Regional diversity of insects in the Pacific Northwest

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ABSTRACT

Provincial and state records for a sample of insect groups from British Columbia, Idaho, Oregon, and Washington show that this region, here termed "the Pacific Northwest", contains about 29% of North American insect diversity, a level that can be extrapolated to suggest that about 26,000 reported species occur in the region. Nearly half of these species are widely distributed in North America. Many species are moreor-less broadly western; 13% of all species essentially are confined to the Pacific Northwest, although some of them occur otherwise only in California, which contains many Pacific Northwestern species, especially in the north. Most of the fauna of British Columbia occurs also in the United States part of the region, and one-third of the species confined in Canada to British Columbia occur also in Idaho, Oregon or Washington. Despite these overall trends, there are wide differences among families and among genera, reflecting the diverse ranges, origins and ecological relationships of the different groups. Detailed studies that would more fully explain the differences are limited, even for groups of North American insects that are taxonomically better known. Nevertheless, the simple but feasible analysis of state and provincial records presented here provides useful indexes of regional occurrence, and indicates groups in the region that are of particular interest.

INTRODUCTION

This paper considers the diversity of the insects of the Pacific Northwest by comparing state and provincial records for selected groups within and beyond the region in North America. The nature of the data requires that entire states or provinces be included in such an analysis, and therefore the Pacific Northwest is defined here as the whole of British Columbia, Idaho, Oregon and Washington, a choice explained further below. An analysis of the insects of this region suggests patterns in the occurrence and restriction of the species there.

METHODS

A sample of relatively well known insect groups for which detailed state-by-state and province-by-province records or maps are available for the whole of North America was chosen for analysis. These groups, chiefly families, were selected as far as possible to represent the whole fauna (see Danks 1994b), including various taxonomic and ecological types, families from different orders, and groups represented most strongly in different parts of North America. The groups essentially are the same as those analyzed for North America by Danks (1994b), but excluding Pompilidae, for which distributional data could not effectively be analyzed for Idaho, Oregon and Washington separately. The sample thus comprises 3322 species, or nearly 4% of the fauna of North America, estimated to be about 90,250 reported species (Danks in press).

The range of each individual species was recorded by marking its occurrence in a

given region, and in the individual province or states of British Columbia, California, Idaho, Oregon and Washington, on to a standardized table of regions. Regional statistics were derived by summing the marked occurrences. Templates or transparent overlays were used to facilitate data extraction from particular combinations of columns in deriving the more complex statistics.

THE PACIFIC NORTHWEST

The Pacific Northwest is a convenient term for the far northwestern regions of North America, typified by relatively high rainfall and evergreen forests containing characteristic western coastal species such as Sitka spruce. Many other characteristic trees such as Ponderosa pine and Douglas fir are more widely distributed in the west. However, the wet coastal strip has some locally dry areas and it grades inland into a series of more or less complex cordilleran ranges with intervening or intermingling valleys and plateaus. Therefore, the habitats of the region are very diverse, with a considerable range in elevation and water supply, and include deserts, meadows, and aquatic, subalpine, alpine and other habitats in addition to moist coniferous forests.

The Pacific Northwest has been defined in various ways. For example, a typical encyclopaedia (Encyclopaedia Britannica 1983) limits it to Oregon, Washington and part of Idaho. The entomologist Melville Hatch, in a series of fascicles on "The beetles of the Pacific Northwest" (1953–1971) included British Columbia, Idaho, Oregon and Washington. Hitchcock *et al.* (1955–1969), in a treatment of the "Vascular plants of the Pacific Northwest", published in the same series of the University of Washington as Hatch's work, used detailed information for plants to circumscribe the area of Washington, Oregon, Northern Idaho, part of Montana, and southern British Columbia. Kavanaugh (1988) used the term for regions inland only to the western slopes of the Coast Ranges, Cascades and Sierra Nevada south to just south of San Francisco, and north to the Aleutian Islands, thereby including parts of Alaska, British Columbia, Washington, Oregon and California.

