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Part Five: Liverworts—Globally and Locally

Chapter Nine: Early Land Plants Today: Liverwort Species Diversity and the Relationship with Higher Taxonomy and Higher Plants

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Abstract

Liverworts (Marchantiophyta) form a conspicuous and important component in many terrestrial ecosystems throughout the world. Despite of their significance and abundance, studies of various aspects on global plant species richness and distribution patterns have almost exclusively focused on vascular plants. Yet, comprehensive studies of liverwort plant diversity have many implications and broad applications. We use a preliminary dataset that unites liverwort nomenclature, taxonomy, and geography based on some 60,000 records. Global maps are produced for the taxonomic ranks of species, genus, and family to provide a rapid guide of diversity across political units worldwide. The usefulness of higher level taxon analyses was investigated at the genus and family level to test the relationship with species richness. A reduced set of taxonomic ranks other than species has been proved to be useful for rapid and costeffective assessment of biodiversity. We provide the first examination of how well this method performs for liverworts. Generic richness was slightly more accurately related to species richness than that of families, indicating surrogacy at this taxonomic level as a promising approach for the prediction of liverwort species richness. Finally, given the fact that vascular plant diversity and distribution patterns are often given high consideration in evaluating global networks of protected areas and biodiversity hotspots, we present a comparison of centers of species richness between liverworts and vascular plants. Several regions of high liverwort species richness lie outside the highest centers of vascular plant species richness. We conclude with ideas for future studies of the dataset, which has many exciting implications and applications for the study of liverwort distribution and diversity patterns.

Introduction

Knowledge of the spatial distribution of biodiversity is also crucial for its further exploration, use, and conservation (Mutke & Barthlott, 2005). Recently, there has been a growing number of studies documenting broad-scale patterns for many major groups of organisms, including vascular plants (Scotland & Wortley, 2003; Barthlott et al., 2005; Kier et al., 2005; Mutke & Barthlott, 2005; Kreft & Jetz, 2007), macrofungi (Mueller et al., 2007), mammals (Ceballos et al., 2005; Ceballos & Ehrlich, 2006), birds (Rangel & Diniz-Filho, 2004; Orme et al., 2005), amphibians (Wiens, 2007), vertebrates generally (Grenver et al., 2006), and epifaunal invertebrates (Witman et al., 2004). Global level datasets supporting richness and endemism analyses now exist and contain information on more than 30,000 species of vertebrates, including birds, mammals, reptiles, and amphibians (Kier et al., 2005).

However, plants are key structural elements of terrestrial ecosystems and are the basis of all terrestrial food webs. They are of great relevance in understanding global distribution of diversity and play a central role as an indicator group (Kreft & Jetz, 2007). Hence, plant richness patterns have been used extensively for global-scale conservation prioritizing (Myers et al., 2000; Mittermeier et al., 2005). Furthermore, detailed information about spatial patterns of phytodiversity is a central prerequisite to fulfill targets set by the Convention on Biological Diversity (CBD) and the Global Strategy on Plant Conservation (GSPC), which include protecting 50% of the most important centers of plant diversity and to conserve 60% of the world's most threatened species in situ by the year 2010 (Barthlott et al., 2005).

To date, papers investigating various aspects of global plant species richness patterns and diversity and global species numbers have almost exclusively focused on vascular plants. Yet, other groups such as liverworts are of critical biological, ecological, and phylogenetic significance. A growing body of evidence identifies liverworts as the earliest diverging lineage of embryophytes. Their sister relationship to all other land plants puts liverworts in a pivotal position in our understanding early land plant evolution (e.g., Mishler et al., 1994; Wellman et al., 2003; Qiu et al., 1998, 2007). Liverworts are an important component of the vegetation in many regions of the world, constituting a major part of the biodiversity in moist forest, wetlands, mountain, and tundra ecosystems (Hallingbäck & Hodgetts, 2000). Liverworts and mosses offer microhabitats that are critical to the survival of a tremendous diversity of organisms such as single-celled eukaryotes, protozoa, and numerous groups of invertebrates (Gerson, 1982). Their structural contribution to levels of diversity might be as significant as that of vascular plants, albeit at a smaller scale. Liverworts, in concert with mosses and hornworts, play a significant role in the global carbon budget (O'Neill, 2000) and CO₂ exchange (De Lucia et al., 2003), plant succession (Cremer & Mount, 1965), net production and phytomass (Frahm, 1990), nutrient cycling (Coxson, 1992), and water retention (Pócs, 1980; Gradstein et al., 2001). These plants also are important environmental and ecological indicators (Rao, 1982; Pitcairn et al., 1995; Gradstein et al., 2001; Giordano et al., 2004) and have been used as indicators of past climate change, to validate climate models, and are potential indicators of global warming (Gignac, 2001).

