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Overlapping fern and bryophyte hotspots: assessing ferns as a predictor of bryophyte diversity

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Abstract

Bryophytes are significant contributors to floristic diversity, but they are often neglected in field surveys and collections. Thus, in order to obtain more accurate estimates of plant richness, there must be reliable estimates of bryophyte diversity. To address this, we examined whether another plant group, namely the ferns, could be used as a surrogate for bryophytes. We used datasets spanning the entire Australian continent for mosses, liverworts, liverworts+hornworts, ferns, and conifers (hornworts were aggregated into the group liverworts+hornworts). Two measures of richness were examined across the continent (as 50 km × 50 km grid cells): uncorrected richness and sample-standardised richness. We calculated the correlations among richness of all of the groups to test the hypothesis that fern diversity predicts bryophyte diversity (because of shared ecological preferences) while conifer diversity does not. Conifers showed very little correlation to either of the four plant groups, whereas ferns were highly correlated to mosses and to a lesser extent to liverworts and liverworts+hornworts. Liverworts, as well as liverworts+hornworts, and mosses were also strongly correlated. These results indicate that surrogates can assist in estimating the diversity and the conservation of other poorly collected plant groups.

Introduction

Although bryophytes are the most species-rich plant group after angiosperms, they are under-studied and under-collected (Delgadillo 1996; Pocs et al. 2011) (herein "bryophytes" is used to refer to the paraphytic assemblage of mosses, liverworts, and hornworts). Thus, in order to make predictions about bryophyte richness, potential surrogates have been assessed. These surrogates are from better-collected groups such as ferns, woody plants, overstorey plants, understorey plants, and vascular plants (Pharo et al. 1999; Chiarucci et al. 2007; Mandl et al. 2010). Of these groups, fern richness best correlates with bryophyte richness (Pharo et al. 1999; Mandl et al. 2010). This is not surprising given that both ferns and bryophytes disperse via spores, share a requirement for water during the sexual reproductive phase of their life cycles, and prefer moist habitats. However, these fern and bryophyte correlations are derived from quadrats – the relationship at larger

geographic scales requires further testing, although ostensibly it appears to hold. For example in the United Kingdom, bryophyte hotspots mirrored pteridophyte hotspots (ferns and lycophytes) (Lawton et al. 1994). Australia provides a good test case since richness patterns of ferns and bryophytes have recently been studied in detail (Stevenson et al. 2012; Nagalingum et al., in revision), and because Australia is considerably larger than the UK, with significantly more environmental diversity.

It is preferable to calculate biodiversity patterns directly from the original data; however, there are cases where the original data are meagre and surrogates could assist with inferring patterns. Surrogates can be either taxonomic groups or environmental conditions (termed "ED" for environmental diversity, see citations for a full discussion) (Humphries et al. 1995; Faith and Walker 1996; Gaston 2000; Moritz et al. 2001). Surrogate groups can be at a higher taxonomic level, such as genera or families for estimating species (Gaston and Williams 1993), or they can be species that share similar distribution patterns (Moritz et al. 2001). Here we test the use of ferns as surrogates for the various bryophyte groups, on the assumption that they have comparable distributions based on similar requirements for water (see above).

To assess broad-scale richness, herbarium collections data are being increasingly used, such as Australia's Virtual Herbarium for plant groups in Australia (Crisp et al. 2001; González-Orozco et al. 2011; Stevenson et al. 2012; González-Orozco et al. 2012; Mishler et al. 2014). One of the factors to consider when inferring richness from herbarium data are sampling biases, which can be categorized as "morphological" and "geographical." Morphological sampling biases occur because of the plants' intrinsic appearance making some preferentially collected over others, such as large versus small plants, or plants with attractive versus dull flower colour (Schmidt-Lebuhn et al. 2013). Differences in geographic sampling are linked to accessibility, or ease of collecting (Funk and Richardson 2002; Graham et al. 2004; Loiselle et al. 2008). This is termed the "roadside effect" where there are more samples along areas such as roadsides, towns and biological stations. In addition, geographic sampling biases may occur among climatic zones where there is uneven collecting among regions with differences in temperature, rainfall, and seasonality (Loiselle et al. 2008). These various geographic biases will lead to apparently greater richness in some areas because they are more thoroughly sampled. To correct for differences in sampling, richness is often standardised by the number of samples (Maurer and McGill 2011). Given that these biases may affect the study groups herein and because under-collecting likely impacts bryophyte richness, we calculated sample-standardised richness alongside unstandardised richness.

The aim of this paper was to test whether fern and bryophyte hotspots are correlated, and whether fern richness can be used as a surrogate for bryophyte richness. As a comparison, we used conifers, which were hypothesized to correlate poorly with ferns and bryophytes. More specifically, this study examined correlations between species richness or corrected species richness for ferns, liverworts, liverworts+hornworts, mosses, and conifers using generalized linear models.

