Search in this book

CHAPTER

2 Biogeography and habitats of carnivorous plants 🔓

J. Stephen Brewer, Jan Schlauer

Abstract

Understanding the processes involved in generating distribution patterns of carnivorous plants requires investigation at multiple scales. Carnivorous plants typically occur in warm or hot and humid or wet climates in subtropical to tropical regions of all continents. Carnivorous plants tend to grow in wet, open, and nutrient-poor habitats. Most carnivorous plants are less tolerant of dry soils than are non-carnivorous plants. The reasons why many carnivorous plants are absent from habitats with nutrient-rich soils remain unclear, but the roles of competition and soil anoxia warrant greater attention. Reduced competition from woody plants (*e.g.*, following fires) contributes to neutral coexistence of carnivorous and noncarnivorous herbs, and there is no evidence to date in support of nutrient-niche partitioning. More studies of interspecific competition are needed to understand better the distribution patterns and drivers of species coexistence of carnivorous and noncarnivorous plants.

Keywords: Carnivorous plants, competition, drought tolerance, niche theory, neutral theory, soil anoxia, species diversity

Subject: Plant Sciences and Forestry, Animal Pathology and Diseases

Collection: Oxford Scholarship Online

2.1 Introduction

Although carnivorous plants are considered to be physiologically specialized, they grow in many different environments and in unevenly distributed locations around the world. Two underlying mechanisms most frequently explain global scale distribution patterns: migration (differentiation during or after dispersal to new locations), and vicariance (differentiation during or after fragmentation of a larger, contiguous original area caused by geological or climatological changes). Even after differentiation, hybridization may cause introgression or polyphyletic speciation wherever two taxa contact one another. At regional and local scales, most investigators (beginning with Darwin [1875]) have hypothesized that botanical carnivory is most beneficial in habitats with nutrient-poor soils. Others, including Juniper et al. (1989), recognized the potential importance of additional factors, including calcium concentration of soils, soil moisture, shade, and competition with noncarnivorous plants.

In this chapter, we discuss global distribution patterns of carnivorous plants with respect to biogeography and climate. We then present data on occurrence of terrestrial carnivorous and noncarnivorous plants in relation to soil fertility, light, and soil moisture within a region (Mississippi, USA) as a case study for testing the hypotheses that carnivory puts carnivorous plants at a competitive disadvantage in shady habitats with dry, nutrient-rich soils. We further consider different hypotheses to explain the high species diversity of wet savannas vis-à-vis mechanisms of coexistence of carnivorous and noncarnivorous herbs. We conclude that additional comparative ecological studies of carnivorous and noncarnivorous plants will be crucial not only for understanding distribution of carnivorous plants but also for understanding general controls of plant diversity and distribution.

2.2 Global biogeography

Carnivory in plants has evolved independently numerous times (Chapter 3), and their evolutionary history has led to a number of geographic "hotspots" with large numbers of species (e.g., *Nepenthes* in Southeast Asia [Chapter 5]; *Drosera* in Australia and South Africa [Chapter 4]; and *Sarracenia* in the Southeast United States [Chapter 9]). Only in comparatively few cases is there reasonable evidence for long-distance dispersal in carnivorous plants, and more or less continuous spread and diversification is clearly the dominant pattern. Biogeographical analogies between unrelated taxa reflect only very general common trends, not synchronous or congruent events (Schlauer 2010). Global-scale distribution patterns, summarized in Table 2.1, can be characterized by floristic composition (Takhtajan 1986) and climatic conditions (Troll and Paffen 1964, Kottek et al. 2006).

Table 2.1 Geographic and climatological distribution of major taxonomic carnivorous plant groups.

Genus-Subgenus-Section	# of spp.	Floristic Region/Province of Takhtajan (1986)*	Köppen-Geiger Climate Classification**	Troll-Paffen Climate Classification***
Lentibulariaceae				
Utricularia-Bivalvaria-Aranella	10	Caribbean, Guyana Highland, Amazonian, Brazilian, Guineo-Congolian & Sudano-Zambezian rr. (65–67, 70, 117, 118, 120, 121, 123, 124, 127, 129)	Af, Am, Aw, Bsh	V_1–V_3
Utricularia-Utricularia-Candollea	1	Sudano-Zambezian r.; Zambezian p. (70)	Aw	V_2
Utricularia-Utricularia-Martinia	1	Guayana Highland & Amazonian rr. (120, 121)	Af, Am	V_1
Utricularia-Bivalvaria-Calpidisca	9	mainly Guineo-Congolian r., Sudano-Zambezian r.; Zambezi & Sudan pp., occasionally Karoo–Namib r.; Namaland p. & Madagascan r.; Eastern Madagascar p. (64–67, 69, 70, 72, 73, 80, 81, 84, 92, 117, ?121, 130, 133)	Af, Am, Aw	V_1, V_2
Utricularia-Bivalvaria-Nigrescentes	3	Sudano-Zambezian r.; Zambezi p. & Madagascan r.; Eastern Madagascar p., Eastern Asiatic, Indian, Indochinese, Malesian & Northeast Australian rr. (16, 18, 20, 21, 23–28, 60, 70, 84, 90–95, 97–105, 108, 109, 113, 131–133)	Af, Aw, Cfa	V_1, V_2, IV_7
Utricularia-Bivalvaria-Meionula	5	Eastern Asiatic r.; Japan–Korea & Southeastern China pp., Indian, Indochinese, Malesian & Northeast Australian rr. (18, 24, 90–92, 94–96, 98–105, 108, 109, 131–133)	Af, Aw, Cfa	V_1, V_2, IV_7
Utricularia-Polypompholyx-Australes	3	Northeast Australian, Southwest Australian & Neozeylandic rr. (133–135, 148, 151)	Cfb, Csb	III_2, IV_1, IV_7
Utricularia-Bivalvaria-Lloydia	1	Caribbean r.; Central American p., Guyana Highland, Amazonian & Brazilian rr., Guineo-Congolian r., Sudano-Zambezian r.; Zambezi p., Eritreo–Arabian r.; Somali–Ethiopian p., Eastern Asiatic r.; Khasi–Manipur p., Indian r.; Upper Gangetic Plain p. (28, 65–67, 70, 73, 93, 117, 120, 121, 124, 126)	Am, Aw, Bsh, Cwa	V_1–V_3
Utricularia-Polypompholyx-Polypompholyx	2	Southwest Australian r. (133–135)	Cfb, Csb	IV_1
Utricularia-Polypompholyx-Tridentaria	1	Southwest Australian r. (135)	Csb	IV_1
Utricularia-Polypompholyx-Pleiochasia	25	Northeast Australian & Southwest Australian rr. (116, 131–135, 148–150)	Aw, Cfb, Csb	IV_1, IV_7, V_3
Utricularia-Utricularia-Orchidioides	10	Caribbean, Guyana Highland, Amazonian & Andean rr. (117, 118, 120–123, 128, 129)	Af, Am, Aw	V_1–V_3

