

# Ecological and taxonomic differences between rare and common plants of southwestern Ontario<sup>1</sup>

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**Abstract:** We compared ecological attributes in rare and common native plants of southern Ontario ( $n = 1,398$  flowering plant species; of these, 375 are identified as provincially rare). Compared with patterns for common species, rare species were significantly ( $P < 0.05$ ) over-represented in one taxonomic order (Fabales) and two families (Boraginaceae and Fabaceae) and significantly under-represented in two orders (Alismatales and Saxifragales) and one family (Salicaceae). Rare species were significantly more likely than common species to be associated with open-habitat communities (tallgrass prairie, alvar, and meadow) and significantly less likely to be found in aquatic habitats. Rare species were also significantly more likely to be insect-pollinated and to have larger fruits than common species. Furthermore, they were less likely to be dioecious, wind-pollinated, shrubby, clonal, or to produce fruits having many seeds. Rare-common differences were examined across nine large, ordinal-level monophyletic groups in order to reduce the phylogenetic influences of derived traits. Results concerning pollination, fruit size, number of seeds per fruit, life form, and clonality were each confirmed within at least one monophyletic group, suggesting that over-abundance of derived traits did not produce these rare-common results. In a separate comparison of rare woody species, rare species were significantly more likely (than common woody ones) to have a short flowering period, animals as dispersers, and large fruits; rare woody species were less likely to be wind dispersed or to inhabit moist/wet substrates. An inability to exploit new habitats or to cope with anthropogenic change appear to be the most important general features associated with rarity. These results support previous conclusions that no single characteristic can reliably predict which species are or will become rare.

**Keywords:** life-history features, habitat change, species rarity, conservation, extinction, ecological comparison.

**Résumé :** Nous avons comparé les caractéristiques écologiques de plantes rares et communes du Sud de l'Ontario grâce à une base de données comprenant 1398 espèces de plantes à fleurs, dont 375 sont identifiées comme rares dans la province. Lorsqu'on les compare aux espèces communes, les espèces rares sont significativement ( $P < 0,05$ ) surreprésentées dans un ordre taxonomique (Fabales) et au sein de deux familles (Boraginaceae et Fabaceae). D'autre part, elles sont sous-représentées dans deux ordres (Alismatales et Saxifragales) et dans une famille (Salicaceae). Les espèces rares sont plus souvent associées aux communautés des milieux ouverts (prairies d'herbes hautes, alvars et prés); on les trouve moins souvent dans les milieux aquatiques. Les espèces rares sont plus susceptibles d'être pollinisées par des insectes et de produire de gros fruits que les espèces communes. De plus, elles sont rarement dioïques, pollinisées par le vent, arbustives ou clonales et elles produisent moins souvent de fruits avec un grand nombre de graines. Les différences entre les espèces rares et communes ont été examinées à l'aide de neuf grands groupes monophylétiques à niveaux ordinaux afin de réduire les influences phylogénétiques des traits dérivés. Les résultats concernant la pollinisation, la taille des fruits, le nombre de graines par fruit, la forme de croissance et la propagation végétative ont tous été confirmés dans au moins un groupe monophylétique, ce qui suggère que la surabondance des traits dérivés n'est pas à l'origine des différences constatées entre les espèces rares et communes. Dans une autre série de comparaisons ayant pour objet les espèces ligneuses, nous avons trouvé que les espèces rares ont plus de chances d'avoir une période de floraison courte, d'être disséminées par les animaux et d'avoir de gros fruits que les espèces communes. Les espèces ligneuses rares sont moins susceptibles d'être disséminées par le vent ou de coloniser des substrats humides. Parmi les principales caractéristiques associées à la rareté, celles qui apparaissent les plus importantes sont l'incapacité de coloniser de nouveaux habitats et la difficulté à faire face aux changements d'origine anthropique. Ces résultats appuyent l'hypothèse qu'il est impossible de prédire avec certitude et à l'aide d'une seule caractéristique quelles espèces sont rares ou celles qui pourraient le devenir.

**Mots-clés :** caractéristiques du cycle de vie, changement d'habitat, rareté des espèces, conservation, extinction, comparaison écologique.

## Introduction

Ironically, rarity is a relatively common biological attribute. Indeed, it is one of the challenges of ecology to explain why the majority of species in any community are relatively rare (Preston, 1948; Gaston & Lawton, 1990; Gaston, 1994; Kunin & Gaston, 1997). Studies indicate that at scales either of local abundances or of regional range sizes,

most species are rare (Pagel, May & Collie, 1991). All species surely are rare somewhere, and most species are rare at the edge of their ranges (Orians, 1997).

Species rarity is not readily attributable to a single cause, except perhaps habitat destruction. Rather, there appear to be particular life-history features that result in lower abundances and/or smaller ranges (Gaston, 1994). Although the ecological processes influencing rare species may not be fundamentally different from those acting on common species, this cannot be assumed to be the case. Direct comparisons of ecological- and life-history features

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in rare and common species, in a range of different taxa, are only now beginning to reveal the essential dimensions of rarity (Gaston, 1994). Many authors have correlated elements of plant biology with distributional status and rarity in regional floras (Harper, 1979; Hodgson, 1986a-d; Kunin & Gaston, 1993; Schwartz, 1993; Daniels & Jayanthi, 1996; Kelly, 1996; Gaston & Kunin, 1997; Kunin & Shmida, 1997; Medail & Verlaque, 1997; Orians, 1997; Hegde & Ellstrand, 1999). However, comparative studies examining reasons why certain plant species are rare and the kinds of life-history and habitat relationships of rare and common species, as well as large-scale, regional patterns of rarity, are still largely unavailable (but see Kunin & Gaston, 1993; Beville & Louda, 1999; Khedr *et al.*, 2002).

Organisms may be rare globally (*i.e.*, across their entire range), or they may be rare within a more restricted part of their total range. Conservationists designate the abundance of organisms accordingly and use a system of global and regional (*i.e.*, sub-national) ranks to represent these (Oldham, 1999). Sub-national abundances (S-ranks) are assembled across the entire range of a species to create global rarity categories (G-ranks). Global ranks have proved extremely useful in assigning conservation priorities.

Here we examine taxonomic and ecological characteristics of the flora of the Carolinian ecoregion of Canada (Maycock & Fahselt, 1987; Argus, 1992) in southwestern Ontario, at the northern limit of the Mixed Wood Plains ecozone (Wiken, 1986). The ecoregion extends from the northern shores of Lake Ontario and Lake Erie (including the archipelago of Erie islands) to lower Lake Huron and the Detroit River (Figure 1) and is one of the most biologically diverse regions in Canada (Allen, Eagles & Price, 1990). The Carolinian ecoregion has the greatest frequency of regionally rare plants of any comparable area in Canada (Argus, 1992). Because Ontario has been entirely glaciated several times, there are very few species endemic to the province. Further-more, because of its mid-continental position, most species that are rare within the boundaries of the province tend to be common to the south, east, or west.