Materials and Methods

Sources of data

To compare richness patterns, herbarium distribution records for ferns, liverworts, hornwort, mosses, and conifers were obtained from three previous studies (Stevenson et al. 2012; Lee 2013; Nagalingum et al., in revision) (Table 1). These data were originally derived from Australia's Virtual Herbarium (AVH, http://avh.ala.org.au/), which hosts collection records from all major herbaria of Australia. After downloading from AVH, the data were cleaned to remove cultivated material, and they were reconciled and updated to consistent taxonomic names (see original publications for full explanations). Data from the hornworts were newly downloaded from AVH and cleaned; because of the small size of the dataset, they were aggregated with liverworts, and analysed as liverworts+hornworts.

Measuring sampling effort and richness

Data were imported into the program Biodiverse v 0.99_004 (Laffan et al. 2010), and richness was measured using 50 km x 50 km grid cells. When there are several collections of the same taxon in a grid cell, the additional records are ignored, leaving a smaller number of records (Table 1, unique records). These unique records can be used as an indication of the number of replicate samples, and thus sampling effort. In addition, the sampling effort can be numerically represented as redundancy where R is richness and N is the total number of collection records (samples), averaged across all of the grid cells:

$$Redundancy = 1 - \frac{R}{N}$$

In the redundancy values presented here, we calculated the redundancy per grid cell, and all grid cell values were averaged for the whole of Australia. The redundancy was calculated separately for each group, and was used to compare the sampling across groups.

Two measures of richness were used, standard uncorrected richness (R) and corrected richness ($R_{Margalef}$). Standard richness is simply the total number of species present in a grid cell. Margalef richness, which can be referred to as corrected richness or sample-standardised richness, was calculated in order to facilitate comparisons among the plant groups. This is particularly useful because our different comparison groups had substantially different collecting effort (total records, Table 1). For each grid cell, R is subtracted by one, then divided by the natural log of N, where N is the total number of collection records (Magurran 2004; Magurran and McGill 2011):

$$R_{Margalef} = \frac{R - 1}{\ln N}$$

Detecting correlations

All of the analyses described below were performed in R (R Core Team 2014). Correlations were assessed for the ferns, liverworts, liverworts+hornworts, mosses, and conifers. Testing for correlations required merging the separate datasets for each group, and we refer to these merged datasets using a hyphen, e.g., ferns-mosses. The term "liverworts/liverworts+hornworts" is used when the results of the liverworts analysis are identical to the liverworts+hornworts analysis.

The individual group datasets were combined in two ways. First, the datasets were merged and restricted to grid cells where *both* plant groups occur; thus, when one group is absent (it has "zero richness") the grid cell was discarded (termed R datasets). Otherwise, the datasets were combined and all grid cells were retained regardless of whether both groups were present, and so for these datasets there were cells with "zero richness" (R_{zero}). The correlations for corrected richness ($R_{Margalef}$) were performed on the R datasets.

An issue when assessing correlations using herbarium records is that the data are not normally distributed, violating one of the key conditions for performing a linear regression (Bolker et al. 2009). Therefore, generalised linear models (GLMs) were employed because they incorporate an additional term to account for data with non-normal distributions, such as Poisson, gamma and binomial. Thus in this study, correlations between each of the study groups were tested using GLMs with Poisson distributions. The Poisson distribution, which describes discrete quantitative data with values greater than zero, was selected because it best describes the richness data (as compared to binomial, gamma and normal distributions). For each GLM, the following were recorded: percent of deviance explained (equivalent to r^2), and the statistical significance of the z score of Wald's test (equivalent to p-value).

Results

Of all the groups, the mosses were the most species-rich with 1,324 species, and they also had the highest number of samples with over 80,000 collection records (Table 1). Liverworts were next highest in terms of number of species, with half of the species diversity of mosses, but only one fifth of the number of collections. Including hornworts with liverworts increased the numbers of collections only modestly (467 collections records). In contrast, ferns had moderate species diversity, but are represented by substantial numbers of collections, while conifers had low diversity and collection records (Table 1). These disparate values were reflected in the ratio of collections to species richness (records per species) and redundancy, where conifers had the highest ratio and redundancy followed by ferns, mosses, and lastly liverworts/liverworts+hornworts (Table 1). When the datasets were examined geographically in grid cells across the Australian continent, the total number of grid cells sampled across the Australian continent was 2,278. Individually, ferns and mosses were found in the most grid cells with 1,986 and 1,231 grid cells respectively (Table 1, Fig. 1) Conifers and liverworts were found in fewer cells with 832 and 829 cells respectively (Table 1, Fig. 1). The hornworts are found in only 130 cells (Table 1, Fig. 1). Inclusion of the hornworts with liverworts did not substantially change the ratio of records to species, redundancy or number of grid cells (Table 1).