Most insect distributions are not known in great detail and for most species only stateby-state or province-by-province records, and not more detailed distributions or habitat information, are readily available in published form. Therefore, the area treated here includes British Columbia (BC), Idaho (ID), Oregon (OR), and Washington (WA), although the diversity of British Columbia as well as of California (CA) also is analyzed separately in relation to the fauna of the region. These and other regions considered in this paper are shown in Figure 1, the caption for which gives the approximate land areas of the regions.

INSECT DIVERSITY IN THE PACIFIC NORTHWEST

North American Comparisons

The occurrence of species of the selected groups in the Pacific Northwest (PNW) as a percentage of the North American fauna is shown in Table 1. Overall, some 29% of North American species have been recorded in the region, while the percentage in each state or province ranges from 16% (ID) to 20% (OR and BC). Nevertheless, there are considerable differences among groups. For example, the characteristic northwestern group Blephariceridae (48% of blepharicerid species occur in the PNW) is much better represented in OR and WA than elsewhere. The predominantly southwestern United States group Bethylidae (only 15% of species in PNW) is poorly represented throughout.

The group Culicidae (38% of species in PNW) is generally widely distributed in North America, and species are evenly distributed across the subregions. Northern syrphids are best represented in BC.

Similar differences are visible among genera in the selected groups. Table 2 lists genera that contain more than 50 species. The fact that overall patterns for these 12 large genera —

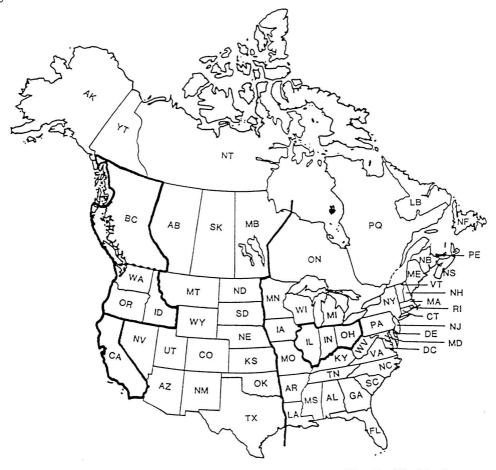


Figure 1. Regions of North America discussed in the text. The Pacific Northwest as considered here (approx. $1,583,000 \text{ km}^2$) comprises British Columbia (949,000), Idaho (213,000), Oregon (249,000), and Washington (172,000). The United States Pacific Northwest (ID–OR–WA, 635,000) is also compared with British Columbia, with California (405,000), with Illinois–Indiana–Ohio (343,000), which contains a similar number of reported species in the east, and with eastern North America.

just over a quarter of the species— are virtually identical to those for the full dataset (compare the two bottom lines of Table 2) suggests that the patterns shown by these samples are representative.

Subregions

The number of species from the Pacific Northwest, and their occurrence in the different subregions, is shown in Table 3. Many species are shared among the subregions

(56–69%) but a substantial proportion of species have not been found in the whole of the region. About 13% of species have been found <u>only</u> in the region, with or without CA as explained below. Two small but distinctive fractions of species restricted to the area would be added if Alaska (for northern species such as some carabids, culicids and syrphids) and Nevada (for some southern elements such as some carabids, chrysidids and butterflies) were to be included in the "Pacific Northwest".

Clues to the different patterns of occurrence are suggested by the differences among families. The presence of groups of more southern or Californian affinity decreases from OR to BC, as in Curculionidae, whereas groups of more northern or Alaskan affinity increase, as in Corixidae, and in Syrphidae, a family within which two better known but chiefly northern genera were analyzed.

British Columbia

British Columbia occupies a large area with a range of habitats including wet coastal forests in the south, dry interior grasslands, and relatively cold alpine and subalpine forests, especially in the north. Its fauna might therefore be expected to diverge from that of the United States Pacific Northwest, but in fact, partly because the northern fauna is relatively depauperate, nearly 80% of the species found there occur in ID, OR or WA too (Table 4). Seven percent of BC's species have been found only in the PNW.