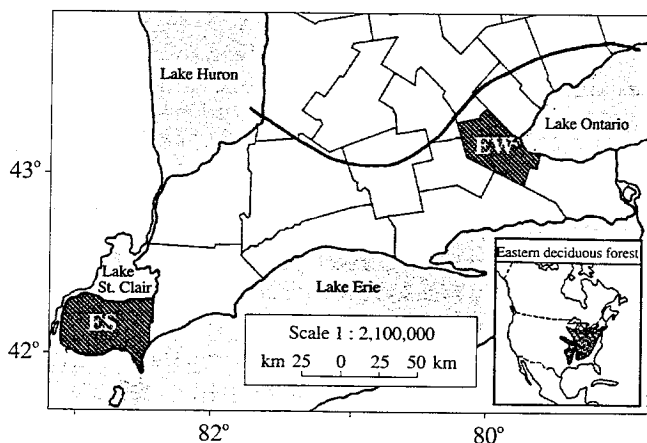


FIGURE 1. The Carolinian ecoregion of southwestern Ontario (the area beneath the undulating line, linking Lakes Ontario and Huron; adapted from Allen, Eagles & Price, 1990) and the two localities from which floristic data were used (ES = Essex County; EW = Hamilton-Wentworth Regional Municipality).

In this paper we compare the frequency of selected traits between common and rare plant taxa from the Carolinian ecoregion. We test the null hypotheses that phylogeny, habitat associations, and life-history traits do not differ between rare and common species.

## Methods

Our general premise is that floras contain valuable information that may reveal ecological patterns among plant life-history attributes (Kelly, 1996; Hegde & Ellstrand, 1999; Cadotte & Lovett-Doust, 2001; Khedr *et al.*, 2002). Two lists of plants were developed: common and rare plants in the Carolinian ecoregion of Canada (Figure 1). The floras from two large localities (straddling, respectively, the southern and northern boundaries of the ecoregion), Essex County (Botham, 1981) and Hamilton-Wentworth Regional Municipality (Goodban, 1993), were used to construct the list of common native species. Rare species were drawn from the list of provincially rare plants (Oldham, 1999), including all rare flowering taxa occurring in any county within the Carolinian ecoregion. Rarity was designated by the provincial ranking (S-rank) of the Natural Heritage Information Centre (Oldham, 1999) as follows:

S1: Extremely rare (critically imperiled); there are five or fewer occurrences.

S2: Imperiled because of rarity; usually between six and twenty occurrences.

S3: Rare to uncommon, usually between 21 and 100 occurrences.

SX: Apparently extinct or extirpated, without expectation that it will be rediscovered.

SH: Historical occurrence, not having been verified in at least 20 years in southwestern Ontario.

Global rarity status (G-rank), determined by the Nature Conservancy, was also recorded; however, life-history analyses were not carried out due to the small sample size ( $n = 21$ ) of globally rare species in the Carolinian ecoregion. Common species were those native taxa not currently identified as rare (*i.e.*, S1-3).

Taxonomic designations follow the Angiosperm Phylogeny Group (APG, 1998), shown in table I. Number of rare species per family was compared (using Pearson correlation analysis) to patterns of global family size and number of globally threatened species per family. Global family sizes and number of threatened species per family were taken from the website *The Families of Flowering Plants* (Watson and Dallwitz, 1992-onwards).

Life-history information, including growth habit, presence of clonal organ (*e.g.*, rhizome, stolon), life cycle, sex habit, length of flowering period, fruit size (longest axis), and number of seeds per fruit, was taken from Gleason (1952). For other details, including information not given by Gleason (such as mating system, nature of seed dispersal, and pollination syndrome), we searched the primary literature. Habitat associations were adapted from Gleason (1952) and categorized as

•Aquatic: species found in lacustrine, wetland, and bog habitats.

TABLE I. The 23 monophyletic groups and their constituent orders (from APG, 1998); the numbers of families and species in southwestern Ontario, and life history attributes (Gleason, 1952). Disp. refers to dispersal syndrome, where A is abiotic, B biotic, and V variable; Poll., pollination syndrome, where A is abiotic, B biotic, and V variable; Life form, where H is herbaceous growth habit, W woody, and V variable; Sex habit, where H is hermaphroditic, DM is dioecious/monoecious, and V is variable. Results of Freeman-Tukey deviates, † indicates value is over-represented ( $P < 0.05$ ); ‡ is under-represented ( $P < 0.05$ ).

Monophyletic group	Order	Number of families in Ontario	Number of species (% rare in Ont.)	Disp.	Life-history attributes <sup>§</sup>		
					Poll.	Life form	Sex habit
Ceratophyllales		1	2 (50.0)				
Laurales		1	2 (0)				
Magnoliales		2	3 (66.6)				
Piperales		2	5 (0)				
Acorales		0	0				
Alismatales		6	46 (10.9)*‡	A	B	H†	V
Asparagales		2	48 (37.5)	B	B	H	H
Dioscorales		1	1 (0)				
Liliales		2	41 (31.7)	V	B	H	V
Pandanales		0	0				
Commelinoids		8	342 (30.1)				
	Arecales	0	0				
	Poales	5	339 (30.1)	A	A	H	V
	Commelinales	2	3 (66.6)				
	Zingiberales	0	0				
Ranunculales		4	45 (20.0)	A	B	H	V
Proteales		1	1 (0)				
Caryophyllales		7	53 (32.1)	A	A	H	H
Santalales		1	1 (100)				
Saxifragales		5	20 (5.0)=‡	A		V	H
Geraniales		1	3 (0)				
Eurosids I		20	263 (25.9)				
	Malpighiales	5	70 (18.6)	A	A	V	V
	Oxalidales	1	2 (0)				
	Fabales	2	44 (54.5)***†	V	B	V	V
	Rosales	6	106 (20.8)	B	V	V	H
	Cucurbitales	1	2 (0)				
	Fagales	4	36 (22.2)	V	A	W	DM
Eurosids II		10	84 (27.4)				
	Myrtales	2	24 (37.5)	A		H	H
	Brassicales	2	27 (14.8)	A	V	H	H
	Malvales	3	14 (50.0)				
	Sapindales	3	19 (15.8)				
Cornales		1	9 (0)				
Ericales		5	38 (15.8)		B	V	H
Euasterids I		15	169 (32.5)				
	Garryales	0	0				
	Gentianales	3	40 (32.5)	A	V	V	H
	Lamiales	9	98 (30.6)	V	V	V	V
	Solanales	2	16 (25.0)				
Euasterids II		8	209 (23.9)				
	Aquifoliales	1	1(0)				
	Apiales	2	30 (30.0)	A	B	H	V
	Asterales	3	153 (22.9)	V	V	H	V
	Dipsacales	2	25 (24.0)	B	B	V	H

§- Life-history attributes given are for orders that have ≥ 20 species; taken from Gleason (1952).  
 \*  $P < 0.05$ ; \*\*\*  $P < 0.001$ ; =  $P = 0.05$ .