Across the whole of the continent, all plant groups had greatest species richness in the Wet Tropics (Fig. 1, red-orange). The ferns, mosses, and liverworts had closely comparable geographic patterns with the majority of richness concentrated along the east coast margin (Fig. 1A–C, yellow-light blue). Hornwort hotspots correspond to the major cities, and they are generally poorly collected across the continent (Fig. 1D). The

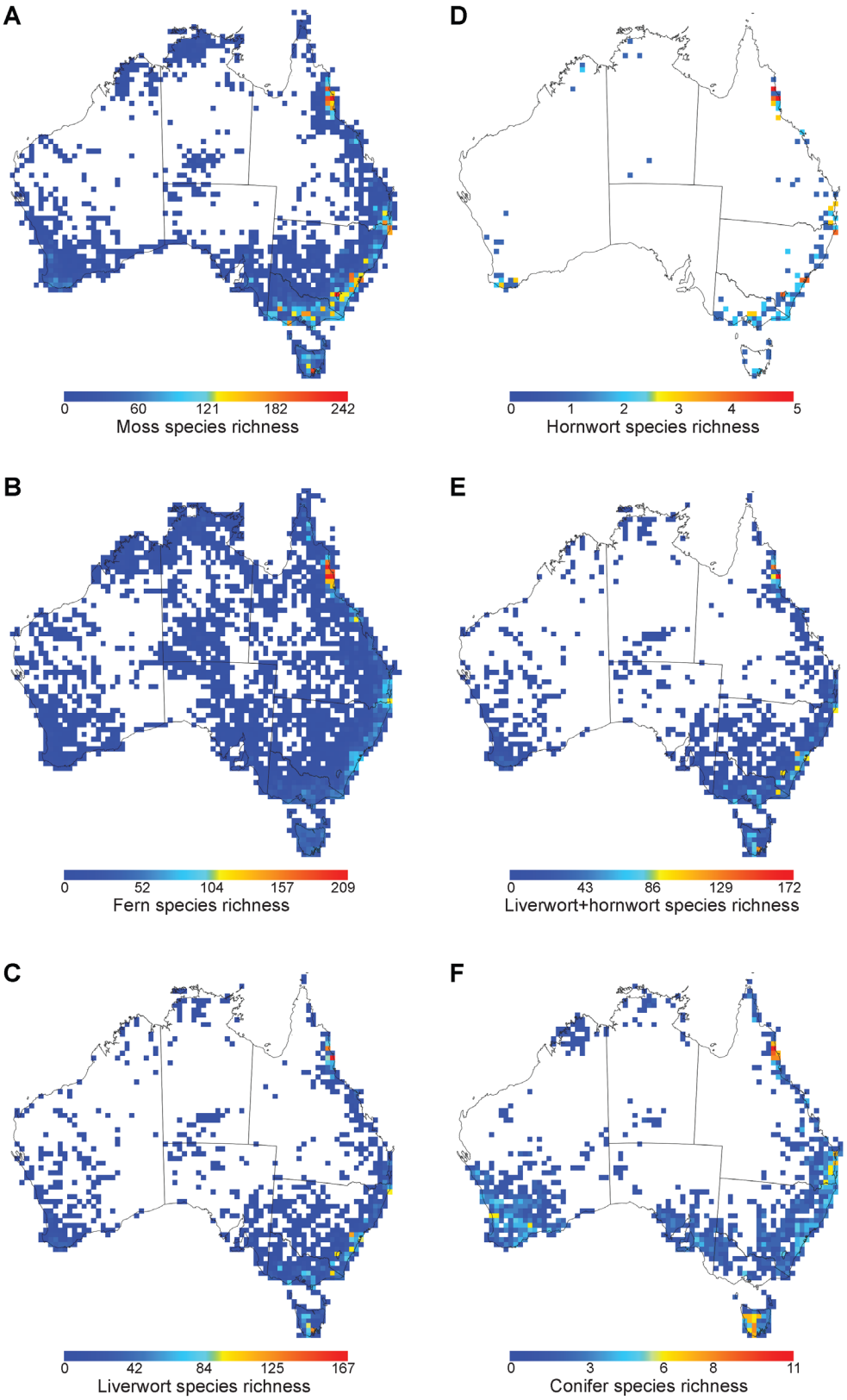

Figure 1. Richness patterns across Australia for all groups examined. A. mosses, **B.** ferns, **C.** liverworts, **D.** hornworts, **E.** liverworts+hornworts, **F.** conifers. Richness is measured as the number of species per 50 km × 50 km grid cell.

aggregated liverwort+hornwort data (Fig. 1E) essentially matches the pattern for liverworts alone (Fig. 1C). Conifers had moderate richness along the east coast, but there were additional significant centres of richness in the Border Ranges at the Queensland-New South Wales border, southwest Australia, and especially Tasmania (Fig. 1F).