Recently, we created the first comprehensive global database uniting liverwort nomenclature, taxonomy, and geography; the preliminary dataset includes the distribution of liverwort species across almost 400 geopolitical units based on some 60,000 records from over 600 publications (von Konrat et al., in press). We contended that this database has much to offer also to the broader biological community, not only through aiding our understanding of liverwort diversity. Moreover, good quality data on liverwort diversity has a multitude of applications, such as powerfully informing biogeographic and conservation research as well as identifying data-deficient regions.

Here we have used this database to 1) provide global maps for liverwort species, genera, and family richness, 2) investigate the relationship between taxon richness at the species level and higher taxonomic levels, and 3) present a comparison of centers of species richness between liverworts and vascular plants. The global maps, presenting political units, summarize the total number of taxa at the rank of species, genus, and family. By examining the relationship between species richness and higher level taxonomy we test Gaston and Williams's (1993) supposition that patterns of species richness can be studied from taxonomic levels higher than species. Finally, the comparison of centers of species richness between liverworts and vascular plants has two immediate implications. First, patterns of vascular plant species richness have been used, as mentioned, for priority setting of global scale conservation networks. Secondly, vascular plant species diversity has been used as a predictor of bryophyte species diversity in some forest systems (Chiarucci et al., 2007).

We close with the conclusion that increased knowledge of liverwort species distribution has far reaching implications and applications. There is an urgent and sustained need to develop such baseline knowledge, from which our understanding of the variability of plant species richness at a global scale ultimately flows.

Methods

Quality of Underlying Data

A brief discussion of the quality of the underlying dataset used here to produce the global maps and statistical analysis is provided by von Konrat et al. (in press). In brief, names obtained primarily from geopolitical checklists were cross-referenced against taxonomic revisions, monographs, and authoritative indices (e.g., Crosby & Engel, 2006) for synonyms and verification of distribution. A very brief assessment on data availability and information needs specifically for liverworts was provided by von Konrat et al. (in press) Our dataset, based on over 600 publications, currently includes some 22,500 published liverwort names ("accepted" taxa and synonyms), 60,000 observations (defined as one taxon recorded from one geopolitical unit), and almost 500 geopolitical units (von Konrat et al., in press). The maps and statistical analysis are based on what we assume to be the approximately 6,500 currently "accepted" binomials to date. All names that could not be reconciled through our cross-referencing, as well as infraspecific taxa, were excluded from the analysis.

Mapping and Statistics

MAPPING-The global distribution maps of species, genera, and family richness were produced using the inventory-based mapping approach, which is explained by Mutke and Barthlott (2005). They reflect numbers per geopolitical unit without standardization for area. The comparison of the top 20% of the centers of species richness between liverworts and vascular plants is defined as >110 spp./10,000 km² for liverworts, and >3,000 spp./10,000 km² for vascular plants (Barthlott et al., 2005). Species richness in this comparison refers to an area of 10,000 km² standardized by the species-area model of Arrhenius (1920, 1921). We used the value 0.25 for the parameter z that determines the slope of the species-area relationship in this model. This value has been widely used (e.g., Rosenzweig, 1995) and is within the range of z-values found in other large-scale analyses of plant diversity patterns (Kier et al., 2005; Qian, 2007). This standard area offers a sufficient spatial resolution and is regarded as suitable for large-scale conservation approaches (Mutke & Barthlott, 2005).