•Open: species occurring in meadows, old fields, prairies, and alvars.

•Woodland: species restricted to deciduous and mixed forests.

•Thickets: species of successional shrublands.

•Aquatic-open: species occurring in aquatic habitats and/or open habitats.

•Open-woods: species found in both open and woodland habitats, or savannas.

•Wet-woods: species found in both woodland and aquatic habitats.

•Disturbed-wasteland: species occurring in arable, degraded, or urban landscapes.

•Various: species found in multiple habitat types.

We compared taxonomic, habitat, and life-history patterns for common native taxa and provincially rare taxa. To compare species frequencies for individual families, we generated expected numbers of rare species per family, using the proportion of either common or rare species per family, which were then compared (using  $\chi^2$  tests) with the frequency of species per family observed for rare species in the region. If, following the null hypothesis, the list of rare species simply represents a random sample of all species,

then no significant differences should occur with respect to the families investigated.

To examine differences between rare and common species in habitat associations and life-history patterns, we used Pearson  $\chi^2$  contingency analysis. This analysis compares only the frequencies of attributes for which information was available. Where required (*i.e.*, 1 degree of freedom), Yates correction was used. If two-way contingency tables showed non-independence ( $P < 0.05$ ), the Freeman-Tukey deviate,

$$(\text{Obs})^{-1/2} + (\text{Obs} + 1)^{-1/2} + (4\text{Exp} + 1)^{-1/2},$$

was used to determine if any individual cell was either over- or under-represented compared to the expected value (Legendre & Legendre, 1998). The observed and expected values are considered significantly different when the absolute value is higher than the critical value:

$$(v\chi^2_{[v,\alpha/n]}/n)^{-1/2}$$

where  $v$  is the degrees of freedom, and  $n$  is the number of cells in the contingency Table, and  $\alpha/n$  is a Bonferroni correction for multiple testing using chi-square ( $\chi^2$ ) test (Legendre & Legendre, 1998).

#### PHYLOGENETIC CONSTRAINTS

A crucial assumption in any comparative approach is that the among-species comparisons are independent of each other. The fact that ancestral species have given rise to closely related genera and families, means that not all species are independent data points (Felsenstein, 1985), and the presence of derived traits may drastically influence results. One possible approach to reducing the effects of phylogeny in a comparative study is analysis of comparisons within taxonomic groups (Kelly & Purvis, 1993). Even though the power of such comparisons may decline with increasing taxonomic level (Kelly & Purvis, 1993), we used the ordinal classification provided by APG (1998). We used monophyletic ordinal groups in an attempt to balance the need for multiple independent phylogenetic samples with sufficiency of sample sizes. We re-analyzed the data for life-history attributes in each of the nine monophyletic groups having  $\geq 10$  common and 10 rare species (Table I).

Re-analysis within monophyletic groups was done using contingency  $\chi^2$  analysis (as above). However, because of smaller sample sizes, there was a propensity for too many sparse cells (*i.e.*, 20% of cells with an observed value  $< 5$ ). In these cases we combined columns to alleviate this effect. Combinations were carried out to retain biological meaning. For example, the two largest (and, separately, the two smallest) fruit-size categories and flowering-period lengths were combined. The Yates correction was again applied for these  $2 \times 2$  contingency tables.

We examined whether differences in the proportion of rare species in each order were due to dominant life-history attributes of these groups. Within each order having  $\geq 20$  species we recorded four life-history attributes for each species (dispersal syndrome, pollination syndrome, life form, and sex habit; see table I). We used rank-based non-parametric tests (Mann-Whitney  $U$  test for categories with two variables and Kruskal-Wallis one-way analysis of variance for  $> 2$  variables) to determine if orders with greater (or lower) proportions of rare species were associated with specific life-history attributes.

#### WOODY SPECIES

We also examined differences between rare and common species for woody species only. The rationale for this analysis is that selective forces and other influences acting on woody taxa may be operating at larger spatial scales (Kelly, 1996), or possibly over longer time spans, thereby producing different patterns than for non-woody species. Unfortunately, due to the small number of woody species ( $n = 237$ ) and especially of rare woody species ( $n = 41$  species in 10 monophyletic groups), we could not compare results across monophyletic groups to determine any rarity-associated attributes that transcend phylogenetic constraints.

#### Results

The two regional floras had a combined total of 1,023 species of common, native flowering plants in southern Ontario. An additional 375 taxa have been designated as regionally or globally rare. Of these rare taxa, 34 (9.1%) are extinct, extirpated, or have not been located in at least 20 years (Rank = SX or SH); 126 (33.6%) are extremely rare (S1); 113 (30.1%) are very rare (S2); 81 (21.6%) are rare (S3); and 21 (5.6%) are rare but current information is insufficient (*e.g.*, S-rank = S2-3). Twenty-one taxa are considered globally rare (G-rank 1-3), with a further 17 possibly globally threatened (G3-4, G3-5).

Of the 1,023 common taxa, 196 are common woody taxa (including shrubs, vines, and trees), while 42 of the 375 rare taxa are woody. Of the 42 rare woody taxa, 9 are ranked as S1, 12 as S2, 13 as S3, and 8 as SX or SH. Three other rare woody taxa are designated as globally rare (G-rank 1-3).

#### TAXONOMIC PATTERNS

The common species were distributed taxonomically among 378 genera and 106 families. The 375 rare taxa were aggregated among 199 genera and 63 families. Rare species occur in families with a lower mean number of species, compared to common species (5.60 versus 8.97). The Fabales was significantly over-represented by rare species ( $P < 0.001$ ), while the Alismatales and Saxifragales were under-represented by rare species (Table I). Table II shows the families that contain the majority of common and rare species. Cyperaceae, Asteraceae, Poaceae, Rosaceae, Orchidaceae, and Lamiaceae contained most native species. Families having highest proportions of rare species were Fabaceae (59.5%), Boraginaceae (53.3%), Apocynaceae (46.7%), Juncaceae (40.0%), Amaranthaceae (38.9%), Orchidaceae (38.5%), Lamiaceae (36.8%), and Scrophulariaceae (33.3%). Families having the lowest proportions of rare species were Salicaceae (0%), Potamogetonaceae (5.3%), Ericaceae (12.0%), and Brassicaceae (15.4%). Table III shows the 20 genera containing the greatest numbers of rare species. Several genera are heavily represented by rare species: *Asclepias* (63.6%), *Desmodium* (58.3%), *Juncus* (40.9%), and *Crataegus* (39.4%). In contrast, two genera had no rare taxa (*Salix* and *Rubus*). Overall, the number of rare species in a family was strongly correlated to the number of common species per family (Pearson correlation coefficient = 0.568;  $P < 0.001$ ) (Figure 2). Similarly, the numbers of rare species per family were also significantly

TABLE II. Southern Ontario families with greatest numbers of native and rare species and genera. ↑ and ↓ indicate families that are significantly over- or under-represented by rare species, respectively (determined by  $\chi^2$  tests, with expected values based on the proportion of native species in each family). \* =  $P < 0.05$ , and \*\* =  $P < 0.01$ , \*\*\* =  $P < 0.001$ .

