C. R. Biologies 337 (2014) 276–282

Contents lists available at ScienceDirect

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Biodiversity/Biodiversité

Does cross-taxon analysis show similarity in diversity patterns between vascular plants and bryophytes? Some answers from a literature review

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ARTICLE INFO

Article history:
Received 10 November 2013
Accepted after revision 13 January 2014
Available online 6 March 2014

Keywords:
Biodiversity conservation
Co-variation
Spatial scale
Species richness
Surrogates

ABSTRACT

The objective of this study was to clarify the taxon surrogacy hypothesis relative to vascular plants and bryophytes. A literature review was conducted to obtain papers that met the following criteria: (i) they examined species richness values; or (ii) they evaluated the species richness within the same study sites, or under the same spatial variation conditions. Twenty-seven papers were accessed. The richness of the two taxa, compared in 32 cases, positively co-varied in about half of the comparisons. The response to the spatial variation in environmental or human-induced factors of the two taxa in terms of species richness was rather variable. Based on current knowledge, the main documented findings regard forest habitats and nival gradients. In forest habitats, co-variation in species richness is likely when similar environments are analysed and seems to be strengthened for boreal forests. Along the nival gradient, a different response in terms of richness of the two taxa suggests that vascular plants cannot be considered good surrogates for bryophytes.

1. Introduction

The characterization of complex biodiversity patterns across ecosystems requires substantial effort, expertise, and financial resources. An approach to limit these challenges is offered by choosing proper indicators or surrogates as a shortcut to predict biodiversity changes in poorly investigated groups from groups where adequate information is available [1]. Surrogate identification is primarily based on cross-taxon congruence analysis and the surrogate strength depends on the taxonomic groups studied and on the scale of analysis [2]. In addition, the response of different taxa to spatial variation in environmental factors should be analysed in cross-taxon congruence analysis, because consistent diversity pattern is a consequence of a similar response to environmental determinants [2–4].

Surrogates are useful in monitoring or solving conservation issues [5], selecting nature reserve networks [6], and evaluating restoration interventions [7]. Lewandowski et al. [8] showed that taxonomic groups having a large number of habitat specialists distributed collectively across broad environmental gradients were the most effective surrogates for complementarity approaches. Vascular plants best represent this suite of attributes; therefore, they were traditionally considered a focal taxon for richness correlation [1] and were chosen as viable surrogates for other taxonomic groups and used to select areas of concern in biodiversity conservation [9,10].

Non-vascular plants are rarely included in floristic and vegetation assessments; consequently, little systematic study has been conducted on their biogeography and community ecology. Some authors have tested possible congruencies between vascular and non-vascular plants in

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http://dx.doi.org/10.1016/j.crvi.2014.01.003

different habitats and locations, at different spatial scales and with different objectives. The results are fragmentary and not systematically organised. A synthesis of the available results might provide some general inferences, which in turn might contribute to the future application of surrogate taxa [8].

The objective of this study was to clarify the taxon surrogacy hypothesis relative to vascular plants or tracheophytes (Tracheophyta) and non-vascular plants or bryophytes (Bryophyta *sensu lato*). Species richness is largely used as an indicator of biodiversity [11], therefore, the hypothesis was tested based on the following outcomes: (i) spatial co-variation in species richness of the two taxa; and (ii) variation in species richness in response to environmental or human-induced factors.

2. Material and methods

A literature review was conducted to obtain papers essential to test our hypothesis. These studies met the following criteria:

(i) they examined species richness values in vascular plants and bryophytes, or;
(ii) they evaluated the species richness within the same study sites, or under the same spatial variation conditions, i.e. environmental or human-induced factors.

First, journal articles were searched in Google Scholar using the following keywords and their combinations: Bryophyta, bryophytes, co-variation, cross-taxon, mosses, multi-taxon, species richness, surrogates, Tracheophyta, tracheophytes and vascular plants. Second, the references section of articles was used to search for additional articles. The following information was extracted from the collected papers: publication year, research objectives, study location, habitat type, scale of analysis and primary findings relative to the cross-analysis congruence between the two taxa. The results relative to congruence between the two taxa were compiled and discussed if any significant correlation was detected between species richness and/or if the variation in species richness was similar when the environmental or human-induced factors varied.

The review is narrative rather than based on a formal meta-analysis. This type of approach is advisable when the data are scarce and/or various measures of congruence used in the studies prevent conducting a meaningful meta-analysis [12].

3. Results

Twenty-seven papers were accessed that addressed cross-taxon analysis between vascular plants and bryophytes [3,6,13–37]. In some cases, several taxon comparisons were reported in the same paper; therefore, only the more relevant ones were considered which totalled 40 comparisons for all the 27 papers (Table 1). If mosses and liverworts were considered independently and the findings were similar for the two groups, for simplicity, only the moss results were evaluated; otherwise, the results of the whole bryophytes were evaluated.