Correlations were performed on reduced datasets in which both plant groups occur in the grid cells (R, richness was greater than or equal to one). Since ferns and mosses were individually in the most grid cells, it is not surprising that the combined fern-moss richness (R) dataset was the largest at over 1,000 grid cells (Table 2). The other four datasets were all similar in size with about 600-700 grid cells, but the conifer-liverwort dataset was significantly smaller at 438 grid cells. Another group of datasets were those where *all* grid cells were merged, that is, when one group had "zero richness" in the cell (R_{zero}, richness was greater than or equal to zero). Consistently, combined datasets incorporating the ferns were the largest with over 2,000 cells (Table 2). The third group of datasets were of sample-standardised richness, $R_{Margalef}$, calculated from the datasets. These were smaller than the original datasets because grid cells that have one collection record yield richness values of zero (this is because the numerator of the calculation is R-1), and so were excluded from the analyses. All of the $R_{Margalef}$ datasets were approximately three quarters to half the size of the original R datasets (Table 2).

Similarities in the maps of geographic richness patterns between ferns, mosses, and liverworts/liverworts+hornworts were further evident when the richness values were plotted against one another (Fig. 2). In the scatterplots, these groups showed corresponding increases in richness (Fig. 2A–E), however, conifer richness did not appear to increase with greater fern, moss, or liverworts/liverworts+hornworts richness as evidenced by a wide scatter of points along both axes of the plots (Fig. 2F–I). These relationships were explicitly tested using generalised linear models (GLMs; Table 2), and all correlations were highly significant at less than 0.005 (not shown). The two groups that had the highest correlation were the ferns-mosses where the

Table 1. Summary of the data for all groups examined in this study. "Records per species" is obtained by dividing the number of records by the number of species, thus, it is a simple measure of collecting effort. "Unique records" refers to the number of records remaining when duplicate records of a species (in a grid cell) are discarded from the dataset. "Redundancy" is an additional measure of sampling quality, where values close to zero indicate possible under-sampling, while those close to one indicate well-sampled cells. Redundancy is measured for all taxa in a grid cell and averaged across all grid cells.

	Collection records	Species	Records/species	Unique records	Redundancy	Grid cells
Mosses	83,639	839	100	24,597	0.29	1,231
Ferns	63,230	386	164	18,050	0.32	1,986
Liverworts	17,454	745	23	7,686	0.21	829
Hornworts	467	14	33	207	0.26	130
Liverworts+hornworts	17,921	759	23	7,893	0.21	836
Conifers	7,536	39	193	1,583	0.46	832

Table 2. Correlations between plant groups using generalized linear regressions. R is uncorrected richness calculated where species richness is ≥1, R_{zero} is uncorrected richness calculated where species richness is ≥0, and $R_{Margalef}$ represents sample-standardised richness. %DE is the percentage of deviance explained, describing the goodness of fit, and is equivalent to r^2. All p-values on the z scores are highly significant below 0.005, except where the superscript NS indicates non-significance.

	R		R_{zero}		$R_{Margalef}$	
	#cells	%DE	#cells	%DE	#cells	%DE
Ferns-mosses	1047	51.1%	2170	51.4%	768	49.5%
Liverworts-ferns	731	38.4%	2084	36.9%	462	39.4%
Liverworts+hornworts-ferns	736	38.6%	2086	37.0%	465	39.8%
Liverworts-mosses	712	48.0%	1348	44.5%	474	53.2%
Liverworts+hornworts-mosses	717	48.1%	1350	44.6%	477	53.5%
Conifers-ferns	716	27.1%	2102	36.0%	307	7.9%
Conifers-mosses	635	17.8%	1428	23.8%	317	2.7%
Conifers-liverworts	483	24.0%	1178	26.7%	204	3.0%
Conifers-liverworts+hornworts	485	19.6%	1183	13.2%	205	2.6%^{NS}