Family	Native species	Native genera	Common species	Genera $\geq 1$ rare species	Rare species	% rare species
Cyperaceae	179	13	122	9		
Asteraceae	143	36	108	18	57	31.8
Poaceae	129	46	94	19	35	24.5
Rosaceae	90	18	70	7	35	27.1
Orchidaceae	39	18	24	8	20	22.2
Lamiaceae	38	16	24	8	15	38.5
Fabaceae	37	18	15	8	14	36.8
Ranunculaceae	34	13	27	15	22↑***	59.5
Liliaceae	33	17	23	6	7	20.6
Scrophulariaceae	33	19	22	9	10	30.3
Apiaceae	26	15	18	8	11	33.3
Brassicaceae	26	8	22	6	8	30.8
Ericaceae	25	13	22	3	4	15.4
Juncaceae	25	2	15	3	3	12.0
Violaceae	23	2	16	2	10	40
Caprifoliaceae	22	8	19	2	7	30.4
Salicaceae	21	2	21	2	3	13.6
Onagraceae	19	5	13	0	0↓*	0
Polygonaceae	19	3	14	3	6	31.6
Potamogetonaceae	19	2	18	1	5	26.3
Amaranthaceae	18	5	11	1	1	5.3
Apocynaceae	15	2	8	2	7	38.9
Boraginaceae	15	6	7	1	7	46.7
				4	8↑*	53.3

TABLE III. Number of rare flowering plant species in southwestern Ontario among the 20 genera having the greatest numbers of native species.

Genera	Native species	Rare species	% rare species
<i>Carex</i> (Cyperaceae)	125	38	30.4
<i>Crataegus</i> (Rosaceae)	33	13	39.4
<i>Aster</i> (Asteraceae)	31	6	19.4
<i>Juncus</i> (Juncaceae)	22	9	40.9
<i>Solidago</i> (Asteraceae)	22	6	27.3
<i>Viola</i> (Violaceae)	22	6	27.3
<i>Panicum</i> (Poaceae)	21	8	38.1
<i>Potamogeton</i> (Potamogetonaceae)	18	1	5.6
<i>Polygonum</i> (Polygonaceae)	16	4	25
<i>Salix</i> (Salicaceae)	16	0	0
<i>Eleocharis</i> (Cyperaceae)	14	5	35.7
<i>Scirpus</i> (Cyperaceae)	14	4	28.6
<i>Quercus</i> (Fagaceae)	14	4	28.6
<i>Cyperus</i> (Cyperaceae)	12	4	33.3
<i>Desmodium</i> (Fabaceae)	12	7	58.3
<i>Galium</i> (Rubiaceae)	12	2	16.7
<i>Asclepias</i> (Apocynaceae)	11	7	63.6
<i>Hypericum</i> (Clusiaceae)	11	3	27.3
<i>Ranunculus</i> (Ranunculaceae)	11	2	18.2
<i>Rubus</i> (Rosaceae)	11	0	0

correlated to both the global number of species per family (Pearson coefficient = 0.488;  $P < 0.001$ ) and the number of globally threatened species per family (Pearson coefficient = 0.494;  $P < 0.001$ ).

Further examination of species membership within families revealed some interesting incongruities. Several families were significantly over-represented by rare species, compared to the expected number of species per family (based upon the proportion of common species; Table II). Two families contained significantly more rare species than expected (Boraginaceae and Fabaceae), and one family (Salicaceae) contained fewer than expected. A further seven, locally small families, were represented solely by

rare species (Annonaceae, Bignoniaceae, Cactaceae, Commelinaceae, Linaceae, Moraceae, and Valerianaceae).

#### HABITAT PATTERNS

The majority (40%) of all rare species were associated with woodland habitats, while a further 45% of rare species were associated with three other habitat types (open, aquatic, or open-woodland). In contrast, although about a third (34.4%) of common native species were also typically associated with woodland, common species in aquatic habitats accounted for 21.3% of species (versus 10.6% for rare species). Table IV summarizes the habitats containing either significantly more rare species (e.g., open habitats) or significantly fewer (aquatic and various). Additionally, rare species appear significantly more likely than common species to inhabit dry soils and significantly less likely to inhabit the wetter soils (or multiple soil moisture levels; see table IV).

#### LIFE-HISTORY PATTERNS

In general, rare species were significantly over-represented for the following life-history traits, compared to patterns for common species: absence of clonal growth and insect pollination (Table V). Rare species were significantly under-represented among the following traits: shrubby growth habit, capacity for clonal growth, dioecy, wind pollination, and many-seeded fruits ( $> 7$ /fruit) (Table V).

Nine monophyletic ordinal groups (having  $\geq 10$  common and 10 rare species) were each independently analyzed for the influence of life-history attributes on the rarity status of species (Table VI). Only a single group (Eurosids I) showed a significant influence of growth form ( $P < 0.05$ ): rare species were under-represented by the shrubby growth habit. Six of the nine groups revealed a significant influence of the presence of a clonal organ ( $P < 0.05$ ); for all six, rare species were significantly under-represented ( $P < 0.05$ ) by clonal species. In one instance (Eurosids I), rare species

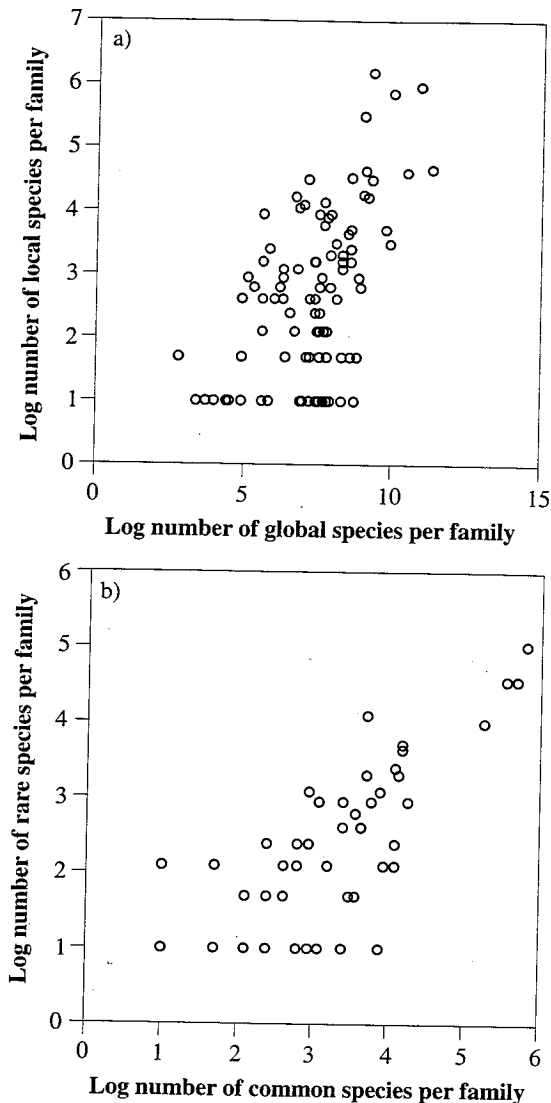


FIGURE 2. The relationship between a) the numbers of local and global species per family ( $P < 0.001$ ; Pearson correlation coefficient = 0.568); and b) numbers of rare and common species per family in southwestern Ontario ( $P < 0.001$ ; Pearson correlation coefficient = 0.756).

