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Pteridophyte richness in the NE Iberian Peninsula: biogeographic patterns

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Abstract

The richness and coexistence of pteridophyte species were studied at the mesoscale level in the NE Iberian Peninsula (Catalonia and Andorra) using a grid system with 10 × 10 km cell-size. The number of pteridophytes, the number of monolete and trilete ferns (two spore patterns), and the number of polyploid and diploid ferns were studied in 371 of such units. The results suggest: (a) a significant relationship of pteridophyte species richness with higher-taxon richness (genera, family, order, class); (b) a significant relationship between pteridophyte richness and maximum altitude (positively related), bedrock type (higher richness in siliceous types), and distance to the coast (interacting with altitude); (c) a significant positive relationship of monolete/trilete ratio with altitude (in the study area) and with latitude (at the European scale); (d) a significantly higher polyploid/diploid ratio for monolete ferns than for trilete ferns, and a significant relation of this ratio with altitude. We conclude that at the scale studied, the distribution of pteridophyte richness is mainly related to terrain and climate parameters and that the monolete/trilete pattern may be explained by the higher polyploidy rate and better migration capacity in monolete species.

Abbreviations: MTR – monolete:trilete ratio; PDR – polyploid:diploid ratio

Introduction

The distribution of the world's biodiversity is poorly known. To reach a conservation objective (e.g., Convention on Biological Diversity, UNEP 1992) more knowledge of the species richness and distribution patterns of the different taxonomic groups is needed.

Pteridophytes represent a very important plant group in biogeography and conservation ecology because they are an ancient group of species with a large number of relict and endemic taxa. They provide us with a lot of information on the evolution of plants and their components, and on evolutionary aspects of biogeography (R. Tryon 1986). They are also quite fragile and vulnerable to disturbances and climate changes due to their microclimatic dependence. Note, for example, that pteridophyte species have a strong dependence on high moisture for sexual reproduction because they have flagellate gametes and external sexual fertilisation. Furthermore, there are no known pteridophytes where dispersion is aided by animals. Given the high dispersability of spores, it could be hypothesised that the occurrence of ferns at a given locality is mainly limited by the suitability of sites for germination and gametophyte establishment (Werth & Cousens 1990); however, life-history and population parameters (e.g., fecundity, antheridiogen response, mating system) are also important (Masuyama & Watano 1990; Peck et al. 1990; Chiou & Farrar 1997) indicating that most diploid species reproduce by outcrossing between gametophytes derived from different spores. The distribution of the pteridophyte species is based on its relationship with the environment and evolutionary history, without the influence of animal vectors for dispersal or pollination.

Basic fine-scale data on the distribution of species are lacking and expensive to acquire. Furthermore, knowledge of organisms at the species level requires a high level of experience. For these reasons, alternative cost-effective sampling methods based on surrogate measures of species diversity have been suggested. For example, it has been hypothesised that higher-taxon richness (e.g., families) may reflect the richness of lower poorly studied taxa (e.g., species; Williams & Gaston 1994; but see also Prendergast Eversham 1997). If this hypothesis were true, the knowledge of higher-taxon richness would provide a first approximation to the distribution of biodiversity and a guide for conservationists and environmental managers. In the present study we have tested this hypothesis for the pteridophytes species in the NE Iberian Peninsula. On the other hand, several studies (Game & Peterken 1984; Ruokolainen et al. 1997) have shown that accurate knowledge of a specific taxon (e.g., pteridophytes) may provide a good indicator of the richness of the regional species pool (e.g., other plant groups).

Species richness is caused by a variety of ecological and evolutionary processes, historical events and geographical circumstances (Ricklefs 1987). This study concerns the richness and coexistence of pteridophyte species on the mesoscale (Ricklefs & Schluter 1993), that is, at the scale where local processes (e.g., resource availability and competition) are less important than regional processes (e.g., climate, dispersal, landscape heterogeneity, and geographical circumstances). For this approach we use a 10 × 10 km grid system in an area of about 33 000 km^2.

Species richness patterns along environmental gradients have been extensively studied (e.g., Currie 1991; Pausas 1994; Austin et al. 1996). Although we do not have direct environmental variables, we use the available terrain parameters (indirect environmental variables; e.g., altitude, distance to coast and bedrock type) to test whether pteridophyte species richness is related to the environment, and to study the spatial distribution of pteridophyte diversity.

