plots replicated twice and the 1 m^2 plots ten times and the plots arranged in a nested manner in the centre of the largest plot. While the 1 m^2 and 100 m^2plots are squares, the 10 m^2 and 1000 m^2plots are rectangles with a length–width ratio of 5:2. Two new variants of Whittaker (WH) plots have been suggested by Stohlgren and co-workers: the 'Modified-Whittaker' (MW; see Table 1) and the 'Long-Thin' (LT) plot designs (Stohlgren, 1995, 2007; Stohlgren et al., 1995). Both use the same four plot sizes as the original, but differ in three aspects: (i) they apply (nearly) identical length–width ratios for all sizes, namely 5:2 or 4:1 in MW plots and 10:1 in LT plots; (ii) the subplots below 1000 m^2 are not nested within each other; (iii) the replicates of the smaller areas are placed as far from each other as possible. In the North Carolina Vegetation Survey (Peet et al., 1998; Fridley et al., 2005; see Table 1), the original Whittaker design is modified by adding two smaller plot sizes (0.1 m^2 and 0.01 m^2), by using square plots for all but the 1000 m^2 areas (which retain the 5:2 shape), and by having four replicates of 10 m^2 size and eight of all smaller sizes. Contrary to MW and LT designs, the smaller plots are fully nested. BIOTA biodiversity observatories, which are widely used for biodiversity monitoring in Africa (www.biota-africa.org; see Jürgens, 2006), are another variant of Whittaker's fundamental approach. Each observatory consists of an area of 1 km × 1 km, subdivided in one hundred 1-ha grid cells, 20 of which are selected for detailed

Table 1
Overview of major characteristics of four typical multi-scale plant diversity sampling schemes compared with the proposal of this paper. Note that 'nestedness' here refers only to the arrangement of the smaller subplots relative to each other. Ultimately, the subplots in any of the five approaches are nested within the single largest plot.

	This proposal (variant of Fig. 2)	Whittaker plot (Shmida, 1984)	Modified-Whittaker plot (Stohlgren, 1995)	CVS (Peet et al., 1998; Fridley et al., 2005)	Dolnik (2003)
Plot size range	0.01–1000 m^2	1–1000 m^2	1–1000 m^2	0.01–1000 m^2	0.0001–900 m^2
Number of plot sizes	6	4	4	6	16
Plot sizes as geometric series	Yes	Yes	Yes	Yes	No
Plot shape(s)	Squares (all)	5:2 rectangles and squares (alternately)	5:2 and 4:1 rectangles (alternately)	5:2 rectangle (1000 m^2); squares (all other)	Squares (all)
Nestedness	Yes	Yes	No	Yes	Yes
Replicates of smallest size	80	10	10	8	1
Spatial distribution of replicates of smaller sizes	Equally distributed	Contiguous in the centre	Around outer perimeter	Slightly aggregated in the centre	–
Position of centroid(s) for replicates of smaller sizes	Central	Central	Central	Central	Corner
Plant counting scheme	Any-part	Rooted presence and any-part (parallel)	Not specified	Rooted presence	≥1 m^2: any-part; <1 m^2: rooted presence
Non-vascular plants recorded	Yes	No	No	No	Yes
Non-terricolous plants recorded	Yes	No	No	No	Yes

analyses, namely recording species lists of vascular plants for 10,000 m^2, 1000 m^2, 100 m^2, and partly also for 10 m^2 and 1 m^2 on nested, non replicated subplots. As in the WH design, plot shapes alternate between squares and 5:2 rectangles.

The fundamental strength of Whittaker plots in all their variants is that they capture the scale dependence of biodiversity by recording species composition and richness at multiple spatial scales. Moreover, they established a series of standard plot sizes for doing so (1 m^2, 10 m^2, etc.), which are equally spaced on logarithmic scale. However, plot shapes that vary between spatial scales in many variants of the Whittaker plots pose a serious problem for analysis because average species richness increases with decreasing compactness of a plot (for review, see Dengler, 2008). Thus, identical shapes would be desirable at all sizes, which is the case only in the LT variant. Stohlgren (1995, 2007) prefers elongated plots to squares because they usually would contain more species. However, in elongated plots the abiotic environment is typically less homogenous than in square plots of the same size and thus the species–environment relationship is less straight (cf. Dengler, 2003). Moreover, elongated plots produce deviating results dependent on whether the long axis is oriented parallel or perpendicular to environmental gradients.

2.3. Other sampling schemes in individual studies

In contrast to common phytosociological practice, some biodiversity studies apply a uniform plot size throughout. Dierßen (2006), for example, suggests using 400 m^2 as a standard for recording plant species richness. The application of the same plot size irrespective of vegetation structure has its merits, but the restriction to only one spatial scale neglects the scale dependency of biodiversity. Moreover, there is no general agreement on such a standard area.