The number of papers exhibited a progressive increase from 1980 to 2013. The papers published during the most recent decade, i.e. 2000–2010 were more than twice the total number published in previous years.

The researchers' objectives were restricted to two main categories (Table 1): biodiversity conservation and monitoring (46%) and ecological assessment (54%).

The scale of analysis was directly addressed in three papers [3,13,31]. Primary results indicated that correlations in species richness became stronger when increasing the plot size.

The richness of the two taxa, compared in 32 cases, positively co-varied in approximately one half of the comparisons. The responses to the spatial variation in environmental or human-induced factors of the two taxa in terms of species richness were rather different (Table 1).

Forests were the most investigated habitat type, and the analyses ranged geographically from Boreal through Mediterranean to Australian forests (Table 1a). All the studies were focalized on the spatial co-variation in species richness of vascular plants and bryophytes, while variation in species richness in response to environmental or human-induced factors was not considered. High and positive correlations between vascular plants and bryophytes richness were obtained for boreal forests at large spatial scale [3,13,14]. The only case of negative correlation was detected in the patchwork of Dutch forests [15]. In Australian rainforests, the correlation was positive [16] while no correlation was found in sclerophyll and *Eucalyptus* forests [17–19]. In the Mediterranean area, the correlation was weakly positive [21] to negative [20,22].

Also, mountain habitats were subjected to several investigations, particularly in Alpine and Fennoscandian areas (Table 1b), where it was mainly the response along the Alpine-nival gradient that was monitored. The spatial co-variation in species richness, analysed just in two cases that considered a longer gradient, including also the temperate belt, was positive [23,24]. Along the gradient the pattern of vascular plant, species richness was mainly unimodal, with a peak above the forest limit, while bryophyte richness was more susceptible to increase with the altitude [24–28].

In disturbed areas (Table 1c), the co-variation in species richness was analysed in six cases and was positive in two of them [6,29]. In meadows [30] and *Picea abies* forests [31], under different management as well as in restored areas [6], no correlation was found. Concerning the responses to the variation in human-induced factors, the two taxa exhibited an opposite trend as a response to fertilization [32] and a similar one as a response to mowing [33].

In aquatic and wet habitats (Table 1d), the co-variation in richness was analysed just in two cases with opposite results [34]. A higher sensibility of vascular plants than of bryophytes to spatial variations of environmental factors was also observed [35,36].

4. Discussion

Cross-taxon congruence analysis between vascular plants and bryophytes generated variable responses.

Table 1

Information on the cross-taxon analysis between vascular plants and bryophytes extracted from the 27 papers accessed.

Reference	Location	Scope		Habitat details	Main findings			Data source
		Biodiversity conservation and monitoring	Ecological assessment		Co-variation in species richness*	Response to environmental or human-induced factors		
						Vascular plants	Bryophytes	
(a) Forests								
[13]	Estonia	*		Boreo-nemoral moist forests and mires–regional scale	Yes +			Page 2160 Fig. 1
				Boreo-nemoral moist forests and mires–ten stand scale	Yes +			
				Boreo-nemoral moist forests and mires–1 ha stand scale	No			
[14]	Western Norway	*		Boreo-nemoral forests	Yes +			Tab. 4
[3]	Sweden		*	Old boreal forests–regional scale–200 m^2 plot	Yes +			Fig. 3
				Old boreal forests–regional scale–1000 m^2 plot	Yes +			Fig. 3
				Young boreal forests–regional scale-200 m^2 plot	Yes +			App. 4
				Young boreal forests–regional scale-200 m^2 plot	Yes +			App. 4
				Boreal forests–landscape scale–0.01 m^2 plot	No			App. 5
				Boreal forests–landscape scale–0.25 m^2 plot	No			App. 5
				Boreal forests–landscape scale–1 m^2 plot	No			App. 5
				Boreal forests–landscape scale–200 m^2 plot	Yes +			App. 5
[15]	Netherlands	*		*Quercus robber*, *Bitola* ssp. and *Pinups sylvestris* forests	Yes –			Pag. 155
[16]	Queensland, Australia	*		Rain forests	Yes +			Tab. 1
[17]	Eastern Australia	*		Open to wet sclerophyll forests	No			Pag. 286
[18]	Eastern Australia	*		Open to wet sclerophyll forests	No			Tab. 2
[19]	Tasmania	*		*Eucalyptus* forests and rainforests	No			Tab. 3
[20]	Tuscany, Italy	*		*Cupressus sempervirens*, *Quercus ilex* and *Arbutus unedo* forests	No			Tab. 2
[21]	Tuscany, Italy	*		*Fagus sylvatica*, *Quercus ilex* and *Abies alba* forests	Weak +			Fig. 3
[22]	Campania, Italy	*		*Fagus sylvatica* and *Quercus cerris* forests	No			Tab. 1
(b) Mountain areas								
[23]	Indian Garhwal Himalaya		*	Temperate to Alpine gradient 1400–3700 m a.s.l.	Yes +			Tab. 1
[24]	Nepal, India		*	Temperate to Alpine gradient 100–5500 m a.s.l.	Yes +	Unimodal (peak 1500–2500 m a.s.l.)	Unimodal (peak 2500–2800 m a.s.l.)	Fig. 3 Tab. 1
[25]	Canadian Rocky Mountains		*	Nival gradient 1000 → 2100 m a.s.l.		No trend	Weak increase with altitude	Page 32
[26]	Norway		*	Nival gradient 310–1135 m a.s.l.		Unimodal peak above forest limit	No trend	Fig. 1 Page 243
[27]	Fennoscandian		*	Nival gradient 275–1525 m a.s.l.		Unimodal peak above forest limit	Sharp increase with altitude	Fig. 3 Tab. 1