A morphological parameter used in the systematics of ferns is the spore type: spores may be trilete (tetrahedral) or monolete (bilateral); this character has not been related to the phylogeny of ferns. However, Ito (1972, 1978) found that the number of monolete ferns increases in relation to the number of trilete ferns (monolete:trilete ratio, MTR) from lower latitudes to high latitudes, and from low altitudes to high altitudes. We tested the validity of this pattern in our study area and at the European scale, and whether differential polyploidy rate (measured as the number of polyploid/number of diploid species; PDR) between monolete and trilete species may explain this pattern. The MTR may not have any direct applicability for conservationists (as opposed to the higher-taxon richness relationship described above), but it does have implications in understanding the evolutionary history of ferns in the study area.

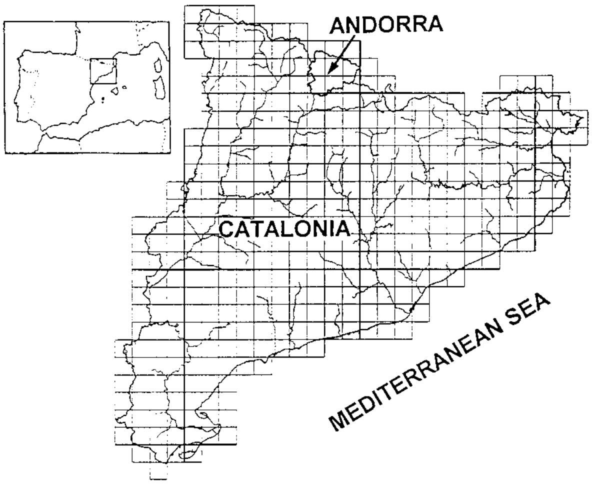

Figure 1. Location map of the study area and the grid system of UTM 10 × 10 km units.

The specific questions addressed in this study are: How many species of pteridophytes are in the study area? Is there any relationship between the diversity of the different taxonomic levels? Is there a geographical pattern to the pteridophyte species richness? If so, can this spatial variation be explained by terrain parameters (at 10 km resolution)? Is there any pattern of MTR at regional and continental scales?

Methods

The study area

The area studied includes Catalonia (ca. 31 900 km^2) and Andorra (464 km^2), the north-east of the Iberian Peninsula (Figure 1); the altitude ranges from sea level to 3143 m (top of Pica d'Estats). It is situated between ca. 0°15′ E and 3°20′ E longitude and 40°30′ N and 42°40′ N latitude. In the northern part of the area (the Pyrenees) the climate is mainly a temperate middle-European type with a cold climate in the higher parts of the mountains. In the remaining area the climate is typically Mediterranean, with a maritime tendency towards the coast (at the east) and a continental and sub-arid tendency inland (towards the west). This transition between temperate and Mediterranean climates (Terradas 1991) makes the area very interesting from the biogeographical and biodiversity point of view.

Terrain parameters

The basic spatial unit of sampling is the Universal Transverse Mercator (UTM) 10 × 10 km grid system. The area studied is composed of 371 of such units included in the zone 31T (squares DH, CH, BH, EG, DG, CG, BG, DF, CF, CE and BE). The UTM system was used for its compatibility with several chorologic atlases that include our study area (Jalas & Suominen 1972; Salvo et al. 1984; Bolòs 1985).

Available variables for each UTM unit were (Bolòs 1985): (a) dominant bedrock type: siliceous (e.g., schist, granite, etc.), calcareous (e.g., limestone, marls, etc.), calcareous bedrock with marked decarbonation processes or where both siliceous and calcareous bedrock were frequent, or UTM units where saline soils are frequent; (b) maximum altitude: $<$500 m, 500–1000 m, 1000–1600 m, 1600–2300 m or $>$2300 m; and (c) distance from the coast measured as the number of UTM squares from the Mediterranean Sea.

The pteridophyte data

The number of pteridophytes in each UTM unit was obtained by an extensive literature search, visits to regional herbaria, and field observations (Sáez 1997). Different taxonomists have different concepts of taxonomic levels, and for the present work the species concept is based on cytogenetic studies (mainly following the criteria of Tutin et al. 1993, see Appendix). To include some genetic variation, we consider species and subspecies, and hereafter we use the term species (and, consequently, species richness) for any taxon at species or subspecies level; that is, subspecies of *Asplenium trichomanes*, *A. obovatum* and *Dryopteris affinis* are also considered in the present work. Varieties, hybrids and naturalised species were not included in the analysis.

The pteridophytes were grouped into 10 taxonomic orders, and these into 4 taxonomic classes (see Appendix): *Lycopsida, Equisetopsida, Ophioglossopsida* and *Filicopsida*. The class *Filicopsida* (ferns) is the most abundant and the richest in species and was subdivided into two groups following their spore morphology: species with monolete spores and species with trilete spores. Heterosporic ferns (*Marsileaceae*) were not considered in this subdivision (Ito 1972). For the UTM units where homosporus ferns were present, the monolete/trilete ratio (MTR) was also studied. MTR values from different European areas were also calculated from available information. On the basis of bibliographic references (Castroviejo et al. 1986; Tutin et al. 1993), each fern was considered to be polyploid, diploid or unknown, and for each UTM cell the ratio of polyploid/ diploid taxa (PDR) was computed, for both monolete and trilete species.