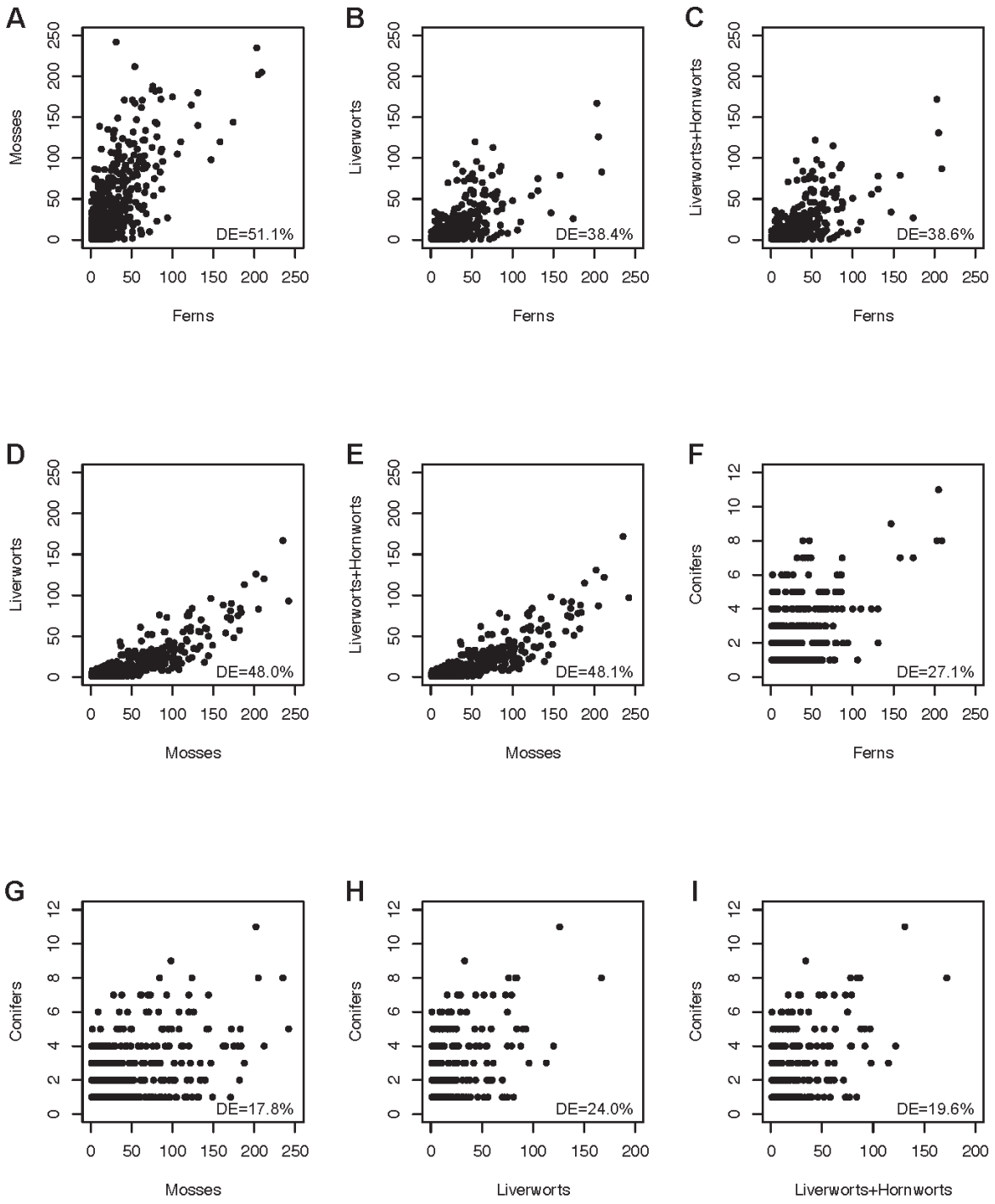

Figure 2. Scatterplots showing relationships between uncorrected richness (R) for all of the groups examined. **A**. ferns and mosses, **B**. ferns and liverworts, **C**. ferns and liverworts+hornworts, **D**. mosses and liverworts, **E**. mosses and liverworts+hornworts, **F**. ferns and conifers, **G**. mosses and conifers, **H**. liverworts and conifers, **I**. liverworts+hornworts and conifers. All x and y axes represent richness, that is the number of species per grid cell. %DE is the percentage of deviance explained and is a measure of the goodness of fit (equivalent to r^2 from linear regressions). All p-values on the z scores are highly significant below 0.005.

