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Elevational patterns of genetic variation in the cosmopolitan moss *Bryum argenteum* (Bryaceae)[1]

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- *Premise of the study:* The Baas Becking tenet posits that 'everything is everywhere, but the environment selects' to explain cosmopolitan distributions in highly vagile taxa. Bryophyte species show wider distributions than vascular plants and include examples of truly cosmopolitan ranges, which have been interpreted as a result of high dispersal capacities and ecological plasticity. In the current study, we documented patterns of genetic structure and diversity in the cosmopolitan moss *Bryum argenteum* along an elevational gradient to determine if genetic diversity and structure is homogenized by intense migrations in the lack of ecological differentiation.
- *Methods:* 60 specimens were collected in the Sierra Nevada Mountains (Spain) between 100 and 2870 m and sequenced for ITS and *rps4*. Comparative analyses, genetic diversity estimators, and Mantel's tests were employed to determine the relationship between genetic variation, elevation, and geographic distance and to look for signs of demographic shifts.
- *Key results:* Genetic diversity peaked above 1900 m and no signs of demographic shifts were detected at any elevation. There was a strong phylogenetic component in elevational variation. Genetic variation was significantly correlated with elevation, but not with geographic distance.
- *Conclusions:* The results point to the long-term persistence of *Bryum argenteum* in a range that was glaciated during the Late Pleistocene. Evidence for an environmentally driven pattern of genetic differentiation suggests adaptive divergence. This supports the Baas Becking tenet and indicates that ecological specialization might play a key role in explaining patterns of genetic structure in cosmopolitan mosses.

Key words: adaptive divergence; Baas Becking tenet; bryophytes; *Bryum argenteum*; cosmopolitan species; elevational gradients; genetic diversity; mountains.

Elevational gradients offer many characteristics that make them extremely suitable for uncovering the underlying causes of spatial variation in diversity because of the dramatic changes in environmental conditions across comparatively short distances (Sanders and Rahbek, 2012). Alpine ecosystems have in particular become an increasing area of research since climate change impacts on alpine and nival vegetation may be more pronounced than on vegetation at lower elevation, with an upward shift of tree lines and range reduction in alpine and nival plant species preceding massive extinctions (Randin et al., 2009).

Bryophytes are among the last land plants to persist in snow beds and other extreme high-elevation habitats up to 5800 m (Mordaunt, 1998; Frey and Kürschner, 2012). In fact, a feature common among most bryophytes is their ability to grow at low temperatures. More than half of the 40 mid-European bryophyte species investigated by Furness and Grime (1982) showed a growth reduction of less than 50% at 5°C compared to growth at their optimal temperature. Most species, including tropical ones, seem to be preadapted to cold and survive temperatures ranging from −10 to −27°C (Glime, 2007). As a result, bryophytes generally have much broader elevation ranges than vascular plants (Vittoz et al., 2010). Previous studies reported partitioning of morphological (Benassi et al., 2011; Pereira et al., 2013) and genetic (Korpelainen et al., 2012b) variation across elevational gradients, but whether this reflects adaptation or dispersal limitations and genetic drift remains ambiguous.

Little evidence of ecotypic differentiation was found in bryophytes (Shaw, 1991). Their cold tolerance varies seasonally (Rütten and Santarius, 1992, 1993), suggesting that they develop tolerance in response to changes in environmental conditions. In fact, it was experimentally shown that incubation at low, but > 0°C, temperatures significantly increases survival rates upon subsequent exposure to negative temperatures (Minami et al., 2005). In the desert moss *Syntrichia caninervis* Mitt., morphological variation of populations from extreme microhabitats results from plasticity (Reynolds and McLetchie, 2011). In *Bryum argenteum* Hedw., plants from clean and heavily polluted environments exhibit indistinguishable growth responses to media supplemented with heavy metals. It may be that this inherent, relatively high level of tolerance makes the evolution of specialized races unnecessary (Shaw et al., 1989; Shaw and Albright, 1990). Although bryophytes are not genetically depauperate and, in fact, display amounts of genetic diversity comparable with angiosperms (Shaw, 2000a), this genetic variation does not appear to be adaptive to specific environments (Shaw and Bartow, 1992). Thus, by contrast with flowering plants, physiological

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acclimatization is much more important for bryophytes than is genetic specialization.

In addition, mosses are traditionally perceived as extremely good dispersers (see Shaw et al., 2011, for review). Regular establishment occurs at the km-scale (Lönnell et al., 2012), while 1% of the regional spore rain is assumed to have a trans- or intercontinental origin (Sundberg, 2013), which is consistent with phylogeographic evidence for recurrent long-distance dispersal in the group (Werner and Guerra, 2004; Devos and Vanderpoorten, 2009; Szövényi et al., 2012). The high dispersal ability of bryophytes appears as a strong homogenizing force that may prevent local differentiation and adaptation and explain the wide distribution of mosses and their low rates of endemism as compared to angiosperms (Vanderpoorten et al., 2010). The high dispersal ability of bryophytes supports the first half of the Baas Becking tenet (Baas Becking, 1934) 'everything is everywhere', which explains the seemingly cosmopolitan distributions typically observed in micro-organisms by invoking a lack of dispersal limitation (see Sul et al., 2013, for review). Meanwhile, the apparent failure of bryophytes to develop ecotypes because of their inherently high ecological plasticity suggests that the second part of the tenet, 'but the environment selects', does not apply.