Statistical analyses

Relations between species richness and higher taxonomic levels, and between species richness and terrain parameters were studied by analysis of deviance. Because dependent variables were discrete data (counts), the Poisson distribution of errors was assumed and a logarithmic link function was used (McCullagh & Nelder 1989). For the relation between richness and terrain parameters, a forward stepwise procedure was employed to enter the variables in the model, and only variables explaining a significant ($P < 0.02$) amount of deviance were included in the statistical model. Interaction terms were also tested. The change in deviance was tested by the F-ratio test. A similar approach has been used elsewhere (Margules et al. 1987; Pausas 1994; Pausas & Carreras 1995; Austin et al. 1996). The terrain parameters tested were: dominant bedrock type, maximum altitude, and distance to the coast. The relation of genera and family richness to species richness was made using the logarithm transformation of the number of species plus one. The relation of MTR and PDR to altitude and latitude was tested using analysis of variance.

Results

Eighty-eight species of pteridophytes included in 20 families have been recorded in the study area (see Appendix for full list). Pteridophytes occur in most (93%) of the units, with a mean number of 9 species per unit, but up to 33 species were co-occurring in a single unit (Table 1).

The number of species is closely related to higher taxon richness (Figure 2). Genus richness, family richness, order richness, and class richness increase

Table 1. Characteristics of the sampled units studied ($n = 371$). For each group the columns are: number of UTM units in which the group occurs (Num. units); number of species in the group found in the whole area, i.e. Catalonia and Andorra (Num. species); the maximum number of species found together in a unit (Max. Num. species); mean number of species found together in all plots (Mean Total); and, mean number of species where the group is present (mean presence).

Group	Num. units	Num. species	Max. num. species	Mean total	Mean presence
Lycopsida	68	11	6	0.30	1.62
Equisetopsida	308	7	5	1.68	2.02
Ophioglossopsida	77	5	2	0.24	1.16
Filicopsida (ferns)	323	65	26	6.86	7.88
Monolete	302	48	21	5.45	6.70
Trilete	285	14	10	1.41	1.84
Total	357	88	33	9.08	9.43

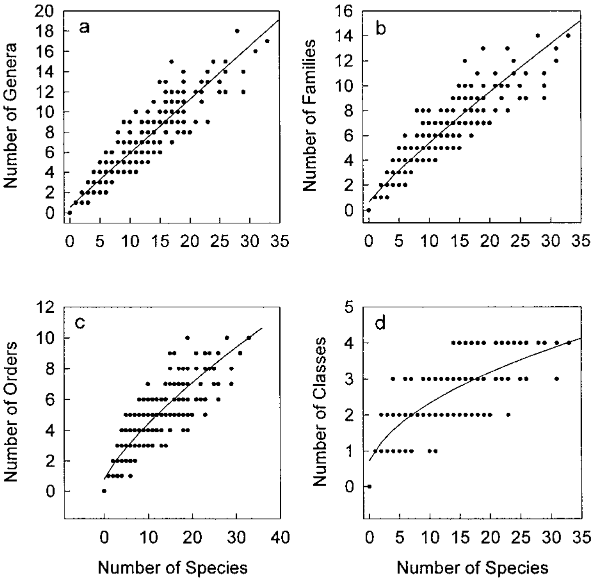

Figure 2. Relationship between the number of genera (a), families (b), orders (c) and classes (c), with the number of species in 10 × 10 km units for the pteridophytes in the NE Iberian Peninsula. Lines are the significant ($P < 0.00001$) logarithmic fit with explained deviance of 90.4, 88.6, 80.7 and 61.2% respectively.

with the increase in species richness (Figure 2), and the explained variance decreases from family richness (90.4%) to class richness (61.2%).

The number of species was significantly related to bedrock type, maximum altitude, and distance from the coast, and the full model explains ca. 56% of the deviance (Table 2). Pteridophyte species richness is higher in UTM units dominated by siliceous bedrock than on the ones with calcareous bedrock, and units with both siliceous and calcareous bedrock types show intermediate richness (Figure 3). The lowest richness is on the units with saline soils. Bedrock type is the variable explaining the most deviance in the model. Species richness is lower when the maximum altitude is <500 m and higher in the other altitude classes. Species richness decreases with distance from the coast (inland) for UTM units with maximum altitudes lower than 2300 m (Figure 4). For UTM units with maximum altitudes higher than 2300 m the opposite pattern was found (Figure 4): there was a tendency towards increasing species richness inland.