were significantly over-represented by biotic-pollination. In two ordinal groups, Lilales and Eurosids I, rare species were significantly ( $P < 0.05$ ) over-represented by smaller fruit sizes. In Eurosids I, rare species were under-represented ( $P < 0.05$ ) by large numbers of seeds per fruit, as well as by abiotic seed-dispersal. Among all nine monophyletic groups, no differences were found for life cycle, sex habit, and flowering-period length (Table VI).

Results of Mann-Whitney  $U$  tests and Kruskal-Wallis ANOVA revealed that order-level differences in the proportion of rare species were not significantly affected by the dominant life-history attributes of these orders ( $P > 0.05$ ).

#### WOODY TAXA

Rare woody species were significantly over-represented by a flowering period limited to a single month, by relatively larger fruits ( $> 50$  mm in diameter), and animal seed dispersal (Table VII). They were also significantly under-

TABLE IV. Results of contingency  $\chi^2$  analysis of numbers of rare and common species occurring in specific habitat types and soil moistures ( $\uparrow$  = significantly [ $P < 0.05$ ] over-represented;  $\downarrow$  = significantly under-represented).

	Rare species	Common species
HABITAT TYPE		
Aquatic	30 $\downarrow$	170
Aquatic-open	8	40
Open	50 $\uparrow$	47
Open-woods	47	99
Woodlands	113	274
Wet-woods	11	48
Thickets	21	51
Disturbed-wasteland	2	32
Various <sup>†</sup>	2 $\uparrow$	36
$\chi^2 = 69.49; P < 0.001$		
SOIL MOISTURE		
Dry	113 $\uparrow$	162 $\downarrow$
Moist/dry	41	114
Moist	91	287
Moist/wet	17	76
Wet	53 $\downarrow$	262
Various <sup>†</sup>	3 $\downarrow$	37
$\chi^2 = 57.76; P < 0.001$		

<sup>†</sup> Taxa that occur in multiple habitat types and/or moisture regimes.

represented among species inhabiting moist and wet soils and whose propagules were wind-dispersed.

#### Discussion

Biological explanation for the occurrence of rarity is necessarily a complex issue, with difficulties surrounding metrics (Gaston, 1994) and the independence of data points (Felsenstein, 1985). The measure of rarity used here, sub-national abundance values (*i.e.*, S-ranks 1-3), though based on numerous field observations by many field workers, is by no means standardized. We believe it is a reliable categorization of relative abundances in comparisons of large numbers of species. Yet two difficulties remain when using S-ranks as measures of rarity: 1) The definition of distinct populations. For example, are the populations small but interconnected, or large and isolated? 2) Differentiation of absolute range size. For example, are there differences between rare species whose centre of range is in Ontario and species that are at the northern edge of their range? These issues remain to be clarified, and various factors, including habitat specificity and range size, might be useful in assessing geographical rarity (Rabinowitz, 1981).

Previous explanations for plant distributions in the Carolinian ecoregion have stressed the importance of abiotic factors such as climate (Maycock, 1963; Argus, 1992) or soil moisture levels (Maycock, 1963). Here we show the importance of several biotic factors, including phylogeny and particular life-history elements.

#### TAXONOMIC / PHYLOGENETIC PATTERNS

Our results indicate that certain taxonomic orders (Fabales) and families of flowering plant (Boraginaceae and Fabaceae) had significantly more rare species than expected, while the Alismatales and Salicales, and the Salicaceae, had significantly fewer rare species than expected. These results are similar to those of Hodgson (1986a,c) and

TABLE V. Results of contingency  $\chi^2$  analysis of numbers of rare and common species having particular life-history attributes ( $\uparrow$  = significantly [ $P < 0.05$ ] over-represented;  $\downarrow$  = significantly under-represented; when  $\chi^2$  values are not indicated, results were not significant).

	Rare	Common
<b>GROWTH HABIT</b>		
Herbaceous	332	825
Shrub & small trees	20 $\downarrow$	132
Tree	18	50
Vine	3	14
$\chi^2 = 42.39; P < 0.001$		
<b>CLONAL ORGAN</b>		
Present	80 $\downarrow$	446 $\uparrow$
Absent	293 $\uparrow$	803 $\downarrow$
$\chi^2 = 26.01; P < 0.001$		
<b>LIFE CYCLE</b>		
Annual-biennial	55	125
Perennial	293	803
<b>SEX HABIT</b>		
Hermaphrodite	275	695
Monoecious	61	174
Gyno-monoecious	18	59
Andro-monoecious	4	14
Diocious	9 $\downarrow$	66
$\chi^2 = 10.33; P < 0.05$		
<b>POLLINATION</b>		
Insect	47 $\uparrow$	83 $\downarrow$
Wind	75 $\downarrow$	299
$\chi^2 = 12.77; P < 0.001$		
<b>NUMBER OF MONTHS DURING WHICH TAXA MAY FLOWER</b>		
1	18	40
2	96	295
3	56	254
4	39	128
5+	2	23
<b>AVERAGE FRUIT SIZE</b>		
0.1-5 mm	192	556
5.1-20 mm	58	212
21-50 mm	14	37
> 50 mm	15	20
$\chi^2 = 7.99; P < 0.05$		
<b>NUMBER OF SEEDS PER FRUIT</b>		
1	176	533
2-4	75	189
5-7	11	33
> 7	54 $\downarrow$	248
$\chi^2 = 9.30; P < 0.05$		
<b>SEED DISPERSAL</b>		
Animal	30	79
Wind	90	342

Schwartz (1993), who studied very different floras. Families having relatively greater proportions of rare species in our data set have no obvious similarities, except perhaps that they have showy or zygomorphic flowers (Boraginaceae and Fabaceae). However, five of the seven Ontario families that contain only rare species are distributed primarily in hot tropical and subtropical regions (Annonaceae, Bignoniaceae, Cactaceae, Commelinaceae, and Moraceae), and so presumably these taxa are at the edges of their respective family's biogeographic ranges. Conversely, diverse higher-level lineages (especially those over-represented by common taxa) may be devoid of rare taxa simply because we are examining rare-common differences within their major

range of distribution. These taxa should then have derived traits adapted to local conditions and possibly maintaining larger populations. These could include species such as those in the Alismatales and Saxifragales, or the Salicaceae.

