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Litter spider succession after clear-cutting in a western coniferous forest

J.D. McIver, G.L. Parsons, and A.R. Moldenke[1]

Systematic Entomology Laboratory, Oregon State University, Corvallis, OR 97331, U.S.A.

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The litter spiders of a coniferous forest in western Oregon were trapped in pitfalls to study the effects of, and recovery after, clear-cutting. Traps were placed in old-growth sites (150–450 years) and in clearcuts of three different ages (4–7, 16–19, and 22–31 years); each age-class was represented by sites that differed along a gradient of moisture availability. A total of 8905 individuals were collected over the 2-year study period, comprising 93 species, 54 genera, and 15 families. Visual pursuit hunting spiders dominated clearcuts, while "sit and wait" microweb and trapdoor spiders dominated mature forests. Most of the common forest species were reestablished in the wettest sites by 30 years after clear-cutting; species composition in dry 30-year-old clearcuts more closely resembled the fauna of shrubby wet 16-year-old clearcuts. Microenvironmental conditions and the availability and species composition of prey are the most likely factors behind variation in spider species composition among sites. Prey and microenvironment are in turn largely influenced by canopy closure and litter depth. The use of litter spiders as bioindicators of litter habitat quality and forest recovery is discussed.

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Les effets de la coupe rase sur les araignées de litière des forêts de conifères ont été étudiés dans l'ouest de l'Orégon à l'aide de pièges fosses. Les pièges furent installés dans des sites à peuplements mûrs (150–450 ans) et dans trois coupes rases d'âge différent (4–7, 16–19 et 22–31 ans). À l'intérieur de chaque classe d'âge, les sites furent sélectionnés en fonction d'un gradient d'humidité des sols. Un total de 8905 spécimens représentant 93 espèces, 54 genres et 15 familles furent récoltés durant les 2 années couvertes par l'étude. Ce sont les araignées chassant par poursuite visuelle qui dominaient les coupes rases tandis que les araignées pratiquant le piégeage dominaient les forêts mûres. La majorité des espèces forestières les plus communes étaient réinstallées dans les sites hydriques environ 30 ans après coupe rase. La composition en espèces des coupes rases de 30 ans à site xérique se rapprochait le plus de celle des coupes rases de 16 ans à site hydrique et à dominance arbustive. Les conditions micro-environnementales et la disponibilité de même que la composition spécifique en proie sont vraisemblablement les facteurs les plus importants après les variations de composition spécifique d'araignées entre les sites. En contre-partie, les proies et les conditions micro-environnementales sont fortement influencées par la fermeture du couvert et l'épaisseur de la litière. L'utilisation des araignées de litière en tant que bio-indicateur de reconstitution forestière et de qualité d'habitat est traitée.

[Traduit par la rédaction]

Introduction

Litter arthropods play fundamental roles in forest decomposition (Wallwork 1970; Lohm and Persson 1977; Swift *et al.* 1979; Anderson *et al.* 1985a; Spence 1985; Cromack *et al.* 1988; Edwards *et al.* 1988; Shaw *et al.* 1991). Oribatid mites, springtails, and millipedes accelerate decomposition directly through fungivory (Sutherland and Fortin 1968; Wiggins and Curl 1979; Newell 1980; Bengston and Rungren 1983), by exposing litter surface to microbes (Seastedt 1984; Anderson *et al.* 1985b), and by transporting inoculum (Visser 1985). Predaceous arthropods such as spiders prey upon decomposers, regulating their populations (Clarke and Grant 1968) and contributing high quality detritus for further decomposition. The extent to which litter arthropod species compositions are influenced by the more common land-use practices may therefore be of interest to forest managers. The purpose of this paper is to describe the changes that occur in the litter spider fauna of a western coniferous forest in the first 30 years after clear-cutting. It is part of a larger study of all arthropod taxa inhabiting the coniferous forest litter and soils of the H.J. Andrews Experimental Forest in western Oregon.

Litter spiders are ideal organisms for understanding the effect of clear-cutting on the forest ecosystem. First, along

with carabid beetles and ants, spiders are the most conspicuous group of arthropod predators in the litter environment of many western coniferous forests (Parsons *et al.* 1991). Spiders represent a large percentage of predator biomass in other temperate forests as well (Moulder and Reichle 1972; Petersen and Luxton 1982) and are known to be capable of regulating populations of soil arthropods (Clarke and Grant 1968). Second, spider species can be placed into functional groups called guilds, which reflect habitat and prey preferences. The guild composition of a spider community can thus be used to make inferences on habitat quality, with respect to both microenvironmental and biotic features (Uetz 1991). Finally, spiders are relatively easy to sample and identify, making them potentially useful as indicator organisms.

This research has two primary objectives: (*i*) to identify the litter spider fauna of mature and old-growth stands in a western coniferous forest; (*ii*) to compare the fauna of mature stands with the fauna of recently clear-cut sites, over a variety of moisture regimes. Both litter spider species composition and guild structure will be examined over succession and moisture gradients.

Site description

Research was carried out between June 1982 and May 1984 in the H.J. Andrews Experimental Forest (HJA), near Blue River, western Oregon (122°09′46″W, 44°13′30″N). The HJA is one of 17 long-term ecological research sites supported by the National

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[1]Author to whom all correspondence should be addressed.