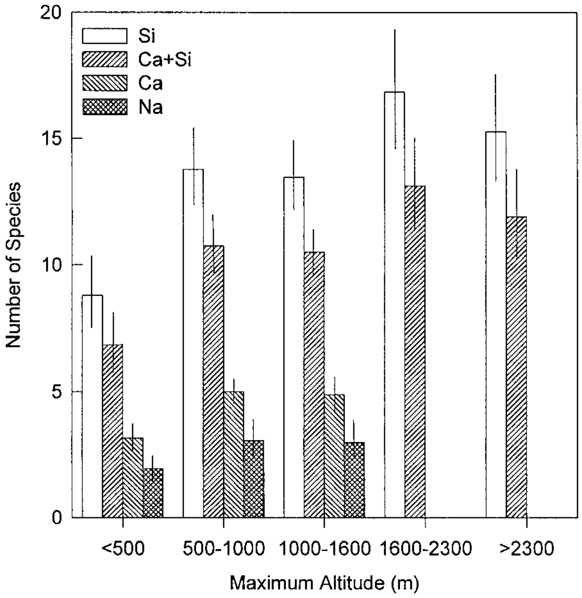

Figure 3. Number of pteridophyte species (and 95% confidence interval) for different maximum altitude values and bedrock types (Si: siliceous; Ca + Si: calcareous with frequent descarbonatations; Ca: calcareous; Na: saline soils). Elaborated from the model in Table 2 with distance to the coast set at 9 units (the median). Note that there are no data with maximum altitude greater than 1600 m and with calcareous or saline bedrock.

Fourteen filicopsida species (ferns) were trilete and 48 were monolete (Table 1), giving an overall MTR for the studied area of 3.43. There was a clear and significant relationship between MTR and altitude (Figure 5). When the variance was explained by altitude, no other variable was significant. High MTR values (i.e., a high number of monolete ferns in relation to trilete ferns) occur in UTM units with high maximum altitude. The overall MTR value for Europe is 3.10 (Table 3), and for different European zones there was a clear positive relationship with latitude

Table 2. Analysis of deviance for total pteridophyte species richness. Variables included in the model are: Bedrock (dominant bedrock type), MaxAlt (range of maximum altitude) and Dist (distance to the coast). The level of significance refers to the change in deviance associated with the addition of the terms (**** $P < 0.0001$; ***$P < 0.001$; *$P < 0.05$).

Model	Deviance	DF	Change in deviance	F	*P*
Null	2023.1	370			
+ Bedrock	1069.5	367	953.6	109.1	****
+ Max Alt	987.7	363	81.83	7.52	****
+ Dist	951.8	362	35.84	13.63	***
+ Max Alt × Dist	894.3	358	57.53	5.75	*
Expl. deviance:	55.80%				

(Table 3, Figure 6), i.e., areas in the south have lower MTR values than areas in the north of Europe. The size of the area considered was not related to the MTR value.

The number of monolete ferns was higher than the number of trilete ferns, and the PDR was also higher for monolete than for trilete ferns (Figure 7). There was a tendency towards increasing the PDR with altitude.

Discussion

The area considered is very rich in pteridophyte species. It is 17 times smaller than France, 18 times smaller than the Iberian Peninsula, and 9 times smaller than Italy, but it has more than 70% of the number of species in these areas (Table 3). Half of the European pteridophyte flora occurs in this area. This high diversity may be due to its privileged location and relief; present here are Mediterranean species, Central-European species and some Macaronesian species. In the area, endemic or very rare species occur, such as: *Asplenium seelosii* subsp. *catalaunicum* (endemic to the study area); *A. celtibericum* (occurring also in the eastern Iberian Peninsula and in the Magreb); *Woodsia pulchella* (present in the study area and reappearing in the Alps); *Pellaea calomelanos* (subtropical element with African affinities that has its only European locality in the study area; Terradas & Brugues 1973); *Cheilanthes maderensis* and *Ophioglossum azoricum* (relict species of Macaronesian affinities). At the UTM scale (10 × 10 km), the number of co-occurring pteridophyte species is also high (a mean of ca. 9 and up to 33 species were found together; Table 1).