#### HABITAT PATTERNS

Hodgson (1986a,b) found that the aquatic and mire (wetland) habitats in the Sheffield region of England had greatest representation of rare taxa, followed by woodland and grassland. Arable and open habitats were associated with the lowest representation of rare species. Our results are in general agreement with those of Hodgson, where natural communities (woodland, aquatic, and open habitats) have the greatest numbers of rare species and open habitats are significantly over-represented by rare species. Similarly, Crins (1997), in an investigation of the habitat preferences of rare and endangered plants in Canada, found that in southern Ontario rare species occurred most often in dry and moist tallgrass prairie, dry and moist hardwood forest (including the eastern deciduous forest and elements of oak savanna habitat), and aquatic habitats. These communities are typical of those that once dominated this region. Undisturbed communities maintain greater habitat heterogeneity than disturbed or degraded communities, and greater habitat heterogeneity may accommodate greater numbers of rare species (Heikkinen, 1998).

Our results concerning habitat differences revolve around two observations. Rare species are significantly over-represented in dry and open habitats and under-represented in aquatic habitats (Table IV). Kelly (1996) concluded that drought/moisture regimes were important determinants of plant rarity in Crete (which has a strong Mediterranean climate) and not very important in Great Britain. The under-representation of rare species in aquatic habitats may have little to do with environmental effects *per se*, but rather with the importance of dispersal on species abundances and community diversity (Hubbell, 2001). Populations in aquatic systems may have greater linkage through dispersal than do terrestrial species. Aquatic species may actually have some of the largest range sizes, while being more likely to belong to species-poor higher taxa.

The association between rare species and dry-open habitats probably has little to do with dispersal, but rather with local habitat history. This region of Ontario has been subjected to massive habitat destruction and intense human population pressure, which have resulted in extensive habitat alterations (Maycock & Fahselt, 1987; Argus, 1992; Catling, 1995; Lovett-Doust & Lovett-Doust, 1995). Furthermore, because of the ease of transition from natural to agricultural ecosystems, the majority of dry-open habitats (which historically were prairies) have been almost entirely wiped out (Robertson, 2000). Hodgson (1986a) showed that in Great Britain, where agricultural pressure has been at least as intense as in Ontario, rarity and extinction in plants were associated with lowland agricultural land transformation.

#### LIFE HISTORY PATTERNS

##### POLLINATION

Our general results, and in particular those for the higher-level monophyletic Eurosids I, reveal that biotic pollina-

TABLE VI. Results of contingency chi-square analysis for life-history attributes among the nine largest monophyletic ordinal groups. \*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ ; ns =  $P > 0.05$ . Arrows refer to results of Freeman-Tukey deviates test; ↓, cell was significantly ( $P < 0.05$ ) under-represented; and ↑, cell was significantly ( $P < 0.05$ ) over-represented.

Monophyletic group	Growth habit	Clonal organ	Life cycle	Sex habit	Life-history attributes				
					Pollination syndrome	Flowering length	Average fruit size	Number of seeds/fruit	Dispersal syndrome
Asparagales	all herbs	*; rare spp. ↓ clonal	all perennial	all hermaphrodite	all biotic	ns	ns	ns	all biotic
Liliales	all herbs	**; rare spp. ↓ clonal	all perennial	ns	all biotic	ns	*; rare spp. ↑ smallest	ns	ns
Commelinoids	all herbs	***; rare spp. ↓ clonal	ns	ns	all abiotic	ns	ns	ns	ns
Ranunculales	all herbs	ns	ns	ns	all biotic	ns	ns	ns	all abiotic
Caryophyllales	all herbs	ns	ns	ns	all abiotic	ns	ns	ns	all abiotic
Eurosids I	*; rare spp. ↓ shrubs	***; rare spp. ↓ clonal	ns	ns	*; rare spp. ↑ biotic	ns, $P > 0.05$	***; rare spp. ↑ 2 <sup>nd</sup> smallest, ↓ largest	*; rare spp. ↓ most seeds/fruit	**; rare spp. ↓ abiotic
Eurosids II	ns	*; rare spp. ↓ clonal	ns	ns	ns	ns	ns	ns	ns
Euasterids I	ns	ns	ns	ns	ns	ns	ns	ns	ns
Euasterids II	ns	***; rare spp. ↓ clonal	ns	ns	ns	ns	ns	ns	ns

tion is associated disproportionately with species having smaller range sizes. The findings of both Harper (1979) and Kelly and Woodward (1996), that rare species are less likely than more abundant ones to be wind-pollinated, are also in accord with our results. Biotic interactions (*e.g.*, insect pollination) are important associates of rarity (Pate & Hopper, 1994), and in order for biotically pollinated species to thrive, habitats must meet the demands of at least two or more species (plant and pollinator) (Kelly & Woodward, 1996). Habitat fragmentation, especially for tallgrass prairie systems, has not only isolated populations of plants but also of insect pollinators. Isolating and reducing the number of populations increases the risk of localized extinction (Hanski, 1982), because of reduced population-saving immigration events, as well as increased susceptibility to stochastic extinctions. Plant species that are insect pollinated experience multiple risks, as a kind of double jeopardy. Not only do plant populations face increased extinction rates, but so do the insect pollinators, which are essential to the long-term survival of these plants.

Kunin and Shmida (1997) studied 113 species of annual Brassicaceae in Israel and determined that rare species were disproportionately likely to be self-compatible. Other studies have also found that rare species rely less on outcrossing and more on asexual modes of reproduction (Kunin & Gaston, 1993; Gaston & Kunin, 1997; Orians, 1997). We note that rare species were significantly under-represented among dioecious species, but we were unable to corroborate this with phylogenetically independent tests.

#### FRUITS AND THEIR DISPERSAL

Our results show significantly more smaller-fruited and possibly fewer many-seeded, regionally rare species than expected, indicating a possible reduced potential in fecundities for rare species. Murray and Westoby (2000) recently reported very significant differences in fecundity in between-population contrasts of low-abundance and higher-abundance populations of certain Australian plant species.

Essentially, species that were "everywhere sparse" showed an approximately ten-fold reduction in seed production, compared to "somewhere abundant" species. Similarly, Pirie *et al.* (2000) showed that among populations of two closely related tree species (*Jatropha* spp., Euphorbiaceae), the one with a restricted range had a reduced crop size compared to the widespread species.