From a Canadian perspective, many species occur in BC, and a significant fraction of all species (13% overall for the groups analyzed here) are confined to that province (Table 5), although there are considerable group-to-group differences. Additional reliable data are available for species distributions in Canada alone (Danks 1993, p. 60), and for these data 19% of 1583 species in 9 families (the whole of the Carabidae and 8 other different groups) have been reported only from BC; the percentage is increased especially because a full third of species of the characteristically western groups Scolytidae and Quediinae (Staphylinidae) are confined to the province (Danks 1993). One third of the species confined to BC (Table 5) nonetheless occur in the U.S. in ID, OR, or WA. Evidently many of these restricted Canadian species are part of the Pacific Northwestern fauna.

California

Habitats in northern California resemble those elsewhere in the PNW, although many different distinctive Californian and southwestern North American habitats occur in southern California. California as a whole therefore cannot be regarded as part of the Pacific Northwest, even though 7% of CA species otherwise occur only in the PNW (Table 6). Nevertheless, because some species centred in the PNW extend to CA, and because many more "southern" species characteristic of CA extend at least into OR, 56% of CA species occur also in the region considered here (Table 6).

Species in common

Within the region, many species are shared (Table 7). For example, 85% of Washington species have been collected also in Oregon; 75% of Oregon species are shared with Washington. About 65% of the United States Pacific Northwestern species occur also in CA, and 63% of them also in BC. However, only 30% of the same species occur in an area with a similar number of species farther east (see Fig. 1).

Once again there are considerable differences from group to group (Table 7). For example, the number of species shared between WA and OR is especially high in groups such as the Lycaenidae. Although relatively few species of characteristically western groups (e.g. Blepharicerids) occur in eastern N. America, the relatively consistent

occurrence in the east of PNW species in most groups is more striking. Indeed, nearly half of all the Pacific Northwest species are found to the east of a line from Manitoba to Texas (see Fig. 1; Table 7): many North American species are widely distributed and occur in different regions.

Range types

Several consistent types of ranges of species that occur in the Pacific Northwest can be detected. A detailed analysis is beyond the scope of this paper, but Kavanaugh (1988) recognized restricted coastal, coast centred, Great Basin, Rocky Mountain and transAmerican species (in addition to mainly northern range types), suggesting that since deglaciation species have entered the PNW by several common routes. In addition, prairie species enter the eastern part of the region not included by Kavanaugh.

Widespread and even transcontinental species are very well represented (Table 7, final column). Many others are more-or-less broadly western. Some species, as already noted, are restricted to the Pacific Northwest. Those that are confined to the PNW and surrounding areas show a variety of patterns, among which characteristic types are northern (e.g. PNW to southeastern Alaska and the Yukon Territory) and southern coastal (e.g. PNW to CA); for sample patterns see Scott (1986), Kavanaugh (1988) and papers cited there, and also compare plant ranges, e.g. Preston (1961). The variety of the individual ranges suggests that current distributions have developed in many different and complex ways. Kavanaugh (1988) emphasized barriers to the dispersal of insect species in the region, noting that centres of endemism include central Idaho, the northern Cascades, and southern and northern coastal centres.

CONCLUSIONS

In the absence of full and detailed data on the ranges and habitats of large numbers of species, analysis of state and provincial records is helpful for characterizing regional diversity (Danks 1993, 1994a, b).

This analysis for the Pacific Northwest — BC, ID, OR, WA — suggests that 29% of the species in North America, some 26,000 reported species, occur in the region (Table 2). Additional species revealed by further collecting, especially in old-growth forest canopies and in some montane habitats, would be expected to augment this number.

Nearly half of the species from the Pacific Northwest are widely distributed in North America; indeed, 30% of them occur in Illinois, Indiana and Ohio alone (Table 7). On the other hand, 13% of all species (or a quarter of the western species) are confined to the Pacific Northwest, with or without occurrence in California, northern parts of which have habitats characteristic of the main part of the zone. Within the region, Oregon and the larger British Columbia have the most species, estimated to be about 18,000 each (Table 2). Almost half of the rich California fauna does not occur in the Pacific Northwest; however, the smaller fauna of BC is dominated by the nearly 80% of species that occur also in WA, OR, or ID.