In sampling species–area data, various authors applied many different approaches. Dolnik (2003) (see Table 1), for example, used a design inspired by the system formerly used in phytosociology to establish so-called minimal areas (e.g. Mueller-Dombois and Ellenberg, 1974) with nested-plots of 0.0001 m^2, 0.0025 m^2, 0.01 m^2, 0.0625 m^2, 0.25 m^2, 1 m^2, 4 m^2, 9 m^2, 16 m^2, 25 m^2, 49 m^2, 100 m^2, 225 m^2, 400 m^2, 625 m^2, and 900 m^2 size. His approach stands out by covering an extremely wide range of plot sizes (nearly seven orders of magnitude) and by thoroughly including non-vascular and non-terricolous plants, but has the smaller subplots not being replicated and their sizes not being equally spaced on log (A) scale, thus giving biased estimates of SAR parameters (see Dengler, 2008). Chiarucci et al. (2001) used a partly nested design (i.e. not all plots were nested within a plot of the next larger size) to characterise species diversity patterns of vascular plants in forests at spatial scales of 1 m^2, 10 m^2, 100 m^2, 500 m^2, 1000 m^2, and 2500 m^2 with different numbers of replicates and different plot shapes at the individual scales. Chiarucci et al. (2006), as final example, sampled vascular plant richness in experimentally manipulated grasslands using nested square plots from 0.004 m^2 to 256 m^2 with a 4-fold increment in area between subsequent sizes and only one replicate per plot size within each series.

2.4. German biodiversity monitoring scheme

In Germany, a national biodiversity monitoring scheme named Ecological Area Sampling (EAS; German: "Ökologische Flächenstichprobe" = ÖFS) has been developed since the mid-1990s (Hoffmann-Kroll et al., 1995, 2000; StBA and BfN, 2000; Dröschmeister, 2001). It aims at assessing state and trends of a wide range of different biodiversity indicators for the so-called "normal landscape" in five-year intervals. For the monitoring, 800 landscape sectors of 1 km^2 have been selected throughout Germany with a stratified-random approach (Hoffmann-Kroll et al., 2000; Dröschmeister, 2001). While at level I, the EAS analyses landscape structure, land-use intensity, diversity and endangerment of biotopes for the complete 1 km^2 sectors (Dröschmeister, 2001), at level II, it aims at addressing species diversity and related indicators. For breeding birds, level II is already implemented Germany-wide, providing reliable data for population trends based on complete censuses of the 800 sample units (e.g. BfN, 2008). By contrast, only in North Rhine-Westphalia level II monitoring is regularly also applied for the flora (König, 2003). The idea of the level II monitoring for plant diversity is to draw randomised subsamples within each of the 1 km^2 squares, stratified according to biotope type, resulting in approximately 22,000 plots in the non-forested part of Germany alone, unevenly spread among sample units and biotope types (StBA and BfN, 2000; Dröschmeister, 2001). This monitoring scheme has several drawbacks: (i) it is incapable of addressing changes in species diversity at landscape scale as it uses predefined biotope types (and even excludes some of them from sampling) and is thus not able to integrate the consequences of changes in proportion and spatial arrangement of biotopes on species diversity, and even less so of the potential emergence of new biotope types within sample units due to land-use and climate change; (ii) by analysing only one spatial scale it fails to address the scale dependence of biodiversity; (iii) due to the use of different plot sizes (8 m^2, 20 m^2, 36 m^2, 400 m^2) and shapes

(squares, 5:4 rectangles, 20:1 rectangles) for different biotope types (see Hoffmann-Kroll et al., 2000; StBA and BfN, 2000; Dröschmeister, 2001), no comparisons among these are possible.

2.5. Swiss biodiversity monitoring scheme

Although similar to the EAS at first glance, the Swiss biodiversity monitoring (BDM; Hintermann et al., 2000) is more sophisticated. For vascular plants, two different spatial scales, 10 m^2 and 1 km^2, are analysed, and in both cases a systematic grid sampling irrespective of biotope types is applied, which allows statistically valid statements over the whole of Switzerland. At the 10 m^2 scale, this approach provided mean richness values of vascular plants and bryophytes in Switzerland for the first time, allowing meaningful comparisons between landscape types (forest, grassland, settlement, ...) and altitudinal belts (colline, montane, subalpine) with surprising results (Koordinationsstelle Biodiversitätsmonitoring Schweiz, 2006). At the 1 km^2 scale, the BDM data provided a sound basis for modelling vascular plant richness patterns in Switzerland dependent on abiotic parameters (Wohlgemuth et al., 2008). However, the 1 km^2 data do not actually quantify the diversity of the whole square kilometre, but only the diversity of a 2.5 m buffer zone on both sides of a transect of 2.5 km length, which is arranged according to certain criteria within the square kilometre (Hintermann et al., 2000; Wohlgemuth et al., 2008). It is unknown which proportion of the species richness on 1 km^2 is captured by this procedure and whether this proportion is constant in different landscape types.