FIG. 1. Site information and sampling protocol.

Clearcut Age (years) — Site Number

Moisture	HB	SH	TR	OG	Series	Sampling
DRY	1: X (2)	2: 19	3: 22	4: 200	Psme/Hodi	
	5: 4	6: 19	7: 28	8: 200	Psme-Tshe/Coco	12 TRAPS per SITE
MOISTURE	9: 7	10: 16	11: 31	12: 200	Tshe/Cach	X
	13: 7	14: 16	15: 31	16: 200	Tshe/Rhma/Gash	8 SEASONS
	17: 7	18: 16	19: 31	20: 200	Tshe/Rhma/Bene	JUNE 1982 / AUG. 1982
	21: 7	22: 16	23: 31	24: 200	Tshe/Acci/Pomu	OCT. 1982 / APR. 1983
	25: 3	26: X	27: 19	28: 200	Tshe/Pomu	JUNE 1983 / AUG. 1983
WET	29: X	30: 16	31: 31	32: 200	Tshe/Pomu-Oxor	OCT. 1983 / APR. 1984

SITE INFORMATION — SAMPLING

⟵ SUCCESSION ➤

FIG. 1. Site information and sampling protocol. Dominant plant species of each site series along the moisture gradient: *Psme*, *Pseudotsuga menziesii*; *Tshe*, *Tsuga heterophylla*; *Hodi*, *Holodiscus discolor*; *Coco*, *Corylus cornutus*; *Cach*, *Castanopsis chrysophylla*; *Gash*, *Gaultheria shallon*; *Bene*, *Berberis nervosa*; *Acci*, *Acer circinatum*; *Pomu*, *Polystichum munitum*; *Oxor*, *Oxalis oregana*; *Rhma*, *Rhododendron macrophyllum*. HB, herb stage; SH, shrub stage; TR, tree stage; OG, old growth. Sites 1, 26 and 29 were not found on H.J. Andrews Experimental Forest at the time of study.

Science Foundation and is representative of northwest coniferous forest habitats. The HJA formerly served as a major biome site for the International Biological Program.

Elevations in the HJA range from 400 to 1600 m, and the topography is mature and well dissected with slopes averaging >50% (Rothacher *et al.* 1967). Climatic conditions are maritime, with mild wet winters and warm dry summers. The weather during the study period was typical of the climate, with mean monthly temperatures ranging from 2°C in January 1982 to 21°C in July 1984. Annual precipitation ranged from 220 cm in 1982 to 260 cm in 1983, with most precipitation falling from October to April as cool rain or snow.

Two distinct vegetational zones are recognized in the HJA, based on the plant classification of Dyrness *et al.* (1974). The present study took place within the low-elevation zone (500–950 m), characterized by a climax community dominated by western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). Based on understory plant species composition data, Dyrness *et al.* (1974) identified 11 climax associations within this zone, differing primarily in slope face, soil characteristics, and distribution of moisture (these are standard designations used by silviculturists throughout the region). The driest sites are characterized by an association of Douglas-fir and *Holodiscus discolor* (ocean-spray), while the wettest sites feature an association of western hemlock, *Polystichum munitum* (sword fern), and *Oxalis oregana* (wood-sorrel) (Fig. 1).

Materials and methods

To examine quantitatively the relation between litter spider species composition and successional stage, we placed pitfall traps in a total of 29 sites within the low-elevation zone (Fig. 1). The successional gradient was sampled by placing traps in the old-growth examples of each association, as well as in clearcuts of three different age-classes: 3- to 7-year-old herb-dominated clearcuts (HB), 16- to 19-year-old shrub-dominated clearcuts (SH), and 22- to 31-year-old tree-dominated clearcuts (TR). Within each age-class, traps were placed in eight sites that differed in presumed moisture availability, following the

classification of Dyrness *et al.* (1974). Of the 32 possible combinations of sites, we were able to find examples in the HJA Forest of 29 (only *Pseudotsuga menziesii / Holodiscus discolor* (HB), site 1; *Tsuga heterophylla / Polystichum munitum* (SH), site 26; *Tsuga heterophylla / Polystichum munitum – Oxalis oregona* (TR), site 29 were not represented). Prior to the initiation of sampling in May 1982, each site was rated on a subjective five-point scale with respect to the degree of canopy closure (1, open; 3, partially closed; 5, closed canopy) and the extent of litter development (1, bare ground; 2, ground patchily covered with litter <1 cm deep; 3, ground evenly covered with litter ca. 1 cm deep; 4, ground evenly covered with litter 1–2.5 cm deep; 5, ground evenly covered with litter >5 cm deep).

Within each of the 29 sites, 12 pitfall traps were established in May 1982. Each trap consisted of a 1-gal (3.8-L) plastic container (diameter = 15 cm; height = 18 cm) buried so that the lip was flush with the ground surface. An aluminum funnel 12 cm in height and 14.5 cm in diameter was then placed neck down so that the upper edge was flush with the top of the plastic container. At the neck of the funnel we attached a sampling cup half filled with ethylene glycol. Traps were placed in convex microtopography and covered by a supported roof to minimize rainwater dilution of the ethylene glycol. At the end of each sampling period, cups were removed and labelled, and traps were closed by pressing the particleboard roof down over the trap opening and securing it to the ground with 20-penny nails.