Despite these generalizations for the fauna as a whole, there are many differences among different groups (e.g. Tables 1, 2). Such differences suggest, for example, that groups with more species in and especially confined to the region, including Blephariceridae and some Carabidae and Curculionidae, would be especially useful for investigation of why these species contribute to the fauna to an unusual degree. The differences confirm too that current distributions depend on a wide variety of ecological and historical factors, reflecting the evolution and dispersal of species and the modification and development of habitats, which have taken place in diverse ways over time. The variety of range types among the species that contribute to the fauna of the Pacific Northwest, and the combinations and intergradations of these range types, attest to the complexity of these processes.

Therefore, analysis of state and provincial records provides useful indexes of regional diversity, but fuller explanations about the nature and origin of the fauna require further systematic and ecological work. Kavanaugh (1979a, b, 1980, 1981, 1988) has been able to develop some explanations from prolonged and detailed studies of carabids of the genus *Nebria*, which contains many restricted northwestern species. Similar studies still are very limited for most of the groups treated here, even though they are among the best known taxonomically in North America.

ACKNOWLEDGEMENTS

This paper was prepared as the basis of a presentation at the 1995 Entomological Society of Canada / Entomological Society of British Columbia symposium on diversity in the Pacific Northwest. I thank Dr. Robb Bennett (BC Ministry of Forests) for stimulating my interest in the region by inviting me to contribute to the symposium, and Dr. David Kavanaugh (California Academy of Sciences) for helpful comments on the manuscript. I again acknowledge the information and advice provided by the many systematists cited in the acknowledgements of an earlier paper on North American diversity (Danks 1994b).

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Order/Family	No. of N.	BC	ID	OR	WA	BC, ID,
	American spp.					OR, WA
Dictyoptera	69	6	6	9	7	9
Hemiptera:						
Corixidae	125	26	9	16	21	36
Pentatomidae	221	18	13	13	10	23
Tingidae	153	14	7	12	9	23
Coleoptera:						
Carabidae (part)	757	19	12	16	16	26
Curculionidae(part)	483	7	9	15	11	18
Diptera:						
Blephariceridae	25	16	20	44	36	48
Culicidae	162	27	29	29	27	38
Dolichopodidae (part) 49	35	24	29	27	47
Syrphidae (part)	83	67	36	45	43	73
Lepidoptera:						
Papilionidae/ Pieridae	e 78	38	32	36	32	44
Nymphalidae	165	39	27	28	29	47
Lycaenidae	124	29	35	35	34	43
Hesperiidae	221	11	13	14	12	18
Hymenoptera:						
Pamphiliidae	71	27	7	17	13	30
Chrysididae	230	20	34	42	25	44
Bethylidae	197	7	10	12	9	15
Dryinidae	109	15	6	6	5	17
TOTAL	3322	20	16	20	17	29

 Table 1

 Occurrence of North American species in selected groups in the Pacific Northwest

 % of these spp. recorded in

Data for this and subsequent tables derived from Atkinson et al. 1991 (Dictyoptera s.s. [cockroaches]), Polhemus et al., 1988, Henry and Froeschner 1992 (Corixidae), Froeschner 1988a (Pentatomidae), Froeschner 1988b (Tingidae), Bousquet and Larochelle 1993 (Carabidae), O'Brien and Wibner 1982 (Curculionidae), Darsie and Ward 1981 (Culicidae), Hogue 1987 (Blephariceridae), Hurley 1985 (Dolicherodidae), Vockeroth 1990, Knutson 1973 (Syrphidae), Scott 1986 (Papilionid Tidae, Nymphalidae, Lycaenidae, Hesperiidae), Middlekauf 1958, 1964, Shinohara and Smith 1983, Eidt 1964 (Pamphiliidae), Behart and Kimsey 1982 (Chrysididae), Evans 1978 (Bethylidae), Olmi 1984, 1989 (Dryinidae)