Utricularia-Utricularia-Iperua	6	Guayana Highland & Brazilian rr. (120, 124, 126, 127)	Af, Am, Aw	V_2
Utricularia-Bivalvaria-Stomoisia	2	North American Atlantic r. and adjacent Canada, Caribbean, Amazonian, Brazilian rr., Guineo-Congolian r.; Upper Guinean p. (15, 29–31, 65, 117, 118, 121, 124)	Af, Am, Aw, Cfb, Dfb	III_8, IV_7, V_1–V_3
Utricularia-Utricularia-Stylotheca	1	Caribbean, Guyana Highland, Amazonian & Brazilian rr. (117, 118, 120, 121, 124)	Af, Am, Aw	V_1–V_3
Utricularia-Utricularia-Choristothecae	2	Guayana Highland r. (120)	Af	V_2
Utricularia-Bivalvaria-Benjaminia	1	Guayana Highland, Amazonian & Brazilian rr. (120, 121, 124, 127)	Af, Am, Aw	V_1–V_3
Utricularia-Bivalvaria-Oligocista	43	Pantropical (18, 21, 23–28, 60, 65–67, 69, 70, 72, 73, 84, 89–109, 113, 116, 117, 120, 121, 124, 126–133, 140)	Af, Am, Aw, Bsh, Cfb, Cwa, Cwb	V_1–V_3
Utricularia-Bivalvaria-Avesicarioides	2	Guineo-Congolian r.; Upper Guinean & Nigeria–Cameroon pp. (65, 66)	Af, Am, Aw	V_1–V_3
Utricularia-Utricularia-Chelidon	1	Guineo-Congolian r.; Nigeria–Cameroon p. (66)	Af, Am, Aw	V_1–V_3
Utricularia-Bivalvaria-Enskide	3	Northeastern Australian r., Malesian r.; Papuan p. (109, 131, 132)	Af, Am, Aw, BSh, Cfa	V_1–V_3
Utricularia-Utricularia-Kamienskia	2	Eastern Asiatic r.; Central & Southeastern Chinese pp. (23, 24)	Cfa	V_2
Utricularia-Bivalvaria-Phyllaria	16	Majority restricted to East Asiatic, Indochinese & Malesian rr., only one species extending to Guineo-Congolian, Usambara–Zululand, Sudano-Zambezian & Indian rr. (21, 23, 25–28, 60, 65–67, 70, 73, 90, 92, 93, 95–98, 100–109)	Af, Am, Aw, Cfa, Cwa	IV_7, V_1–V_3
Utricularia-Utricularia-Oliveria	1	Guineo-Congolian, Usambara–Zululand, Sudano-Zambezian & Madagascan rr. (66, 67, 70, 84)	Af, Am, Aw, Cwa	V_1–V_3
Utricularia-Utricularia-Psyllosperma	10	Madrean r.; Mexican Highland p., Caribbean r.; Central American p., Guyana Highland, Amazonian, Brazilian & Andean rr. (64, 117, 120, 121, 124–127, 129, 140)	Af, Am, Aw	V_1–V_3
Utricularia-Utricularia-Foliosa	13	Caribbean r.; Central American p., Guyana Highland, Amazonian, Brazilian & Andean rr. (117, 118, 120–122, 124–129, 140)	Af, Am, Aw	V_1–V_3
Utricularia-Utricularia-Sprucea	1	Caribbean, Amazonian, Brazilian, Andean & Chile–Patagonian rr. (117, 120, 121, 123)	Af, Am, Aw, Cfa, Cfb	V_1–V_3
Utricularia-Utricularia-Avesicaria	2	Guayana Highland, Amazonian & Brazilian rr. (120, 121, 124)	Af, Am, Aw	V_1–V_3

Utricularia-Utricularia-Mirabiles	2	Guayana Highland r. (120)	Af	V_2
Utricularia-Utricularia-Steyermarkia	3	Guayana Highland r. (120)	Af	V_2
Utricularia-Utricularia-Lecticula	2	North American Atlantic, Caribbean & Guyana Highland rr. (15, 29, 30, 117, 118, 120)	Af, Am, Aw, Cfb, Dfb	III_8, IV_7, V_1–V_3
Utricularia-Utricularia Setiscapella	9	Pantropical & subtropical, but predominantly American (15, 28–30, 39, 65–67, 69, 70, 72, 80, 84, 98, 101–103, 117, 118, 120–129, 131–133, 140)	Af, Am, Aw, Cfa, Cfb, Dfb	V_1–V_3
Utricularia-Utricularia-Nelipus	3	Indochinese, Malesian & Northeast Australian rr. (96, 97, 99, 101, 102, 108, 131–133)	Af, Am, Aw, Cfa	V_1–V_3
Utricularia-Utricularia-Utricularia	38	Almost cosmopolitan (1–18, 20–33, 36, 39–42, 44, 45, 49, 51, 54, 55, ?57, 60, 62–74, 78, 80, 81, 84, 87, 88, 90–109, 113, 115–135, 140, ?148, ?149)	azonal (aquatic)	azonal (aquatic)
Utricularia-Utricularia-Vesiculina	3	North American Atlantic, Caribbean, Guyana Highland, Amazonian, Brazilian, Andean & Chile–Patagonian rr. (15, 29, 30, 117, 118, 120, 121, 124, 127, 129, 140)	Af, Am, Aw, Cfa, Cfb, Dfb	III_8, IV_6–IV_7, V_1–V_3
Utricularia-Utricularia-Biovularia	3	North American Atlantic, Caribbean, Guyana Highland, Amazonian, Brazilian & Andean rr. (29, 30, 117, 118, 120, 121, 124, 129)	Af, Am, Aw, Cfb, Dfb	III_8, IV_7, V_1–V_3
Pinguicula-Isoloba-Isoloba	6	North American Atlantic r.; Atlantic & Gulf Coastal Plain pp. (30, 118)	Cfa	IV_7
Pinguicula-Isoloba-Cardiophyllum	3	Circumboreal r; Atlantic European p. & Mediterranean r; Southwestern Mediterranean, Ligurian–Tyrrhenian, Adriatic & Eastern Mediterranean pp. (2, 39, 43–45)	Csa, Csb, Cfb	III_2, IV_1
Pinguicula-Isoloba-Ampullipalatum	5	Andean r.; Northern Andes, Central Andes, Chile–Patagonian r.; Patagonia & Magellania pp. (128, 129, 139, 141, 142)	Cfb, Cfc, ET	III_1, III_2, V_1, V_2
Pinguicula-Pinguicula-Pinguicula (without P. vulgaris)	21	Circumboreal r.; Pontus Euxinus p., Mediterranean r. (5, 39, 41, 43–45)	Csa	IV_1
P. vulgaris (P.-P.-Pinguicula)	1	Circumboreal, Eastern Asiatic, Rocky Mountain & Mediterranean rr. (1–4, 7–11, 14, 15, 17, 18, 32, 39, 41, 43, 44)	Cfb, Csa, Csb, Cwa, Cwb, Dfb, Dfc, Dfd, Dwb, Dwc	I_4, II_2–II_3, III_2–III_8, III_{11}, IV_1
Pinguicula-Temnoceras-Temnoceras	5	Madrean r.; Mexican Highlands p., Caribbean r.; Central America p. (64, 117)	Bsh, Cwa, Cwb	V_1–V_3
Pinguicula-Temnoceras-Crassifolia	4	Madrean r.; Mexican Highlands p. (64)	Bsh, Cwa, Cwb	V_1–V_3
Pinguicula-Temnoceras-Longitubus	5	Madrean r.; Mexican Highlands p., Caribbean r.; Central America p. (64, 117)	Bsh, Cwa, Cwb	V_1–V_3