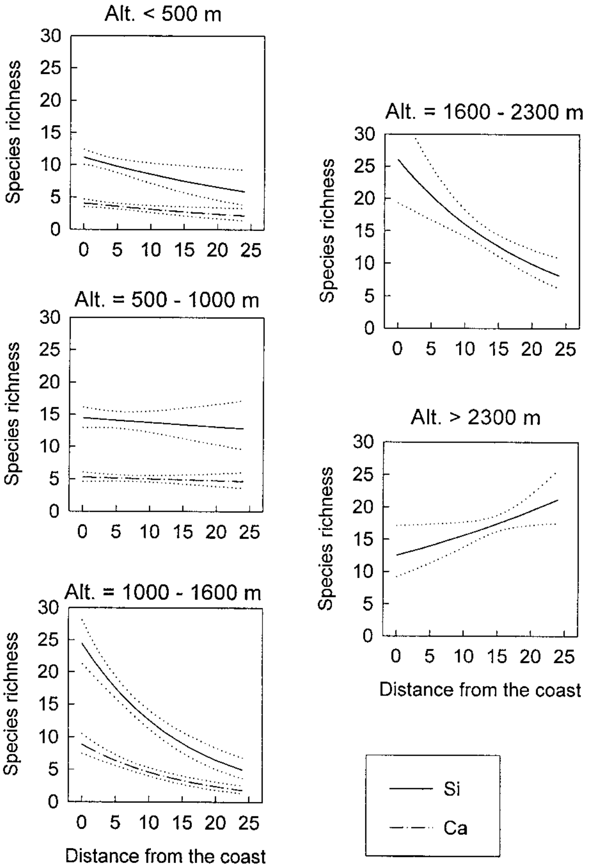

Figure 4. Number of pteridophyte species (and 95% confidence interval) for 5 altitude classes (<500 m, 500–1000, 1000–1600 m, 1600–2300, >2300 m) along the distance-from-coast gradient. Distance from the coast is measured as the number of 10 × 10 UTM units to the Mediterranean Sea. Elaborated from the model in Table 2.

Table 3. Number of pteridophyte species, number of monolete fern species, number of trilete fern species and the monolete/trilete ratio (MTR) in different European areas. Data is sorted by the MTR (descending order). See also Figure 6.

	Total pteridophyte species	Num. of monolete ferns	Num. of trilete ferns	Monolete trilete ratio	Ref.[a]
Finland	64	30	3	10.0	1
Sweden	71	35	4	8.75	1
Germany	77	43	4	8.60	1
Norway	72	36	5	7.20	1
Belgium + Luxembourg	54	30	4	6.00	1
Britain	71	40	7	5.71	1
Catalonia + Andorra	88	51	11	4.63	2
France	120	65	16	4.06	3
Europe[b]	175	93	30	3.10	1
Italy	119	59	16	3.68	4
Iberian Peninsula	120	66	20	3.30	5
Balearic Islands, Spain	38	21	7	3.00	6
Valencia Region, Spain	39	20	10	2.00	7
West Andalucia, Spain	54	27	15	1.80	8

[a] Data source: 1. Tutin et al. 1993; 2. Present study; 3. Prelli & Boudrie 1992; 4. Pignatti 1982; 5. Castroviejo et al. 1986; 6. Rosselló et al. 1992; 7. Herrero-Borgoñón et al. 1989; 8. Valdés et al. 1987.

[b] Overall Europe except Macaronesian islands (Canary Islands, Madeira, Azores, etc.).

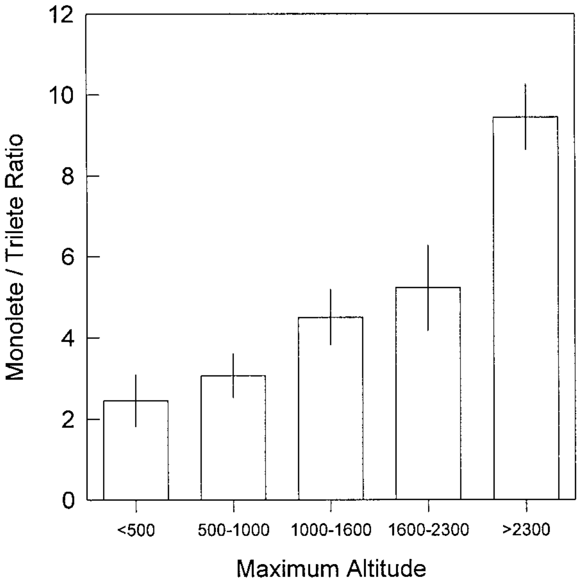

Figure 5. Monolete/trilete ratio values (and 95% confidence interval) for different maximum altitude values. The statistical model is highly significant ($F_{4,259} = 51.5$; $P < 0.0001$).