In the present paper, we revisit the Baas Becking tenet, taking the cosmopolitan *Bryum argenteum* as a model. *B. argenteum* has one of the widest distributions of all plants on Earth. It is found on all continents in contrasting climates from the equator up to polar and alpine habitats. In addition to sexual reproduction, *B. argenteum* can produce large numbers of deciduous bulbils and branchlets that can detach and serve as a primary mode of local dispersal (Selkirk et al., 1998). The dual mating system of *B. argenteum*, along with its preference for disturbed soils, makes the species a typical colonist (sensu During, 1992) whose high dispersal capacity makes it capable of efficiently tracking ephemeral habitats at both short and long distances. The species is morphologically extremely variable, but this variation does not appear to be adaptive (Longton, 1981; Shaw et al., 1989; Shaw and Albright, 1990). Consequently, patterns of genetic diversity and variation are expected to show no geographic structure among populations sharing the same evolutionary history. This hypothesis is tested here along an elevational gradient in the Sierra Nevada Mountains of southern Europe. If this hypothesis is rejected, we attempt to (i) determine whether populations from low, mid, and high elevation experienced contrasting demographic histories and (ii) disentangle the roles of dispersal limitations and ecological specialization in spatial patterns of genetic variation.

MATERIALS AND METHODS

***Sampling design and molecular protocols*—**Sixty specimens of *Bryum argenteum* were collected from 15 localities in the mountains of Sierra Nevada, Spain, along an elevational gradient from 100 to 2870 m a.s.l. All accessions but two were sterile at the time of collection. Voucher information, including elevation of each locality, geographic coordinates, and GenBank accession numbers, is given in Appendix 1. Samples from within each locality were separated from each other by at least 1 m. The maximum distance between any two localities was 52 km. Samples were air dried and stored until DNA extraction. Total genomic DNA was extracted using a modified version of the NaOH extraction protocol (Werner et al., 2002) in which 5 µl of crude NaOH extract were diluted by the addition of 45 µl of 100 mM Tris – 1 mM EDTA (pH 8.3), stored frozen at –18°C, and used as template for PCR. The ITS1- 5.8S rDNA—ITS2 nuclear genomic fragment was amplified by PCR using primers (5′-CCGATTGAATGGTCCGGTGAAGTTTTCG and 5′-GCTGGGCTCTTTCCGGTTCGCTCGCCGTTAC) specifically redesigned for *B. argenteum* from sequences obtained with universal primers. The *rps4* cpDNA was amplified using the primers rps5 (Nadot et al., 1995) and trnas (Buck et al., 2000). PCR reactions were performed in a thermo cycler using 2 µl of the DNA solution in a 50 µl final volume. The reaction mix contained 1.5 µl of each primer (10 µM), 5 µl 10× reaction buffer with $MgCl_2$, 2 µl (1 U μl^{-1}) DNA polymerase (Biotools, Madrid, Spain), 2 µl 10 mM dNTP mix, 1 µl 10% skim milk powder in water, and 35 µl nuclease free water. ITS amplification included the following steps: (1) initial denaturation for 3 min at 95°C; (2) 40 cycles each of 94°C for 30 s, 60°C for 30 s and 72°C for 75 s; and (3) a final extension at 72°C for 5 min. Amplification for the *rps4* marker started with 3 min denaturation at 95°C; 40 cycles each of 94°C for 30 s, 55°C for 30 s and 72°C for 60 s; and a final extension at 72°C for 5 min. We used agarose electrophoresis to test for amplification of single fragments before cleaning PCR products with the GenElute PCR Clean-Up Kit (Sigma-Aldrich Co., St. Louis, Missouri, USA). Forward and reverse sequence fragments for both ITS1 and ITS2 and for *rps4* were generated using BigDyeTerminator v3.1 (Applied Biosystems, Foster City, California, USA) and separated on an ABI-Prism3730 sequencing machine (Applied Biosystems). In addition to the amplification primers, the primers 5.8R and 5.8F (Stech and Frahm, 1999) were used in the sequencing reactions of the ITS region. Forward and reverse sequence fragments were edited and assembled using Bioedit ver.7.0.5 (Hall, 1999) and every polymorphism was checked from the chromatograms. The sequences were aligned by eye, allowing gaps where necessary to conserve homology among sequences. No polymorphism was observed in the 5.8S gene, which was excluded from further analyses.