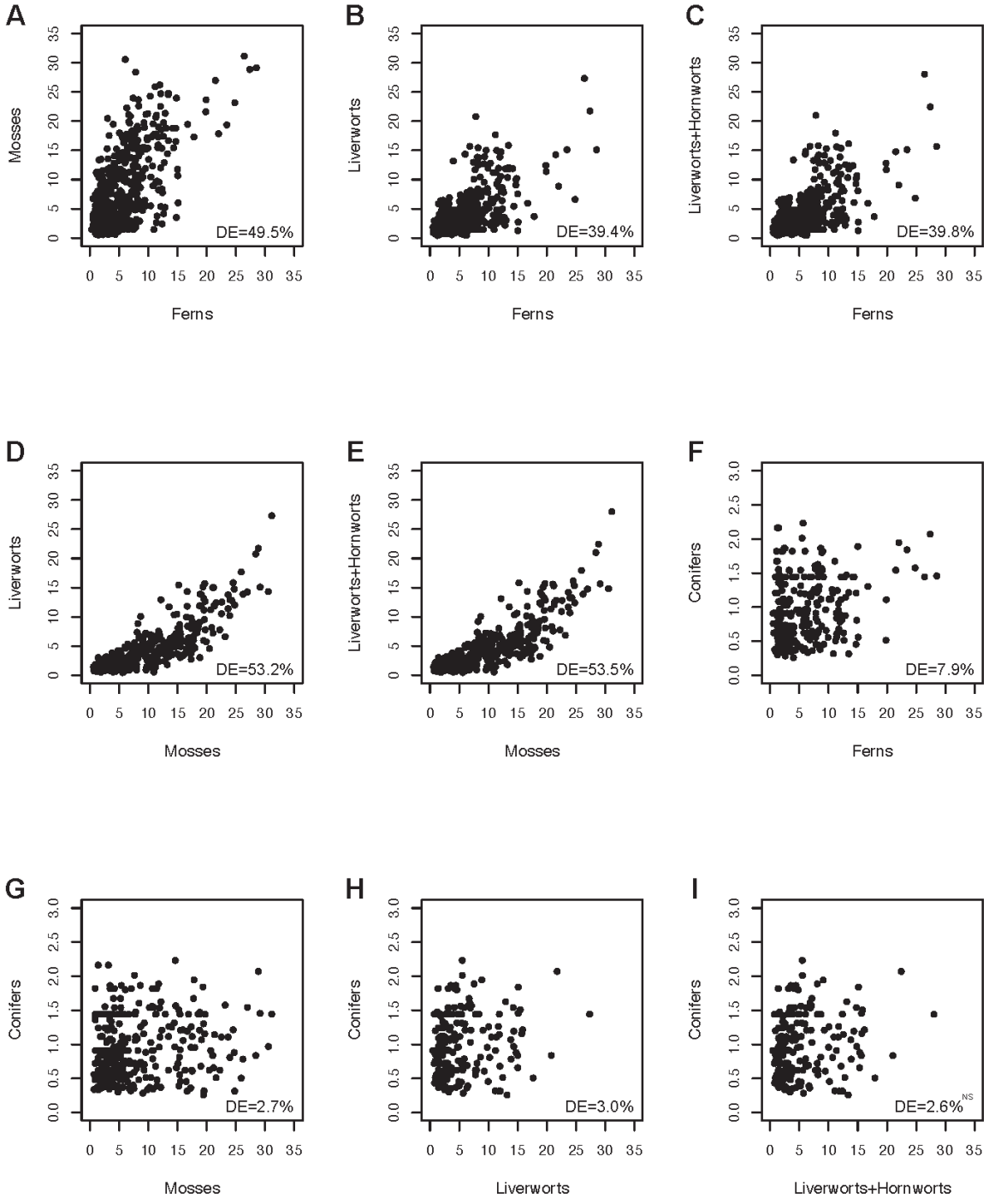

Figure 3. Scatterplots showing relationships between sample-standardised richness ($R_{Margalef}$) for all of the groups examined. A. ferns and mosses, **B**. ferns and liverworts, **C**. ferns and liverworts+hornworts, **D**. mosses and liverworts, **E**. mosses and liverworts+hornworts, **F**. ferns and conifers, **G**. mosses and conifers, **H**. liverworts and conifers, **I**. liverworts+hornworts and conifers. All x and y axes are equal to Margalef richness, that is the number of species per grid cell corrected by the number of samples in that grid cell. %DE is the percentage of deviance explained and is a measure of the goodness of fit (equivalent to r^2 from linear regressions). All p-values on the z scores are highly significant below 0.005, except where the superscript NS indicates non-significance.

GLM accounted for 51.1% of the deviance explained (DE=the proportion of deviance explained by the GLM, which is equivalent to r^2 of a linear model). Richness of liverworts-mosses had a similar correlation at 48.0%, and liverworts-ferns were lower at 38.4% (Table 2). In comparison, all correlations involving conifers had lower correlation values ranging from 17.8% to 27.1% (Table 2). Using cells that had richness values either greater than or equal to one for both groups (R) or greater than or equal to zero (R_{zero}) did not yield any pronounced differences in the correlation values (Table 2). Since we cannot discern whether the zero values are the result of undersampling or true absences, we focused on the results from the R correlations. Correcting richness for differences in sampling, $R_{Margalef}$, did not substantially change any of the correlations among ferns, mosses, and liverworts/liverworts+hornworts (Table 2; Fig. 3). However, there were even poorer correlations between conifers and the other plant groups, ranging from 3.6% to 7.9% (Table 2). These poor correlations are apparent in the plots showing widely scattered points in no apparent pattern (Fig. 3G-I). For all of the analyses conducted, R and $R_{Margalef}$, inclusion of the hornworts with liverworts, resulted in almost no changes to the plots and correlation values (Figs 2, 3, Table 2).

Discussion

Using generalized linear models, we found that the best-correlated groups were the mosses, liverworts/liverworts+hornworts, and ferns; and depending on the richness measure used, the pairs that had the highest correlations were ferns-mosses or mosses-liverworts/liverworts+hornworts. For both richness measures, the ferns-mosses were correlated with values around 50%; however, ferns-liverworts had the lowest correlations with values typically below 40%. Since all of these correlations were significant, our results indicate that ferns can potentially be used as a proxy for moss diversity, and to a lesser extent for the liverworts, although the predictive power is only moderate. An additional avenue for further assessing ferns as surrogates for mosses and liverworts/liverworts+hornworts is to conduct the analyses within particular biomes. It is expected that the correlations would improve, especially for liverworts/liverworts+hornworts-ferns, when the data are limited to wetter biomes (see below).