Pinguicula-Temnoceras-Microphyllum	7	Madrean r.; Mexican Highlands p. (64)	Bsh, Cwa, Cwb	V_1–V_3
Pinguicula-Temnoceras-Orcheosanthus	13	Madrean r.; Mexican Highlands p., Caribbean r.; Central America p. (64, 117)	Bsh, Cwa, Cwb	V_1–V_3
Pinguicula-Temnoceras-Agnata	4	Madrean r.; Mexican Highlands p. (64)	Bsh, Cwa, Cwb	V_1–V_3
Pinguicula-Temnoceras-Heterophyllum	5	Madrean r.; Mexican Highlands p. (64)	Bsh, Cwa, Cwb	V_1–V_3
Pinguicula-Temnoceras-Homophyllum	18	Madrean r.; Mexican Highlands p., Caribbean r.; Central America & West Indies pp. (64, 117, 118)	Bsh, Cwa, Cwb	V_1–V_3
Pinguicula elongata (P.-Temnoceras-Heterophylliformis)	1	Andean r.; Northern Andes p. (128)	Af	V_1
Pinguicula-Temnoceras-Micranthus	1	Circumboreal & Eastern Asiatic rr., Central Asiatic r.; Tibetan p. (1–3, 8–12, 22, 23, 25, 27, 60)	Cfb, Cwa, Cwb, Dfb, Dfc, Dfd, Dwb, Dwc	I_3, II_2–II_3, III_2–III_8, III_{11}
Pinguicula-Temnoceras-Nana	4	Circumboreal, Eastern Asiatic & Rocky Mountain rr. (1, 8–18, 32)	Dfc, Dfd, Dwb, Dwc, ET	I_3, II_1–II_3, III_8
Genlisea-Tayloria-Tayloria	8	Brazilian r.; Central Brazilian Upland p. (124, 126)	Bsh	V_2
Genlisea-Genlisea-Genlisea	13	Mainly Guyana Highland, Amazonian & Brazilian rr. (117, 118, 120, 121, 123, 124, 126, 127)	Bsh, Aw	V_2
Genlisea-Genlisea-Africanae	9	Guineo-Congolian r., Sudano-Zambezian r.; Zambezian p. (65–67, 70, 72)	Af, Am, Aw	V_1–V_3
Genlisea-Genlisea-Recurvatae	3	Sudano-Zambezian r.; Zambezian p., Madagascan r.; Eastern Madagascan p. (70, 84)	Af, Am, Aw	V_1–V_3
Droseraceae				
Drosera-Regiae-Regiae	1	Cape r. (130)	Csb	IV_1
Drosera-Arcturia-Arcturia	2	Southeast Australian & Tasmanian pp., Neozeylandic r. (133, 134, 148–150)	Cfb	III_2, IV_7
Drosera-Ergaleium-Phycopsis	1	Northeast Australian, Southwest Australian & Neozeylandic rr. (133–135, 148–151)	Cfb, Csb	IV_1, IV_7
Drosera-Ergaleium-Bryastrum	49	Northeast Australian, Southwest Australian (most) & Neozeylandic rr. (133–135, 148–150)	Cfb, Csb	IV_1, IV_7
Drosera-Ergaleium-Meristocaulis	1	Guayana Highland r.; Guyana p. (120)	Af	V_1

Drosera-Ergaleium-Ergaleium	31	Mainly Southwest Australian r., few in Eastern Asiatic, Indochinese, Malesian, Neocaledonian, Northeast Australian & Neozeylandic rr. (18, 21, 23, 24, 26–28, 60, 90–94, 97–99, 104, 106, 108–109, 131–135)	Am, Aw, Cfa, Cfb, Csb, Cwa	IV_1, IV_7, V_2–V_3
Drosera-Ergaleium-Erythrorhiza	12	Northeast Australian (few) & Southwest Australian (most) rr. (133, 135)	Csb	IV_1
Drosera-Ergaleium-Stoloniferae	4	Southwest Australian r. (135)	Csb	IV_1
Drosera-Ergaleium-Coelophylla	1	Northeast Australian & Southwest Australian rr. (133–135)	Cfb, Csb	IV_1, IV_7
Drosera-Ergaleium-Lasiocephala	15	Northeast Australian r. (108, 109, 131, 132)	Aw	V_2–V_4
Drosera-Drosera-Arachnopus	11	Guineo-Congolian, Sudano-Zambezian, Madagascan, Indian, Eastern Asiatic, Indochinese, Malesian & Northeast Australian rr. (18, 21, 24, 65–67, 70, 84, 90–92, 96–100, 103–107, 109, 131–133)	Af, Aw, Cfa	V_1, V_2, IV_7
Drosera-Drosera-Prolifera	3	Northeast Australian r.; Queensland p. (132)	Am	V_2
Drosera-Drosera-Thelocalyx	2	Trop. Asia, Northeast Australian, Amazonian & Brazilian rr., ?Guineo-Congolian r. (18, 21, 24, 28, ?65, 90–92, 94–98, ?99, ?100, ?101, 102–109, 113, 121, 123, 124, 126, 131–133, 136)	Af, Am, Aw	V_1–V_3
Drosera-Drosera-Stelogyne	1	Southwest Australian r. (135)	Csb	IV_1
Drosera-Drosera-Psychophila	2	Chile–Patagonian & Neozeylandic rr. (141, 142, 148–150, 152)	Cfb, Cfc, ET	I_4, III_1, III_2, III_{10}
Drosera-Drosera-Drosera	11	Trop. Africa, especially Sudano-Zambezian r.; Zambesi p. (65–70, 72, 84)	Aw	V_3
	14	Cape r. (130)	Csb	IV_1
	40	Central & South America, mainly Guyana Highland, Amazonian & Brazilian rr. (119–129, 140–142)	Af, Am, Cwb	V_1, V_2
	6	North American Atlantic r.; mainly Atlantic & Gulf Coastal Plain pp. (29–33, 117, 118)	Cfa	IV_7
	3	Circumboreal & Eastern Asiatic rr. (1–18, 21–24, 41, 43, 45, 46, 61, 115)	Cfb, Dfb, Dfc	II, III
	4	Eastern Asiatic, Indochinese, Malesian, Neocaledonian, Northeast Australian & Neozeylandic rr. (18, 21, 24, 97, 103–105, 107–109, 113, 116, 132–134, 148–150)	Af, Cfb, Cwa	III_2, V_1, V_2
Dionaea	1	North American Atlantic r.; Atlantic & Gulf Coastal Plain pp. (30)	Cfa	IV_7
Aldrovanda	1	Widespread in Old World (3, 5, 6, 7, 16, 18, 43, 44, 53, 65, 67, 70–72, 94, 106, 131, 133)	azonal (aquatic)	azonal (aquatic)