***Phylogenetic analyses*—**Indels were coded with SeqState 1.25 (Müller, 2005) using simple coding (Simmons and Ochoterena, 2000) and added to a separate binary character matrix. The nucleotide substitution models HKY+G and TPM3uf were selected based upon the AIC and BIC criteria as implemented by JModeltest2 (Darriba et al., 2012) for the ITS and *rps4* partitions, respectively. A model implementing identical forward and backward transition rates was applied to the indel matrix. Independent phylogenetic analyses of each cpDNA and nrDNA dataset were performed in MrBayes 3.1.2 (Ronquist and Huelsenbeck, 2003). For each dataset, two Metropolis-coupled Markov Chain Monte Carlo (MCMC) analyses, including three hot chains and one cold chain, were run for 10^7 generations and sampled every 10^4 generations. To confirm that the chains had reached stationarity and converged, we (1) graphically inspected the values of the log-likelihoods of the two MCMC analyses; (2) made sure that the standard deviation of split frequencies was below 0.01 at the completion of the analysis; and (3) made sure that the potential scale reduction factor for each of the parameters shown in the summary statistics of the analyses was close to 1. The first 200 trees were discarded as burn-in and the remaining trees were used to construct a 50% majority rule consensus tree. The *rsp4* analysis resolved two haplotypes that correspond to the two main clades identified in the ITS analysis (see below under RESULTS). The partitions were therefore congruent and combined within a heterogeneous Bayesian analysis employing the nucleotide substitution models indicated above for each partition. The other settings were identical as those described above.

The generalized least square models implemented by the Continuous option of BayesTraits (Pagel, 1997) were used to investigate the phylogenetic component of elevational variation through the scaling parameter lambda (λ). A value of $\lambda = 1$ indicates that the tree correctly predicts the patterns of elevational variation observed, whereas $\lambda = 0$ points to the phylogenetic independence of trait evolution (Freckleton et al., 2002). We employed an MCMC analysis to sample values of λ depending on their posterior probability. At each iteration, the chain selects a tree and a value of λ, and the combination is assessed though the Metropolis-Hastings algorithm. We then reran the analysis, setting λ to 0, and determined whether imposing complete phylogenetic independence in elevational variation ($\lambda = 0$) significantly decreases the log-likelihood by computing the Bayes factors. The latter were measured as twice the difference in the harmonic means of the log-likelihood of the two analyses, and differences of 2, 5, and 10 were considered as evidence, strong evidence, and very strong evidence for differences of fit between the models, respectively (Pagel et al., 2004).

***Population genetics analyses*—**Haploid diversity corrected for sample size (uh) and nucleotide diversity (pi) were calculated with GENEALEX 6.5 (Peakall and Smouse, 2006) along the elevational gradient partitioned into three elevational belts that correspond to vegetation zones in the Sierra Nevada Mountains of southern Europe: low elevation, < 800 m; mid-elevation, 800-1900 m; and high elevation > 1900 m (Anderson et al., 2011). Tajima's *D* (Tajima, 1989) and Fu's *Fs* (Fu, 1996) were calculated in Arlequin 3.5 (Excoffier et al., 2005) for each of the three elevation levels to seek for a signature of demographic changes in patterns of genetic diversity. Both statistics