Table 1 (*Continued*)

Reference	Location	Scope		Habitat details	Main findings			Data source
		Biodiversity conservation and monitoring	Ecological assessment		Co-variation in species richness*	Response to environmental or human-induced factors		
						Vascular plants	Bryophytes	
[28]	Switzerland		*	Alpine/nival gradient 2400–3200 m a.s.l.		Sharp decrease with altitude	Weak decrease with altitude	Tab. 1 Fig. 1
(c) Disturbed areas								
[29]	Ontario, Canada		*	Areas affected by mining and smelting activities and restored	No			Tab. 2
				Areas affected by mining and smelting and activities and not restored	Yes +			
[6]	Austria		*	Agricultural landscape	Yes +			Tab. 1
[30]	Austria		*	Meadows under different management	No			Tab. 6
[31]	Northern Sweden		*	*Picea abies* forests along a gradient of impact of forestry–1 ha stand scale	No			Tab. 4
				Picea abies forests along a gradient of impact of forestry–0.25 ha stand scale	No			
(d) Aquatic and wet habitats								
[34]	NE Iberian peninsula		*	Temporary wetlands in Mediterranean areas	Yes +			Tab. 8
			*	Temporary wetlands in steppe areas	No			Tab. 8
[35]	Western Carpathian		*	*Sphagnum*-rich mires		Related to pH, conductivity and water level dynamics	No relationships	Tab. 1
[36]	Sub-Alpine Europe		*	Sub-Alpine springs		Related with altitude and conductivity	No relationships	Tab. 1
(e) Multiple habitats								
[37]	Global	*		Tropical zone	Yes+	Increase with precipitation and coastline length	Increase with precipitation, area and energy input	Fig. 1 Tab. 2
		*		Temperate zone	No	Increase with precipitation and coastline length	Increase with precipitation, area and energy input	Fig. 1 Tab. 1

* +: Positive correlation; –: negative correlation.

Vascular plants did not perform well enough to encourage their use as surrogates for bryophytes without carefully considering habitat type, environmental and human-induced factors, and assessment scale. In selected habitats, a positive correlation between the richness of the two groups at the regional and landscape scales makes a strong case for generality [3], but results were less conclusive in other cases.

A temporal trend in the literature demonstrated an increased interest in this topic from the early 1990s. Cross-taxon congruence analysis has received particular attention during the last twenty years in response to a growing demand for documentation concerning the biodiversity of neglected taxonomic groups, particularly for selection of target conservation areas [38,39]. Most manuscripts with the primary aim of establishing surrogate taxa consistently evaluated the effectiveness of vascular plants to identify areas of specific relevance to overall plant biodiversity [5]. A strong contribution to ecological assessments along altitudinal gradients, which can provide a foundation (and baseline data) to evaluate climate change effects on plant distribution [40], was also given. The two considered types of outcomes (i) spatial co-variation in species richness of the two taxa and (ii) variation in species richness in response to environmental or human-induced factors, allowed to gather a large range of cases in different habitats and locations.

4.1. Spatial co-variation

Spatial co-variation strength between vascular plant and bryophyte richness varied among different locations and habitats, as already reported for, the comparisons between several taxonomic groups [1].