2.6. European forest monitoring scheme

For European forests, a supra-national monitoring scheme has been developed within the 'International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests' (ICP Forests), the so-called 'Level II monitoring' (Schulze et al., 2000; Seidling, 2005; BMELV, 2006; Aamlid et al., 2007). On level II sites, data on ground vegetation (including terricolous bryophytes and lichens) shall be sampled on a common standard area (CSA) of 400 m^2; however, the sampling protocol does not define the shape of this CSA and even allows the combination of several incontiguous subplots (Aamlid et al., 2007). In practice, methodology varies even more, with plot sizes ranging from 10 m^2 to 1200 m^2 and non-vascular plants being only partly included (Schulze et al., 2000). If epiphytic cryptogams are sampled at all, this is done with a methodology deviating from the one used for the ground vegetation (BMELV, 2006).

2.7. Overall assessment

As shown, many different, often incompatible biodiversity sampling schemes are presently applied. Moreover, these methodologies are often documented insufficiently or only in 'grey' literature, and they largely ignore important methodological considerations for small-scale species richness sampling and analysis (reviewed in Dengler, 2008). Major weaknesses of most approaches concern the following aspects: (i) plot sizes and shapes are not standardised or reached by the combination of incontiguous subplots; (ii) despite the inherent scale dependence of biodiversity, studies are often confined to only one plot size; (iii) if different plot sizes are included, the smaller subplots are often not replicated or – if replicated – the replicates are arranged inadequately; and (iv) despite the ecological significance of non-vascular plants and their high contribution to total biodiversity, bryophytes and lichens, and particularly non-terricolous cryptogams, are usually disregarded or sampled with deviating schemes.

3. Proposal of a new approach

My proposal of an approach for standardised assessment of plant species richness patterns at multiple spatial scales has been developed and tested since 2004 and has already been mentioned shortly in several publications (Dengler et al., 2004; Dengler, 2006; Dengler and Allers, 2006; Allers and Dengler, 2007; Dengler and Boch, 2008b). In the following, I will describe it in detail (see Table 1). It consists of a basic (minimum) variant, which can be intensified or extended, depending on specific questions and available resources.

3.1. Plot sizes

To address the scale dependence of biodiversity parameters, it is indispensable to sample biodiversity data at various spatial scales (e.g. Shmida, 1984; Peet et al., 1998). For the selection of plot sizes three criteria are decisive: (i) they should cover as wide a range as possible (preferably five orders of magnitude or more) because otherwise discrimination of different species–area models is hardly possible (cf. McGill, 2003; Dengler, 2008); (ii) they should be evenly spaced on logarithmic scale (i.e. form a geometric series) since otherwise species–area analyses would be biased (Dengler, 2008), and (iii) they should preferably match frequently used plot sizes of other sampling schemes.

Accordingly, a 10-fold increment between plot sizes with 1 m^2 as basis is a reasonable solution. Compared to a 4-fold increment (e.g. Chiarucci et al., 2006) this solution allows to cover wider plot-size ranges with less effort, and it avoids odd area sizes such as 64 m^2 or 0.0625 m^2. Moreover, these sizes correspond with those used in Whittaker plots and all their variants (see Section 2) and some of the most frequently used plot sizes in phytosociology (1 m^2; 9 m^2 or 10 m^2; 100 m^2; see Chytrý and Otýpková, 2003; Dengler et al., 2006). As basic sampling variant, I thus suggest to analyse *0.01 m^2, 0.1 m^2, 1 m^2, 10 m^2, and 100 m^2*. If resources allow, the studied range should be extended to 0.0001 m^2 and to 1000 m^2. For specific questions, even smaller or larger plots can be added. For example, Dengler et al. (2004) and Dengler (2006) used 0.000001 m^2 (=1 mm^2) as smallest plot size in their study of dry grasslands.

While for SAR analyses the ratio between largest and smallest plot size should be as large as possible, it is less relevant whether, for example, 0.01–100 m^2 or 0.1–1000 m^2 are studied because SAR parameters are relatively little scale-variant (e.g. Dengler, 2005, 2009; Fridley et al., 2005). However, the time demanded for (near) complete sampling at larger scales can be very high: Dolnik (2003) needed up to 14 h for 900 m^2 plots in nemoral forests (including non-vascular plants and one series of nested subplots), and Klimeš et al. (2001) reported that after 3 h, an experienced researcher had only found 85% of the vascular plant species occurring on 4 m^2 of a semi-dry grassland. Hence, areas larger than 100 m^2 should only be included in studies when researchers are willing to spend sufficient time to produce reliable richness counts at these scales.

In previous variants of the presented approach (e.g. Dengler et al., 2004; Allers and Dengler, 2007), we used 9 m^2 instead of 10 m^2 and so forth because of easier delimitation of such areas as squares. This modification poses no serious problem for species–area analyses because plot sizes are still spaced approximately evenly on logarithmic scale. To allow direct comparability with Whittaker plots, I now suggest to use precise powers of ten as plot sizes and to accept the awkwardness caused by delimitating, for example, a 10 m^2 square as 3.16 m × 3.16 m.

