

Life history, diversity and distribution: a study of Japanese pteridophytes

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Many studies address the relationships between diversity or distribution and attributes of the physical environment. However, how these relationships are connected to variation in life history is poorly understood. This is particularly true in the case of pteridophytes. Japanese ferns and their allies comprise one of the best-known pteridophyte floras in the world. We analyzed ca 600 species of Japanese pteridophytes for which there is detailed information on distribution, reproduction, and chromosome number. Species richness was greatest in groups with a single reproductive mode (sexual, followed by apogamous), but distribution was greatest in species groups with multiple reproductive modes: sexual plus either sterile (irregular in meiosis) or apogamous. Geographical ranges varied greatly among species with small chromosome numbers but were uniformly small among species having high chromosome numbers. Seasonally green (mostly summer green) species had significantly larger distribution ranges than evergreen species. Endemic species had higher proportions of apogamy and sterility than non-endemic species. Seasonally green species had significantly larger distributional ranges, and a smaller proportion of species with apogamous reproduction, than evergreen species. There was no clear relationship between distribution and spore size, either among endemic species, non-endemic species, or all species combined. There was no relationship between spore size and chromosome number when all species were combined. However, positive relationships were detected within three of the nine largest genera, suggesting potential phylogenetic effects. We concluded that habitat availability, rather than dispersability, may be the limiting factor for the distribution of pteridophytes in Japan.

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Considerable research has been devoted to understanding the determinants of species diversity, abundance, and distribution (Huston 1994, Rosenzweig 1995). However, most work has focused on physical factors (e.g. Richard et al. 2000), and the relationships between diversity or distribution and life-history traits, such as leaf phenology, ploidy, reproduction mode, and dispersal, have not been thoroughly investigated (Ehrendorfer 1980, Brown 1984, 1995, Ricklefs and Renner 1994, Petit and Thompson 1999). One of the reasons for this neglect is the limited data on plant life history traits for a given flora.

In contrast to many seed plants, most pteridophytes are herbaceous perennials (a few are annuals or tree-like) and they have a long geological history. Pteridophytes are strongly associated with mesic and warmer habitats and therefore are distributed primarily in lower latitudes (Parris 1985, Given 1993). Because pteridophytes disperse widely by means of small spores, they exhibit lower endemism and less frequent speciation than seed plants (e.g. Smith 1972, Page 1979a, b, Kato 1993, Kramer 1993). Because of these unique features in pteridophytes, the contrasting patterns of diversity and distribution in relation to geology and life

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history traits between pteridophytes and seed plants have attracted much attention recently (e.g. Klekowski 1972, Kato 1993, Kramer 1993, Guo et al. 1998). Consequently, pteridophytes may “offer an independent test of how broadly biogeographic principles may be applied” (Barrington 1993).

Hypotheses relating diversity and distribution to life-history characteristics have not yet been satisfactorily tested (Iwatsuki 1994). Even among seed plants, for which numerous studies address patterns of diversity and distribution, few relate these patterns to life histories (see Rees 1995, Petit and Thompson 1999, Guo et al. 2000). The Japanese pteridophyte flora is among the best-studied in the world and is particularly well suited to an analysis of the relationship between life history attributes and distribution and diversity. Much information is available regarding species composition, genetics, and geography (e.g. Kurata and Nakaike 1979–97, distribution, spores; Iwatsuki et al. 1995, morphology, chromosome number, distribution, habitat; Takamiya 1996, chromosome number, ploidy level, reproductive mode). This provides a unique opportunity to overcome the major difficulty in examining the diversity/distribution-life history relationships caused by limited data.

The Japanese pteridophyte flora is diverse because of Japan's 1) favorable climates, 2) proximity to continental Asian areas of high diversity, and 3) island nature with enriched floristic elements though several land bridge connections to continental Asia and Taiwan in the geological past. One of the advantages of studying the Japanese pteridophytes is the ability to examine the relatively independent development of a unique flora with many endemic forms (Iwatsuki 1994). Although the total separation of Japan from continental Asia after the last ice age occurred only ca 30 000 yr BP (Iwatsuki 1994, Kimura 2000), the Japanese islands might nonetheless have retained many old elements of their previously isolated flora.

In this study, we relate diversity and distribution of Japanese pteridophytes to the following life-history traits: spore size, chromosome number, ploidy level, and reproductive mode. We also examine the possible interrelationships between life-history traits from several aspects. We ask the following questions: 1) what are the relationships between species diversity or distribution and ploidy level (or chromosome numbers), reproductive mode, and spore size (e.g. do species with multiple reproductive modes have larger distribution ranges)? 2) How is species richness in a particular genus or family related to the distribution range of the component species (or are the species range and the number of species in a particular genus related)? 3) At what taxonomic level (i.e. family, genus, and species) do life-history characteristics matter with regard to species diversity or distribution? Accordingly, we make the following predictions: 1) all life history traits contribute

more or less independently to variation in species diversity and distribution; for example, species with multiple reproductive modes have broader distributions; 2) the average size of the ranges of individual species is inversely related to the total number of species in a family or genus; and 3) the relationships between diversity, distribution and overall life history characteristics exist at all three taxonomic levels (i.e. family, genus, and species) and relationships between life history traits may also exist across higher taxa.

Materials and methods

Japan's pteridophytes included 34 families, 117 genera, and ca 600 species (Kurata and Nakaike 1979–97). The species are generally indigenous and include only a few naturalized species, e.g. *Pityrogramma calomelanos* (L.) Link. Among the 634 described taxa (species and subspecies; Iwatsuki 1994), chromosome numbers were known for 596 and distribution maps were available for 600. To examine the relationship between distribution and ploidy level, we used only species for which there was both chromosome and distribution information.