Traps were located at least 5 m apart and at least 25 m from the nearest habitat edge. Since each site was to some degree heterogeneous in microhabitat type, the 12 traps were situated so as to maximize the coverage of within-site variability. Catches from each set of 12 traps were then combined to provide the species composition and relative abundance data for each site.

Traps were opened for 3 weeks on eight occasions over the 2-year study period: 26 June – 18 July 1982, 28 August – 19 September 1982, 18 October – 9 November 1982, 13 April – 4 May 1983, 16 June – 7 July 1983, 23 August – 14 September 1983, 18 October – 9 November 1983, and 18 April – 10 May 1984. No samples were taken from late autumn to early spring owing to snow accumulation. With this sampling plan, we collected a total of 2784 pitfall trap samples, representing eight moisture regimes, four successional stages, and eight seasonal sampling intervals. Individual spiders were sorted out, identified to species, and counted. Most immatures could be assigned to species by association, although very young individuals and some dwarf spiders could not be confidently assigned and were excluded from quantitative analysis.

Pitfall trap data are analyzed and presented in two different ways: (*i*) by a standard guild composition analysis; and (*ii*) with the use of detrended correspondence analysis (DCA), an ecological ordination technique developed by Hill (1979). Data are interpreted with the understanding that pitfall trap catches are better estimates of activity rather than density; therefore no statements about absolute abundance *per se* will be made. It is also expected that species will vary in their tendency to be captured, but we assume that distribution patterns will be unaffected by this bias. Support for this assumption is provided by litter samples taken at the same sites over the course of the study: both Micryphantidae and Linyphiidae show similar distribution patterns for both pitfall and litter sample collections (J.D. McIver, G.L. Parsons, and A.R. Moldenke, personal observation).

To assess the extent to which guild composition corresponded to the moisture and succession gradients, the 36 most frequently captured species were assigned to guilds, based on their hunting techniques. Species catches per site were then combined based on guild membership (see Post and Reichert 1977), and guild catches were presented by histogram. Guild analysis can be especially useful in studies that focus on spiders as indicator species, because of the typically close correspondence between hunting technique and features of habitat quality.

Like other ordination techniques, DCA offers the potential for discovering subtle patterns of variation and can identify more than one critical factor associated with species distribution patterns. In

Schizocosa mccooki

FIG. 2. Pitfall trap catch of *Schizocosa mccooki* for each of eight sampling periods (June 1982 – April 1984) and for all periods combined (TOTAL). Center of distribution (*) is the mean position along moisture and successional gradients. For plant species abbreviations, see Fig. 1 caption.
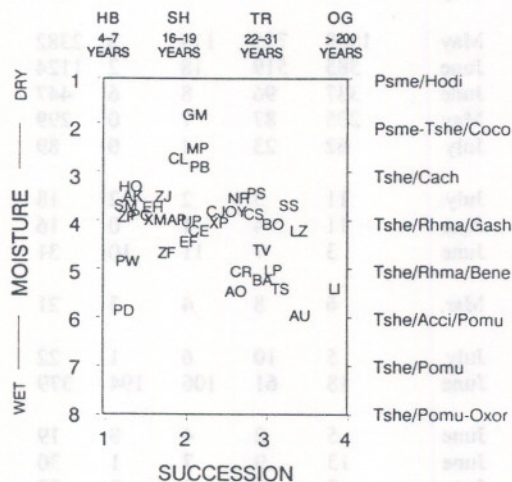

FIG. 3. Centers of distribution for the 36 most common species of litter spiders collected by pitfall trapping. For spider species abbreviations, see Table 1.

particular, factors other than succession and moisture may be associated with litter spider distribution patterns in the HJA; these may be undetectable by simpler techniques. DCA is superior to other ordination techniques because it corrects for distortion problems common to other reciprocal averaging procedures (Gauch 1982) and assigns sample scores that more accurately reflect equivalent differences in species composition (Hill and Gauch 1980). For the present study, we ran DCA on a matrix of the 36 most frequently captured species in 232 sites (29 sites sampled during 8 seasons). Data are represented graphically and interpreted within the context of the known biology of each species.

Results

A total of 8905 litter spiders were collected during the 2-year study period, representing 93 species, 54 genera, and 15 families. Most species were uncommon or rare: 57 species (61%) were represented by fewer than 15 individuals, or 4.0% (354/8905) of the total sampled abundance.

The 36 most frequently captured species (total abundance > 17 individuals) represented 28 genera and 11 families, and 96.0% (8551/8905) of the total sampled abundance (Table 1). Trap catches were highest in the herb-dominated clearcuts (3–7 years old), with an average catch of 559 individuals per site. Average trap catch declined steadily with clearcut age, to 166 per site in tree-dominated clearcuts (22–31 years old). Much of the difference in catch among sites is due to the abundance of four species of wolf spiders in new clearcuts: 81% of the total catch in 3- to 7-year-old clearcuts were wolf spiders, or 32% of the entire catch of common species (2717/8551).