For both R and $R_{Margalef}$ the correlations between mosses and liverworts/liverworts+hornworts were around 50%, rising slightly when sample standardisation was used. These results indicate that mosses can serve as a proxy for liverworts/liverworts+hornworts. Correlations between liverworts/liverworts+hornworts-ferns also improved slightly using standardised richness, increasing by 1%.

The somewhat greater correlation values between ferns-mosses, rather than ferns-liverworts suggest differences in the distribution of mosses and liverworts, relative to ferns. Indeed statistically significant differences have been found in the distribution of liverworts compared to mosses in Australia (Stevenson et al. 2012). In general, liverworts are more sensitive to drier conditions than mosses, whereas mosses and ferns are able to grow in drier environments such as dry sclerophyll forests and even under arid conditions (N. S. Nagalingum, pers. obs.; M. A. Renner, pers. comm.). Therefore, moss and fern tolerances are more similar, and thus their distribution and species richness patterns show greater congruence. However, these patterns may be confounded by collection bias, such that liverworts are collected preferentially in wet areas (since there is greater richness there) as compared to more arid regions.

The conifers were included here as a comparison surrogate to the ferns, and correlations involving conifers are all quite low, albeit significant. Of the various groups, conifers were most highly correlated to ferns (DE=27.1%), which is not surprising given that ferns have greater tolerance for drier conditions compared to liverworts, hornworts and mosses. Given the low values involving conifers, they have very little predictive power for any of the groups examined here.

Other analyses comparing fern richness to bryophyte richness have found similar correlations as recovered here (Pharo et al. 1999; Mandl et al. 2010). In a study of coastal lowlands plots in eastern Australia (where bryophytes were examined collectively) the r^2 was 0.708, which is equivalent to DE of 70.8% (Pharo et al. 1999); in comparison the DE values recorded herein are lower at 46.2-51.1% (Table 2). Given the limit of the study sites to coastal lowlands all with high rainfall, the stronger correlation is not surprising. By comparison, our investigation includes multiple climatic zones and rainfall regimes, which likely reduces the strength of the correlation. In another study, plots in tropical montane forests in Ecuador yielded similar results to our findings. There, the r^2 value between ferns-epiphytic mosses was 0.54 (ferns and terrestrial mosses was 0.21), and 0.53 and 0.64 for ferns-liverworts (epiphytic and terrestrial, respectively) (Mandl et al. 2010). The congruence of our results at a continental-scale covering multiple biomes and climatic zones to these two smaller plot-based analyses indicates that small-scale patterns are applicable at the large scale. The results further suggest that additional broad-scale analyses in other regions could potentially be used to infer bryophyte hotspots using ferns.

From a conservation-planning standpoint, our results suggest that using surrogates, such as ferns and mosses, can assist in the conservation of other plant groups, for instance the liverworts. However, potential surrogates that have different ecological preferences to the target groups (for example, conifers compared to liverworts) have very limited applicability as proxies.

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References

Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White J-SS (2009) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends In Ecology & Evolution* 24: 127–135. http://dx.doi.org/10.1016/j.tree.2008.10.008

Chiarucci A, D'auria F, Bonini I (2007) Is vascular plant species diversity a predictor of bryophyte species diversity in Mediterranean forests? *Biodiversity and Conservation* 16: 525–545. http://dx.doi.org/10.1007/s10531-006-6733-1

Crisp MD, Laffan S, Linder HP, Monro A (2001) Endemism in the Australian flora. *Journal of Biogeography* 28: 183–198. http://dx.doi.org/10.1046/j.1365-2699.2001.00524.x

Delgadillo C (1996) Moss conservation in Mexico. *Anales del Instituto de Biología serie Botánica* 67: 177–181.

Faith DP, Walker PA (1996) Environmental diversity: on the best-possible use of surrogate data for assessing the relative biodiversity of sets of areas. *Biodiversity and Conservation* 5: 399–415. http://dx.doi.org/10.1007/BF00056387

Funk VA, Richardson KS (2002) Systematic data in biodiversity studies: use it or lose it. *Systematic Biology* 51: 303–316. http://dx.doi.org/10.1080/10635150252899789

Gaston KJ (2000) Global patterns in biodiversity. *Nature* 405: 220–227. http://dx.doi.org/10.1038/35012228

Gaston KJ, Williams PH (1993) Mapping the world's species – the higher taxon approach. *Biodiversity Letters*, 1: 2–8. http://dx.doi.org/10.2307/2999642