Nepenthaceae

Nepenthes-Nepenthes-Nepenthes	15	Eastern Asiatic r.; Khasi–Manipur p., Madagascan, Indian, Malesian & Neocaledonian rr. (28, 84, 89, 90, 107–109, 116)	Af (most), Am, Aw	V_1 (most)–V_3
Nepenthes-Nepenthes-Urceolatae	5	Indochinese, Malesian, Polynesian & Northeast Australian rr. (96–98, 100–105, 107–109, 113, 132)	Af (most), Am, Aw	V_1 (most)–V_2
Nepenthes-Nepenthes-Tentaculatae	9	Malesian r.; Borneo & Celebes pp. (103, 107)	Af	V_1
Nepenthes-Nepenthes-Insignes	12	Malesian r.; Borneo, Philippines, Celebes & Moluccas pp. (103,104,107,108)	Af	V_1
Nepenthes-Nepenthes-Villosae	19	Malesian r.; Borneo, Philippines (103, 104)	Af	V_1–V_2
Nepenthes-Nepenthes-Regiae	48	Malesian r.; Borneo, Philippines, Celebes, Moluccas & Papua pp. (103, 104, 107–109)	Af	V_1–V_2
Nepenthes-Nepenthes-Pyrophytae	23	Indochinese r., Malesian r.; Malaya, Borneo, Sumatra (few) pp. (96, 98, 100–103, 105)	Af (most), Am, Aw	V_1–V_3
Nepenthes-Nepenthes-Montanae	29	Malesian r.; Borneo (few), Sumatra (most) & South Malesia (few) pp. (103, 105, 106)	Af (most), Am, Aw	V_1–V_2

Sarraceniaceae

Heliamphora	23	Guayana Highland r.; Guyana p. (120)	Af	V_1
Darlingtonia	1	Rocky Mountain r.; Vancouver p. (32, ?62)	Csb	III_1
Sarracenia	11	North American Atlantic r.; predominantly in Atlantic & Gulf Coastal Plain pp. (15, 29, 30)	Cfa	IV_7

Byblidaceae

Byblis-Byblis-Anisandra	2	Southwest Australian r. (135)	Csb	IV_1
Byblis-Byblis-Byblis	6	Northeast Australian r.; North Australia & Queensland pp., just reaching nearby New Guinea (108, 131, 132)	Aw	V_2–V_4

Roridulaceae

Roridula	2	Cape r. (130)	Csb	IV_1

Cephalotaceae

Cephalotus	1	Southwest Australian r. (135)	Csb	IV_1

Drosophyllaceae

Drosophyllum	1	westernmost Mediterranean r. (39)	Csb	IV_1

Dioncophyllaceae

| *Triphyophyllum* | 1 | Guineo-Congolian r.; Upper Guinean p. (65) | Af, Am | V_1 |

Carnivorous plants are most abundant and diverse in tropical to subtropical regions of all continents and have a preference for warm to hot, humid to wet climates. In contrast, they tend to be rare or absent in polar ice deserts, in arid to dry climates, or on remote oceanic islands (Table 2.1). The speciose genera of carnivorous plants occupy contrasting ↳

centers of high diversity: *Nepenthes* in tropical Asia (frequently at elevated altitudes), *Drosera* in Australia, *Pinguicula* in Central America and the Mediterranean (predominantly at elevated altitudes), *Genlisea* in tropical South America and Africa, and *Utricularia* in tropical America, Africa, and Australia. More details on the biogeography and distribution of each family and genus are provided in the chapters devoted to each taxon (Chapters 4–10).

2.3 Habitat specificity defines regional distributions

Carnivorous plants do not grow in all habitats, either because they have not yet reached some of them (§2.2) or because they have particular adaptations that allow them to survive in nutrient-poor soils (Darwin 1875). Darwin based his hypothesis that botanical carnivory is an adaptation to nutrient-poor soils on the observation that *Drosera* grows on nutrient-poor soils and the related inference that this habitat specificity is related to poorly developed roots. Thus, the evolution of modified leaves to capture nutrients from insects and other small animals is seen as an alternative to additional investment in roots in nutrient-poor soils (Tilman 1988, Juniper et al. 1989).

2.3.1 Hypotheses concerning co-occurrence of carnivorous and noncarnivorous plants

p. 14 In general, carnivorous plants have weak root systems (e.g., Juniper et al. 1989, Adamec 2005a, Adlassnig et al. 2005b, Brewer et al. 2011), and understanding the benefits of carnivory in part centers around understanding the relative advantages of ↳ plants investing in additional root absorptive area versus investing in carnivory. If increased root allocation and carnivory are simply different ways to accomplish the same goal in nutrient-poor habitats, then carnivorous plants should co-occur with noncarnivorous plants that have either relatively large root systems or have other adaptations for surviving in nutrient-poor soils (e.g., mycorrhizae or *Rhizobia*). Carnivorous plants would not be expected to be at a competitive disadvantage in such habitats, but rather nutrient niche complementarity (Brewer 2003), dispersal limitation, or other stochastic processes (Myers and Harms 2009) would result in their coexistence with noncarnivorous plants. Alternatively if carnivorous and noncarnivorous plants with equally effective adaptations for nutrient-poor soils do not co-occur, then environmental factor(s) other than soil nutrient availability (Givnish et al. 1984, Juniper et al. 1989; Brewer et al. 2011) or interspecific competition may limit the distribution of carnivorous plants.

Juniper et al. (1989) emphasized the role of calcium concentration in the soil, suggesting that most carnivorous plants are "calcifuges" (unable to tolerate conditions related directly or indirectly to high soil or water calcium concentrations) restricted to acidic soils with low nutrient availability. Although calcium toxicity has been demonstrated in a couple of species (Adlassnig et al. 2006), others are associated with high calcium or ultrabasic soils (Adlassnig et al. 2005b, van der Ent et al. 2015). Givnish et al. (1984) and Juniper et al. (1989) also identified that carnivorous plants grow mainly in nutrient-poor habitats that also are wet and unshaded.

Givnish et al. (1984; Chapter 18) explained this pattern using an evolutionary cost/benefit model based on the photosynthetic benefit of carnivory. Light-saturated photosynthesis of leaves of a noncarnivorous shrub is strongly and positively correlated with leaf nitrogen, which in turn requires greater investment of carbon to roots when soil nitrogen is in low supply (Gulmon and Chu 1981). By extension, the increased marginal photosynthetic benefit resulting from increased nutrient capture associated with additional marginal investment in carnivory should decline with increasing availability of substrate nutrients and with decreasing availability of water and light (Givnish et al. 1984; Chapters 17–19). In a review of studies purporting to test the cost/benefit model, Ellison (2006) concluded there were inadequate data to assess the prediction that carnivorous plants should be competitively disadvantaged in dry, shady, or nutrient-rich habitats.

2.3.2 Regional patterns of co-occurrence

To compare regional distributions of carnivorous and noncarnivorous plants, we evaluate the available evidence to test the prediction that terrestrial carnivorous plants are more likely to be associated with wet, unshaded, nutrient-poor habitats. We also address the related prediction that noncarnivorous plants are under-represented in habitats in which carnivorous plants occur. Support for the second prediction would support the cost/benefit model and could imply that carnivorous plants have a competitive advantage in wet, unshaded, nutrient-poor habitats, which would also support the cost/benefit model (Ellison 2006).

Carnivorous plants are more strongly associated with wet habitats than with nutrient-poor habitat in wet pine savannas of southern Mississippi, USA (Brewer et al. 2011). Carnivorous plants and noncarnivorous plants with deep, aerenchymatous roots were more strongly associated with the wettest microsites (Brewer et al. 2011). Variation in soil nutrient availability within the wet savannas was negligible and explained virtually no variation in abundance or occurrence of carnivorous plants (Brewer et al. 2011). Finally, carnivorous plants are disproportionately associated with wet habitats and wetter microsites within wet pine savannas, but these habitats also have some of the highest total plant species richness in the region (Peet and Allard 1993, Palmquist et al. 2014, Noss et al. 2015). This result suggests that the same factors responsible for the general restriction of carnivorous plants to wet, unshaded, nutrient-poor habitats simultaneously are responsible for extraordinarily high plant diversity overall (Peet et al. 2014).