The additional inclusion of intermediate plot sizes may improve comparability with plot sizes frequently applied in a certain vegetation type. Dengler et al. (2004), for example, analysed 4 m^2 in addition to the areas of the present approach because this size is

widely applied in dry grassland studies (e.g. Dengler et al., 2006). For European forests, it would be useful to add 400 m^2 to allow direct comparisons with ICP Forest data (see Section 2.6). To avoid bias, such 'intermediate' plot sizes should be excluded when SAR models are fitted (Dengler, 2008).

3.2. Shape of plots

For a given plot size, species richness depends on the shape of the plot, and normally increases with decreasing compactness (Kunin, 1997; Dengler, 2003, 2008; Stohlgren, 2007). Admittedly, as long as the shape is not too elongated, the richness increase in rectangular vs. square plots, is not very pronounced (typically 0.5–5% more species in 4:1 rectangles) and may not be significant (Keeley and Fotheringham, 2005; for review, see Dengler, 2008). The combination of species lists from incontiguous subplots to achieve species richness values for a certain plot size (e.g. Stohlgren et al., 1995; Aamlid et al., 2007; Chong and Stohlgren, 2007) is completely unreasonable because incontiguous areas normally contain much more species than contiguous areas of the same size (cf. Dengler, 2008; Hui, 2008). Generally, uniform plot shapes should be applied from the smallest to the largest areas. Compact shapes such as circles, squares, or regular hexagons are preferable over rectangles as used in most Whittaker plot variants (see Section 2.2) because they contain the least environmental heterogeneity on average, and their results do not depend on their orientation in space (Dengler, 2003). Of all shapes, circles are the most compact, but the minor difference in compactness usually does not result in significant differences in species richness compared to squares (Stohlgren, 2007). However, circles, in contrast to squares and hexagons, do not allow continuous tessellation of an area, which could be desirable in intensive biodiversity sampling schemes. In such continuous tessellations, hexagons have the advantage over squares that all six adjacent plots of a plot are equally distant, while squares have four closer and four more distant neighbours. While these small disadvantages compared to circles and hexagons are irrelevant in most biodiversity studies, *squares* stand out by allowing easy and clear delimitation, and thus are recommended.

3.3. Replication and spatial arrangement of subplots

Traditional approaches of SAR sampling with only one replicate per plot size (e.g. Mueller-Dombois and Ellenberg, 1974; Dolnik, 2003) have several disadvantages: (i) usually the environmental conditions of a single subplot differ from the average conditions within the largest plot, leading to biases in the SAR model selection (Dengler, 2008; Dengler and Boch, 2008b); (ii) many statistical techniques are only applicable to mean species richness values because small count data deviate strongly from normal distribution, while means of counts are normally distributed (Quinn and Keough, 2002); (iii) only with several replicates of each size the floristic, structural, and environmental heterogeneity and its potential contribution to the richness on the larger spatial scale can be assessed. Thus, *several replicates of all smaller plot sizes* should be sampled. Since the variation coefficient of species richness decreases exponentially with log-transformed area (Dengler, 2006), increasingly more replicates would be necessary for smaller plots to estimate mean species density with identical precision. In the study of Dengler (2006), on average a 24-fold and, in the worst case, a 208-fold increase in replicate number was necessary to maintain precision when plot size was reduced to 10^{-6} of the starting size. Actually, some authors increase replicate numbers successively towards smaller plots (e.g. Shmida, 1984; Barkman, 1989; Peet et al., 1998; Dengler et al., 2004), but hardly as much as the case study suggests. Moreover, the delimitation and sampling of high numbers of small subplots would be time-consuming and detrimental to the studied vegetation. Thus, only a moderate increase in replicates numbers towards smaller sizes can be recommended.

While most studies on SARs and other scale-dependent properties of biodiversity apply a nested-plot design (e.g. Reed et al., 1993; Chiarucci et al., 2001, 2006; Dolnik, 2003; Dengler et al., 2004; Fridley et al., 2005), some authors claim this approach to be inappropriate since it would not allow regression analyses due to non-independence of species counts in nested-plots (Barkman, 1989; Connor and McCoy, 2001; Stohlgren, 2007). Instead, Barkman (1989) suggests a fully random placement of all subplots, while Stohlgren (2007) favours a systematic and non-overlapping placement of all plots within the largest. The criticism of these authors, however, is not justified for several reasons (see also Dengler, 2008): (i) only hypothesis testing is affected by the non-independence of data points but not the estimation of model parameters and goodness-of-fit metrics (Quinn and Keough, 2002); (ii) when comparing different mathematical models for the same nested-plot data, the model selection itself is not biased since the data are equally non-independent in each model; (iii) plots that are non-overlapping but located nearby are similarly affected by spatial autocorrelation (Legendre, 1993). On the other hand, non-nested designs – apart from the higher effort for locating, marking, and sampling – also result in more stochasticity in the recorded richness data and thus may lead to the selection of inappropriate SAR models (Dengler and Boch, 2008b). Thus, *nested-plot sampling* is the most appropriate method for biodiversity assessment as with this method plot of different sizes vary only in area, but not in mean environmental conditions, which would inevitably be the case for non-overlapping sampling schemes (Dengler, 2008). Additionally, complete nestedness (i.e. all plots of a certain size are nested in the plots of the next larger size and not only within the largest plot) allows direct comparison of data, irrespective of the size of the largest plot.