González-Orozco CE, Brown AHD, Knerr N, Miller JT, Doyle JJ (2012) Hotspots of diversity of wild Australian soybean relatives and their conservation in situ. *Conservation Genetics* 13: 1269–1281. http://dx.doi.org/10.1007/s10592-012-0370-x

González-Orozco CE, Laffan SW, Miller JT (2011) Spatial distribution of species richness and endemism of the genus *Acacia* in Australia. *Australian Journal of Botany* 59: 601–608. http://dx.doi.org/10.1071/BT11112

Graham CH, Ferrier S, Huettman F, Moritz C, Peterson AT (2004) New developments in museum-based informatics and applications in biodiversity analysis. *Trends In Ecology & Evolution* 19: 497–503. http://dx.doi.org/10.1016/j.tree.2004.07.006

Humphries C, Williams PH, Vane-Wright RI (1995) Measuring biodiversity value for conservation. *Annual Review of Ecology and Systematics* 26: 93–111. http://dx.doi.org/10.1146/annurev.es.26.110195.000521

Laffan SW, Lubarsky E, Rosauer DF (2010) Biodiverse, a tool for the spatial analysis of biological and related diversity. *Ecography* 33: 643–647. http://dx.doi.org/10.1111/j.1600-0587.2010.06237.x

Lawton JH, Prendergast JR, Eversham BC (1994) The numbers and spatial distributions of species: analyses of British data. Pp. 177–195. In *Systematics and conservation evaluation* Forey P, Humphries C, Vane-Wright RI (eds). (Clarendon Press, Oxford, U.K.)

Lee AC (2013) Phylogenetic diversity and endemism: metrics for identifying critical regions of conifer conservation in Australia. University of California, Berkeley, Undergraduate Honors Thesis.

Loiselle BA, Jørgensen PM, Consiglio T, Jiménez I, Blake JG, Lohmann LG, Montiel OM (2008) Predicting species distributions from herbarium collections: does climate bias in collection sampling influence model outcomes? *Journal of Biogeography* 35: 105–116.

Magurran AE (2004) Measuring biological diversity. (Blackwell Science Ltd, Oxford, U.K.)

Magurran AE, McGill BJ (2011) Challenges and opportunities in the measurement and assessment of biological diversity. Pp. 1–7. *Biological diversity: frontiers in measurement and assessment* Magurran AE, B.J. McGill BJ (eds). (Oxford University Press, Oxford, U.K.)

Mandl N, Lehnert M, Kessler M, Gradstein SR (2010) A comparison of alpha and beta diversity patterns of ferns, bryophytes and macrolichens in tropical montane forests of southern Ecuador. *Biodiversity and Conservation* 19: 2359–2369. http://dx.doi.org/10.1007/s10531-010-9839-4

Maurer BA, McGill BJ (2011) Measurement of species diversity. Pp. 55–65. *Biological diversity: frontiers in measurement and assessment* Magurran AE, McGill BJ (eds). (Oxford University Press, Oxford, U.K.)

Mishler BD, Knerr N, González-Orozco CE, Thornhill AH, Laffan SW, Miller JT (2014) Phylogenetic measures of biodiversity and neo-and paleo-endemism in Australian *Acacia*. *Nature Communications* 5. http://dx.doi.org/10.1038/ncomms5473

Moritz C, Richardson KS, Ferrier S, Monteith GB, Stanisic J, Williams SE, Whiffin T (2001) Biogeographical concordance and efficiency of taxon indicators for establishing conservation priority in a tropical rainforest biota. *Proceedings of the Royal Society B: Biological Sciences* 268: 1875–1881. http://dx.doi.org/10.1098/rspb.2001.1713

Nagalingum NS, Knerr N, González-Orozco CE, Thornhill AH, Miller JT, Mishler BD (in revision) Continental scale patterns and predictors of fern richness and phylogenetic diversity.

Pharo EJ, Beattie AJ, Binns D (1999) Vascular plant diversity as a surrogate for bryophyte and lichen diversity. *Conservation Biology* 13: 282–292. http://dx.doi.org/10.1046/j.1523-1739.1999.013002282.x

Pócs T, Sass-Gyarmati A, Naikatini A, Tuiwawa M, Braggins J, Pócs S, Konrat von M (2011) New liverwort (Marchantiophyta) records for the Fiji Islands. *Telopea* 13: 455–494. http://dx.doi.org/10.7751/telopea20116031

R Core Team (2014) R: A language and environment for statistical computing.

Schmidt-Lebuhn AN, Knerr NJ, Kessler M (2013) Non-geographic collecting biases in herbarium specimens of Australian daisies (Asteraceae). *Biodiversity and Conservation* 22: 905–919. http://dx.doi.org/10.1007/s10531-013-0457-9

Stevenson LA, González-Orozco CE, Knerr N, Cargill DC, & Miller JT (2012) Species richness and endemism of Australian bryophytes. *Journal of Bryology* 34: 101–107. http://dx.doi.org/10.1179/1743282012Y.0000000004

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