These results suggest that it is important not only to address why carnivorous plants have high habitat specificity but also what allows them to coexist with noncarnivorous plants in the same habitats. Explanations for the absence of carnivorous plants ↳ in other habitats include competitive exclusion or lack of environmental tolerance.

p. 15

Nutrient availability and competitive exclusion.

Both Darwin's hypothesis and the cost/benefit model predict that carnivorous plants will be at a competitive disadvantage in nutrient-rich soils. Numerous studies have examined variation in carnivory investment or variation in performance in relation to substrate nutrient availability (reviews in Juniper et al. 1989, Adamec 1997a, Ellison and Gotelli 2009; Chapters 17–19). Most studies have focused on one or a few carnivorous species grown without competition from noncarnivorous plants, and have found that investment in carnivory decreases with substrate nutrient addition or increased nutrient availability (Adamec 1997a, Ellison 2006: Chapter 17). In some cases, decreased investment in carnivory with increasing substrate nutrient availability is adaptive (Thorén and Karlsson 1998, Zamora et al. 1998, Thorén et al. 2003), but in others increased nutrient deposition reduces both trap production and individual plant fitness (Ellison and Gotelli 2002, Gotelli and Ellison 2002).

These studies do not address the question of competitive disadvantage in nutrient-rich soils (Ellison 2006). A shift in allocation by a carnivorous plant from trap production to increased chlorophyll concentrations in leaves or to leaves with greater surface area is functionally similar to a noncarnivorous plant increasing its leaf-to-shoot ratio as a function of increased substrate nutrient supply (Olff et al. 1990); both can prevent or delay competitive displacement (Dybzinski and Tilman 2007). Demonstration that carnivorous plants are so disadvantaged in nutrient-rich substrates that their distribution would be affected requires data showing that either carnivorous plants are affected more negatively by increased nutrient availability than are noncarnivorous plants; or noncarnivorous plants competitively suppress or exclude carnivorous ones in nutrient-rich substrates.

Although a few investigators have examined competition between carnivorous and noncarnivorous plants (Wilson 1985, Svensson 1995, Brewer 1998a, 1999b, 1999c, 2003), only one has examined soil fertility-related differences in competitive effects (Abbott and Brewer 2016). That study examined the competitive

effects of noncarnivorous plants on *Sarracenia alata* transplanted from its native bog into a productive, nutrient-rich marsh within its dispersal range, but where no carnivorous plants grew. Although the growth rate and survival rate of transplants of pitcher plants were indeed significantly lower in the marsh and in marsh soil than in the bog or bog soil, there was no evidence of a competitive effect in either the bog or the marsh (Figure 2.1). The poor performance of transplants in savanna soil with marsh neighbors intact indicated the potential for competitive exclusion in the marsh, a potential not realized, however, because of the greater importance of the harsh edaphic conditions (i.e., lower redox potential) in marsh soil (Figure 2.1). With but scant data, there is little support for the hypothesis that carnivorous plants are competitively excluded from nutrient-rich habitats. Abiotic stress factors also need to be evaluated to determine why carnivorous plants do not grow in many open and unshaded but nutrient-poor sites.
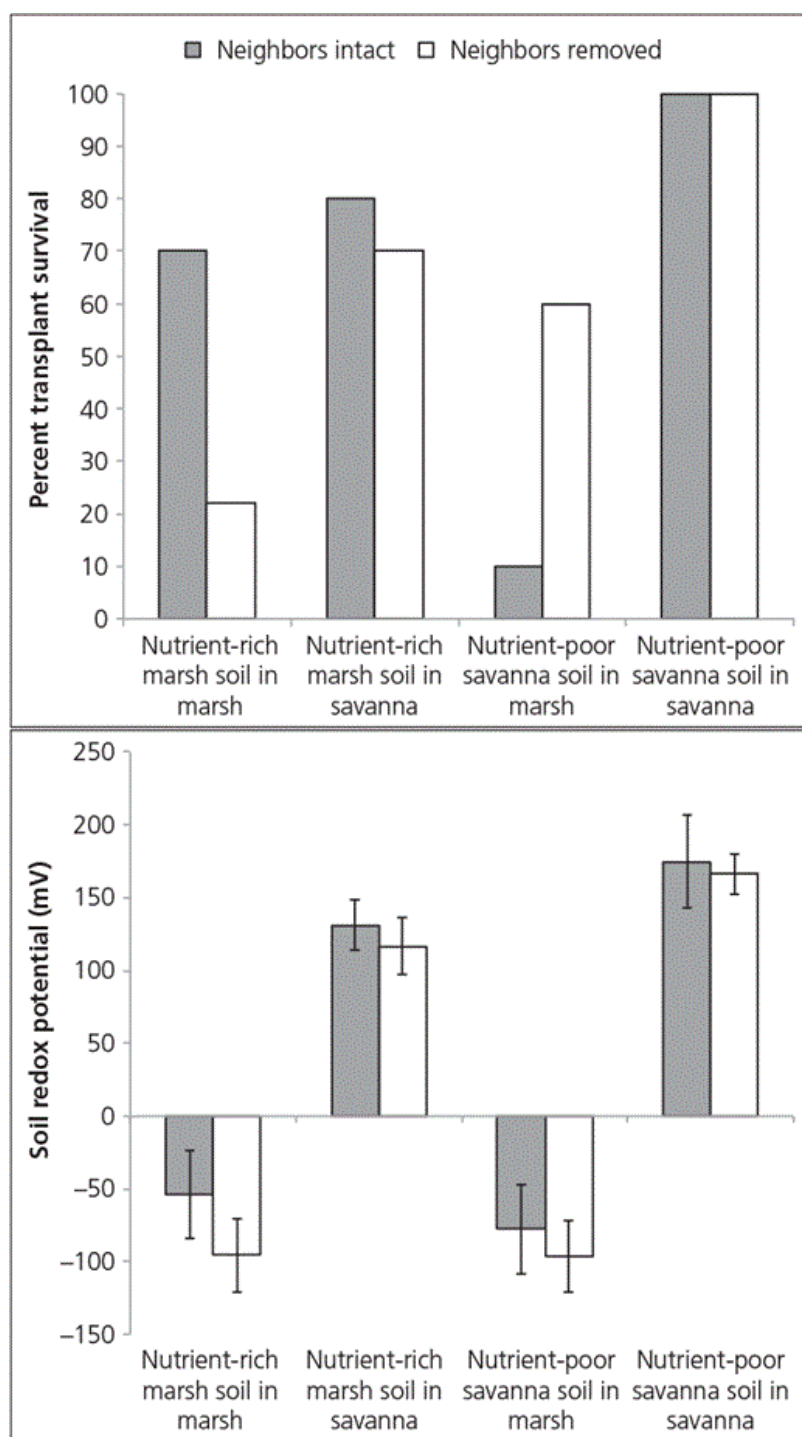
Figure 2.1 Percent survival of transplanted *Sarracenia alata* and soil redox potential (means ± 1 standard error of the mean) as a function of site (marsh, wet savanna), soil (nutrient-rich marsh soil, nutrient-poor savanna soil), and neighbor removal (neighbors intact, neighbors removed).

Data from Abbott and Brewer (2016).

Light.