In general, however, we have found an absence of dispersal effects. It may be that our categories, biotic versus abiotic, are too broad. As discussed above, aquatic dispersal may maintain larger, inter-connected populations and reduce the potential for allopatric speciation, but our dispersal results combine wind (which the majority of species utilize) with other forms of abiotic dispersal. Kelly and Woodward (1996) also found evidence suggesting that small range sizes were associated with animal pollination, though that did not necessarily translate to an equally strong relationship with animal dispersal. They attributed this to a plant's "looser" dependence on animals for dispersal than for pollination. Obligate dependence is more important for insect pollination, where a plant's reproduction may necessitate interaction with insects because of the physical arrangement of reproductive parts (Silvertown & Lovett-Doust, 1993). Conversely, a dispersal (and birth event) for an animal-dispersed species does not necessarily require an animal vector for success every time.

#### VEGETATIVE REPRODUCTION

Kelly and Woodward (1996) hypothesized that in Britain clonal species ought to have smaller range sizes, because clonal species have superior adaptations to highly localized habitat conditions. Our results show that, in southwestern Ontario, rare species across many monophyletic groups are under-represented among clonal species. Other authors have hypothesized that vegetative reproduction may confer on species a greater ability to invade new communities and thereby expand their range (Baker, 1974; Pysek, 1997). We have noted elsewhere (Cadotte & Lovett-Doust,

TABLE VII. Results of contingency  $\chi^2$  analysis of the number of rare and common woody species utilizing different habitats and life-history strategies ( $\uparrow$  = significantly over-represented;  $\downarrow$  = significantly under-represented; when  $\chi^2$  values are not indicated, results were not significant).

	Rare woody	Common woody
<b>HABITAT</b>		
Woodland	20	66
Woodland & open	3	23
Woodland & thicket	13	32
Aquatic	2	26
<b>SOIL MOISTURE</b>		
Dry (or moist-dry)	11	59
Moist	24	75
Wet (or moist-wet)	3 $\downarrow$	38
$\chi^2 = 6.01; P < 0.05$		
<b>GROWTH HABIT</b>		
Shrub or small tree	20	132
Tree	50	18
Liana	3	14
<b>POLLINATION SYNDROME</b>		
Insect	18	47
Wind	12	58
<b>SEX HABIT</b>		
Dioecious	4	42
Hermaphrodite	24	113
Monocious	13	39
<b>MONTHS IN FLOWER</b>		
1	11 $\uparrow$	35
2	15	116
3+	2	35
$\chi^2 = 7.19; P < 0.05$		
<b>AVERAGE FRUIT SIZE (mm)</b>		
0.1-5	4	33
5.1-20	21	115
20.1-50	8	18
> 50	9 $\uparrow$	4 $\downarrow$
$\chi^2 = 25.41; P < 0.001$		
<b>SEEDS PER FRUIT</b>		
1	13	80
2-4	17	55
5-7	4	9
8+	6	49
<b>SEED DISPERSAL</b>		
Animal	28 $\uparrow$	70
Wind	2 $\downarrow$	42
$\chi^2 = 9.13; P < 0.005$		

2001) that a high proportion of southwestern Ontario species are clonal. The high extent of clonal capacity in the flora could mean that species lacking clonal ability may be competitively inferior.

Another reason why non-clonal species may have smaller range sizes and/or lower densities could be the highly fragmented and degraded nature of many communities in southwestern Ontario. As indicated above, reduced population sizes and increased isolation may be increasing a population's risk of stochastic extinction in a fragmented landscape (Hanski, 1982). Environmental stochasticity can have major influences on population extinction probabilities (Kalisz & McPeck, 1993). Clonal species may be able to inflate (at least temporarily) their population sizes, which will mitigate extinction risks associated with random processes and environmental stochasticity.

## Conclusion

While the various correlates observed here cannot be assigned as either causes or consequences of rarity, they may well represent high risk traits that could be useful in identifying other species already at risk or potentially at risk of becoming rare. Our results suggest that plant species that may not be suited to success in degraded and fragmented landscapes are more likely to be listed as rare by conservation authorities. Generally, these rare taxa have traits that make them poor colonizers, and they appear to be restricted to less-degraded, natural habitats. Conservation efforts should take into account species-specific life-history attributes, habitat requirements, and co-evolved biotic interactions.

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## Literature cited

- Allen, G. M., P. F. J. Eagles & S. D. Price (ed.), 1990. Conserving Carolinian Canada: Conservation Biology in the Deciduous Forest Region. University of Waterloo Press, Waterloo, Ontario.
- Angiosperm Phylogeny Group (APG), 1998. An ordinal classification for the families of flowering plants. *Annals of the Missouri Botanical Garden*, 85: 531-553.
- Argus, G. W., 1992. The phytogeography of rare vascular plants in Ontario and its bearing on plant conservation. *Canadian Journal of Botany*, 70: 469-490.
- Baker, H. G., 1974. The evolution of weeds. *Annual Review of Ecology and Systematics*, 5: 1-24.
- Bevill, R. L. & S. M. Louda, 1999. Comparisons of related rare and common species in the study of plant rarity. *Conservation Biology*, 13: 493-498.
- Botham, W., 1981. Plants of Essex County: A Preliminary List. Essex Region Conservation Authority, Essex, Ontario.
- Cadotte, M. W. & J. Lovett-Doust, 2001. Ecological and taxonomic differences between native and introduced plants of southwestern Ontario. *Écoscience*, 8: 230-238.
- Cadotte, M. W., R. Franck, L. Reza & J. Lovett-Doust, 2002. Tree and shrub abundance and diversity in fragmented littoral forest of southeastern Madagascar. *Biodiversity and Conservation*, 11: 1417-1436.
- Catling, P. M., 1995. The extent of confinement of vascular plants to alvars in southern Ontario. *Canadian Field-Naturalist*, 109: 172-181.
- Crins, W. J., 1997. Rare and endangered plants and their habitats in Canada. *Canadian Field-Naturalist*, 111: 506-519.
- Daniels, R. J. & M. Jayanthi, 1996. Biology and conservation of endangered plants: The need to study breeding systems. *Tropical Ecology*, 37: 39-42.
- Felsenstein, J., 1985. Phylogenies and the comparative method. *American Naturalist*, 125: 1-15.
- Gaston, K. J., 1994. *Rarity*. Chapman and Hall, London.
- Gaston, K. J. & J. H. Lawton, 1990. The population ecology of rare fishes. *Journal of Fish Biology*, 37: 97-104.