Nearly 600 species were classified according to ploidy level, leaf phenology, and endemism, and reproductive information was available for 286 of the 600 species. Chromosome number, ploidy level, and reproductive mode were based on Iwatsuki et al. (1995) and Takamiya (1996). Reproductive mode was determined using cytological and/or spore evidence. The reproductive mode of most homosporous ferns was determined by observing the number of spore mother cells (SMCs) or spores in a sporangium. Reproductive modes were categorized as “sex” (sexual), “ster” (sterile), or “apo” (apogamous), and their combinations. Spore sizes were determined using the photos in Kurata and Nakaike (1979–97) as the maximum length \times maximum width of the spores, excluding the perispores. Three species with photos of megaspores were excluded from our analysis.

Distribution data (presence/absence) and other complementary data (e.g. leaf phenology) used in this study were obtained from Kurata and Nakaike (1979–97), Iwatsuki et al. (1995) and Takamiya (1996). Species distributions in Japan were based on 134 grid cells of equal size that cover the geographic extent of Japan. Each cell is ca 2820 km² in area but only about half of the 134 cells were fully covered by land. Distribution maps, along with the number of collections and the list of locations where the species were recorded, provided a unique opportunity to detect potential sampling bias by comparing species that occupied geographical ranges of similar size but that might have been collected from different numbers of locations (e.g. He and Gaston 2000).

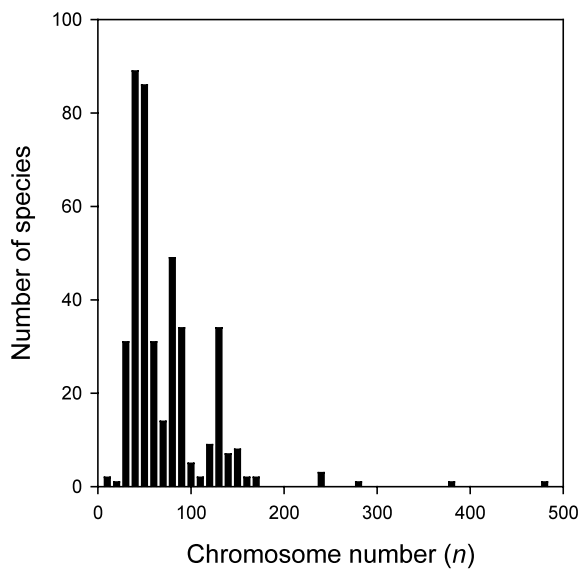


Fig. 1. Species frequency distribution based on gametic chromosome numbers (n).

There is no satisfactory study on the phylogeny of Japanese pteridophytes. To detect the possibility of higher-level phylogenetic effects on relationships between distribution and life history traits and among species traits (i.e. chromosome number, spore size), we performed a hierarchical analysis of variance (ANOVA) based on species, genus, and family effects. This analysis estimates the distribution of variance in measurements between levels and the correlations between variables at each level. Calculations were performed using the SAS NESTED procedure (Anon. 1990; see also Niklas 1994). Hierarchical ANOVA partitions variance at each taxonomic level, wherein relationships at higher levels might represent the earlier diversification of the major lineages of ferns, and more

ecologically-driven relationships might appear at lower levels in the hierarchy.

To further investigate the life history relationships and distribution patterns at different taxonomic levels, we also examined the distribution-life history relationships within the nine largest genera, belonging to seven families, and within all the 34 families of pteridophytes. The nine genera were (in order of size): *Dryopteris* (51 spp., Dryopteridaceae), *Asplenium* (40 spp., Aspleniaceae), *Diplazium* (32 spp., Woodsiaceae), *Polystichum* (31 spp., Polypodiaceae), *Athyrium* (26 spp., Woodsiaceae), *Pteris* (25 spp., Pteridaceae), *Thelypteris* (22 spp., Thelypteridaceae), *Arachniodes* (18 spp., Dryopteridaceae), *Lycopodium* (16 spp., Lycopodiaceae).

Results

Diversity and life history

Among the 600 species examined, 102 were endemic to Japan. Of the 406 species with records of leaf phenology, 302 were evergreen and 104 were seasonally green (mostly summer green). Among the 596 species for which chromosome numbers were known, 249 (42%) were polyploid, 80 (13%) included two or three cytotypes within the same taxon (i.e. intraspecific or intravarietal polyploids), and 77 (13%) (17% in Iwatsuki 1994) taxa were apogamous. This value is greater than the world's average of 10% (Takamiya 1996). Most species had gametic chromosome numbers (n) ranging from 30 to 90 (Fig. 1). Most species for which data were available had sexual reproduction, followed by apo, sex + ster, sex + apo, and ster (Table 1, 2). Four relatively large genera, *Cryptogramma*, *Diplazium*, *Dryopteris*, and *Pteris* accounted for most of the species with asexual reproduction. More than 80% of the species have spore sizes (length \times width) of 800–2500 μm^2 (Fig. 2).

Table 1. Comparisons of distribution, ploidy level, and reproductive mode between endemics and non-endemics and between evergreen and seasonally green species of Japanese pteridophytes (mean \pm SD)*. Bold-faced means (\pm SD) were significantly different values from each other in each pair in t-tests or G-tests ($p < 0.05$).

	Endemism		Leaf phenology	
	Endemics	Non-endemics	Evergreen	Seasonally green
Distribution (no. cells)	11.51 (\pm 17.38)	29.92 (\pm 28.88)	24.41 (\pm 26.33)	39.97 (\pm 31.87)
Spore size (μm^2)	1494 (\pm 729)	1627 (\pm 729)	1606 (\pm 762)	1555 (\pm 774)
Chromosome no. (n)	66.78 (\pm 41.44)	66.00 (\pm 47.07)	67.51 (\pm 41.99)	70.16 (\pm 63.75)
2n	122.12 (\pm 88.97)	108.40 (\pm 86.79)	103.47 (\pm 64.35)	122.79 (\pm 150.71)
Sex (%)	68.89	75.83	71.59	91.48
Apo (%)	24.44	15.83	23.52	1.59
Sex + apo (%)	2.22	7.08	2.35	7.94
Sex + ster (%)	0.98	2.61	2.32	4.81
Ster (%)†	4.44	1.25	4.71	0
Polyploid (%)	42.86	52.90	55.17	42.11

* The comparisons for reproductive modes are based on 286 species for which reproductive information is available and the comparisons between evergreen and seasonally green species are based on 406 species for which leaf phenology is known. † Including three natural hybrids and two of uncertain origin (see Table 2).