The cost/benefit model predicts that carnivorous plants are intolerant of shade or are poor competitors for light, and most species are associated with open, herbaceous habitats (Juniper et al. 1989, Givnish 1989). With the possible exception of *Drosophyllum lusitanicum*, which could be considered a dwarf tree, there are no carnivorous trees, and even *D. lusitanicum* grows in sunny sites. Although *Triphyophyllum peltatum* is somewhat shade-tolerant (Juniper et al. 1989), it is carnivorous only during part of its life (Chapter 10). Like *Triphyophyllum*, other carnivorous plants that grow in forested habitats (e.g., *Nepenthes*; Chapter 5), tend to be climbers that rely on trees to get above the tree canopy or stolons to move into gaps or edges to take advantage of increased light availability. *Triphyophyllum* does not require production of carnivorous leaves to make the transition from rosette to liana; nutrient deficiency, not light, appears to trigger the production of carnivorous traps in the field, but the mechanism for the ontogenetic shift remains unknown (Bringmann et al. 2002). In Sierra Leone, *Triphyophyllum* often is found at forest edges and in secondary forests with reduced overstory canopies (Jonathan 1992), a finding that is consistent with a hypothesis of light-triggered investment carnivory.

p. 16 Field studies demonstrating competitiveness as a function of light availability or differential shade tolerance are rare. Zamora et al. (1998) reported reduced performance of *Pinguicula vallisneriifolia* when shaded in the field but they did not examine competition for light. A field competition experiment examining above- versus below-ground competitive effects of neighboring vegetation on *Drosera capillaris* failed to show that shade was the primary factor excluding it from dense woody thickets within a wet pine savanna (Brewer 1999b). However, *D. capillaris* showed increased emergence from a bank of dormant seeds following fire, and this was a response to shade reduction, not fire-mediated changes in the soil (Brewer

p. 17 1999b; Chapter 22). Nevertheless, reduction of above-ground biomass in ↳ woody thickets where the abundance of *D. capillaris* was low had no greater positive effect on seedling emergence than did such reduction in open sedge meadows, where *D. capillaris* was abundant (Brewer 1999b). Growth of adult transplants of *D. capillaris* was lower in woody thickets than in open sedge meadows, but it did not benefit more from a reduction in above-ground biomass in the former than in the latter, suggesting that below-ground competition with woody neighbors was more important than above-ground competition. In sum, support for the hypothesis that carnivorous plants are poor competitors for light remains weak. Although carnivorous plants are rare in shady forests, it seems likely that factors other than light availability play a role in their absence.

Substrate moisture.

Among habitats with similarly nutrient-poor soils, the cost/benefit model predicts that carnivorous plants will be at a disadvantage in drier soils. Noncarnivorous plants can adapt to poor, dry soils (via natural selection or phenotypic plasticity) by increasing allocation to roots. In contrast, if investment in carnivory conflicts with investment in roots, then the reduced benefit-to-cost ratio of investment in carnivory as soil moisture declines puts carnivorous plants at a disadvantage. Demonstrating that this disadvantage is large enough to affect their distributions requires evidence either that carnivorous plants are less tolerant of dry soils or that they cannot compete with noncarnivorous plants for water in drier soils; such evidence is lacking.

As with data on performance in different light environments, support for the soil-moisture hypothesis is inferred from studies of phenotypic plasticity in carnivorous investment and growth responses by individual species in response to substrate moisture supply. Zamora et al. (1998) found that growth of *Pinguicula vallisneriifolia* responded more positively to increased light and prey when water was not limiting, which is consistent with the prediction that carnivory is less beneficial in drier substrates. Some carnivorous plants do grow in seasonally dry habitats (e.g., *Drosera* in Western Australia) and rely on seed or bud

dormancy or water storage to persist through dry periods (Dixon and Pate 1978, Juniper et al. 1989, Luken 2007). How *Drysophyllum lusitanicum* thrives in consistently dry soils along the Mediterranean coast of Iberia and North Africa is unclear but may be related to foliar absorption of sea mist or the production of deep roots (Juniper et al. 1989, Müller and Deil 2001, Correia and Freitas 2002, Adlassnig et al. 2005a, Paniw et al. 2015).

Reduced performance and efficiency of carnivory when water availability is low could indicate greater sensitivity to drought, but a proper test requires comparative studies. Brewer et al. (2011) examined the responses of carnivorous and noncarnivorous plants to experimentally manipulated soil moisture availability in the field (via substrate elevation in a wet savanna) and found that *Drosera* and *Sarracenia* spp. responded more negatively to elevating the substrate (reduced water availability) than did co-occurring noncarnivorous plants. In the same study, structural equation modeling and non-parametric multiplicative regression were used to quantify the potential role that competition played in determining distributions of these species along a moisture gradient from a mesic savanna ecotone to wet savanna. Consistent with the results of the substrate elevation experiment, the statistical models revealed that carnivorous plants were associated more strongly with wetter microsites. Abundances of carnivorous plants were low in the drier, mesic soils, irrespective of the abundance of mesophytic noncarnivorous plants with deep roots. Hence, the greater relative frequency of carnivorous plants in the wetter microsites largely resulted from a lower tolerance by carnivorous plants of drier soils. Hydrophytic noncarnivorous plants with well-developed root aerenchyma, however, also appeared to be intolerant of dry soils. Hence, the lack of tolerance of carnivorous plants to dry soils is comparable to that of obligate wetland noncarnivorous ones, and competition for water did not appear to determine species distributions along a moisture gradient in the savanna.

Although it is generally the case that carnivorous plants are less tolerant of low soil moisture, the cost/benefit model is not the only explanation for why they are more strongly associated with wet habitats than noncarnivorous plants. Many carnivorous plants are obligate wetland species and carnivory could be an alternative to the production of deep roots with well-developed aerenchyma as ↳ a means of maximizing nutrient uptake in hypoxic substrates (Brewer et al. 2011). Instead of producing well-developed root aerenchyma (Seago et al. 2005), carnivorous plants may avoid substrate hypoxia by producing shallow roots (Brewer et al. 2011). To compensate for the reduced access to soil nutrients, carnivorous plants invest in traps to capture nutrients above-ground. One consequence of producing shallow roots (or no roots), however, is extreme sensitivity to dry conditions. Other functional plant types with specialized adaptations for nutrient capture but which do not generally produce shallow roots (e.g., legumes) rarely are restricted to wet habitats (Depuy and Dreyfus 1992, Cornelissen et al. 2003) and in some cases cannot tolerate wet substrates (Saur et al. 2000).

2.4 Mechanisms of coexistence in wet, unshaded, nutrient-poor soils

In the absence of experimental data, Juniper et al. (1989) asserted that carnivorous plants were, generally speaking, poor competitors with noncarnivorous ones, a conclusion at odds with that of Lloyd (1942). Furthermore, contrary to their claim that carnivorous plants typically grow only in close association with other carnivorous plants, *Sphagnum*, and a few orchids (Juniper et al. 1989: 24), some plant communities known to have among the highest local plant species diversity in temperate North America have numerous species of carnivorous and noncarnivorous plants growing together (Peet and Allard 1993, Palmquist et al. 2014, Noss et al. 2015). We suggest that a better understanding of two aspects of coexistence of carnivorous and noncarnivorous plants—niche complementarity and fire-mediated stochasticity—will improve our understanding of general mechanisms of plant species coexistence.