- Gaston, K. J. & W. E. Kunin, 1997. Rare-common differences: An overview. Pages 12-29 in W. E. Kunin & K. J. Gaston (ed.). *The Biology of Rarity: Causes and Consequences of Rare-Common Differences*. Chapman and Hall, London.
- Gleason, H. A., 1952. *The New Britton and Brown Illustrated Flora of the Northeastern United States and Adjacent Canada*. Three volumes. Hafner Press, New York.
- Goodban, A. G., 1993. A checklist of the vascular plants of Hamilton-Wentworth region, Ontario. Pages 4(1)-4(72) in A. E. Heagy (ed.). *Hamilton-Wentworth Natural Areas Inventory: Volume I*. Hamilton Naturalists Club, Hamilton, Ontario.
- Hanski, I., 1982. Dynamics of regional distribution: The core-satellite species hypothesis. *Oikos*, 38: 210-221.
- Harper, K. T., 1979. Some reproductive and life history characteristics of rare plants and implications of management. *Great Basin Naturalist Memoirs*, 3: 129-137.
- Heikkinen, R. K., 1998. Can richness patterns of rarities be predicted from mesoscale atlas data? A case study of vascular plants in the Kevo reserve. *Biological Conservation*, 83: 133-143.
- Hegde, S. G. & N. C. Ellstrand, 1999. Life history differences between rare and common flowering plant species of California and the British Isles. *International Journal of Plant Sciences*, 160: 1083-1091.
- Hodgson, J. G., 1986a. Commonness and rarity in plants with special reference to the Sheffield Flora. Part I: The identity, distribution and habitat characteristics of the common and rare species. *Biological Conservation*, 36: 199-252.
- Hodgson, J. G., 1986b. Commonness and rarity in plants with special reference to the Sheffield Flora. Part II: The relative importance of climate, soils and land use. *Biological Conservation*, 36: 253-274.
- Hodgson, J. G., 1986c. Commonness and rarity in plants with special reference to the Sheffield Flora. Part III: Taxonomic and evolutionary aspects. *Biological Conservation*, 36: 275-296.
- Hodgson, J. G., 1986d. Commonness and rarity in plants with special reference to the Sheffield Flora. Part IV: A European context with particular reference to endemism. *Biological Conservation*, 36: 297-314.
- Hubbell, S. P., 2001. *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton.
- Kalish, S. & M. A. McPeck, 1993. Extinction dynamics, population growth and seed banks: An example using an age-structured annual. *Oecologia*, 95: 314-320.
- Kelly, C. K., 1996. Identifying plant functional types using floristic data bases: Ecological correlates of plant range size. *Journal of Vegetation Science*, 7: 417-424.
- Kelly, C. K. & A. Purvis, 1993. Seed size and establishment conditions in tropical trees. *Oecologia*, 94: 356-360.
- Kelly, C. K. & F. I. Woodward, 1996. Ecological correlates of plant range size: Taxonomies and phylogenies in the study of plant commonness and rarity in Great Britain. *Philosophical Transactions of the Royal Society of London, Series B*, 351: 1261-1269.
- Khedr, A. H., M. W. Cadotte, A. El-Keblawy & J. Lovett-Doust, 2002. Phylogenetic diversity and ecological features in the Egyptian flora. *Biodiversity and Conservation*: in press.
- Kunin, W. E. & K. J. Gaston, 1993. The biology of rarity: Patterns, causes and consequences. *Trends in Ecology and Evolution*, 8: 298-301.
- Kunin, W. E. & K. J. Gaston, 1997. *The Biology of Rarity: Causes and Consequences of Rare-Common Differences*. Chapman and Hall, London.
- Kunin, W. E. & A. Shmida, 1997. Plant reproductive traits as a function of local, regional, and global abundance. *Conservation Biology*, 11: 183-192.
- Legendre P. & L. Legendre, 1998. *Numerical Ecology*. 2<sup>nd</sup> English Edition. Elsevier Science B. V., Amsterdam.
- Lovett-Doust, L. & J. Lovett-Doust, 1995. Wetland management and conservation of rare species. *Canadian Journal of Botany*, 73: 1019-1028.
- Maycock, P. F., 1963. The phytosociology of the deciduous forests of extreme southern Ontario. *Canadian Journal of Botany*, 41: 379-438.
- Maycock, P. F. & D. Fahselt, 1987. An inventory of ecologically significant natural vegetation in the province of Ontario: Essex County. *Canadian Field-Naturalist*, 101: 474-486.
- Medail, F. & R. Verlaque, 1997. Ecological characteristics and rarity of endemic plants from southeast France and Corsica: Implications for biodiversity conservation. *Biological Conservation*, 80: 269-281.
- Murray, B. R. & M. Westoby, 2000. Properties of species in the tail of rank-abundance curves: The potential for increase in abundance. *Evolutionary Ecology Research*, 2: 583-592.
- Oldham, M. J., 1999. *Natural Heritage Resources of Ontario: Rare Vascular Plants*. 3<sup>rd</sup> Edition. Natural Heritage Information Centre, Ontario Ministry of Natural Resources, Peterborough, Ontario.
- Orians, G. H., 1997. Evolved consequences of rarity. Pages 190-208 in W. E. Kunin & K. J. Gaston (ed.). *The Biology of Rarity: Causes and Consequences of Rare-Common Differences*. Chapman and Hall, London.
- Pagel, M. D., R. M. May & A. R. Collie, 1991. Ecological aspects of the geographical distribution and diversity of mammalian species. *American Naturalist*, 137: 791-815.
- Pate, J. S. & S. D. Hopper, 1994. Rare and common plants in ecosystems, with special reference to the south-west Australian flora. Pages 293-325 in E. D. Schulze & H. A. Mooney (ed.). *Biodiversity and Ecosystem Function*. Springer-Verlag, New York.
- Pirie, C. D., S. Walmsley, R. Ingle, A. Perez Jimenez, A. S. Magallanes & C. K. Kelly, 2000. Investigations in plant commonness and rarity: A comparison of seed removal patterns in the widespread *Jatropha standleyi* and the endemic *J. chame-lensis* (Euphorbiaceae). *Biological Journal of the Linnean Society*, 71: 501-512.
- Preston, F. W., 1948. The commonness and rarity of species. *Ecology*, 29: 254-283.
- Pysek, P., 1997. Clonality and plant invasion: Can a trait make a difference? Pages 405-427 in H. de Kroon & J. van Groenendael (ed.). *The Ecology and Evolution of Clonal Plants*. Backhuys Publishers, Leiden.
- Rabinowitz, D., 1981. Seven forms of rarity. Pages 205-217 in H. Synge (ed.). *The Biological Aspects of Rare Plant Conservation*. John Wiley & Sons, Chichester.
- Robertson, K. R., 2000. The tallgrass prairie. *Plant Talk*, 20: 21-25.
- Schwartz, M. W., 1993. The search for pattern among rare plants: Are primitive species more likely to be rare? *Biological Conservation*, 64: 121-127.
- Silvertown, J. W. & J. Lovett-Doust, 1993. *Introduction to Plant Population Biology*. Blackwell Science, Cambridge.
- Watson, L. & M. J. Dallwitz, 1992-onwards. *The families of flowering plants: Descriptions, illustrations, identification, and information retrieval*. Version 14<sup>th</sup> December 2000. [Online] URL: <http://biodiversity.uno.edu/delta/> [May 2001].
- Wiken, E., 1986. *Terrestrial Ecozones of Canada*. Ecological Land Classification Series No. 19. Land Directorate, Environment Canada, Ottawa, Ontario.