Table 2. Comparison of species richness, distribution, and life history characteristics in different reproductive modes and the results of ANOVA*. Bold-faced mean (\pm SD) was a significantly different value from others within the same row in ANOVA ($p < 0.05$).

	Sex	Apo	Sex + ster	Sex + apo	Ster	F	DF	p
No. species	213	49	14	5	5	–	–	–
No. distribution cells	33.24 \pm 30.39	32.63 \pm 25.84	54.29 \pm 27.21	55.25 \pm 32.27	12.60 \pm 11.78	2.92	4	0.022
Endemics (%)	14.55	22.45	7.14	0	40	–	–	–
Chromosome no. (n)	55 \pm 26.90	106 \pm 28.01	54 \pm 25.16	35 \pm 6.93	–†	45.5	3	<0.001
Polyploid (%)	11.27	20.41	71.43	100	40	–	–	–
Spore size (μm^2)	1600 \pm 775	2045 \pm 648	1742 \pm 931	1765 \pm 360	1262 \pm 786	4.98	4	0.06

* Based on 286 species for which reproductive information was available. Cautions should be given to the analytical results as the analyses were based on the assumption that the taxa with reproductive information were randomly chosen. However, we have no evidence that these taxa were chosen without bias. Sex = the taxon reproduces sexually; the n chromosome number is half the 2n number; Apo = an apogamous taxon; n = 2n; Ster = sterile (plants displaying irregular meiosis).

† Chromosome data not available.

Almost all seasonally green species (91.5%) had only sexual reproduction, while the figure for evergreen species was lower (71.6%) but the proportion of apo species was significantly higher (23.5 vs 1.6%). Of 39 apo species with known leaf phenology 38 were evergreen, whereas among 177 “sex” species, 118 were evergreen. Six out of 11 sex + apo species and all four sex + apo species were evergreen (Table 1).

There was no significant difference in mean spore size between endemics and non-endemics or between evergreen and seasonally green species. Similarly, gametic chromosome numbers (n or 2n) and proportion of each reproductive mode or proportion of polyploid species varied little with respect to endemism or leaf phenology. Also, no clear difference was found in proportions of other reproductive modes or polyploidy (Table 1).

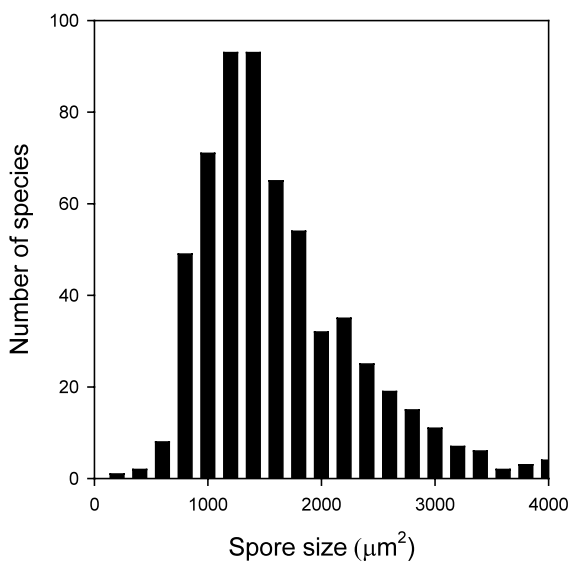


Fig. 2. Frequency distribution of spore sizes of Japanese pteridophytes (no. species = 597).

Spore sizes were marginally different across reproductive modes, with the largest average spore size occurring in apo species, partly due to the reduced number (32 vs 64) of spores produced in each sporangium in apogamous leptosporangiate ferns (Walker 1979). Apogamous species have greater gametic chromosome numbers than the other three reproductive categories. However, because ca 75% apo species were $3\times$ in both sporophytes and unreduced gametophytes, such direct comparison in gametic chromosome numbers might not be accurate (Kato 1992). For example, with regard to gametic chromosome numbers, $3\times$ apo was equivalent to $6\times$ sexual species with $3\times$ gametophytes. Gametic chromosome numbers did not differ significantly between other reproductive categories. Most apo species were either $3\times$, $2\times$, or $2\times + 3\times$ while most sex species were $2\times$, $4\times$, or $2\times + 4\times$. Sterile species had higher polyploidy levels (from $3\times$ to $6\times$) while sex + ster species had the highest polyploidy levels, ranging from $2\times$ to $8\times$. Sex + apo species were either $2\times$ or $3\times$. Sex species had the lowest proportion of polyploid species (Table 2).

Distribution

Distribution ranges were largest in species with multiple reproductive modes: sex + ster, sex + apo, followed by species with a single mode, i.e. sex, apo, and ster. Ster species had the smallest distributions and also the highest percentage of endemic species (Table 2). The ster species classified here perhaps were hybrids that arose recently and were still restricted to the areas of origin. There were 66 species that occupied only one geographic grid cell. The species with the largest distribution range was *Pteridium aquilinum* var. *latiusculum*, which occupied 122 of the 134 cells.