I suggest placing the chosen number of subplot series systematically and equally spaced within the largest plot. As a minimum variant (Fig. 1), three series of subplots (arranged on a diagonal) should be analysed to receive reasonable information on within-plot heterogeneity, but also variants with four, five (Fig. 2), or nine subseries are possible. If the numbers of replicates for the next smaller subplots is kept constant, each of them should be placed in the centre of the superior plot (Fig. 1). Otherwise, the subplots should be evenly spread within the next larger plots (Fig. 2). Various subplot arrangements of different sampling effort are possible in accordance with these 'rules' (Figs. 1 and 2), which allows the adaptation to specific requirements of a project without loosing comparability.

While the reference for area measurement makes little difference in plains, in hilly regions, the area of 1000 m^2 projected to the ground plane and 1000 m^2 of the inclined plane defined by the actual earth surface differ significantly. For both reference systems, reasons can be brought forward. In the field, however, only the (idealized) actual earth surface can be used as reference without substantial additional effort. Thus, if biodiversity parameters shall be related to the vertically projected area, such data have to be gained by interpolation afterwards.

3.4. Recording of species

While most publications on plant diversity restrict their analyses to vascular plants, it is crucial to include also all other groups of 'plants' to get the whole picture. In Germany, for example, there are 3755 vascular plant species (Wißkirchen and Haeupler, 1998), but the 1051 bryophyte (Koperski et al., 2000) and 2325 lichen species (Scholz, 2000) together contribute a near-equal share to national

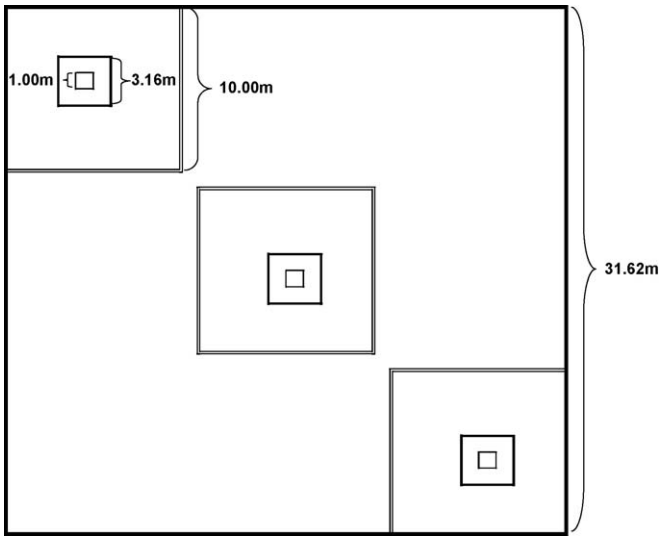

Fig. 1. Minimum variant of the proposed sampling approach with 1000 m^2 as largest plot. Every 1 m^2 plot contains one subplot of 0.1 m^2 and one of 0.01 m^2 (not shown). For the plots of all sizes, species lists of all macroscopically visible plants are to be recorded. Additionally, complete vegetation relevés are compiled at one or several of the spatial scales. Note that for sake of easy delimitation (avoidance of 'odd' values for the coordinates of the corners) the smaller plots may be placed slightly outside the centre of the respective next larger plot.

species diversity. The proportion of endangered species is even higher for lichens (61.3% of the taxa are red-listed in Germany) and bryophytes (45.8%) than for vascular plants (31.5%; Ludwig and Schnittler, 1996). Also at small scales (10^{-6}–10^4 m^2) non-vascular plants typically contribute significantly to species diversity, both in certain vegetation types, such as forests, mires, and dry grasslands, and at landscape scale (e.g. Dolnik, 2003; Dengler, 2005; Dengler and Löbel, 2006; Allers, 2007). Bryophytes and lichens have high ecological significance and 'behave' differently from vascular plants in many ways (see Shaw and Goffinet, 2000; Nash, 2008). Especially species–environment and species–area relationships deviate strongly between vascular plants, bryophytes, and lichens (e.g.