2.4.1 Niche complementarity

Brewer (2003) asked why pitcher plants do not compete with noncarnivorous plants for nutrients. An obvious answer is that the growth and reproduction of the different species are limited by difference nutrients. If the hypothesis that carnivory is an alternative to producing deep roots with well-developed aerenchyma is correct, then these alternative adaptations could represent different nutrient-capture niches. If so, as predicted by the competitive exclusion principle, a lack of niche overlap could permit coexistence. Testing the competitive exclusion principle requires experimental manipulation of the niche of one of the competitors so that it is more similar to that of the other competitors. Although such experimental niche manipulation had been done before by manipulating root co-occurrence (e.g., Berendse 1982), it was easier to manipulate the nutrient-capture niche of *Sarracenia alata.* Because *S. alata* produced shallower and less extensive roots than most of its noncarnivorous neighbors (Brewer 2003), Brewer predicted that it might be a relatively poor competitor for soil resources (including soil nutrients). To test this idea, Brewer (2003) measured how the growth of juvenile *S. alata* individuals responded to being denied prey and to the reduction of neighbors (most of which were noncarnivorous). Prey was excluded from *S. alata* by filling the pitchers with fabric batting; noncarnivorous neighbors were reduced by clipping them to the ground repeatedly over the course of a growing season and by uprooting plants in the immediate vicinity of *S. alata.* Hence, he attempted to reduce both above- and below-ground competition.

The growth of *S. alata* (but not survival) increased dramatically in response to the sustained reduction of the neighbors (Brewer 2003); there was clear evidence of competition. However, the competitive release was not consistent with different nutrient niches (Figure 2.2). *Sarracenia alata* did not show significantly reduced growth when denied prey but when neighbors were left intact. Rather, the negative effect of denying prey was significant only when the neighbors were reduced (Figure 2.2). Brewer (2003) interpreted these results as evidence that *S. alata* increased its demand for prey upon receiving more light, which occurred when he reduced its neighbors. This result is likely an example of adaptive phenotypic plasticity in response to varying light levels, whereby the demand for nutrients (and thus the negative effect of prey exclusion) increases with reduced competition for light (Brewer 2006). Alternatively, competition for prey and light among conspecifics limited prey capture and growth. Prey capture was indeed greater when neighbors were removed (although not on a per pitcher volume basis Brewer [2003]). Gibson (1991a) found reduced prey capture in *Drosera tracyi* when conspecifics were ↳ added. Greater negative effects of pitcher-plant neighbors relative to noncarnivorous ones could promote species coexistence, provided the latter also exhibit density dependence (Chesson 2000).
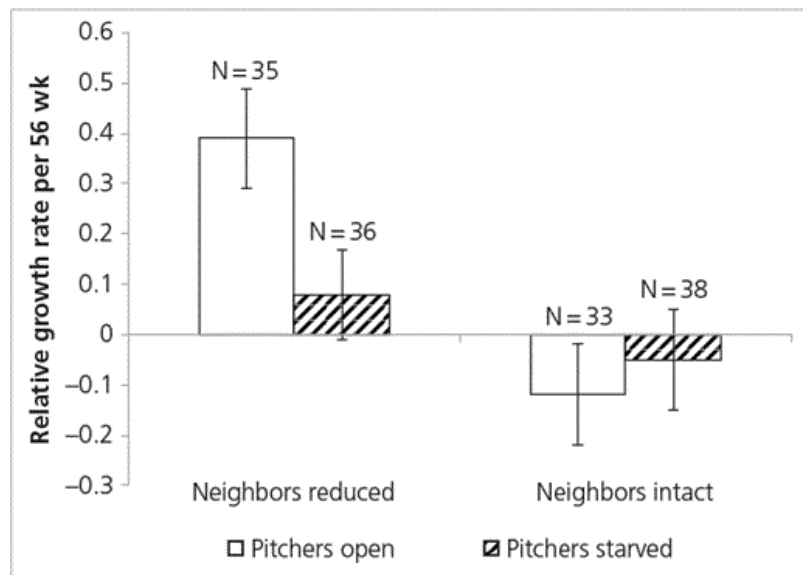
p. 19

Figure 2.2 Effects of neighbor removal and prey exclusion on relative growth rate over a 56-week period. Least-squares means (± 1 SE of the mean) of relative growth rate are adjusted for the initial diameter of the largest pitcher on each target plant.

Figure modified from Brewer (2003) and reproduced with permission from the Ecological Society of America.

2.4.2 Fire-mediated stochasticity

Absent niche complementarity, another possible explanation for coexistence of carnivorous and noncarnivorous herbs is that they compete for resources equally well (or poorly) in wet pine savannas, and repeated fires maintain nonequilibrium populations of each. The reduction of competition by repeated fires benefits both carnivorous plants (Roberts and Oostings 1958, Folkerts 1982, Barker and Williamson 1988, Schnell 2002, Correia and Freitas 2002, Garrido et al. 2003, Kesler et al. 2008, Paniw et al. 2015), and many co-occurring herbaceous noncarnivorous ones (Glitzenstein et al. 2003, 2012, Hinman and Brewer 2007, Palmquist et al. 2014).

To test whether losses of herbaceous species associated with prolonged fire exclusion in wet pine savannas in southern Mississippi were stochastic or deterministic, Brewer analyzed effects of natural additions of competitively dominant trees and associated shrubs on assemblages of carnivorous and noncarnivorous herbs (Brewer 2017). Losses of herb species associated with shrub thickets that develop underneath mature slash pines (*Pinus elliottii*) that established during a period of fire exclusion provides a long-term (up to 65-yr) "natural" competition experiment. The establishment of trees in wet pine savannas reduces dispersal limitation of shrubs but not herbs, nucleating the addition of dominant woody competitors (Hinman et al. 2008). If herb species losses associated with tree and shrub establishment resulted from deterministic processes such that certain herb species consistently were more vulnerable to competitive displacement than were others, then herbaceous beta diversity of areas near trees (i.e., spatial variation in species composition *sensu* Anderson et al. 2011) should be lower than in open areas. Thus, resulting assemblages near trees would be compositionally more similar to one another than would be assemblages in open areas away from trees. One way in which beta diversity could decline near trees is if certain functional groups (e.g., carnivorous herbs) consistently were excluded from the neighborhoods of the dominant woody plants (Figure 2.3). Alternatively, if losses of herb species associated with tree and shrub establishment resulted from local stochastic processes, then herbaceous beta diversity of areas near trees should be similar to that in open areas. Assuming no dispersal or resource niche differences between carnivorous and noncarnivorous herbs (Myers and Harms 2009), competitive displacement of either group would be equally likely (Figure 2.3).