There were strong positive relationships between distribution and collecting records for both endemics and

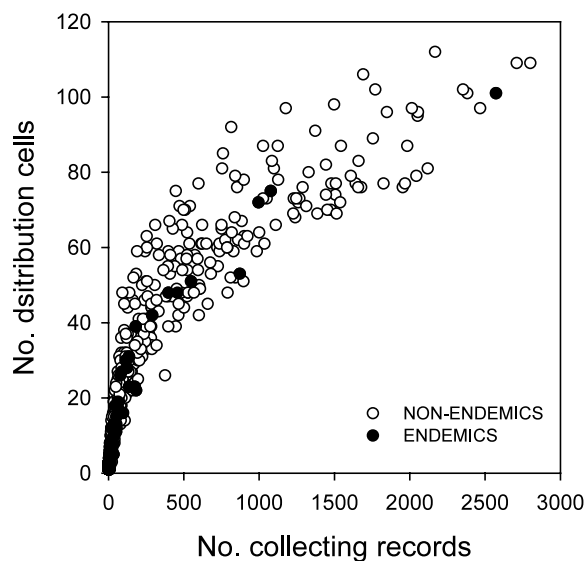


Fig. 3. Relationships between number of distribution cells each species occupies and the number of collection records (i.e. locations where the species was recorded or specimens of the species were collected) for endemics and non-endemics, respectively.

non-endemics (Fig. 3). Evergreen species also exhibited smaller distribution ranges than seasonally green species. There was no relationship between the average range size of the component species and the number of species in each family but there was a triangular-shaped relationship between the average range size of the component species and the number of species in each genus (Fig. 4; see Appendix). Species with small chromosome numbers varied greatly in the extent of their distributions (i.e. which could be either small or large) but those with high numbers had restricted distributions (Fig. 5; see Appendix). Among all species and among both endemic and non-endemic species (data not shown), there was no clear relationship between distribution and spore size (Fig. 6).

No clear relationship between spore size and gametic chromosome number (n) was found. Examination of the nine largest genera showed no relationships between distribution and chromosome number or between distribution and spore size within each genus. However, significant positive relationships between spore size and chromosome number were found within three genera (Fig. 7). At the family level, only two positive relationships were detected between spore size and chromosome number (n) out of a total of 34 families, Dryopteridaceae ($r^2 = 0.27$, $F = 40.19$, $p < 0.001$) and Ophioglossaceae ($r^2 = 0.68$, $F = 29.47$, $p < 0.001$). In many families, the relationships between distribution and chromosome numbers were triangular, such as that in Fig. 5, suggesting that species with high chromosome numbers tended to have restricted distributions while those with low numbers might have restricted or broad

distributions. No other relationships among distribution, chromosome number, and spore size were detected among species in all other families.

Nested ANOVAs showed that the distribution of variance at the levels of family, genera within families, and error (species within genera) differed among life history traits. Most of the variance in distribution (number of cells) occurred at the species level (species = 85%, genus = 15%, family = 0%) while variance in chromosome number (n ; 66%, 15%, 20%) and spore size (45%, 28%, 27%) was distributed more towards higher levels. There was a negative relationship between distribution and chromosome number at the genus level, a positive relationship between distribution and

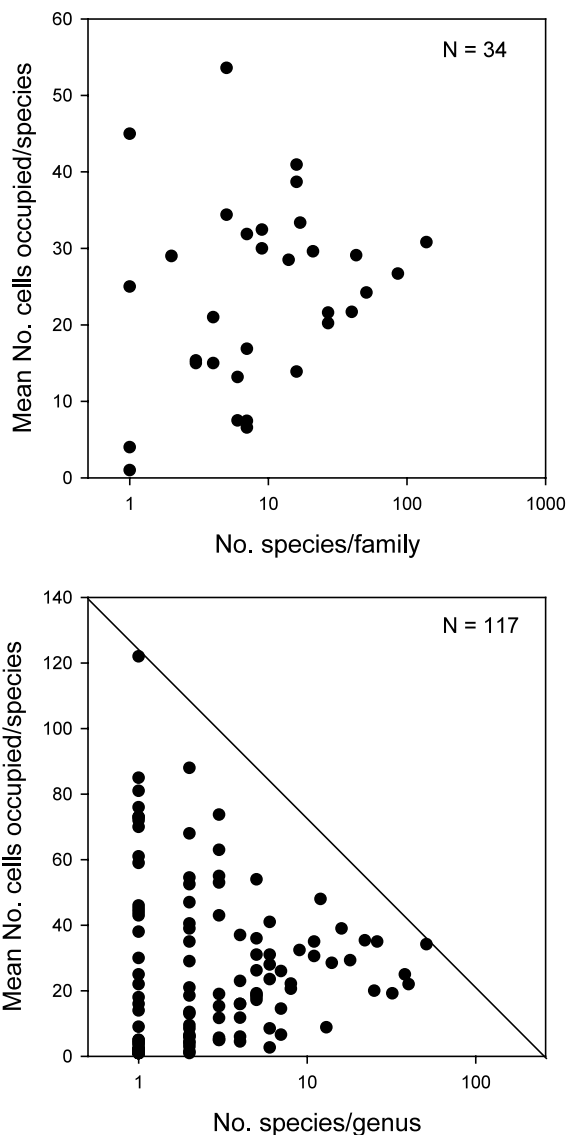


Fig. 4. Relationship between the average distribution range (number of cells occupied) of each component species and the number of species in each family (above) and genus (below).

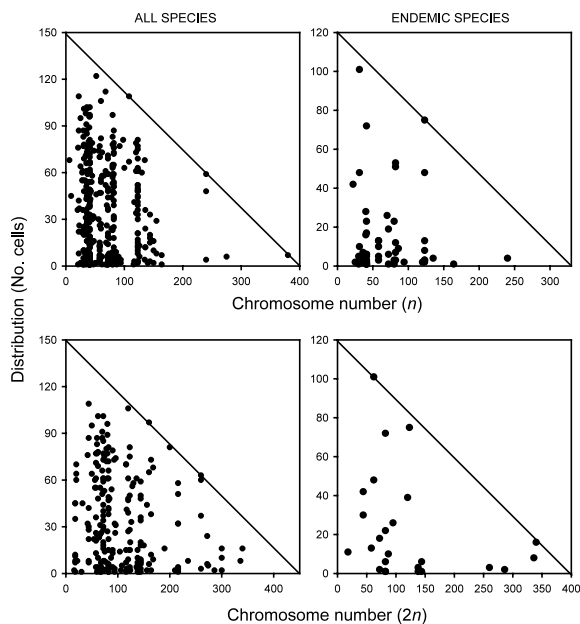


Fig. 5. Relationships between distribution and gametic (n , above) and somatic ($2n$, bottom) chromosome numbers of Japanese pteridophytes (left: all species, right: endemic species).