Most species exhibited characteristic patterns of distribution among sites and among seasons. The wolf spider *Schizocosa mccooki*, for example, was associated primarily with herb- and shrub-dominated clearcuts, and intermediate on the moisture gradient in June and July (Fig. 2, top). If the effect of season is removed, the among-site catch distribution of *Schizocosa mccooki* can be further reduced to two index values, the coordinates of its mean position along the successional (X) and moisture (Y) gradients, which we designate as its center of distribution (Fig. 2, bottom). When index values for all 36 common species are plotted together, their centers of distribution can be viewed relative to one another and to the sampling design (Fig. 3). With this method, it is clear that

TABLE 1. The 36 most common litter spider species collected by pitfall trapping, June 1982 – April 1984 at H.J. Andrews Experimental Forest, western Oregon

Family and species	Abbreviation*	Guild†	Estimated reproductive time‡	HB	SH	TR	OG	Total
Agelenidae								
Blabomma oregonensis Chamb. & Ivie	BO	FW	Aug.	3	5	45	21	74
Calymmaria emertoni (Simon)	CE	FW	Aug.	32	36	19	23	110
Cicurina jonesi Chamb. & Ivie	CJ	FW	Feb.	32	25	28	44	129
Cybaeus reticulatus Simon	CR	FW	Aug.	164	312	443	382	1301
Amaurobiidae								
Callobius severus (Simon)	CS	HB	June	5	5	10	14	34
Antrodiaetidae								
Antrodiaetus occultus Coyle	AO	TR	Sept.	16	91	33	66	206
Antrodiaetus pacificus (Simon)	AP	TR	Aug.	54	60	31	13	158
Antrodiaetus pugnax (Chamberlin)	AU	TR	Aug.	6	6	46	87	145
Clubionidae								
Castianeira longipalpa (Hentz)	CL	DR	June	11	30	6	2	49
Phrurotimpus borealis (Emerton)	PB	DR	June	27	102	67	6	202
Gnaphosidae								
Gnaphosa muscorum (Koch)	GM	NR	Aug.	3	11	7	0	21
Micaria pulicaria (Sundevall)	MP	DR	July	1	19	6	0	26
Zelotes fratris Chamberlin	ZF	NR	May	32	37	12	4	85
Zelotes josephine Platnick & Shad.	ZJ	NR	May	84	115	30	4	233
Zelotes puritanus Chamberlin	ZP	NR	May	26	18	5	0	49
Linyphiidae								
Bathyphantes alameda Ivie	BA	SW	June	4	7	15	17	43
Lepthyphantes zelatus Zorsch	LZ	SW	Mar.	0	1	13	12	26
Lepthyphantes zibus Zorsch	LI	SW	Mar.	0	0	6	36	42
Linyphantes pualla Chamb. & Ivie	LP	SW	Mar.	46	87	159	283	575
Pelecopsis sculptum (Emerton)	PS	SW	Aug.	1	10	5	11	27
Scironis sima Chamberlin	SS	SW	Mar.	1	4	19	21	45
Tachygyna vancouverana Chamb. & Ivie	TV	SW	May	9	9	25	31	74
Lycosidae								
Alopecosa kochi (Keyserling)	AK	DP	May	1528	735	114	5	2382
Pardosa californica Keyserling	PC	DP	June	585	519	18	2	1124
Pardosa dorsalis Banks	PD	DP	June	337	96	8	6	447
Pardosa wyuta Gertsch	PW	DP	May	205	87	7	0	299
Schizocosa mccooki (Montgomery)	SM	DP	July	62	23	4	0	89
Salticidae								
Evarcha hoyi (Peck. & Peck.)	EH	DS	July	11	3	2	2	18
Habronattus oregonensis (Peck. & Peck.)	HO	DS	June	11	4	1	0	16
Neon reticulatus Blackwell	NR	DS	June	3	7	11	10	31
Telemidae								
Usofila pacifica Banks	UP	SL	Mar.	6	8	4	3	21
Theridiidae								
Euryopis formosa Banks	EF	SL	July	5	10	6	1	22
Theridion sexpunctatum Emerton	TS	SL	June	18	61	106	194	379
Thomisidae								
Ozyptila yosemitica Schick	OY	DA	June	5	2	4	8	19
Xysticus montanensis Keyserling	XM	DA	June	13	9	7	1	30
Xysticus pretiosus Gertsch	XP	DA	June	7	2	3	8	20
Total individuals caught				3353	2556	1325	1317	8551
Average individuals caught per site				559	365	166	165	294

*The first letters of the genus and specific epithet.
†FW, funnel web; HB, hackled band; TR, trapdoor; DR, diurnal running; NR, nocturnal running; SW, sheet line weaver; DP, diurnal pursuit; DS, diurnal stalk; SL, scattered line; DA, diurnal ambush.
‡Based on peak adult activity.
§HB, 3- to 7-year-old herb-dominated clearcuts; SH, 16- to 19-year-old shrub-dominated clearcuts; TR, 22- to 31-year-old tree-dominated clearcuts; OG, old growth.

species can be arranged linearly along both the succession and moisture gradients, although the relative importance of the two gradients, as well as the significance of seasonality, cannot be deduced with this analysis alone.