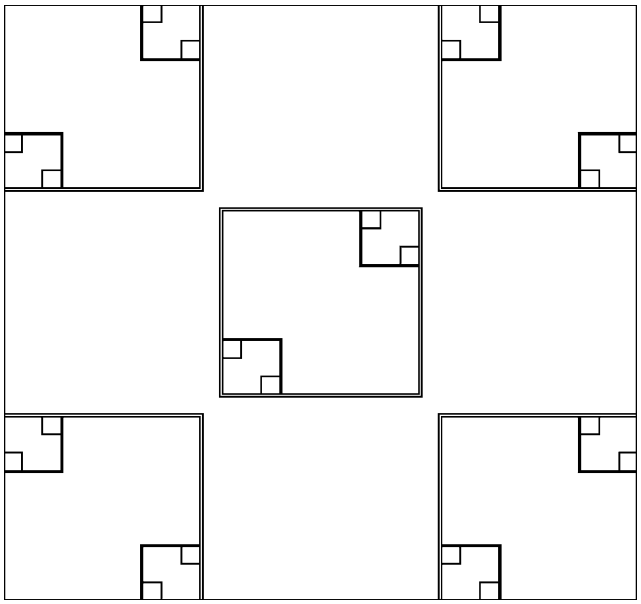

Fig. 2. A more intensive variant of the proposed sampling approach (see also Table 1). Within the 1000 m^2 plot, five 100 m^2 plots are analysed, and towards each smaller scale down to 0.01 m^2, the number of subplot replicates is doubled. (The plots of 0.1 m^2 and 0.01 m^2 size not shown in the drawing.)

Herben, 1987; Löbel et al., 2006; Allers, 2007). Because of the peculiarities of these three taxonomic groups vascular plant richness is only partly suitable as surrogate for non-vascular diversity (Pharo et al., 1999; Dynesius and Zinko, 2006). Finally, bryophytes and lichens are important in bioindication for assessing site conditions (Ellenberg et al., 1991), environmental pollution (Kirschbaum and Wirth, 1997; Frahm, 1998), or land-use history (Coppins and Coppins, 2002; Friedel et al., 2006), and for discriminating vegetation types (Dengler, 2003; Berg and Dengler, 2005). Contrary to the suggestion by Crawley and Harral (2001), also planted taxa should be recorded and included in the analyses (see Allers, 2007) as they are part of the total diversity and use resources that otherwise would be available for spontaneous taxa.

Not only terricolous taxa should be recorded, but also those lichens, bryophytes, and – where applicable – vascular plants that inhabit different substrates, such as other plants (epiphytic taxa), dead wood (lignicolous taxa), or stones (saxicolous taxa). While non-terricolous taxa are usually disregarded in relevés (e.g. Dierschke, 1994; BMELV, 2006), they are relevant in bioindication and may contribute significantly to the total plant diversity of a community (for detailed discussion, see Dengler, 2003). In nemoral forest communities, non-terricolous plants constitute 40–70% of the total plant species richness at the 400 m^2 scale (Dolnik, 2003), and Boch and Dengler (2006) demonstrated that saxicolous taxa increased the plant species richness of certain dry grassland types by 12% on average at the 4 m^2 scale. Thus, I suggest including all 'plants' in the sense of macroscopically visible species from photoautotrophic groups of organisms in the standard scheme for assessing plant species richness, namely *all vascular plants, bryophytes, lichens, as well as macroscopic algae and cyanobacteria, irrespective of whether they grow on soil or not*. Regarding epiphytic species, some limitations must be accepted since in forests tree crowns, which host many epiphytes, are not directly accessible. However, at least in nemoral forests most epiphytes can be captured without climbing the trees by carefully checking the woody plants within accessible height, by analysing fallen branches, and by use of binoculars (see Dolnik, 2003). Finally, it is crucial to record all groups of plants on exactly the same plots of the same size and not to use different plot sizes or approaches for non-terricolous taxa or even non-woody plants (as opposed to trees and shrubs) as suggested by some authors (Schuhwerk, 1986; Gillet and Gallandat, 1996; USDA Forest Health Monitoring, see Stohlgren, 2007).

Williamson (2003) has demonstrated that for small-scale species–area studies the way in which plants are counted on plots is far more important than generally assumed. Grid-point system and any-part system ('shoot presence') denote the two fundamental possibilities, with 'rooted presence' being a not so clearly defined intermediate solution (Williamson, 2003; Dengler, 2008). In the grid-point system each plant is thought of as a point (without spatial extent) that is always assigned to only one of several adjacent plots, while in the any-part system the presence of a species is recorded for any plot in which the vertical projection of the superficial parts of its representatives falls. Towards small areas, the *z*-values (increments) of power-law SARs in the grid-point system approach 1 and in the any-part system 0 (Dengler, 2003, 2009; Williamson, 2003). Since, however, this artefact is more pronounced for the grid-point and the mathematically similar rooted-presence system (Williamson, 2003), the *any-part system* should be used for species richness recording. Moreover, the grid-point system is hardly applicable to clonal plants, while rooted presence fails for rootless plants, such as bryophytes and lichens.