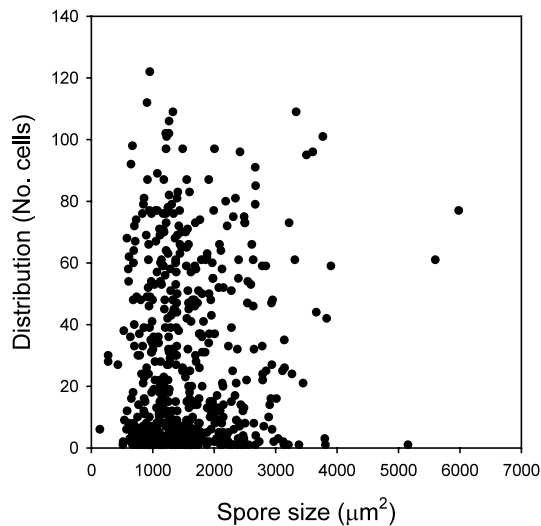


Fig. 6. Relationship between distribution and spore size among all species.

spore size at the genus level, and a strongly negative relationship between chromosome number and spore size at the family level, with a weaker but significant positive relationship at the species level (Table 3).

Discussion

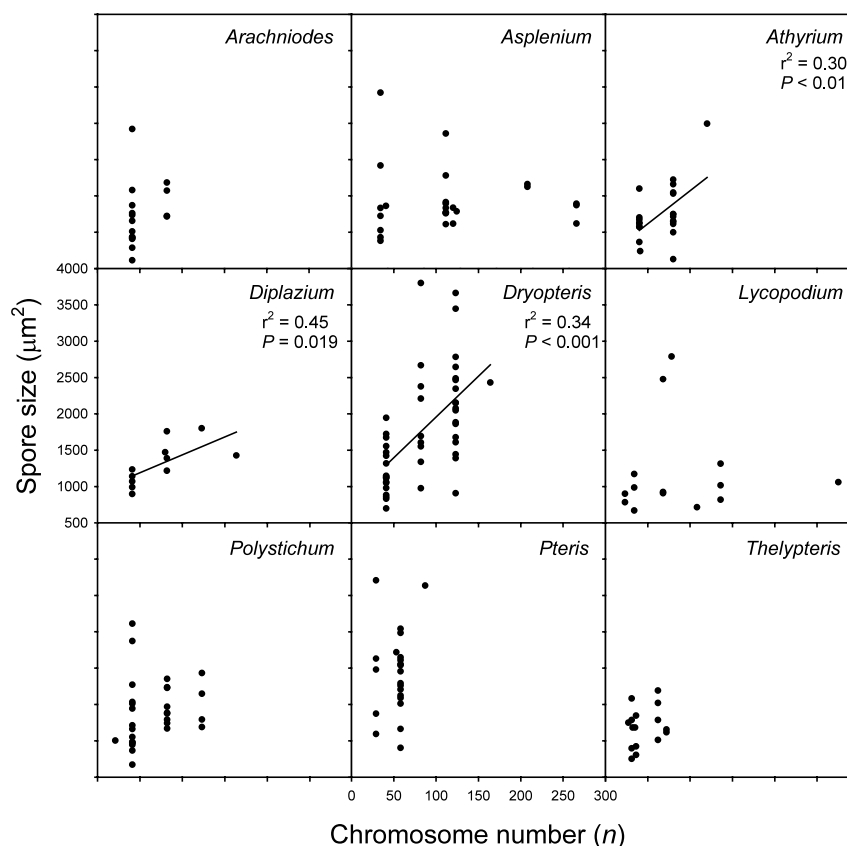
Despite some limitations, especially with respect to phylogenetic relationships, our study showed strong

links between morphology or life history and diversity or distribution. Morphology and life history are the outcomes of ecological and evolutionary adaptations of organisms to changing environments that ultimately influence the nature of diversity and distribution (Karr and James 1975, Ricklefs and Miles 1993). Consequently, many life history traits are interrelated to each other and their relationships interact with physical factors to determine taxonomic diversity and distribution. For example, the species in the family Dennstaedtiaceae have broader mean distribution ranges than other fern species in Japan (t-test on the number of cells, $p = 0.07$), and many of them have invaded disturbed habitats. This could reflect the wide range of life histories exhibited within the family, including such notable characteristics as indeterminate frond growth and extensive starch-storing surface rhizomes, which together contribute to colonization ability (Smith and Taylor 1986).

The distribution of pteridophytes may be promoted by their higher dispersal abilities but restricted by habitat availability (e.g. Richard et al. 2000). The smaller distribution ranges of evergreen species relative to seasonally green species probably results from the limited availability of more humid and warmer habitats required by evergreen taxa, which are restricted to southern Japan (Numata 1974). In general, pteridophytes are more strongly associated with mesic and warmer habitats than seed plants (Parris 1985, Given 1993). This can be seen from their generally lower latitudinal distributions toward the tropics relative to seed plants (e.g. Klekowski 1972, Kramer 1993). The greater dispersability of pteridophytes can be in part demonstrated by the relative lower endemism (17%) in Japan compared with that of flowering plants (ca 40%, Anon. 1992) (Tryon 1970, Klekowski 1972). Unlike seed plants, whose abundance (number of individuals) and distribution are often constrained by seed size (dispersal) (Guo et al. 2000), the absence of a strong relationship between distribution and spore size indicates that spore size is not a limiting factor for dispersal and distribution in pteridophytes. Thus, even the largest spores appear to be wind dispersed over large areas (Smith 1972, 1993, Page 1979a, b). Given data limitations, we could not determine whether a trade-off exists between spore number and size comparable to the number-size trade-off of seeds in seed plants (Harper et al. 1970).