	% of these spp. recorded in					
Family / Genus	No. of N. American spp.	BC	ID	OR	WA	BC, ID, OR, WA
Carabidae:						
Agonum	71	44	15	18	30	45
Cicindela	90	8	8	11	8	16
Chlaenius	51	12	4	8	12	12
Nebria	54	26	15	24	30	48
Curculionidae:						
Apion	154	5	8	12	12	14
Listronotus	76	13	16	20	11	22
Anthonomus	102	12	11	25	16	29
Conotrachelus	60	2	0	0	2	2
Sphenophorus	64	8	14	16	16	20
Culicidae:						
Aedes	76	41	39	38	37	51
Syrphidae:						
Platycheirus	70	63	33	37	39	69
Chrysididae:						
Chrysis	79	27	47	48	35	58
TOTAL (These genera)	947	20	17	21	20	31
TOTAL (All genera)	3322	20	16	20	17	29

Table 2
Occurrence of North American species in selected larger genera in the Pacific Northwest

Oregon and Washingt	on					
	,	%	of these sp	p. recorded	in	
						% recorded only from
					· · · ·	BC, ID,
	No. of spp.					OR, WA,
	n BC, ID,	DO	TD		117 A	with or
	DR, WA	BC	ID	OR	WA	without CA
Dictyoptera	6	67	67	100	83	0
Hemiptera:						
Corixidae	45	73	24	44	58	18
Pentatomidae	51	76	57	55	45	6
Tingidae	35	63	29	51	40	11
Coleoptera:						
Carabidae (part)	198	74	44	60	63	27
Curculionidae (p	art) 86	42	51	83	64	27
Diptera:						
Blephariceridae	12	33	42	92	75	42
Culicidae	62	71	76	76	69	5
Dolichopodidae (part)	23	74	52	61	57	17
Syrphidae (part)	61	92	49	61	59	8
Lepidoptera:	01	12	.,		•••	
Papilionidae/ Pieridae	34	88	74	82	74	6
Nymphalidae	78	83	58	60	62	4
Lycaenidae	53	68	83	83	79	2
Hesperiidae	39	64	72	77	67	10
Hymenoptera:			40,07748			
Pamphiliidae	21	90	24	57	43	5
Chrysididae	101	47	78	95	57	2
Bethylidae	30	47	67	77	60	0
Dryinidae	19	84	37	37	26	11
TOTAL	954	68	56	69	61	13

 Table 3

 Occurrence of Pacific Northwest species in selected groups from British Columbia, Idaho, Oregon and Washington

in Idaho, Oregon and Wash	nington		
			% of BC spp.
		% of BC spp.	otherwise only
No	o. of spp.	recorded also	in ID, OR,
record	led from	in ID, OR,	WA, with or
Order/Family	BC	WA	without CA
Dictyoptera	4	100	0
Hemiptera:			
Corixidae	33	58	9
Pentatomidae	39	82	5
Tingidae	22	50	5
Coleoptera:			
Carabidae (part)	147	77	16
Curculionidae (part)	36	92	11
Diptera:			
Blephariceridae	4	100	0
Culicidae	44	89	2
Dolichopodidae (part)	17	76	12
Syrphidae (part)	56	75	36
Lepidoptera:			
Papilionidae/ Pieridae	30	83	33
Nymphalidae	65	69	2
Lycaenidae	36	94	3
Hesperiidae	25	96	0
Hymenoptera:			
Pamphiliidae	19	53	0
Chrysididae	47	96	0
Bethylidae	14	79	7
Dryinidae	16	56	0
TOTAL	654	78	7

Table 4

Occurrence of species from British Columbia in selected groups in relation to occurrence in Idaho. Oregon and Washington

 Table 5

 Occurrence of species, confined in Canada to British Columbia, in Idaho, Oregon and Washington