At very small scales, it is generally problematic to decide whether a certain species is present in a plot or not – either because one can hardly look up or down in an exactly perpendicular

manner or because plants are slightly moving in the wind. For low vegetation types (≤1 m in height), a construction similar to a point-frequency frame (e.g. Mueller-Dombois and Ellenberg, 1974), but with the possibility to attach square tops of 10 cm^2; 1 cm^2, 10 mm^2, and 1 mm^2 size to the poles, allows the objective assessment of species densities (Dengler et al., 2004). For such small squares laid out on the forest floor, it is even harder to decide whether their perpendicular projection will 'hit' any parts of a tree crown. Here, I suggest using probabilities of occurrence (e.g. 0.5), based upon the visual inspection of the crown sector above the plot (i.e. the question to be answered is with which probability would an arrow with a tip of the respective size hit parts of the tree if shot vertically into the air).

The date of recording should be chosen so that all occurring plant taxa can be expected to be visible. When in certain vegetation types, such as therophyte-rich grasslands, geophyte-rich forests, or ephemeral wetlands, not all occurring plant taxa can be encountered at one single point of time, it is necessary to mark the plot in the field precisely and to resample it some other time (e.g. Dierschke, 1994). Both for biodiversity analyses and for vegetation classification it is desirable that each species list represents the 'integral' over one whole year (Dengler, 2003).

According to the proposed sampling scheme, complete species lists are recorded for all plot sizes, but at least for one of the replicated sizes additionally complete relevés with data on stand structure and cover estimations for each individual species should be made to allow the assignment of the stand to phytosociological units. To meet recent standardisation proposals (Chytrý and Otýpková, 2003; Dengler, 2003), 10 m^2 in open vegetation and 100 m^2 in forests seem most suitable for phytosociological relevés. Due to analytical problems with the combination of cover and abundance in the widespread Braun-Blanquet scale (see Dengler, 2003), either direct estimates of coverage (in %) or a pure cover scale (e.g. the Londo scale or the modified Braun-Blanquet scale by Dengler; see Dengler, 2003: p. 131) should be applied.

3.5. Marking of the plots and environmental data

The position of biodiversity plots should generally be marked permanently, for example by wooden stakes or buried magnets. This step offers the option to gain more from the initial 'investment' by allowing a repetition of the sampling in the future, even if monitoring was not the aim of the original study. At least, all plots should be located as precisely as possible (longitude, latitude, altitude) with a global positioning system (GPS). Moreover, aspect and inclination should be recorded as fundamental data.

Regarding further environmental data, such as presence of certain microhabitats, microrelief, and physical and chemical soil properties, it is generally useful to have them recorded, but it is beyond the scope of this paper to propose a standardised sampling scheme for these, too. Generally, such environmental parameters should be preferred that are applicable throughout a wide range of vegetation types in an identical way. Moreover, it is advantageous to measure environmental parameters in several subplots of a certain scale (preferably the scale of the vegetation relevés) separately instead of providing only a single or a mean value for the whole plot. By doing so, the abiotic heterogeneity can be assessed and related to species richness and spatial species turnover.

3.6. Placement of nested-plot series

The sampling approach suggested here is applicable in four different situations, each of which requires a different strategy for the spatial arrangement of the largest plots:

(1) If the aim is to monitor environmental changes in specific situations, for example the population dynamics of rare plants, the plot(s) must be placed subjectively in accordance with the research question.
(2) If the aim is to analyse biodiversity patterns along environmental gradients or successional stages, the plots should be placed systematically along the gradient(s) in focus.
(3) If the aim is to analyse biodiversity patterns of specific vegetation types or habitats or to compare them with those of other such entities, the plots must be placed within the predefined units according to a stratified-random scheme. This approach requires a certain degree of within-plot homogeneity as the whole area of the largest plot must belong to the same vegetation or habitat type.
(4) If the study aims at assessing or monitoring biodiversity patterns of landscape sectors, the plots have to be placed completely randomly or systematically within the research area, irrespective of plot homogeneity, because otherwise all parameter estimates would be biased (Bunce and Shaw, 1973; Palmer, 1995; Dengler and Allers, 2006). Typically some of the plots will contain more than one vegetation type, be strongly influenced by human activity (buildings, streets, gardens) or be vegetationless. To receive unbiased biodiversity estimates at landscape scale, one must not disregard plots whose random coordinates fall within villages or on private ground as did Diekmann et al. (2007). To deal with situations where certain plot locations chosen by the systematic or random procedure are inaccessible, the whole investigation area should be pre-stratified into a number of major habitat types. Within each of the strata, more plot coordinates than actually needed should be generated in a defined sequence. If a certain plot fails, the next 'free' plot of the same stratum should replace it.

4. Biodiversity indicators based on the approach

The proposed sampling scheme already in its basic variant provides a large number of different meaningful biodiversity indicators. The most important indicators are the *species richness values (S) for a wide range of different standard areas*. By using replicated smaller subplots, the approach does not only provide mean richness values, but also information on their variability, which in turn can be used to estimate the precision of the calculated mean. For plots on which cover data have been recorded, diversity indices can be calculated additionally that account for the varying performance of different species. Examples are cover-based variants of evenness (E), Shannon index (H'), Simpson index, and Berger-Parker index (see van der Maarel, 1997).