Tryon (1970) has shown that the most successful colonizers of oceanic islands are also the most abundant species on the closest continents (Barrington 1993). It is also possible that species in open habitats could disperse more readily. Page (1979a, b) noticed that some closely related tropical species growing under forest canopies also occurred on many small islands, suggesting that escape of spores from forests occurs. However, this observation is confounded by habitat preference, i.e. although spores of endemic species in

Fig. 7. Relationships between spore size and gametic chromosome numbers (n) among species in nine largest genera.



the forests can be dispersed from forests, they may be unable to establish in open habitats. Experimental study may help separate such confounding effects (Page 1979a, b).

As expected, species with multiple reproductive modes (e.g. *Lycopodium clavatum*) had broader distribution ranges. Such species have the potential to overcome harsh environments where multiple reproductive modes are necessary to maintain a viable population. It is also possible that a broadly distributed species encompasses a broader range of conditions that subsequently select for multiple reproductive modes. Certainly asexual reproduction permits persistence with low population size, which would enhance colonizing abilities and the ability to withstand harsh conditions.

It should be pointed out that only 19 (6.6%) out of 286 species for which the reproductive modes were known had multiple reproductive modes.

Our analyses showed that species with high chromosome numbers had restricted distributions. Earlier researchers had noticed this phenomenon in some taxa of pteridophytes (e.g. Stebbins 1950, Smith 1972, Wagner and Wagner 1980). It has been suggested that the ages of the polyploids may be responsible for this pattern. For example, many polyploids are either paleopolyploids that might be relicts resulting from prolonged environmental changes in the past or neopolyploids that have had little time to adapt to new environments and spread. Neopolyploidy may result from hybridization, which enables pteridophytes to colonize stressful

Table 3. Results of nested analysis of variance showing nested correlations among distribution (no. cells), chromosome number (n), and spore size (bold-faced represent significant correlations). Chromosome number (n) and spore size were log-transformed for normality before analysis.

Covariance source	Distribution vs log (n)		Distribution vs log (spore)		Log (n) (vs log spore)	
	DF	Correlation	DF	Correlation	DF	Correlation
Total	411	-0.04	599	0.09	411	0.01
Family	24	0	33	0	24	-0.82
Genus	67	-0.34	84	0.52	67	0.08
Species	320	-0.03	482	0.06	320	0.32

habitats with smaller distributional ranges to avoid competition with other species (Page 1979a, b, Nelson and Elisens 1999). In this case, polyploidy only permits colonization and adaptation to the new environments but may not necessarily lead to an increase in species' range, particularly when the hybrid must compete with presumably well adapted parental species (Ehrendorfer 1980, Song et al. 1995). This issue may not be resolved until we can take history, dispersal, and colonization into account (Smith 1993, Petit and Thompson 1999).

Earlier evidence has shown that, in general, species at higher latitudes have broader distribution ranges (i.e. Rapoport's rule; see Stevens 1989) and the frequency of polyploids increases from lower latitudes to higher latitudes (e.g. Ehrendorfer 1980). Yet, many studies (e.g. Wagner and Wagner 1980) and our results showed polyploids to have smaller distribution ranges. This seeming incongruity may arise because polyploid species represent only a small fraction of floras at high latitudes. Alternatively, pteridophytes may be exceptions to such "rules" because, compared with seed plants, pteridophytes are restricted to warmer and more humid environments at lower latitudes.

Our results do not support the "genetic depauperization hypothesis" (i.e. the absence of inherited variability in disjunct populations; Klekowski 1972; see also Tryon 1970), which predicts lower levels of heterozygosity in the non-endemic taxa in comparison to populations in their respective source areas. Our conclusion follows from our assumption that asexual reproduction is associated with reduced genetic diversity and our observation that the proportion of apogamous species is higher in non-endemics than in endemics (24 vs 16%; Table 1). The ancestral sexual species of many Japanese apogamous species occur in China, suggesting that these species might have migrated from China.

Frequently, the species in each genus have similar life-history characteristics; for example, almost all species in some genera are seasonally green (e.g. *Botrychium*, *Polypodium*, *Woodsia*) and most species of *Cyrtomium*, *Dryopteris* and *Pteris* are apogamous. Therefore, phylogenetic relationships may also constrain their distribution patterns. Since the phylogenetic relationships among Japanese pteridophytes have not been well resolved, we compared the results from statistical analyses on all Japanese pteridophytes to those of the largest genera to identify consistent elements of distribution patterns. We found the patterns differ among genera in some respects, indicating possible phylogenetic constraints.

The hierarchical analysis of variance showed that most of the variation in geographic range was concentrated at the level of species within genera (85%), indicating a high degree of lability in this trait. This variation in range size at the species level was unrelated to variation in either chromosome number or spore size. However, the smaller proportion of the variance in

range size at the level of genera within families (15%) was positively related to spore size ($r = 0.52$) and negatively related to chromosome number ($r = -0.34$). Thus, hierarchical analysis can clarify the relationships between variables, particularly by sorting out the ecological lability characteristic of the lowest taxonomic level. Clearly, large spore size is not an impediment to distribution and may enable some taxa to become established in a wide range of environments. The association between high chromosome number and restricted distribution on the genus level may reflect the ecological specialization of allopolyploids. Our observations on the proportion of total variation at each taxonomic level were quite different from those of Niklas (1994) on seed plants in which most of the variation in vegetative and reproductive traits tended to be located at the family level. This in part, could be because pteridophytes have a longer geological history and many unique life history features compared with seed plants or simply because different variables were used in the analyses.