When the 36 common litter spider species are ordinated with DCA, the position of each species along the first axis closely corresponds to their catch distributions relative to successional age (Fig. 4; $r^2 = 0.89$). Early successional
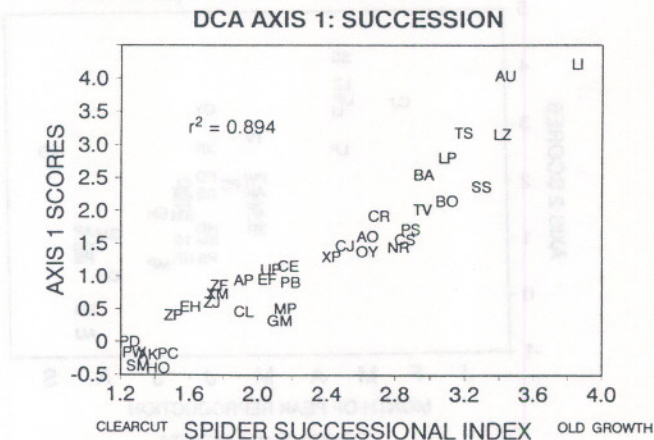
DCA AXIS 1: SUCCESSION

FIG. 4. Correspondence between DCA axis 1 species scores and litter spider successional index (mean position of each species along successional gradient (Fig. 3); see Table 1 for species acronyms).
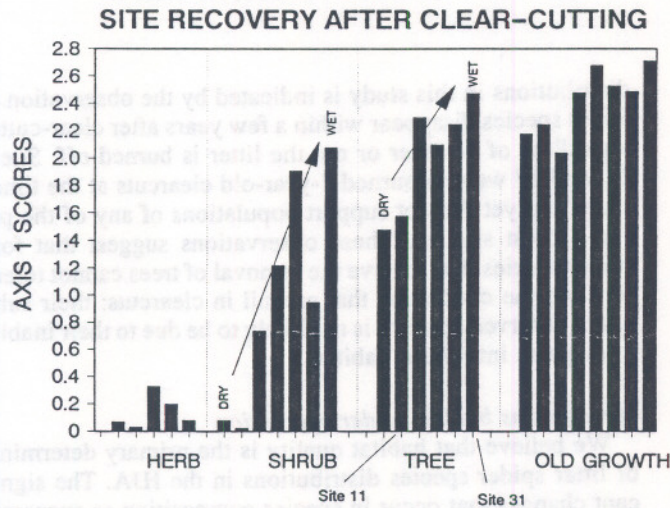
SITE RECOVERY AFTER CLEAR–CUTTING

FIG. 5. DCA axis 1 scores for herb (3- to 7-year-old clearcuts), shrub (16- to 19-year-old clearcuts), tree (28- to 31-year-old clearcuts; tree sites <23 years postcut were omitted) and old-growth sites, for eight seasons combined. Within each successional stage, sites are ordered from dry to wet, based on the plant species characterization of Dyrness, *et al.* (1974).

species like *Schizocosa mccooki*, with their relatively low successional index values, are assigned low axis 1 scores, while forest species like the sheet-web spinner *Lepthyphantes zibus*, with their relatively high successional index values, are assigned high axis 1 scores. The ordination of sites shows a similar pattern, reflecting a high eigenvalue of 0.692, a measure of the percent correspondence between sites and species. Site scores increase by an order of magnitude from 0–0.2 in herb-dominated clearcuts to above 2.0 in the old-growth sites (Fig. 5).

The prime importance of the successional gradient is clearly represented by changes in litter spider guild composition, from a dominance of diurnal pursuit hunters in 3- to 7-year-old clearcuts to a dominance of sheet-web, funnel-web, and trapdoor spiders in 30-year-old clearcuts and old-growth sites (Fig. 6). Nocturnal running spiders occur in clearcuts of all ages, but disappear along with diurnal pursuit hunters in old-growth sites.
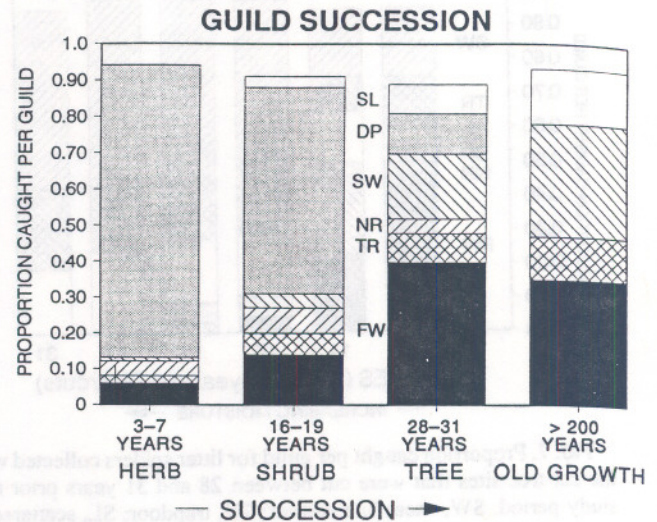
GUILD SUCCESSION

FIG. 6. Proportion caught per guild for litter spiders collected in 3- to 7-year-old clearcuts (herb sites), 16- to 19-year-old clearcuts (shrub sites), 28- to 31-year-old clearcuts (tree sites), and >200-year-old old-growth sites. SL, scattered line weaver; DP, diurnal pursuit; SW, sheet line weaver; NR, nocturnal running; TR, trapdoor; FW, funnel web weaver.