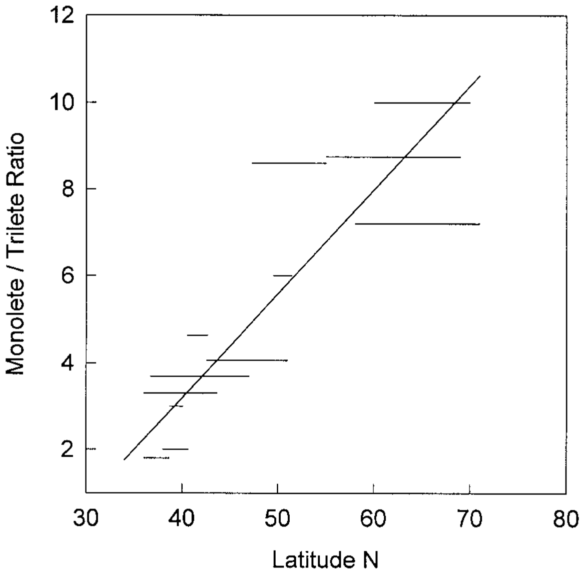

Figure 6. Monolete/trilete ratio for different European areas (see Table 3). Horizontal lines refer to the latitudinal range of the area considered. Regression line ($r^2 = 0.92$) is calculated from the mean latitude of each area.

There is a relationship between species richness and higher taxon richness, suggesting that genera or family richness may be a good surrogate for species richness. Similar results were found for British ferns at 100 × 100 km grid squares by Williams & Gaston (1994). Pteridophytes have also been suggested

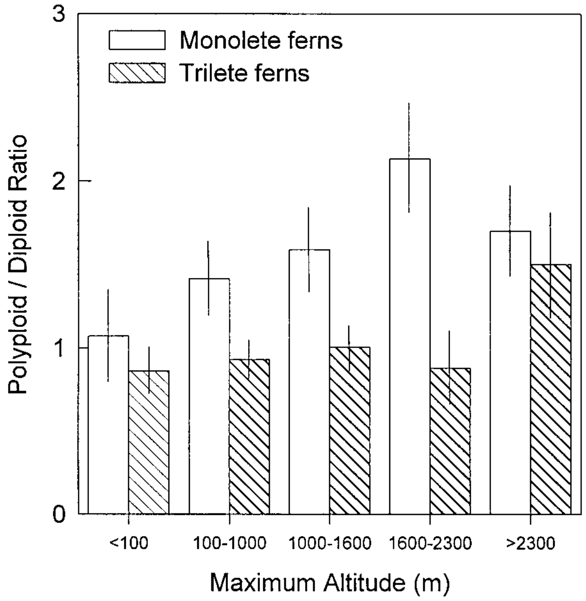

Figure 7. Mean number of polyploid ferns in relation to the number of diploid ferns (and 95% confidence interval) for the monolete and trilete species and for the different maximum altitude values. ANOVA: Monolete ferns: $F_{4,231} = 6.56$, $P < 0.0001$; Trilete ferns: $F_{4,230} = 3.54$; $P < 0.01$; All together: $F_{4,273} = 9.43$, $P < 0.0001$. Note that the sample size (*n* value) is different for each group (236, 237, 278 respectively) because it depends on the UTM units with number of diploid species >0.

as an indicator for tree species richness in tropical rainforests because of the difficulty in identifying tree species in these ecosystems (Ruokolainen et al. 1997). Several studies support the idea that comprehensive biodiversity protection may be attained by targeting a subset of taxa (e.g., Game & Peterken 1984; Ruokolainen et al. 1997).

There is a clear relationship between species richness and terrain parameters. Bedrock type is a very important parameter in explaining the pteridophyte richness, as has been found in other studies for vascular plant species richness (e.g., Pausas 1994; Pausas & Carreras 1995). However, the pattern found for pteridophyte richness (higher richness on siliceous bedrock than on calcareous one; Figures 2 and 3) is the opposite of the pattern found in vascular species richness in Pyrenean forests (i.e., higher richness on calcareous than on siliceous bedrock types; Pausas 1994; Pausas & Carreras 1995). This pattern may be due to the fact that siliceous bedrocks often produce substrates with higher water-holding capacity and moister environments for nurturing gametophyte growth and fertilisation.

Altitude and distance to the coast have also been shown as significant parameters in explaining pteridophyte richness (Figures 2 and 3), probably due to their relation to climate and moisture patterns in the study area. Moisture is a well known factor for the occurrence of most pteridophyte species. Tryon (1989) found a unimodal pattern of pteridophyte species richness along an altitude gradient in tropical mountains, but his data includes a larger altitudinal gradient (0–4500 m) than our study. In general, UTM units with high maximum altitude and low distance to the coast have higher moisture (higher rainfall), and this is followed by higher pteridophyte richness (Figures 2 and 3). However, at the highest altitude (in the Pyrenees), the influence of the Atlantic winds from the west produces a wet corner in the north-west of the area. This pattern is also followed by an increase in pteridophyte richness (Figure 4). Several species of Atlantic distribution appear only in this corner (e.g., *Dryopteris remota, Lastrea limbosperma, Phegopteris connectilis*). All this suggests a strong dependence of pteridophyte richness on climate.