STATISTICS—We explored the relationship between species richness and genus richness, and species richness and family richness through linear regression analysis, because we were primarily interested in the nature of the relationship between these pairs of variables. We established that the relationship between the variables was significant with an ANOVA, and used the Residual mean squares from the ANOVA as the primary basis for our comparison of the fit of our data to linear and various simple polynomial models. Analysis and graphics were produced and performed using SPSS 15.0 for Windows (SPSS Inc., Chicago, IL, USA).

Results and Discussion

Described Species Over Time

Figure 1 depicts the number of novel liverwort species, excluding new combinations that have been described over the last 250 years. The first major peak corresponds to the works of several early 19th century botanists, including Synopsis Hepaticarum by Gottsche, Lindenberg, and Nees (1844–1847). The three decades leading into, but prior to the highest peak, between 1860 and 1890, corresponds to the publications by a number of prominent bryologists including W. Mitten, J. D. Hooker, T. Taylor, and V. Schiffner. The second and highest peak of almost 1,200 names, in the early 1900s corresponds largely to the plethora of taxa described by Stephani (1898-1924) in his monumental work Species Hepaticarum. The periods of highest rates of new species described in the 1830s and around 1900 are the same for seed plants (Mutke & Barthlott, 2005). The third peak over the four decades between 1950 and 1980 can be attributed mainly to the works of R. M. Schuster, H. Inoue, and S. Hattori. The decline in newly described species since 1970 does not necessarily wholly translate to the supposition that taxonomists are closer to discovering all known species.

The almost 200 novel liverwort species that have been described in less than the past six years alone still represent a significant number, considering the relatively few liverwort taxonomists and monographers. Moreover, bryological exploration has been very uneven in many parts of the world; for example, many areas of the Neotropics still remain without a single bryophyte record (Gradstein et al., 2001). Paradoxically, scores of new species are still being discovered and described in relatively well-studied areas such as New Zealand; e.g., 12 new taxa in Lepidozia (Engel & Schuster, 2001). Recent attention to cryptic speciation in bryophytes is also revealing novel liverwort species; e.g., Szweykowski et al. (2005). The combination of collecting in yet-tobe explored areas, the continued discovery of species in well-studied regions, and an increased understanding of the biology of liverworts (including cryptic speciation), will lead to a significant number of newly discovered species into the foreseeable future. The corollary of this, coupled with increased monographic and revisional work, will be the increased discovery and the unraveling of synonymy.

Despite the fact that discovery and description of liverworts has continued for over 250 years, there has been no central source working toward a synthesis of nomenclature, taxonomy, and global distributional data until recently. This has been a major impediment for the study and analysis of species richness, distribution patterns, and conservation at a regional and global scale. There remains no reliable quantitative data with which the global number of liverwort species can be estimated objectively. Nevertheless, reliable figures of the global number of extant species are in great demand and have been seen as a fundamental descriptor of life on Earth (Gaston & Hudson, 1994) as well as important to assist conservation and decision-making (Govaerts, 2001). With support from the bryological community, we are



FIG. 1. The number of novel liverwort species described over 250 years from 1750 to the present (numbers exclude new combinations and are based on our unpublished dataset).

now working toward centralizing this information; e.g., Söderström et al. (this volume) and von Konrat et al. (in press). Below, we apply that dataset to providing a summary of global diversity, including species, genera, and family numbers, on a global scale, the relationship of liverwort species richness to higher taxonomy, and a comparison of centers of species richness between liverworts and vascular plants.

Numbers of Species, Diversity, and Distribution

Species richness is the simplest way to describe community and regional diversity (Magurran, 1988), and this variable-number of speciesforms the basis of many ecological models of community structure (MacArthur & Wilson, 1967; Connell, 1978; Stevens, 1989). Mutke and Barthlott (2005) produced a world map of species numbers per country/state for mosses and stated that the documentation of patterns of bryophyte diversity is still very incomplete. Pócs (1996) provided an evaluation of 1,000 epiphyllous liverwort species on a global scale, assessing their diversity, degree of threat, and conservation. Recently, von Konrat et al. (in press) produced the first-ever preliminary global map of species richness of liverworts, presenting species density values for standard area sizes of 10,000 km² throughout the world. Here, we present the number of liverwort species, genera, and families per geopolitical unit (Figs. 2–4) offering an easy and quick guide to identifying richness across the three taxonomic ranks worldwide based on our preliminary global dataset. It must be stressed that these numbers only offer a guide to liverwort diversity and the dataset is in a constant state of flux as 1) new data comes to hand, 2) increased monographic and revision work takes place, and 3) data are acquired from undercollected regions of the world.