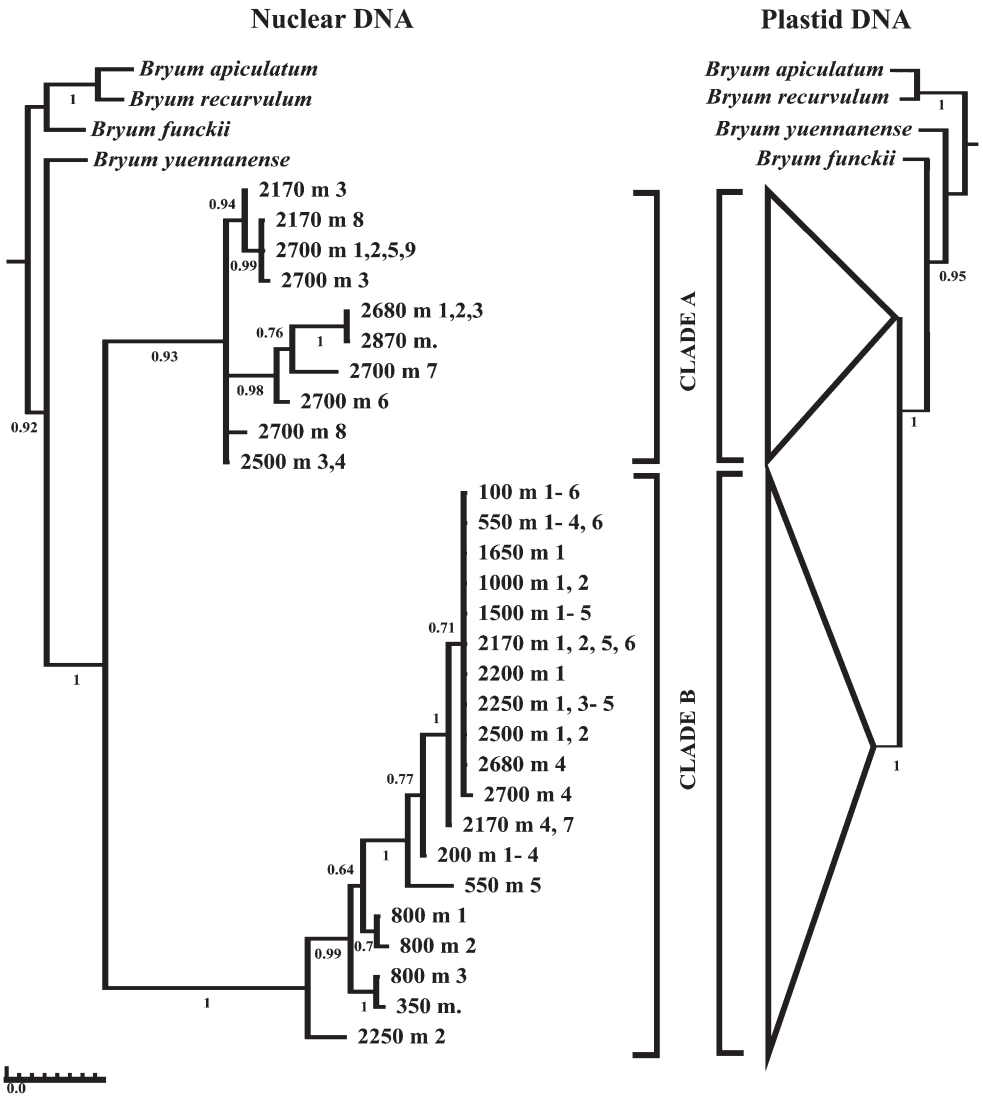

Fig. 1. Fifty percent majority-rule consensus with branch length averaged across the trees sampled from the posterior probability distribution from the Bayesian analysis of ITS and *rps4* sequences in the moss *Bryum argenteum* along an elevation gradient in the Sierra Nevada Mountains of southern Europe. Numbers below the branches are the posterior probabilities.

measure whether variation at the locus considered is consistent with the hypothesis that the populations are at neutral mutation-drift equilibrium. If *D* and *Fs* do not significantly depart from 0, there is no evidence for changes in population size or for selection at the locus. Significantly negative *D* and *Fs* point to purifying selection or expansion, while a positive value of those statistics is suggestive of bottleneck or dominant selection.

Mantel's tests were used to measure the correlation between genetic distances on the one hand, and geographical distance and elevational gradients on the other. We therefore computed kinship coefficient among individuals, *Nij*, which is analogous to J. Nason's *Fij* estimator as defined by Loiselle et al. (1995), but takes the phylogenetic relationship among alleles into account (Vanderpoorten et al., 2011). Phylogenetic distance among alleles was measured from a Tamura 3-parameter model distance matrix with Mega 5 (Tamura et al., 2011). The significance of the slope of the regression of *Nij* on the logarithm of spatial distance between individuals, ln(*dij*), was tested by means of 10^4 random permutations of population locations in SPAGeDi 1.3 (Hardy and Vekemans, 2002). The same test was then applied between the matrix of *Nij* and of the elevational difference among pairs of individuals. To obtain a graphic representation of the change in genetic similarity with increasing elevational difference among individuals, the mean *Nij* values were computed over *i*, *j* pairs separated by predefined elevational intervals. Threshold distance separating intervals were 0, 250, 670, 1300, 2000, and 2600 m, the first interval corresponding to pairs of individuals from the same population. To remove the potentially confounded signal of geographic distance in the matrix of elevational differences, partial Mantel's tests were used. The latter were employed to test the correlation between matrices of kinship coefficients and of elevational difference among individuals, while controlling for the information present in the geographic distance matrix. Partial Mantel's tests were performed with ZT (Bonnet and Van de Peer, 2002), and the significance of the correlations was tested by means of 10^4 randomization runs.

RESULTS

There were 112 (80 indels and 32 mutations) and 6 polymorphic positions (no indels) in the ITS and *rps4* matrices, respectively. Two clades, hereafter labeled as A and B, were resolved with full support in the *rps4* tree. These two clades also corresponded to the first dichotomy in the ITS phylogeny (Fig. 1). In the combined analysis, these two clades were supported with posterior probabilities of 0.97 and 1.00, respectively. Specimens from clade A are restricted to localities above 1900 m,

TABLE 1. Unbiased haploid diversity ± SD (uh ± SD), nucleotide diversity ± SD (pi ± SD), Tajima's *D* and Fu's *Fs* statistics and associated *P*-values, sample size (N), and number of haplotypes (*n*) in the moss *Bryum argenteum* along an elevational gradient in the Sierra Nevada Mountains of southern Europe.