The monolete-trilete ratios (MTR) have been shown to increase significantly with altitude and with latitude (Figures 5 and 6), confirming the pattern found at a larger scale in Asia and Oceania by Ito (1972, 1978). This pattern also suggests that different taxonomic groups have different environmental niches, as has been shown for other taxonomic groups like eucalypts (Austin et al. 1996) and cacti (Mourelle & Ezcurra 1996). There is no intuitive cause-effect relation between the spore pattern and these climatic related variables (latitude and altitude), and the explanation is more probably related to differential evolutionary history. There are more monolete than trilete species in our study area (mean MTR = 3.43) and in Europe overall (mean MTR = 3.10). Trilete species are a phylogenetically older group of ferns occurring earlier in the fossil record and evolving mainly in the tropics (A.F. Tryon 1986), while most monolete species are probably in phylogenetically derived families (e.g., Aspleniaceae, Dryopteridaceae and Thelypteridaceae), most of which have become adapted to colder environments.

There is more polyploidy (in relation to the number of diploid species) in monolete species than in trilete species (Figure 7), and also there is some relationship between increasing polyploidy and altitude (Figure 7). The increase in poliploidy in relation to altitude and latitude has been reported elsewhere for different taxonomic groups (Grant 1971; Rosenzweig

1995). The number of hybrid taxa in the study area (not considered in the present study) is also higher for monolete species (15 monolete hybrid vs. 1 trilete hybrid; Sáez 1997); for example, at least 7 hybrids of the genus *Asplenium* have been found in the study area (Herrero et al. 1995; Sáez 1997; Sáez et al. 1997). Some monolete species are very active from the speciation point of view (Bouharmont 1977; Cubas 1989), and have a large number of subspecies (e.g., see genus *Asplenium* and *Dryopteris* in the Appendix). Both developmental studies of fern gametophytes and genetic studies of natural sporophyte populations (see review by Masuyama & Watano 1990) indicate that most diploid species are not capable of successfully reproducing from a single isolated spore (the result of long-distance dispersal), either because of failure to become functionally bisexual or because of high inbreeding depression. Polyploid species tend to be capable of self-fertilisation (Haufler 1987; Masuyana & Watano 1990) and thus are better long-distance migrators. Polyploid species are thus better able to disperse between mountains and perhaps have exceeded diploids in the ability to recolonise the northern latitudes following deglaciation. Furthermore, differential spore morphology may also provide different aerodynamic properties (e.g., crests and folds, sometimes with a large aerolae, are frequent in some monolete genus such as *Asplenium* and *Dryopteris*) that could have implications for their dispersability and distribution. The joint effect of the large number of monolete polyploids and their better migration capacity may explain the MTR pattern in relation to altitude and latitude (Figures 5 and 6). However, further study in this topic is needed before we can unambiguously provide any causal relationship.

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Appendix 1. Taxonomic list of all pteridophyte (Division Pteridophyta) species and subspecies found in the study area (Catalonia and Andorra). Hybrids and naturalised species are not included. Families of ferns (Class Filicopsida) with an asterisk (∗) are families with trilete spore pattern.

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1. Cl. LYCOPSIDA
1.1. O. LYCOPSIDALES
F. Lycopodiaceae
Huperzia selago (L.) Bernh. ex Schrank & C.F.P. Mart.
Lycopodium annotinum L.
Lycopodium clavatum L.
Diphasiastrum alpinum (L.) J. Holub

1.2. O. SELAGINELLALES
F. Selaginellaceae
Selaginella selaginoides (L.) P.B. ex Schrank & C.F.P. Mart.
Selaginella denticulata (L.) Spring

1.3. O. ISOETALES
F. Isoetaceae
Isoetes lacustre L.
Isoetes setaceum Lam.
Isoetes velatum A. Braun subsp. *velatum*
Isoetes echinosporum Durieu
Isoetes durieui Bory

2. Cl. EQUISETOPSIDA
2.1 O. EQUISETALES
F. Equisetaceae
Equisetum variegatum Schleicher ex Webber & Mohr
Equisetum hyemale L.
Equisetum ramossisimum Desf.
Equisetum telmateia Ehrh.
Equisetum arvense L.
Equisetum fluviatile L.
Equisetum palustre L.