Second most important is the *characterisation of the species–area relationship*. Either this can be done by selecting the most suitable model from the wide range of different function types suggested (e.g. Tjørve, 2003; Dengler, 2009) on the basis of adequate selection procedures (see Dengler, 2009) or the fitted parameters of these models can be used as biodiversity indicators themselves. For the latter approach, the regular power function is most suitable as it provides two meaningful and readily interpretable parameters (Dengler, 2009): c is the modelled species richness on one unit area, while z denotes the relative richness gain per increase of log-transformed area. Typically, z takes values between 0.15 and 0.40 (Hobohm, 1998; Fridley et al., 2005), but is higher for taxa with spatially clumped distribution and lower for those that are particularly evenly distributed across the area of investigation. The application of the power law as universal model allows to test whether and how the steepness of the species–area curve itself depends on spatial scale (Crawley and Harral, 2001; Turner and Tjørve, 2005; Dolnik and Breuer, 2008) by asking whether z varies

significantly with scale (Dengler, 2009). Because of the replication of the subplots, this question is easily addressable with statistical tests (Dengler, 2009).

Further, the *frequency distributions of species* at different spatial scales both among subplots of one plot and for different plots in one study provide meaningful diversity information. They allow, for example, determining the most frequent taxa of a landscape sector at different spatial scales (see Allers, 2007; Allers and Dengler, 2007).

Finally, the sampling approach with several replicates of all smaller plot sizes, representatively distributed within the largest plot, allows the meaningful *assessment of spatial heterogeneity* of floristic, structural, and abiotic parameters. For the characterisation of small-scale heterogeneity, for example, standard deviations of these parameters among the replicates of a certain size within a single plot or the mean floristic distances between subplots may be used.

All mentioned groups of parameters cannot only be assessed at *various spatial scales*, but also for the *total plant diversity or separately for its different components*. For example, plant diversity can be subdivided according to taxon (vascular plants, bryophytes, lichens), substrate (terricolous, epiphytic, lignicolous, saxicolous), life form (phanerophytes, chamaephytes,...), floristic status (indigenous plants, archaeophytes, neophytes, cultivated plants), red-list status, and various other criteria.

While many studies and monitoring schemes aim at quantifying *plant diversity at landscape scale*, most of them are doomed to failure because they try to achieve this important goal by studying specific vegetation or biotope types (e.g. Dröschmeister, 2001; Billeter et al., 2008; Tasser et al., 2008). However, it is impossible to derive valid landscape scale biodiversity parameters based on relevés in such predefined units (see Diekmann et al., 2007). Here, the sampling variant (4) of section 3.6 provides a statistically valid approach for generating meaningful data (similar to the 10 m^2 data of the Swiss BDM programme). This solution is also most meaningful for monitoring the cumulative effect of global change (climate change, land-use change,...) on various biodiversity components because it integrates these changes at landscape scale and is thus not confounded when proportions of habitats or habitat preferences of species change over time.

5. Conclusions and outlook

As biodiversity is essentially a scale-dependent phenomenon (Reed et al., 1993; Peet et al., 1998; Turner and Tjørve, 2005), both assessment and monitoring approaches need to look at different spatial scales if they want to draw conclusions of general relevance. Testing of ecological hypotheses and documenting the effect of global change on biodiversity depends on large amounts of data sampled with the same or at least compatible methods. Presently, such comprehensive analyses are hindered by the variety of applied sampling approaches for plant diversity, which are often incompatible or involve artefacts the researchers are unaware of (Dengler, 2008). Here, the proposed approach offers a powerful instrument because (i) it is applicable to any biome worldwide; (ii) it provides a large number of meaningful and standardised biodiversity indicators; (iii) it can easily be extended in order to address nearly any question typically posed in the field of small-scale plant richness patterns; and (iv) it achieves a good comparability with several other wide-spread biodiversity assessment approaches. I thus suggest to use it for newly set-up national and international monitoring programmes and to consider modifying existing programmes such as ESA in Germany, ICP Forest in Europe, and BIOTA in Africa so that they become fully compatible with this standard. Although the usefulness of the application of such a standardised scheme may not be immediately evident in the case of specific biodiversity studies, I urge researchers to consider whether a variant of the proposed approach could serve their aims equally well as a specifically developed incompatible scheme, while providing full comparability with a much larger pool of data. Regarding other sampling schemes, case studies should be conducted to quantify the effects of different methodologies (e.g. rectangles vs. squares; 9 m^2 instead of 10 m^2; rooted presence instead of any-part system; see Table 1) in order to allow the approximate transformation of data.

In conclusion, the proposed standardised yet flexible approach offers a solution for both applied biodiversity research (e.g. monitoring) and for pure science how to get more as well as more meaningful biodiversity indicators without much more effort.

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