			% of Canadian	% of spp. confined in Canada to BC
	No. of	% of N.Am.	spp. confined	that occur in
Order/Family	Canadian spp.	spp. in Canad		ID, OR, WA
Dictyoptera	7	10	0	
Hemiptera:				
Corixidae	69	55	10	43
Pentatomidae	63	29	17	18
Tingidae	35	23	34	7
Coleoptera:				
Carabidae (part)	286	38	14	67
Curculionidae (part)	105	22	15	25
Diptera:				
Blephariceridae	7	28	0	
Culicidae	74	46	7	40
Dolichopodidae (part	.) 39	80	15	33
Syrphidae (part)	73	88	15	36
Lepidoptera:				
Papilionidae/ Pierida	e 46	59	13	17
Nymphalidae	89	54	9	25
Lycaenidae	55	44	13	14
Hesperiidae	55	25	9	0
Hymenoptera:				
Pamphiliidae	45	63	18	0
Chrysididae	61	27	23	0
Bethylidae	25	13	4	100
Dryinidae	38	35	3	100
TOTAL	1172	35	13	33

Idaho, Oregon, and Washi	ngton	Ç Î	
			% of CA spp.
		% of CA spp.	otherwise only
	No. of spp.	recorded also	in ID, OR,
	recorded from	in ID, OR,	WA, with or
Order/Family	CA	WA	without BC
Dictyoptera	14	29	0
Hemiptera:			
Corixidae	24	67	17
Pentatomidae	68	51	4
Tingidae	32	40	3
Coleoptera:			
Carabidae (part)	185	44	13
Curculionidae (part)	94	63	14
Diptera:			
Blephariceridae	16	75	31
Culicidae	48	77	2
Dolichopodidae (part)	12	83	25
Syrphidae (part)	27	85	7
Lepidoptera:			
Papilionidae/ Pieridae	36	69	6
Nymphalidae	59	73	4
Lycaenidae	64	75	2
Hesperiidae	60	52	7
Hymenoptera:			
Pamphiliidae	18	72	6
Chrysididae	164	57	1
Bethylidae	79	33	0
Dryinidae	23	35	0
TOTAL	1023	56	7

Table 6

Occurrence of species from California in selected groups in relation to occurrence in Idaho. Oregon, and Washington

Table 7

Occurrence of species in selected groups from the Pacific Northwest in adjacent and in distant regions

Order/Family	% spp. from WA also in OR	% spp. from OR also in WA	% spp from ID- OR-WA also in CA	% spp. from ID- OR-WA also in BC	% spp. from ID- OR-WA also in IL- IN-OH	% spp. from ID- OR-WA also east of MB to TX
Distrontors	100	83	67	67	02	0.2
Dictyoptera Hemiptera:	100	83	07	0/	83	83
Corixidae	62	80	52	61	26	50
Pentatomidae	62 70	80 57	32 80	73		52
Tingidae	70	56	80 54		41	50
Coleoptera:	/1	30	54	46	33	42
-	77	80	50	69	29	27
Carabidae (part)					28	37
Curculionidae (pa	11) 87	68	73	41	33	44
Diptera:	00	7 2	100	22	0	
Blephariceridae	89	73	100	33	0	0
Culicidae	91	83	65	68	44	65
Dolichopodidae (part)	100	93	53	68	11	42
Syrphidae (part)	86	84	49	89	26	62
Lepidoptera:		• •		07	20	02
Papilionidae/	96	86	86	86	28	59
Pieridae					20	
Nymphalidae	88	89	75	79	32	47
Lycaenidae	95	91	94	67	31	45
Hesperiidae	85	73	82	63	37	45
Hymenoptera:						
Pamphiliidae	100	75	100	77	0	31
Chrysididae	95	57	95	46	26	41
Bethylidae	89	70	93	39	43	64
Dryinidae	40	29	67	75	25	92
TOTAL	85	75	65	63	30	47

Summary of the diversity of species in	n the regions discussed	d
%	o of spp. reported in	Estimated total no.
Region	selected groups	of spp. reported
North America	(100)	90,250
Canada	35	31,590
Pacific Northwest (BC, ID, OR, WA)	29	26,170
U.S. Pacific Northwest (ID, OR, WA)) 24	21,660
British Columbia (BC)	20	18,050
Oregon (OR)	20	18,050
Washington (WA)	17	15,340
Idaho (ID)	16	14,440
California (CA)	31	27,980
Middle states (IL, IN, OH)	26	23,460

 Table 8

 Summary of the diversity of species in the regions discussed