The interdependence between systematic classification and biogeographical distribution makes our results especially useful for informing taxonomic treatments of Japanese pteridophytes (Smith 1993). For example, it would be interesting to examine whether *Struthiopteris niponica* (Blechnaceae), which occupies 101 of the 134 cells in Japan (Fig. 1; outlier on the far right), is truly an endemic species to Japan or an endemic that is secondarily expanded under human influences. This species prefers higher level of light and disturbance therefore often exists in open forests or forest edges close to trail or roadside. One possibility is that the species is combined with the very closely related species, *Blechnum hancockii* that also occurs in Taiwan. Also, the different relationships among distribution, spore size, and chromosome number in different genera or families may have significant implications for future phylogenetic studies and taxonomic treatments of pteridophytes. Spore size and chromosome number may be positively related within some families or genera because polyploids tend to have larger cells that contain more genetic material (DNA). The negative relationship across different families (Table 3) is puzzling in this regard and may indicate greater differences in evolutionary histories and habitat preferences among families.

A complete phylogenetic tree for the Japanese pteridophytes would help clarify some of the relationships we observed. The following issues need to be addressed in future studies: 1) latitudinal distribution of each pteridophyte group based on ploidy levels, reproductive mode (mating systems), and other life history traits (e.g. lifespan or growth rate for which we still lack much information); 2) the ecologic and biogeographic consequence of many unique life-history traits of pteridophytes, particularly the relative freedom from

herbivory and lack of reliance on animals for reproduction and dispersal; and finally 3) the effects of human activities and climatic change on the distribution of peridophytes (e.g. Given 1993).

The last issue is especially critical as human activities create many new (open) habitats that can greatly alter the overall species diversity and distribution patterns (Kurata and Nakaike 1979–97). For example, Iwatsuki (1996) stated that biodiversity might be increased in some developed areas due to the increase of agamosporous and agamosperous species that do not reproduce sexually and whose further evolutionary development is therefore greatly diminished. However, such areas may serve as hybrid zones that allow interspecific and intraspecific hybridization to occur in higher frequencies. This will eventually give rise to apogamous species or races as a way of escaping from hybrid sterility. Further studies that compare similar habitats with different human disturbance regimes may shed light on these issues. As new data become available in the near future, we should be able to test whether human activities and global change have significantly increased the number of neopolyploids but decreased the number of paleopolyploids in a given flora. In short, this study shows a clear need for more extensive studies on the relationships between diversity or distribution and life history traits, as physical factors only cannot fully explain many observed patterns.

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References

- Anon. 1990. SAS/STAT user's guide, ver. 6. – SAS Inst., Cary.
- Anon. 1992. Global biodiversity: status of the earth's living resources. – Chapman and Hall.
- Barrington, D. S. 1993. Ecological and historical factors in fern biogeography. – *J. Biogeogr.* 20: 275–280.
- Brown, J. H. 1984. On the relationship between abundance and distribution of species. – *Am. Nat.* 124: 255–279.
- Brown, J. H. 1995. Macroecology. – Univ. of Chicago Press.
- Ehrendorfer, F. 1980. Polyploidy and distribution. – In: Lewis, W. H. (ed.), *Polyploidy: biological relevance*. Plenum Press, pp. 45–60.
- Enquist, B. J., Gordan, M. A. and Brown, J. H. 1995. Connections between ecology, biogeography, and paleobiology: relationship between local abundance and geographic distribution in fossil and recent mollusks. – *Evol. Ecol.* 9: 586–604.
- Given, D. R. 1993. Changing aspects of endemism and endangerment in pteridophyta. – *J. Biogeogr.* 20: 293–302.
- Guo, Q., Ricklefs, R. E. and Cody, M. L. 1998. Vascular plant diversity in eastern Asia and North America: historical and ecological explanations. – *Bot. J. Linn. Soc.* 128: 123–136.
- Guo, Q. et al. 2000. Constraints of seed size on plant abundance and distribution. – *Ecology* 81: 2149–2155.
- Harper, J. L., Lovell, P. H. and Moore, K. G. 1970. The shapes and sizes of seeds. – *Annu. Rev. Ecol. Syst.* 1: 327–356.
- He, F. and Gaston, K. J. 2000. Estimating species abundance from occurrence. – *Am. Nat.* 156: 553–559.
- Huston, M. 1994. Biological diversity. – Cambridge Univ. Press.
- Iwatsuki, K. 1994. Comparison of pteridophyte flora between North America and Japan. – In: Mayawaki, A., Iwatsuki, K. and Grandtner, M. (eds), *Vegetation in eastern North America*. Univ. of Tokyo Press, pp. 89–97.
- Iwatsuki, K. 1996. Has biodiversity increased under human influences? – In: Zhang, A. L. and Wu, S. G. (eds), *Floristic characteristics and diversity of eastern Asian plants*. China Higher Education Press and Springer, pp. 437–439.
- Iwatsuki, K., Kato, M. and Yamazaki, T. 1995. Flora of Japan, Vol. 1 (Pteridophyta and gymnospermae). – Kodansha, Tokyo.
- Karr, J. R. and James, F. C. 1975. Ecomorphological configuration and convergent evolution in species and communities. – In: Cody, M. L. and Diamond, J. M. (eds), *Ecology and evolution of communities*. Belknap Press, pp. 258–291.
- Kato, M. 1992. What is ploidy in ferns? – *Proc. Sem. Asian Perid.* 2: 31–35.
- Kato, M. 1993. Biogeography of ferns: dispersal and vicariance. – *J. Biogeogr.* 20: 265–274.
- Kimura, M. 2000. Paleogeography of the Ryukyu Islands. – *Tropics* 10: 5–24.
- Klekowski, E. J. Jr. 1972. Genetic features of ferns as contrasted to seed plants. – *Ann. Mo. Bot. Gard.* 59: 138–151.
- Kramer, K. U. 1993. Distribution patterns in major pteridophyte taxa relative to those of angiosperms. – *J. Biogeogr.* 20: 287–291.
- Kurata, S. and Nakaike, T. 1979–97. Illustrations of pteridophytes of Japan. Vols 1–8. – Univ. of Tokyo Press.
- Nelson, A. D. and Elisens, W. J. 1999. Polyploid evolution and biogeography in *Chelone* (Scrophulariaceae): morphological and isozyme evidence. – *Am. J. Bot.* 86: 1487–1487.
- Niklas, K. J. 1994. Plant allometry: the scaling of form and process. – Univ. of Chicago Press.
- Numata, M. 1974. The flora and vegetation of Japan. – Elsevier.
- Page, C. N. 1979a. The diversity of ferns: an ecological perspective. – In: Dyer, A. F. (ed.), *The experimental biology of ferns*. Academic Press, pp. 9–56.
- Page, C. N. 1979b. Experimental aspects of fern ecology. – In: Dyer, A. F. (ed.), *The experimental biology of ferns*. Academic Press, pp. 552–589.
- Parris, B. S. 1985. Ecological aspects of distribution and speciation in Old World tropical ferns. – *Proc. R. Soc. Edinburgh B* 86: 341–346.
- Petit, C. and Thompson, J. D. 1999. Species diversity and ecological range in relation to ploidy level in the flora of the Pyrenees. – *Evol. Ecol.* 13: 45–66.
- Rees, M. 1995. Community structure in sand dune annuals: is seed weight a key quantity? – *J. Ecol.* 83: 857–863.
- Richard, M., Bernhardt, T. and Bell, G. 2000. Environmental heterogeneity and the spatial structure of fern species diversity in one hectare of old-growth forest. – *Ecography* 23: 231–245.
- Ricklefs, R. E. and Miles, D. B. 1993. Ecological and evolutionary inferences from morphology: an ecological perspective. – In: Wainright, P. C. and Reilly, S. (eds), *Ecological morphology: integrative organismal biology*. Univ. of Chicago Press, pp. 13–41.
- Ricklefs, R. E. and Renner, S. S. 1994. Species richness within families of flowering plants. – *Evolution* 48: 1619–1636.