Forest habitats were the most investigated. In boreal forests, the co-variation was always positive. In other cases, it was absent, weak or negative, probably because the analysis in each case study was extended to several forest types, e.g., open to wet sclerophyll forests [17,18]. The significant co-variation obtained in Australian rainforest [16] seems to confirm this hypothesis. The positive correlation between the richness of vascular plants and bryophytes at the regional and landscape scales in boreal forest makes a strong case for generality. In these habitats, conservation of communities rich in vascular plant species can ensure the maintenance of bryophyte species richness, even if fewer stands are needed to maintain bryophytes than vascular plant species pools [13]. In other forest types, it is more relevant to combine compositional and structural surveys with species richness assessment in monitoring programs. For example, in old Mediterranean forest stands characterised by old growth trees, high tree basal areas, a broad range of diameter classes, and understorey diversity are good indicators of bryophytes richness [41]. Similar findings emerged for coniferous and deciduous broad-leaved forests [42–45].

The two cases of co-variation analysed along an altitudinal gradient [23,24] are promising, but not sufficient for a generalization.

In disturbed areas, few cases of co-variation were generally observed particularly along a gradient of impact of agricultural or forestry management. Anand et al. [29], based on the lack of co-variation in species richness in restored areas, suggested that the conservation of diversity relationships might be more important in protection efforts than simply by conserving diversity levels, because the relationships can be better indicators of ecosystem health and function.

Concerning aquatic and wet habitats, just one paper considered the spatial co-variation in richness between the two taxa [34], giving opposite answers under different climatic conditions. Nevertheless, findings referring to other taxonomic groups in inland aquatic ecosystems are not encouraging for these habitat types [12,46].

The contrasting results obtained in different habitats seem to mirror those obtained at the global scale for multiple habitats where opposite findings were obtained for tropical and temperate zones [37].

The different findings in spatial co-variation may be partly caused by the effect of the scale of analysis on richness, i.e. the different rates of accumulation of species as area increases [47]. Indeed, vascular plants and bryophytes exhibited different accumulation rates as area increased [48], as already reported for the Estonia Important Plant Areas [49], and for Mediterranean forests [15]. The scale of analysis requires then particular attention, as important patterns in species richness appeared to vary among different spatial scales [13], which was generally observed in evaluating the effectiveness of biodiversity indicators [50].

4.2. Variation in species richness in response to environmental or human-induced factors

Besides the scale, the spatial effect species on richness of the two taxonomic groups was also conditioned by the responses to independent environmental factors [51] or by different sensitivity to human activities [1].

Richness in the two taxonomic groups was affected similarly by the same environmental factors in some case studies and differently in others. For example, species richness responded similarly to precipitation [37] and moisture [3], but not to pH, conductivity and water level dynamics [35].

In mountain areas along the nival gradient, bryophyte richness showed a more gradual decrease in species richness with increased elevation than vascular plants, because a higher dependence of bryophytes on humidity than on temperature contrary to vascular plants [28], a wider tolerance to elevation-correlated factors of bryophytes in comparison with that of vascular plants [25], and a different demands from bryophytes than from vascular plants for climatic variables along the nival gradient, e.g. available energy [24].

The response to human-induced factors, evaluated under different type of interventions, gave different and not generalizable answers. Vascular plants and bryophytes showed a different sensitivity to human activities, such as agricultural practices. Nevertheless, management cessation, which is considered a serious problem for vascular plant diversity conservation [52,53] has had similar impacts on bryophytes, since under certain conditions, land-use intensity increases species richness for both taxa compared to unmanaged areas [54]. Mowing meadows as a nature conservation strategy may be very promising for both vascular plants and bryophytes [33].

5. Conclusions

Based on the current knowledge, the main documented findings regard forest habitats and nival gradients. In forest habitats, co-variation in species richness is related to habitat homogeneity and seems to be strengthened for boreal forests. Along the nival gradient, a different response in terms of richness of the two taxa suggests that vascular plants cannot be considered a good surrogate for bryophytes.

Nevertheless, in spite of the issues that emerged from the cross-taxon analysis based on a lack of congruency in some results, other findings encourage further insights and may be a sound basis to direct future research.

All the literature results collected in this review were valuable to understand and to determine the relationships between species richness patterns of vascular plants and bryophytes and determine the primary distribution drivers (i.e. environmental and human-induced factors) into different habitat types. Understanding the patterns of congruence has more than theoretical importance; all the available information contributed to support the local and global scale demands on the diversity drivers from different taxonomic groups for effective conservation policies. The discrepancies among cross-taxon analysis results in different habitats and at different spatial scales suggested that care must be taken in generalizing the findings of isolated surrogacy tests.

Disclosure of interest

The author declares that she has no conflicts of interest concerning this article.

Acknowledgements

This research was funded by the PAULIS project (Regione Sardegna, CRP-24943).

Joanna Schultz (http://www.writescienceright.com/) edited the English text.

I thank the anonymous referees for their valuable comments on the manuscript and their constructive suggestions.

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