Areas representing the highest class of between 501–777 liverwort species numbers include 601 documented binomials for New Zealand (Engel & Glenny, 2008), 615 for Japan (Furuki & Mizutani, 2004), 561 for Costa Rica (Dauphin, 2005), 514 for the Philippines (Tan & Engel, 1986), 608 for the island of Borneo (Menzel, 1988), 752 for Colombia (Bernal et al., 2007), and 606 for continental Ecuador (León-Yánez et al., 2006). The latter three areas (Borneo, Colombia, and Ecuador) do not coincide with the global maxima of liverwort species after being standardized for

area as presented by von Konrat et al. (in press). In some regions such as India, the data have been aggregated at the country level because there are no reliable data at a smaller scale. Hence, India, too, falls into the highest class. However, the majority of the species, over 500, occur in the north of India (e.g., Kashmir and the Himalayas), whereas the remaining regions of India (e.g., Punjab, Rajastahn, Gujarat, central India, the Gangetic Plain, and south India) have less than 250 species. The unrealistically low class of 16-50 documented binomials in areas such as Gabon, Congo, and the Malayan Peninsula where there are over 3,000 vascular plant species per 10,000 km² (Mutke & Barthlott 2005), is a direct reflection of our dataset that illustrates a lack of adequate information on liverworts from those regions. Equally, Figure 2 illustrates areas without or with very few species, the class representing 1–15, including large parts of the Sahara and the Kalahari Desert, as well as the arid and semiarid regions of central and south Australia; this almost certainly reflects genuine lack of diversity. These minima coincide with a lack of either available ambient energy or humidity, which limits plant growth and corresponds to the low number of vascular plants (Barthlott et al., 2005).

Interestingly, the areas with the highest number of species do not necessarily correspond precisely to those with the highest number of genera or families (Figs. 3, 4). For instance, New Zealand and Japan are represented by the highest classes of 501-777, 128-151, and 46-49 for species, genus, and family, respectively. Colombia, by contrast, is represented in the highest class for species and genus, but only the third highest class of 36-40 for family. Similarly, Ecuador, which also falls into the highest class for species, falls in the second highest class for genus, and the third highest class for family. These slight differences can be attributed to the relatively large number of endemic genera or monotypic genera that occur in areas such as New Zealand. On the other hand, areas such as Colombia, which lie in the tropics, are represented by a disproportionate number of members representing Lejeuneaceae. Lejeuneaceae is the largest family of liverworts with an extant diversity of approximately 1,000 species in some 90 genera (Gradstein, et al., 2003), and in some areas of tropical lowland forests, Lejeuneaceae can make up 70% of all liverwort species (Cornelissen & Ter Steege, 1989; Zartman, 2003; Gradstein, 2006). The section below explores the relationship between species richness and higher level taxonomy.

Despite the constraints and challenges in obtaining high quality data to quantify global liverwort diversity, we now have a dataset that can be applied to investigate liverwort distribution patterns. Future global mapping of liverwort species richness needs to be explored by ecoregion rather than by political units in a fashion similar to what Kier et al. (2005) have produced for vascular plants. This will lead to more biologically and ecologically meaningful interpretation of liverwort diversity patterns. Lack of a totally resolved taxonomy with all "accepted" species named and their range defined, although hampering, should not preclude us from making such analyses. As in any other field of science, taxonomy will always be in flux, aptly quoted by May (1990) "taxonomy is the destiny" because new data will always come to hand. Yet, for future global mapping and distribution analyses, it will be essential to consider and distinguish between those species that remain poorly documented, and thus too poorly known for analyses, and those species that are widely accepted as accurate descriptors of biological diversity.