Diversity and Neutral test statistics	All	< 800 m	800-1900 m	> 1900 m
uh ± SD	0.177 ± 0.011	0.068 ± 0.012	0.082 ± 0.015	0.381 ± 0.017
pi ± SD	0.008 ± 0,004	0.001 ± 0,001	0.002 ± 0.001	0.010 ± 0.005
Tajima's *D* (*P*-value)	0.397 (0.74)	−0.805 (0.24)	0.472 (0.70)	1.424 (0.95)
Fu's *Fs* (*P*-value)	14.601 (1.00)	5.610 (0.98)	6.249 (0.99)	16.380 (1.00)
N(*n*)	59(16)	16(5)	11(4)	29(9)

whereas specimens from clade B were sampled from the whole elevational range (Fig. 1). There was a strong phylogenetic component in elevational variation. In fact, the posterior probability of lambda ($\lambda = 0.87$, min = 0.54, max = 0.99) did not encompass 0, and constraining λ to 0 resulted in a Bayes factors of 100.7, unambiguously indicating that a phylogenetically dependent model describes patterns of elevational variation significantly better than a phylogenetically independent one.

Both haploid diversity and nucleotide diversity were lowest at low elevation and highest at >1900 m (Table 1). Tajima's *D* and Fu's *Fs* were not significant at any of the elevation belts. The slope of the regression between *Nij* and geographic distance (isolation-by-distance test) was not significant ($P > 0.05$). Mantel's tests between *Nij* and elevation difference among individuals were significant. On average, mean *Nij* per class of altitudinal difference decreased with increasing altitudinal difference among individuals (Fig. 2). This relationship remained significant after removal of the geographical component of the matrix of elevational difference among individuals (partial Mantel's test, $r = 0.055$, $P < 0.01$).

DISCUSSION

Striking levels of genetic diversity, similar to the highest levels of ITS divergence reported within moss species (e.g., Shaw, 2000b), were found in ITS sequences of *Bryum argenteum* along an elevation gradient in the Sierra Nevada Mountains, confirming previous reports of high ITS diversity in the species (Longton and Hedderson, 2000). The ITS region has been and remains one of the most widely exploited sources of molecular variation at the species level (e.g., Nagy et al., 2012; Pettigrew et al., 2012; Kučera et al., 2013), but there has been an increasing concern about its reliability for phylogenetic reconstruction, especially due to the existence of paralogs and pseudogenes (see Nieto Feliner and Rosselló, 2007, for review). The 5.8S gene was completely invariant among *B. argenteum* accessions, rendering the pseudogene hypothesis unlikely. The hypothesis that several paralogous copies were sequenced is also weakened by two lines of evidence. First, no conflicting base calls during sequencing were observed. Second, although the levels of polymorphisms in *rps4* were low, there was a congruent phylogenetic signal between *rps4* and ITS. Altogether, these observations suggest that the variation observed reflects actual diversification of orthologous ITS sequences.

There was a substantially higher genetic diversity at high elevation as compared to that observed at mid and low elevations, ruling out our primary hypothesis that everything is everywhere in the absence of dispersal limitations and ecological differentiation along the elevational gradient. Similar patterns were reported in previous studies and have been interpreted as evidence of adaptation to severe conditions at high elevation, human factors, or demographical shifts associated with climate change (see Ohsawa and Ide, 2008, for review). Since Tajima's *D* and Fu *Fs* statistics did not significantly depart from 0, there was no evidence for changes in population size, weakening the latter hypothesis. Intense migration from lower areas could potentially erase any signature of bottlenecks associated with founding events and lead to nonsignificant *Fs* and *D* statistics (Busch et al., 2007), but this hypothesis is not compatible with the observed partitioning of genetic diversity. The results thus suggest that *Bryum argenteum* successfully persisted in a high-elevation range that was extensively glaciated during the Late Pleistocene (Anderson et al., 2011). This parallels molecular support for