DCA axis 1 also reflects the influence of moisture, especially in the intermediate-aged shrub and tree sites (Fig. 5). Dry sites show systematically lower axis 1 scores for each age-class, indicating that spider fauna recovery depends to some degree on moisture: dry 30-year-old clearcuts are more similar to 16- to 19-year-old clearcuts than to old-growth sites. Variability among site scores in the 30-year age-class is clearly reflected in litter spider guild composition (Fig. 7). For example, dry 30-year-old clearcut site 11 has an axis 1 score of only 1.5 (see Fig. 5), and a fairly even abundance of each of six guilds is represented there. On the other hand, wet 30-year-old clearcut site 31 has the highest axis score of any 30-year-old clearcut (2.45), but is represented by only three guilds. Diurnal and nocturnal running spiders, common in site 11, were not found in site 31. The influence of moisture on litter spider distributions is most likely due to its concomitant effect on plant growth: canopy closure and litter development indices were significantly correlated with 31-year site scores of axis 1 (canopy closure $r^2 = 0.75$; litter development $r^2 = 0.72$). After 28–31 years, the vegetation in sites 7 and 11 had not succeeded far enough to eliminate open-ground clearcut spiders or to encourage the sheet-web and trapdoor spiders so typical of more mature forests.

The second axis of the ordination was primarily an expression of seasonality, with axis 2 scores correlated with time of reproduction (Fig. 8). This interpretation stems from the assumption that the time of peak adult activity is closely related to the time of reproduction; since adults of most species were typically much more readily caught than juveniles, trap catch variation over each year therefore reflects variation in time of reproduction. Winter and early spring reproducers (the sheet-web spiders *Scironis sima*, *Linyphantes pualla*, and *Lepthyphantes zebus*; and the funnel-spider, *Cicurina jonesi*) were assigned high second axis scores, summer reproducers (many of the wolf, running, and crab spiders) had intermediate scores, while fall reproducers (trapdoor spiders, some funnel-web spiders) typically had the lowest scores.
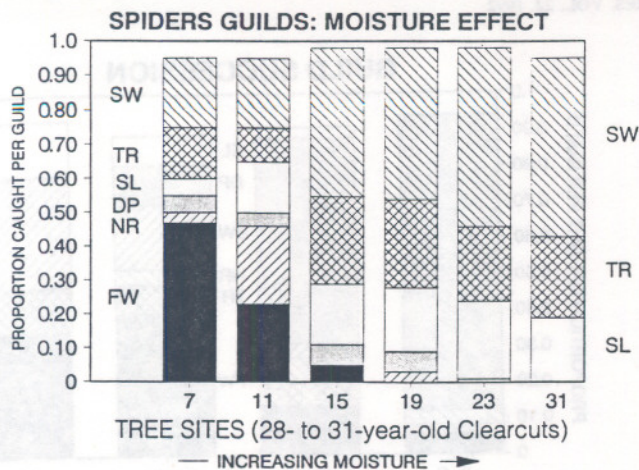
FIG. 7. Proportion caught per guild for litter spiders collected within the six tree sites that were cut between 28 and 31 years prior to the study period. SW, sheet line weaver; TR, trapdoor; SL, scattered line weaver; DP, diurnal pursuit; NR, nocturnal running; FW, funnel web.
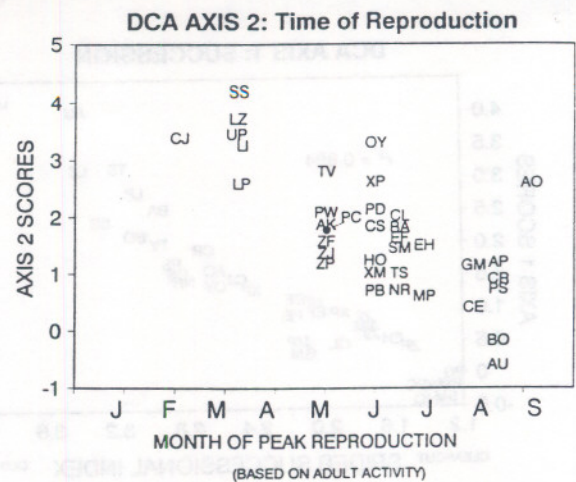

FIG. 8. Correspondence between DCA axis 2 species scores and month of peak reproduction for 36 litter spider species. Estimates of reproductive times are based on the time of peak adult activity. For identity of spider species abbreviations, see Table 1.

When species scores for the first two axes are viewed simultaneously, the interaction between the two most important descriptors of the variation in litter spider species composition are portrayed (Fig. 9). On axis 1 the species are arranged primarily on the basis of their position along the successional and to a lesser extent the moisture gradient, while axis 2 orders the species on the basis of reproductive time. Interestingly, most of the typical clearcut species have intermediate axis 2 scores, owing to reproduction in the dry summer months, while the species typical of more forested habitats have both high and low scores, reflecting reproductive times covering a wide range of seasonal moisture regimes.

Axes 3 and 4 of the ordination exhibited no interpretable patterns of association between sites and species: among-site variation in litter spider catch in this study is due principally to successional stage, followed by moisture and reproductive time.