Species Richness and Higher-Level Taxonomy

Species richness is a fundamental measure of biodiversity, and declining species richness in many regions of the world is a major ecological, economical, and cultural problem (Bergamini et al., 2005). The practical challenges in describing and enumerating species richness, including the problem of the enormous amount of resources (e.g., time, money, taxonomists) have urged conservation biologists to identify reliable surrogate measures for explaining patterns in biodiversity (Balmford et al., 1996; Heino & Soininen, 2007). These surrogacy methods include environmental characteristics, indicator taxon groups and individual indicator species, and use of higher taxonomic levels (Gaston & Blackburn, 1995; Faith & Walker, 1996; Williams et al., 1997; McGeogh, 1998; Ward et al., 1999; Heino et al., 2003; Fleishman et al., 2005; Wolters et al., 2006). Recently, Moreno et al. (2007) provided a brief review of these rapid alternative routes for appraising species diversity.

Gaston & Williams (1993) suggested that patterns of species richness could be studied from higher taxonomic levels. Their preliminary analyses indicated that predictions might be quite reasonable, cost effectiveness might be high, and that substantial bodies of data already existed. Another crucial advantage is the retention of broad biological information that allows the understanding of distribution patterns (Eggleton et al., 1994; Williams et al., 1994; Gaston & Blackburn, 1995) and more efficiency in the definition of conservation priority areas (Williams, 1993; Williams et al., 1994; Vanderklift et al., 1998; Balmford et al., 2000). Numbers of higher taxa can also provide some measure of another dimension of diversity, the dissimilarity or disparity between organisms (Williams, 1993). Higher taxa have also proven to be useful in environmental and impact studies (Beattie & Oliver, 1994; Somerfield & Clarke, 1995).

This approach has since been applied to a variety of biological groups, with studies showing significant positive correlations between higher taxon richness and species richness (e.g., Gaston & Williams, 1993; Williams & Gaston, 1994; Roy et al., 1996; Balmford et al., 1996, 2000; Cardoso et al., 2004; Villaseñor et al., 2005). Diversity at higher taxonomic levels has also long been regarded as a good surrogate for diversity at the species level by palaeontologists (Sepkoski, 1992). On the other hand, some studies have found that higher taxon analyses are weak predictors of species richness (Prance, 1994; Andersen, 1995; Fjeldsa, 2000), suggesting that this is not necessarily an infallible remedy when it comes to estimating the patterns of species richness (Grelle, 2002).

We here examine the utility of using higher taxa as potential surrogates for liverwort species richness by testing the relationship between species richness and the numbers of higher taxa, i.e., genera and families.

SPECIES VS GENERA-Box plots for the raw number of species and number of genera were both positively skewed (Appendix I). A scatterplot of number of species against number of genera (Fig. 5) and a plot of residuals against predicted number of species (not shown) from a linear regression analysis both suggested a nonlinear relationship between these two variables. The boxplots of species and genera were both strongly positively skewed. The nature of the species vs. genera relationship appears quadratic. For simple polynomial models of the form $y=a+x^2$, by defining $w = x^2$, we get a simple linear model, y = a + bw, with which we can estimate x^2 using traditional linear regression procedures. The boxplots for species were only slightly positively skewed after the data was square-root



FIGS. 2–4. Maps of the numbers of liverworts per political unit: 2, Species numbers; 3, Genus numbers; 4, Family numbers.

transformed (Appendix I). A plot of residuals against predicted number of species from a linear relationship substituting w for x shows no evidence of a nonlinear relationship. Following transformation, plots of residuals against genera showed a cloud-like distribution, suggesting homogeneity of variances (not shown).

The *t*-test and the ANOVA F-test cause us to reject the null hypothesis that the slope of both linear and quadratic regressions equals zero (Appendices 2 & 3). The r^2 indicates that we can explain about 88% of the total variation in species number with the linear relationship, but about 95% with the quadratic relationship. Pearson's correlation coefficient is also higher for the quadratic model (0.974 vs. 0.940), indicating that this relationship is stronger than the linear. The Residual Mean Squares are less for the quadratic (882.16 vs. 1994.74), which means that the points all lie closer to the line than in the linear. This indicates again that the quadratic is a better fit, and this can be seen visually (Fig. 5).