(a) Niche-Based Coexistence of Carnivorous and Non-Carnivorous Herbs
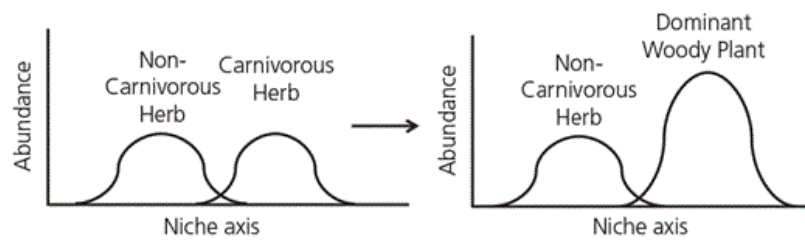
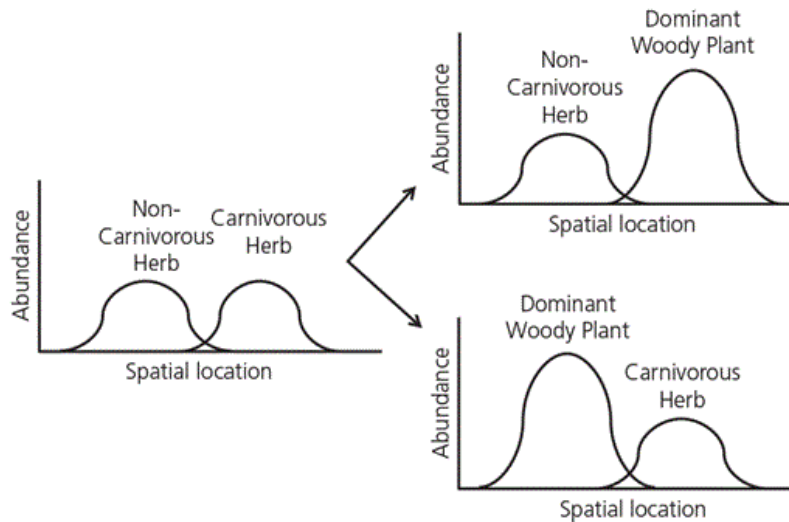**(b) Neutral Coexistence of Carnivorous and Non-Carnivorous Herbs**

Figure 2.3 Predicted patterns of competitive displacement of herbs by dominant woody plants in wet pine savannas when coexistence of carnivorous and noncarnivorous herbs results from either niche differences (**a**) or neutrality and chance (**b**).

Brewer (2017) contrasted alpha and beta diversity of neighborhoods associated with slash pine/shrub thickets to those in open areas away from thickets in each of three wet pine savanna sites in southern Mississippi (Wolf Branch, Sandy Creek, and Little Red Creek) using a permutation–based dispersion ↳ test (Permdisp: M.J. Anderson 2006). To ensure that differences in multivariate dispersion (and thus beta diversity) were not the result simply of differences in alpha diversity (which was significantly lower near slash pine trees than away from them; Brewer 1998b), Brewer calculated Raup–Crick distances using the raupcrick function in the R vegan package (Chase et al. 2011).

In all three savannas, beta diversity did not differ significantly between tree/shrub thickets and open areas away from thickets (Wolf Branch $F_{1,28}$ = 0.019; p = 0.91; Sandy Creek $F_{1,30}$ = 0.43; p = 0.49; Little Red Creek $F_{1,30}$ = 0.72; p = 0.41), and Brewer concluded that trees or associated shrubs stochastically eliminated herb species from their neighborhoods. If this conclusion is true, herbaceous species that coexist in open areas do not differ functionally from one another in ways that affect their ability to compete with the dominant woody species. Hence, we suggest that increases in dominant woody competitors following reductions in fire frequency (Hinman et al. 2008) result in random losses of herbaceous species and that carnivorous herbs are no more or less vulnerable to competitive exclusion than are noncarnivorous herbs. These results do not mean that niche differences were unimportant entirely. Negative feedbacks unrelated to how herbs compete with woody plants could contribute to long–term species coexistence (Adler et al. 2010).

2.5 Future research

A recurring theme throughout much of this chapter is that our understanding of the biogeography and ecology of carnivorous plants requires comparisons with noncarnivorous plants. For whatever reasons, such comparisons are rarely done (Ellison 2006, Brewer et al. 2011), and research in these areas has ↳ focused on phenotypic plasticity of carnivorous effort or have compared differences among carnivorous plant species. Contrasting the drivers of distributions of carnivorous and noncarnivorous plants will improve our understanding of both limits to carnivorous plant distribution and to mechanisms of plant coexistence in diverse assemblages (Figure 2.4).
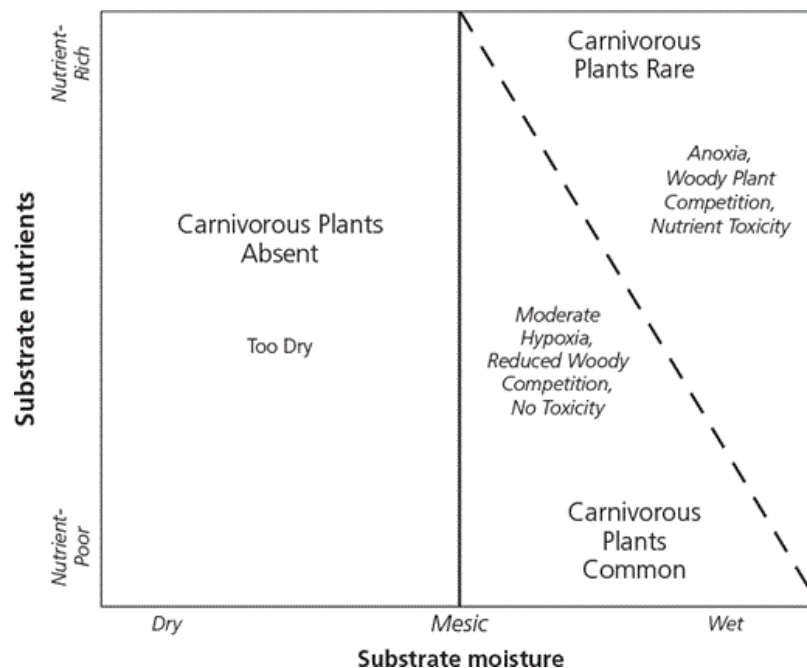

Figure 2.4 Predicted habitat distributions of terrestrial, wetland carnivorous plants and hypothesized environmental factors determining their distributions.

Data available to date suggest that terrestrial carnivorous plants generally are less tolerant of dry soils than are most noncarnivorous ones (Juniper et al. 1989). Exceptions arise in seasonally dry habitats, where carnivorous plants reduce or suspend investment in carnivory during the dry season, persisting as tubers, rhizomes, leafless stipule clusters, or dormant seeds (Chapter 22). *Drosophyllum lusitanicum* is an exception to this general rule, and additional research is needed to determine if it relies on absorption of sea mist through its leaves or absorption of water through deep roots.

In the southeastern United States, the positive association of carnivorous plants with nutrient-poor soils is not as strong as their association with wet soils. This difference between carnivorous plants and noncarnivorous plants may result from carnivorous plants being less tolerant of dry soils than of nutrient-rich soils. Many carnivorous plants are absent from some habitats with nutrient-rich soils, but the reasons why remain unclear. To date, there is no evidence to support the hypothesis that carnivorous plants simply cannot compete with noncarnivorous plants in nutrient-rich soils. More competition experiments are needed (including those that manipulate competition for water with woody plants), and alternative explanations (nutrient toxicity, anoxia intolerance) need to be explored more fully.

Carnivorous herbs are outcompeted by woody plants (and in some cases, large grasses) but do not appear to be less competitive than co-occurring noncarnivorous herbs. Traits that carnivorous and noncarnivorous

herbs share that make them vulnerable to competition from woody plants (e.g., small size, slow growth) deserve greater attention.

Finally, explanations for coexistence of carnivorous and noncarnivorous herbs when woody plants are reduced by fire or other disturbances remain elusive. There is some limited evidence for neutral coexistence of carnivorous and noncarnivorous herbs in wet pine savannas and no evidence yet supports partitioning of nutrient niches. The roles played by intraspecific competition for prey by carnivorous plants and soil-mediated negative feedbacks on noncarnivorous neighbors in promoting coexistence need to be examined.