Discussion

Dispersal and litter spider distributions

Patterns of litter spider species distributions in HJA could be explained either by differences among species in dispersal ability or by differences in response to habitat quality. Many of the wandering spiders typical of clearcuts are known to be excellent dispersers: both wolf spiders and gnaphosids balloon readily as first or second instars (Gertsch 1979). This tendency must in part explain their appearance in early successional habitats: three of the most common HJA clearcut species (*Alopecosa kochi*, *Schizocosa mccooki*, *Zelotes fratris*) are also common ground spiders in commercial peppermint fields of western Oregon (McIver and Belnavis 1986). However, ballooning is a documented mode of dispersal utilized by many taxonomically unrelated spiders, including many of the species found in old-growth and mature forest litter of the HJA (Greenstone *et al.* 1987). In addition, forest-dwelling trapdoor spiders wander considerably as adult males, suggesting that it is not the lack of dispersal ability that limits their distribution within the HJA. On the other hand, the importance of habitat conditions in explaining litter spider

distributions in this study is indicated by the observation that forest species disappear within a few years after clear-cutting, regardless of whether or not the litter is burned off. Sites 9, 13, and 17 were unburned 7-year-old clearcuts at the time of study and yet did not support populations of any of the principal forest species. These observations suggest that forest spider species that survive the removal of trees cannot tolerate for long the conditions that prevail in clearcuts: their subsequent observed absence is not likely to be due to their inability to disperse into these habitats.

Mechanisms behind spider succession

We believe that habitat quality is the primary determinant of litter spider species distributions in the HJA. The significant changes that occur in species composition as succession proceeds can be placed in perspective by describing the difference in the habitat of the ground surface between an old-growth and a clearcut site. Three features that appear to be most closely associated with the variation in litter spider species composition among sites are canopy closure, litter development, and prey availability.

The presence of a closed forest canopy has major influences on microenvironmental conditions at the forest floor. The habitat at ground level under a closed canopy is characterized by more constant microenvironmental conditions relative to a clearcut (Jiquan 1990). Light, humidity, temperature, and wind all fluctuate with less amplitude in the forest environment, allowing for the colonization and persistence of ground surface species that have limited tolerance for environmental extremes. When the trees are removed by clear-cutting, the ground surface habitat is exposed to the wider range of fluctuations in macroenvironmental conditions typical of the climatic region. It is likely that the majority of the common litter spider species in the HJA are active from April through November, and hence the hot dry summer months would present a critical problem in exposed habitats. Species sensitive to these extreme fluctuations would be unable to persist and would be replaced by more tolerant species characteristic of exposed open places.

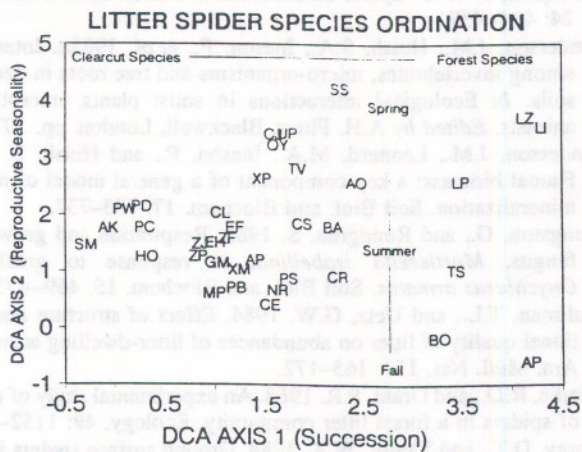## LITTER SPIDER SPECIES ORDINATION

FIG. 9. DCA scores for litter spider species, axes 1 and 2. For species abbreviations, see Table 1.

Other studies have documented similar patterns in ground spider distributions along gradients that differ in the degree of canopy closure. Lowrie (1948) described ground spider species composition along a gradient from dune to forest in the Chicago area. He listed wolf spiders and other non web building wandering spiders as dominant in the open dunes habitat, while dwarf spiders and araneids (orb-web spiders) were dominant in the forest habitat. Huhta (1971) reported a similar trend during early succession in a Finnish coniferous forest, with forest species eliminated after clear-cutting and replaced by wandering spiders for the first 7 years postcut.

It is not possible to distinguish at the present time whether litter spiders respond directly to changes in moisture availability, or whether they respond to the moisture environment that is influenced by canopy closure. No doubt both mechanisms are to some extent responsible for observed patterns of distribution. Almquist (1971) showed experimentally that dune-inhabiting spiders had a significantly higher resistance to desiccation than forest-inhabiting species from the same geographic region, and that both temperature and moisture regimes were correlated with vegetative cover (Almquist 1973). Vollmer and MacMahon (1974) also reported a correlation between resistance to desiccation and habitat, and further suggested that behavior is closely tied to habitat choice, with spiders varying in their ability to adjust their position based on temporal changes in environmental conditions.

A second important process in forest recovery that is likely to influence litter spider species composition among sites is litter development. Litter depth and structure are widely recognized as critical features of habitat structure to which spiders respond (Uetz 1991). An old-growth forest floor is characterized by a deep layer of litter, the top portion of which many spiders use as placement sites for their webs (Huhta 1971). The litter habitat is inhabited by microarthropods, chiefly mites and collembola, which serve as the primary source of food for juvenile and small-bodied adult litter spiders. After clear-cutting and broadcast burning, the litter habitat is virtually destroyed, and the typical community of litter spiders disappears, along with about 90% of the microarthropod food base (Moldenke and Fichter 1988; Moldenke 1990). The forest community is replaced with a set

of species that does not build webs, does not establish nest sites in litter, and feeds on prey species common on low-growing herbs and shrubs.