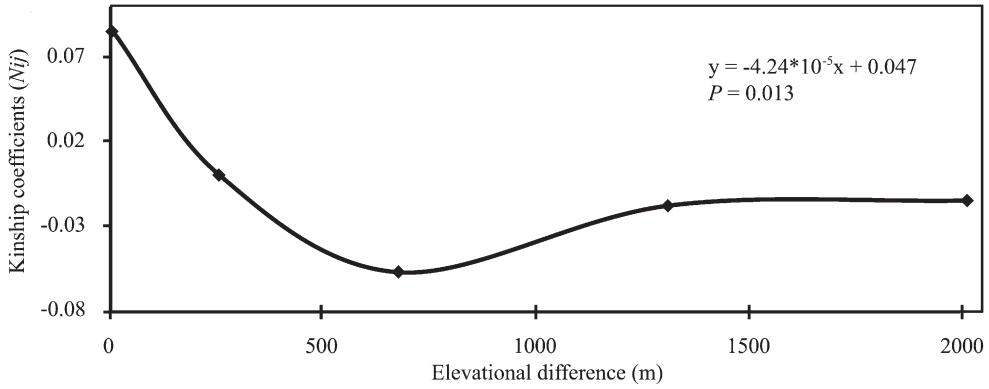

Fig. 2. Mean kinship coefficients *Nij* between pairs of individuals of the moss *Bryum argenteum* based on their sequence variation at ITS and *rps4* depending on the elevational difference among them in the Sierra Nevada Mountains. The slope of the regression between pairwise *Nij* and elevational difference and its *P*-value are indicated in the upper right corner.

Pleistocene persistence of the species in continental Antarctica (Hills et al., 2010) and, more generally, of temperate bryophyte species in microrefugia across largely glaciated landscapes (Désamoré et al., 2012).

Bryophytes are almost never deliberately introduced and *Bryum argenteum* is not a species that is harvested for commercial purposes, so that the high levels of genetic diversity found at the highest elevations cannot be attributed to human factors, such as lower collection or exploitation intensity at high elevation, which has been reported for some commercially valuable taxa (Wen and Hsiao, 2001; Maghuly et al., 2006). Human factors could potentially play a role in generating higher disturbance levels at low elevation, but recent evidence suggests that moss populations from natural and disturbed areas display similar levels of genetic diversity (Korpelainen et al., 2012a, but see Patiño et al., 2010), especially in a colonist species (sensu During, 1992) such as *B. argenteum* with a life-history typically adapted to highly disturbed environments. Altogether, this suggests that although the influence of human factors in the patterns of genetic diversity of *B. argenteum* along the elevation gradient cannot be ruled out, it is unlikely to account for the substantially higher diversities observed at high elevation.

A third possibility to explain the peak of genetic diversity at high elevation is that the severe conditions at high elevation trigger adaptation, and in particular, adaptive divergence fostering genetic diversity (Porter and Rice, 2013). In *Bryum argenteum*, in fact, genetic variation was significantly correlated with elevation. Furthermore, the elevational range displayed by the species has a significant phylogenetic component, pointing to heritable elevational preferences. Such a genetic differentiation along a steep ecological gradient was unexpected, because in bryophytes in general (Shaw, 2000a), and in *B. argenteum* in particular (Longton, 1981; Shaw et al., 1989; Shaw and Albright, 1990), physiological plasticity rather than ecotypic differentiation is thought to account for the ability to occur in contrasting ecological conditions. The results presented here therefore support yet provide scant evidence (Shaw and Beer, 1999; Hutsemekers et al., 2010; Horsley et al., 2011) that although ecologically highly plastic, moss species also develop ecotypes to adapt to a wide range of environmental conditions and achieve large distribution ranges. As in other organisms, such as tardigrades (Faurby et al., 2012), the present results fully support the Baas Becking tenet and indicate that ecological specialization might play a much more important role than dispersal limitation in explaining patterns of genetic structure in cosmopolitan mosses.

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APPENDIX 1. Identification of samples studied (arranged by collection elevation), species name, herbarium and voucher number, publication source if published previously, sample provenance, geographic coordinates, haplotype number, and GenBank accession numbers. GenBank codes located in the middle of ITS1 and ITS2 columns correspond to full ITS1-5.8S-ITS2 sequences.