SPECIES VS. FAMILY—Quadratic models again provide a better explanation of the data by the same metrics as described above (Appendices 4 & 5). The scatterplot of number of species against number of families also exhibits a nonlinear relationship (Fig. 6). The r^2 indicates that we can explain about 59% of the total variation in species number with the linear regression, but about 69% with the quadratic equation. Pearson's correlation coefficient is also higher for the quadratic (0.829 vs. 0.770), indicating that this relationship is stronger than the linear. Yet, the fact that the Residual Mean Square is much higher for this



FIG. 5. Relation of generic richness to species richness.



FIG. 6. Relation of familial richness to species richness.

model means that the relationship is not so tight as between species and genera. The scatter of points around the regression line is considerably positively skewed in this relationship, and this is reflected in a plot of residuals against predicted number of species.

HIGHER-TAXON ANALYSIS AS A SURROGATE FOR SPECIES RICHNESS—Analyses based on our dataset showed that generic richness was slightly more related to species richness than that of the families. Quadratic models also appear to explain a greater variation of species number than linear models. In summary, it is suggested that the higher-taxon approach at the generic level might be a useful surrogate of species richness. The higher-taxon α -diversity, especially at the generic level, has now been shown to be a useful surrogate across a wide biological spectrum. For mammals (Grelle, 2002), ants (Andersen et al., 2004), spiders (Cardoso et al., 2004), macrofungi (Balmford et al., 2000), macrolichens (Bergamini et al., 2005), and plants (Balmford et al., 1996; Villaseñor et al., 2005), the higher-level taxon surrogate approach at the generic level is useful, but the relationships between number of species and families or orders are weaker.

This dataset has the potential to be explored in more detail and the reliability tested depending on habitat, biogeography, and sampling effort. The data can be partitioned and geographical variability at a regional scale can be explored. Partitioning of the data sets by taxon and geography also will aid in identifying the potential problem of para- and polyphyletic taxa as well as assessing the impact that genera and families are not necessarily comparable units because of their different life histories. We can also begin to explore such questions as: Can total liverwort species richness be predicted by the richness of liverwort genera alone or particular liverwort genera? and Do liverwort genera alone reflect compositional shifts in liverwort communities? Diversity patterns of higher taxa might also provide valuable insight into evolutionary, historical, and biogeographical influences on contemporary diversity (Ricklefs, 1987).

Comparison of Liverwort and Vascular Plant Species Richness Patterns

Diversity patterns of vascular plants have almost always been included in analyses for priority setting of global scale conservation networks (e.g., Myers et al., 2000; Olson & Dinerstein, 2002; Mittermeier et al., 2005). We therefore evaluated the relationship between the top 20% centers of species richness for liverworts and vascular plants (Fig. 7), which is defined as >110 sp./10,000 km² for liverworts, and >3,000 spp./10,000 km² for vascular plants (Barthlott et al., 2005); the top 10% is also illustrated for liverworts which equates to >251 sp./10,000 km². Many centers with high liverwort species richness, e.g., New Zealand and Japan, are outside the top 20% centers of vascular plant species richness. However, because of the extraordinary high rate of vascular plant endemism coupled with the degree of habitat threat, these regions have been designated biodiversity hotspots (Myers et al., 2000; Olson & Dinerstein, 2002; Mittermeier et al., 2005). Figure 7 illustrates other areas with high liverwort species richness such as Costa Rica, the Himalayas, and the island of Borneo which coincide with the top 20% centers of vascular plant species richness. These same areas are also part of designated global biodiversity hotspots, i.e., Mesoamerica, Himalaya, and Sundaland hotspots, respectively (Mittermeier et al., 2005).

Conversely, it is also apparent that there are many regions that exhibit significantly high levels of liverwort species richness but do not coincide with any of the top 20% centers of vascular plant species richness. These areas include southern Chile, the British Isles, Taiwan, and Tasmania and Queensland of Australia. Nor do any of these areas coincide with any existing biodiversity hotspot region as defined by Mittermeier et al. (2005). Considering that bryophytes are a conspicuous and dominant feature in many ecosystems throughout these regions, further analysis is warranted. In summary, a potential weakness of approaches that are heavily weighted towards vascular plant species richness and endemism for identification of global biodiversity hotspots is that they neglect very important centers of



FIG. 7. Map of centers of high species richness of liverworts and vascular plants.

liverwort diversity, which lie outside exisiting biodiversity hotspots.