Several studies have documented a correspondence between spider species composition and structural features of the habitat (Luczak 1966; Sudd 1972; Uetz 1975; Muma 1980; Stevenson and Dindal 1982; Bultman and Uetz 1984; Corey and Taylor 1988; Dobel *et al.* 1990). In general, relatively small changes in habitat structure can have profound effects on spider species composition and relative abundances (Duffey 1978). For example, Uetz (1979) showed a distinct transition in wandering spider species along an artificially produced gradient of deciduous litter depth, with wolf spiders replaced by crab and running spiders as litter depth increased. Dobel *et al.* (1990), working in an intertidal marsh, observed that wandering spiders were largely replaced by web-building species along a gradient from matted *Spartina patens* grass to lower elevation *Spartina alterniflora*. Robinson (1981) demonstrated that web-building spiders respond to changes in the structural complexity of their web-building sites, with species segregating on the basis of habitat geometry.

Though it is easiest to appreciate the physical changes that occur in the litter environment during succession, biological changes are of potentially equal importance. Both prey availability and the abundance and species composition of competing predaceous arthropods may contribute to variation in litter spider species composition among sites.

Abundance of potential herbivorous prey fauna is several orders of magnitude greater in 7- to 15-year-old clearcuts relative to 30-year-old clearcuts and old-growth sites (A.R. Moldenke, unpublished data). Herbivorous Orthoptera and Heteroptera abound in pitfall traps in early stages of succession, probably because abundant edible vegetation is near the ground surface. The abundance of both diurnal pursuit hunters and large herbivorous insects in pitfall traps suggests an association between the two trophic levels. Numerous observations of predation by wolf spiders on grasshoppers in the field (J.D. McIver, personal observation) support the contention that large herbivorous insects are the primary prey of clearcut litter spiders. No such association exists between diurnal pursuit hunters and the abundance of Collembola (springtails) and Acari (mites) in the litter habitat. Springtails and mites virtually disappear in burned clearcut sites, yet diurnal pursuit hunters are as common in burned as in unburned sites. Finally, the peak in lycosid reproduction in early summer closely matches the flush of herbivore prey availability in clearcuts, which is consistent with the hypothesis that low-growing vegetation supports much of the primary prey of clearcut spiders.

The majority of invertebrate predator biomass in clearcuts is represented by the several species of ants that forage diurnally in the litter habitat and in all layers of vegetation (*Camponotus* spp., *Formica* spp., *Lasius* spp., *Aphaenogaster* spp., *Tapinoma sessile*, A.R. Moldenke, unpublished data). In the old-growth habitat, only the carpenter ant *Camponotus modoc* is abundant, and this large-bodied species forages primarily in the canopy. The great abundance of ants in clearcuts, having a variety of different body sizes, may exclude predaceous arthropods that cannot avoid encounters with them or compete effectively for food. Active visual pursuit hunters and nocturnal running spiders may be the only hunting strategies that favor coexistence with ants in the clearcut habitat.

This community approach has thus revealed not only how individual taxa respond to physical and biological gradients but also how functional groups (hunting guilds) are differentially successful as the nature of their environment changes. The utility of spiders as indicators of community change rests in our ability to distinguish divergent functional roles played by groups of taxa. The shifting emphasis of different hunting guilds suggests emergent properties of the total community that cannot be discerned by a species by species approach.

Litter spiders as bioindicators

The use of species composition data for the bioassessment of habitat quality has been a common practice in recent years, especially in aquatic systems (Lenat 1988; Plafkin *et al.* 1988). The value of bioassessment in aquatic systems is twofold: (*i*) aquatic organisms, especially fishes and certain invertebrates, are relatively easy to sample and identify; (*ii*) aquatic organisms respond to a complex array of chemical and physical factors that are difficult to measure directly. Water quality can thus be assessed quickly without resorting to the use of sophisticated instruments and procedures (Higler 1974; Hilsenhoff 1982, 1987).

Bioassessment might also be useful in forest management. If the quality of the forest floor habitat is linked to important ecosystem processes, such as decomposition rates and nutrient cycling, then it might be useful to develop a means for assessing changes in this habitat that occur as a result of the more common management practices. Understory plant species composition would normally be the most appropriate bioassay of forest floor habitat quality. However, litter spiders would be more useful than plants under at least two circumstances: (*i*) Because most understory plant species are perennial, their distribution patterns would not closely reflect short-term changes in habitat quality, nor would they be good early predictors of habitat change. On the other hand, since litter spiders are short-lived (some species have longevities of less than a few months), short-term changes in habitat quality would be expected to profoundly affect their distribution and abundance. (*ii*) A litter spider assay would be more useful in areas that had been treated postcut (shrub removal or prescribed burning), such that the typical understory plant species composition no longer reflected habitat quality.

Because of their abundance, ease of sampling and identification, presumed ecological ties to the litter microarthropods, and clear response to changes in habitat quality, litter spiders have potential for use as indicator species in forest planning.

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