Sample ID	Species	Herbarium	Original publication	Location	Geographic Coordinates	Haplotype	ITS1	ITS2	*rps4*
100 m 1	*Bryum argenteum*	MUB 40250	—	Spain, Granada province	N 36.75117 W 003.19887	hap. 1	KC493840		KC493936
100 m 2	*Bryum argenteum*	MUB 40251	—	Spain, Granada province	N 36.75117 W 003.19887	hap. 2	KC493841		KC493937
100 m 3	*Bryum argenteum*	MUB 40252	—	Spain, Granada province	N 36.75117 W 003.19887	hap. 2	KC493842		KC493938
100 m 4	*Bryum argenteum*	MUB 40253	—	Spain, Granada province	N 36.75117 W 003.19887	hap. 2	KC493843		KC493939
100 m 5	*Bryum argenteum*	MUB 40254	—	Spain, Granada province	N 36.75117 W 003.19887	hap. 2	KC493844		KC493940
100 m 6	*Bryum argenteum*	MUB 40255	—	Spain, Granada province	N 36.75117 W 003.19887	hap. 2	KC493845		KC493941
200 m 1	*Bryum argenteum*	MUB 40220	—	Spain, Granada province	N 36.84465 W003.50905	hap. 3	KC493868	KC493894	KC493911
200 m 2	*Bryum argenteum*	MUB 40221	—	Spain, Granada province	N 36.84465 W003.50905	hap. 3	KC493873	KC493899	KC493912
200 m 3	*Bryum argenteum*	MUB 40222	—	Spain, Granada province	N 36.84465 W003.50905	hap. 3	KC493874	KC493900	KC493914
200 m 4	*Bryum argenteum*	MUB 40223	—	Spain, Granada province	N 36.84465 W003.50905	hap. 3	KC493872	KC493898	KC493913
350 m 1	*Bryum argenteum*	MUB 40256	—	Spain, Granada province	N 36,80025 W 003.21738	hap. 4	KC493867	KC493893	KC493942
550 m 1	*Bryum argenteum*	MUB 40257	—	Spain, Granada province	N 36,80025 W 003.21738	hap. 2	KC493875	KC493901	KC493944
550 m 2	*Bryum argenteum*	MUB 40258	—	Spain, Granada province	N 36,80025 W 003.21738	hap. 2	KC493876	KC493902	KC493945
550 m 3	*Bryum argenteum*	MUB 40259	—	Spain, Granada province	N 36,80025 W 003.21738	—	KC493877	KC493903	—
550 m 4	*Bryum argenteum*	MUB 40260	—	Spain, Granada province	N 36,80025 W 003.21738	hap. 2	KC493878	KC493904	KC493947
550 m 5	*Bryum argenteum*	MUB 40261	—	Spain, Granada province	N 36,80025 W 003.21738	hap. 5	KC493858	KC493884	KC493943
550 m 6	*Bryum argenteum*	MUB 40262	—	Spain, Granada province	N 36,80025 W 003.21738	hap. 2	KC493879	KC493905	KC493946
800 m 1	*Bryum argenteum*	MUB 40263	—	Spain, Granada province	N 36.79475 W 003.24682	hap. 6	KC493865	KC493891	KC493948
800 m 2	*Bryum argenteum*	MUB 40264	—	Spain, Granada province	N 36.79475 W 003.24682	hap. 7	KC493864	KC493890	KC493949
800 m 3	*Bryum argenteum*	MUB 40314	—	Spain, Granada province	N 36.79475 W 003.24682	hap. 8	KC493866	KC493892	KC493950
1000 m 1	*Bryum argenteum*	MUB 40248	—	Spain, Granada province	N 37.16320 W 003.46658	hap. 2	KC493882	KC493908	KC493934
1000 m 2	*Bryum argenteum*	MUB 40249	—	Spain, Granada province	N 37.16320 W 003.46658	hap. 2	KC493839		KC493935
1500 m 1	*Bryum argenteum*	MUB 40224	—	Spain, Granada province	N 37.00218 W 003.27027	hap. 2	KC493824		KC493910
1500 m 2	*Bryum argenteum*	MUB 40225	—	Spain, Granada province	N 37.00218 W 003.27027	hap. 2	KC493825		KC493915
1500 m 3	*Bryum argenteum*	MUB 40226	—	Spain, Granada province	N 37.00218 W 003.27027	hap. 2	KC493826		KC493916
1500 m 4	*Bryum argenteum*	MUB 40227	—	Spain, Granada province	N 37.00218 W 003.27027	hap. 2	KC493827		KC493917
1500 m 5	*Bryum argenteum*	MUB 40228	—	Spain, Granada province	N 37.00218 W 003.27027	hap. 2	KC493828		KC493918
1650 m 1	*Bryum argenteum*	MUB 40265	—	Spain, Granada province	N 37.12633W 003.43677	hap. 2	KC493869	KC493895	KC493951
2170 m 1	*Bryum argenteum*	MUB 40236	—	Spain, Granada province	N 37.09725 W 003.39753	hap. 2	KC493881	KC493907	KC493924
2170 m 2	*Bryum argenteum*	MUB 40237	—	Spain, Granada province	N 37.09725 W 003.39753	hap. 2	KC493880	KC493906	KC493925
2170 m 3	*Bryum argenteum*	MUB 40238	—	Spain, Granada province	N 37.09725 W 003.39753	—	KC493862	KC493888	—
2170 m 4	*Bryum argenteum*	MUB 40239	—	Spain, Granada province	N 37.09725 W 003.39753	hap. 10	KC493833		KC493926
2170 m 5	*Bryum argenteum*	MUB 40240	—	Spain, Granada province	N 37.09725 W 003.39753	hap. 2	KC493834		KC493928
2170 m 6	*Bryum argenteum*	MUB 40241	—	Spain, Granada province	N 37.09725 W 003.39753	hap. 2	KC493835		KC493927
2170 m 7	*Bryum argenteum*	MUB 40242	—	Spain, Granada province	N 37.09725 W 003.39753	hap. 10	KC493836		KC493929
2170 m 8	*Bryum argenteum*	MUB 40243	—	Spain, Granada province	N 37.09725 W 003.39753	hap. 9	KC493837		KC493930
2200 m 1	*Bryum argenteum*	MUB 40266	—	Spain, Granada province	N 37.10975 W 003.41837	hap. 2	KC493870	KC493896	KC493952
2250 m 1	*Bryum argenteum*	MUB 40229	—	Spain, Granada province	N 37.09725 W 003.39753	hap. 2	KC493829		KC493919
2250 m 2	*Bryum argenteum*	MUB 40235	—	Spain, Granada province	N 37.09725 W 003.39753	hap. 11	KC493863	KC493889	KC493923
2250 m 3	*Bryum argenteum*	MUB 40231	—	Spain, Granada province	N 37.09725 W 003.39753	hap. 12	KC493830		KC493920
2250 m 4	*Bryum argenteum*	MUB 40232	—	Spain, Granada province	N 37.09725 W 003.39753	hap. 12	KC493831		KC493921
2250 m 5	*Bryum argenteum*	MUB 40233	—	Spain, Granada province	N 37.09725 W 003.39753	hap. 2	KC493832		KC493922
2500 m 1	*Bryum argenteum*	MUB 40244	—	Spain, Granada province	N 37.09512 W 003.38668	hap. 2	KC493838		KC493932
2500 m 2	*Bryum argenteum*	MUB 40245	—	Spain, Granada province	N 37.09512 W 003.38668	—	KC493883	KC493909	—
2500 m 3	*Bryum argenteum*	MUB 40246	—	Spain, Granada province	N 37.09512 W 003.38668	hap. 12	KC493861	KC493887	KC493931
2500 m 4	*Bryum argenteum*	MUB 40247	—	Spain, Granada province	N 37.09512 W 003.38668	hap. 12	KC493860	KC493885	KC493933
2680 m 1	*Bryum argenteum*	MUB 40276	—	Spain, Granada province	N 37.07605 W 003.37648	hap. 13	KC493854		KC493961
2680 m 2	*Bryum argenteum*	MUB 40277	—	Spain, Granada province	N 37.07605 W 003.37648	hap. 13	KC493855		KC493962
2680 m 3	*Bryum argenteum*	MUB 40278	—	Spain, Granada province	N 37.07605 W 003.37648	hap. 13	KC493856		KC493963
2680 m 4	*Bryum argenteum*	MUB 40279	—	Spain, Granada province	N 37.07605 W 003.37648	hap. 2	KC493871	KC493897	KC493964
2700 m 1	*Bryum argenteum*	MUB 40267	—	Spain, Granada province	N 37.0,943 W 003.38662	hap. 9	KC493846		KC493953
2700 m 2	*Bryum argenteum*	MUB 40268	—	Spain, Granada province	N 37.0,943 W 003.38662	—	KC493847		—
2700 m 3	*Bryum argenteum*	MUB 40269	—	Spain, Granada province	N 37.0,943 W 003.38662	hap. 9	KC493848		KC493954