Conclusion

Liverworts, together with mosses and hornworts, are of great ecological and biological significance worldwide. To date, papers investigating various global plant species richness and diversity patterns have almost exclusively focused on vascular plants. The bryological community is now working toward developing a high quality dataset quantifying global liverwort diversity. Many promising areas of research are now possible with this new dataset and can contribute toward understanding the forces that shape spatial and temporal variation in liverwort diversity as well as for conserving and managing liverwort biodiversity. The global maps produced here provide a quick overview of richness on a global scale at different levels of taxonomic hierarchy. Future global mapping efforts should include liverwort species richness by ecoregions and investigations of the environmental and potential historical determinants of liverwort richness. Endemism should also be assessed in future mapping efforts.

Ideally, the study of patterns of biodiversity should be carried out using species-based datasets. However, in some instances, identification of reliable surrogate measures for explaining patterns in biodiversity might be warranted. The analyses performed here showed that higher taxon analysis, especially at the generic level, has potential to be used as a reasonable surrogate for species richness. It is now important to determine the degree to which higher taxa perform as species-level biodiversity surrogates in regions differing in species diversity and in other taxonomic groups.

Greater consideration of liverworts can now be made in evaluating global networks of protected areas. This is underscored by the importance and abundance of liverworts in many habitats throughout the world and the fact that some centers of species richness lay outside many centers of vascular plant species richness, which are often used to create these networks. In future studies, it would be interesting to investigate the underlying factors, e.g., geological, climatological, or historical, that might explain the lack of total overlap between centers of liverwort diversity with those of vascular plants and different animal groups. Many applications of this dataset are now possible and can contribute towards the creation of a comprehensive global biodiversity strategy for the terrestrial realm where already large datasets occur for vascular plants, mammals, birds, and amphibians.

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Appendix I. Boxplots for transformed variables.

Species, skew = 0.375 (mild positive skew). Square root species, skew = 0.077 (where 0 is no skew).



Square root species

	Coefficient	Standard error	Standardized coefficient	t	Р
Intercept	-50.90	4.4		-11.57	< 0.001
Slope	4.08	0.08	0.940	48.38	< 0.001
Correlation coe	fficient (r) = 0.940, r^2 =	=0.883			
Source	df	MS	F	Р	
Regression	1	4668941.7	2340.6	< 0.001	
Residual	311	1994.7			

Appendix II. Linear regression statistics: species vs. genera.

Appendix III. Quadratic regression statistics: species vs. genera.

	Coefficient	Standard error	Standardized coefficient	t	Р
Intercept	1.871	3.955		0.473	0.637
Slope	0.027	0.01	0.732	19.830	< 0.001
Correlation coe	fficient $(r) = 0.974, r^2 =$	=0.948			
Source	df	MS	F	Р	
Regression	2	2507917.61	2842.92	< 0.001	
Residual	310	882.16			

Appendix IV. Linear regression statistics: species vs. family.

	Coefficient	Standard error	Standardized coefficient	t	Р
Intercept	-59.571	9.800		-6.079	< 0.001
Slope	9.200	0.432	0.770	21.285	< 0.001
Correlation coe	fficient (r) = 0.770, r^2 =	=0.593			
Source	df	MS	F	Р	
Regression	1	3136332.508	453.048	< 0.001	
Residual	311	6922.740			

Appendix V. Quadratic regression statistics: species vs. family.

	Coefficient	Standard error	Standardized coefficient	t	Р
Intercept	26.688	12.376		2.157	0.032
Slope	0.312	0.032	1.082	9.692	< 0.001
Correlation coe	fficient (r) = 0.829, r^2 =	=.688			
Source	df	MS	F	Р	
Regression	2	1818502.050	341.182	< 0.001	
Residual	310	5330.002			