- Rosenzweig, M. L. 1995. Species diversity in space and time. – Cambridge Univ. Press.
- Smith, A. R. 1972. Comparison of fern and flowering plant distribution with some evolutionary interpretation for ferns. – *Biotropica* 4: 4–9.
- Smith, A. R. 1993. Phytogeographic principles and their use in understanding fern relationships. – *J. Biogeogr.* 20: 255–264.
- Smith, R. and Taylor, J. (eds) 1986. *Bracken: ecology, land use, and control technology*. – Parthenon, Lancaster.
- Song, K. et al. 1995. Rapid genome change in synthetic polyploids of *Brassica* and its implications for polyploid evolution. – *Proc. Natl. Acad. Sci. USA* 92: 7719–7723.
- Stebbins, G. L. 1950. *Variation and evolution in plants*. – Columbia Univ. Press.
- Stevens, G. C. 1989. The latitudinal gradient in geographical range: how so many species coexist in the tropics. – *Am. Nat.* 133: 240–256.
- Takamiya, M. 1996. *Index to chromosomes of Japanese pteridophyta*. – Nippon Print Center, Tokyo.
- Tryon, R. M. 1970. Development and evolution of fern floras of oceanic islands. – *Biotropica* 2: 76–84.
- Wagner, W. H. and Wagner, F. S. 1980. Polyploidy in pteridophytes. – In: Lewis, W. L. (ed.), *Polyploidy: biological relevance*. Plenum Press, pp. 199–213.
- Walker, T. W. 1979. The cytogenetics of ferns. – In: Dyer, A. F. (ed.), *The experimental biology of ferns*. Academic Press, pp. 87–132.

Appendix. Statistical (randomization) tests used in this study

To examine whether any relationships between average distribution (number of cells) of all component species and the number of species per family or genus can be distinguished from null hypotheses of random association, we performed randomization tests (Fig. 4). These tests were also used to evaluate to the extent to which the data points for all the species fell within a hypothesized “triangular envelope” of the distribution – number of species per family (or genus) relationship. The triangular envelope was constructed by connecting the data point with the highest distribution with a second data point, such that the resulting triangular envelope

contained all the remaining data points. We then tested the null hypothesis by comparing the area of the triangular envelope with the areas of triangular envelopes generated by random combinations of distribution and the number of species per family (or genus). The values of distribution of a species were paired with the number of species per family (or genus) drawn at random from the raw data. We repeated this process drawing values for each species without replacement until all values were drawn. For each such random species assemblage, the area of a hypothetical triangular envelope was computed and this procedure was repeated 5000 times. The probability of obtaining this result under the null hypothesis was estimated by determining the number of simulated values that were less than or equal to the observed value. Such tests were also performed separately for the relationships between distribution (number of cells) and chromosome number (Fig. 5), between distribution and spore size (Fig. 6), and between spore size and chromosome number (the same test was used in Guo et al. 2000; a similar randomization test was developed by Enquist et al. 1995).

Randomization tests of the observed data showed that, at the family level, the null hypothesis of no association between average distribution of the component species and the number of species in each family was not rejected ($p > 0.05$) but at the genus level, the null hypothesis was rejected ($p < 0.05$), indicating that when the number of species in the genus is very large, the average distribution of the component species is always small (Fig. 4). However, when the number of species in each genus is small, the distribution of the component species can vary greatly. The null hypothesis of non-relationship between distribution and chromosome number was rejected in all cases (i.e. all species or endemics only; $p < 0.05$; Fig. 5). Such randomization tests on the relationships between distribution and spore size (Fig. 6) and between spore size and chromosome number at the species level did not reject the null hypotheses ($p > 0.05$).