Appendix 1. Continued.

Sample ID	Species	Herbarium	Original publication	Location	Geographic Coordinates	Haplotype	ITS1	ITS2	*rps4*
2700 m 4	*Bryum argenteum*	MUB 40270	—	Spain, Granada province	N 37.0,943 W 003.38662	hap. 2	KC493849		KC493955
2700 m 5	*Bryum argenteum*	MUB 40271	—	Spain, Granada province	N 37.0,943 W 003.38662	hap. 9	KC493850		KC493956
2700 m 6	*Bryum argenteum*	MUB 40272	—	Spain, Granada province	N 37.0,943 W 003.38662	hap. 15	KC493851		KC493957
2700 m 7	*Bryum argenteum*	MUB 40273	—	Spain, Granada province	N 37.0,943 W 003.38662	hap. 14	KC493859	KC493885	KC493958
2700 m 8	*Bryum argenteum*	MUB 40274	—	Spain, Granada province	N 37.0,943 W 003.38662	hap. 16	KC493852		KC493959
2700 m 9	*Bryum argenteum*	MUB 40275	—	Spain, Granada province	N 37.0,943 W 003.38662	hap. 9	KC493853		KC493960
2870 m 1	*Bryum argenteum*	MUB 40280	—	Spain, Granada province	N 37.07153 W 003.37355	hap. 13	KC493857		KC493965
Bryum apiculatum Schwägr.	*Bryum apiculatum*	HBNU	Wang and Zhao (2009)	China, Yunnan province	—	—	EU878213		FJ593892
Bryum funckii Mitt.	*Bryum funckii*	HBNU	Wang and Zhao (2009)	China, Hunan province	—	—	EU878209		AY078332
Bryum recurvulum Schwägr.	*Bryum recurvulum*	HBNU	Wang and Zhao (2009)	China, Hebei province	—	—	EU878217		FJ593887
Bryum yuennanense Broth.	*Bryum yuennanense*	HBNU	Wang and Zhao (2009)	China, Yunnan province	—	—	EU878211		FJ593890