3. Cl. OPHIOGLOSSOPSIDA
3.1. O. OPHIOGLOSSALES
F. Botrychiaceae
Botrychium lunaria (L.) Swartz
Botrychium matricariifolium (Retz.) A. Braun ex Koch

F. Ophioglossaceae
Ophioglossum lusitanicum L.
Ophioglossum azoricum C. Presl
Ophioglossum vulgatum L.

4. Cl. FILICOPSIDA
4.1. O. OSMUNDALES
F. Osmundaceae ∗
Osmunda regalis L.

4.2. O. POLYPODIALES
F. Polypodiaceae
Polypodium cambricum L.
Polypodium interjectum Shivas
Polypodium vulgare L.

4.3. O. PTERIDALES
F. Sinopteridaceae ∗
Cheilanthes acrostica (Balbis) Tod.
Cheilanthes maderensis Lowe
Cheilanthes tinaei Tod.
Notholaena marantae (L.) Desv.
Pellaea calomelanos (Swartz) Link

F. Cryptogrammaceae ∗
Cryptogramma crispa (L.) R. Br.

F. Adiantaceae ∗
Adiantum capillus-veneris L.

F. Hemionitidaceae ∗
Anogramma leptophylla (L.) Link
Cosentinia vellea (Aiton) Tod. subsp. *vellea*

4.4. O. MARSILEALES
F. Marsileaceae
Marsilea quadrifolia L.
Marsilea strigosa Willd.
Pilularia globulifera L.

4.5. O. DENNSTAEDTIALES
F. Hypolepidaceae ∗
Pteridium aquilinum (L.) Kunhn subsp. *aquilinum*

4.6. O. ASPIDIALES
F. Thelypteridaceae
Phegopteris connectilis (Michaux) Watt
Lastrea limbosperma (All.) J. Holub & Pouzar
Thelypteris palustris Schott

F. Aspleniaceae
Asplenium marinum L.
Asplenium petrarchae (Guérin) DC. subsp. *petrarchae*
Asplenium trichomanes L. subsp. *trichomanes*
Asplenium trichomanes subsp. *quadrivalens* D.E. Meyer emend. Lovis
Asplenium trichomanes subsp. *inexpectans* Lovis
Asplenium trichomanes subsp. *hastatum* (Christ.) Jessen
Asplenium csikii Kummerle & Andrazovsky [=*A. trichomanes* subsp. *pachyrachis* Lovis & Reichst.]
Asplenium trichomanes-ramosum L.
Asplenium fontanum (L.) Bernh.
Asplenium foreziense Le Grand ex Héribaud
Asplenium obovatum Viv. subsp. *obovatum*
Asplenium obovatum subsp. *lanceolatum* (Fiori) Pinto da Silva
Asplenium onopteris L.
Asplenium adiantum-nigrum L. subsp. *adiantum-nigrum*
Asplenium septentrionale (L.) Hoffm.
Asplenium celtibericum Rivas-Martínez subsp. *celtibericum*
Asplenium seelosii Leybold subsp. *catalaunicum* (O. Bolòs & Vigo) P. Monts.
Asplenium ruta-muraria L. subsp. *ruta-muraria*
Asplenium scolopendrium L. subsp. *scolopendrium*
Asplenium sagittatum (DC.) A.J. Bange
Asplenium ceterach L. subsp. *ceterach*

F. Woodsiaecae
Woodsia alpina (Bolton) S.F. Gray
Woodsia pulchella (Bertol.) A. & D. Löve

F. Athyriaceae
Cystopteris fragilis (L.) Bernh. subsp. *fragilis*
Cystopteris fragilis subsp. *huteri* (Hausm. ex Milde) Prada & Salvo

Appendix 1. Continued.

Cystopteris alpina (Lam.) Desv.
Cystopteris montana (Lam.) Desv.
Gymnocarpium dryopteris (L.) Newman
Gymnocarpium robertianum (Hoffm.) Newman
Athyrium filix-femina (L.) Roth
Athyrium distentifolium Tausch ex Opiz

F. Dryopteridaceae
Dryopteris filix-mas (L.) Schott
Dryopteris affinis (Lowe) Fraser-Jenkins subsp. *affinis*
Dryopteris affinis subsp. *borreri* (Newman) Fraser-Jenkins
Dryopteris affinis subsp. *cambrensis* Fraser-Jenkins
Dryopteris oreades Fomin
Dryopteris submontana (Fraser-Jenkins & Jermy) Fraser-Jenkins
Dryopteris remota (A. Braun ex Döll) Druce
Dryopteris carthusiana (Vill.) H. P. Fuchs
Dryopteris expansa (C. Presl.) Fraser-Jenkins & Jermy
Dryopteris dilatata (Hoffm.) A. Gray
Polystichum lonchitis (L.) Roth
Polystichum setiferum (Forsskal) Woynar
Polystichum aculeatum (L.) Roth

4.7. O. BLECHNALES
F. Blechnaceae
Blechnum spicant (L.) Roth subsp. *spicant*