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Seasonal variation in insect abundance among three Australian rain forests, with particular reference to phytophagous types

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Abstract

Monthly sweep net and light trap samples were used to examine seasonal changes in the abundance of insects in subtropical, warm and cool temperate rain forest in New South Wales. Maximum insect abundance, especially of phytophages, coincided with leaf flushing in the canopy trees. Cool temperate insect numbers were highest during the month just following the beech leaf flush, a rapid and synchronous growth event. Conversely, numbers of subtropical insects fluctuated over a longer period, in a pattern similar to the continuous growth of leaves that occurred throughout spring and summer there. The warm temperate was intermediate in its vegetation growth phenology and insect patterns. Rain forest insect abundance varied both temporally and spatially.

Introduction

Insects have a significant role in the forest community, affecting both primary production by their grazing activities, and nutrient turnover by their roles as decomposers. Phytophagous insects are probably the most extensively studied due to economic interests in controlling defoliators (Kulman 1971). Populations of herbivorous insects have been assessed for a number of forest communities, including eucalypt (Morrow 1977a,b), African dry forest (Denlinger 1980), North American hardwood (Whittaker 1952; Futuyma & Gould 1972), and neotropical forests (Janzen 1973). Few studies exist, however, that have examined seasonal changes in insect populations of rain forests, and none within Australia.

There are a number of logistic problems associated with sampling insects in rain forest. There is evidence that many insects occur high in the canopy (Sutton & Hudson 1980), thus rendering a census by ground sweeping alone inadequate. Different rain forest sites, even in close proximity, may have highly variable insect populations due to subtle differences in environmental factors or plant composition (Janzen & Schoener 1968); and numbers may fluctuate greatly within one site, although this has not been thoroughly examined (but see Elton 1973). Seasonal variability of arthropods can be extremely high, reflecting periodic food supplies or environmental changes such as rainfall (Denlinger 1980) or temperature (Mani 1968). Lastly, the problems simply associated with the numbers and taxonomy of these organisms may be a deterrent to quantifying the results of rain forest insect surveys.

The study presented in this paper related seasonal changes in insect populations of rain forests to the dynamics of vegetation growth. Within the rain forests of New South Wales, most trees exhibit distinct seasonal periods of growth (Lowman 1982). Since insects (particularly phytophagous types) rely on the vegetation in most aspects of their behaviour, it is suggested that the seasonality of insect populations may reflect the phenology of the vegetation. To examine this, an insect sampling programme was conducted at monthly intervals over 18 months (including two growing seasons) in three rain forest formations: subtropical, warm and cool temperate.

Methods

Description of study sites

I sampled insects in three rain forest formations located in north-central New South Wales on the New England Tableland. This area has altitudinal gradients of subtropical through warm temperate to cool temperate rain forest in close proximity to one another, thereby eliminating latitudinal variability among sites. The region is underlain by basalt and trachyte, and the soils are rich, loamy and volcanic, as is characteristic for many areas of Australian rain forest (Beadle 1954). Although structurally similar, Australian subtropical rain forest is climatically quite different from the archetypal tropical lowland rain forest, having cooler temperatures and lower humidity, as a consequence of location in a more temperate region atop an escarpment. Meteorological data are illustrated in Fig. 1, representing mean annual temperatures and rainfall for Bellingen, located centrally among the three forests.

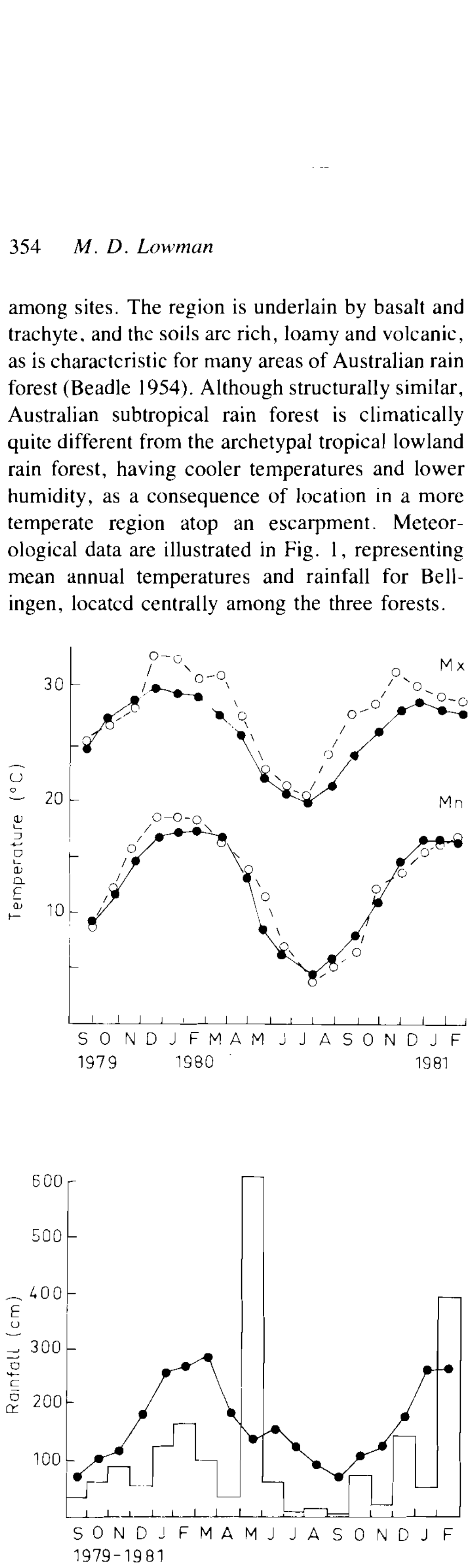

FIG. 1. Temperature and rainfall data for Bellingen, NSW (22.9 m elevation) during the years of insect sampling (1979–81) as compared to long-term averages. Courtesy of the State Meteorological Bureau.Temperature: mean maximum (Mx), mean minimum (Mn); ●25 year average, ○ 1979–1981. Rainfall: ● 58 year average.

The rain forest sites are sumarized as follows:

1. Cool temperate rain forest. This is classified as microphyll fern forest by Webb (1959), and is dominated by Antarctic beech *(Nothofagus moorei).* The study area is located within New England National Park at an elevation of 1200 m. The canopy height extends to 30 m, and is stratified into two layers. Its seasonal growth pattern involves one synchronous flush in early spring (September–October), at which time the beech canopy replaces approximately half its leaves annually (Lowman 1982).

2. Warm temperate rain forest. Situated within Dorrigo National Park (Never Never Region) at 900 m, this site is classified as simple notophyll vine forest (Webb 1959). The canopy extends to 35 m and is composed of five to ten dominant species, including coachwood *(Ceratopetalum apetalum),* sassafras *(Doryphora sassafras),* Dorrigo plum *(Endiandra tortosa)* and others. The canopy is intermediate in its growing season between the other two rain forest types: a major leaf flush occurs in spring (October–November), but intermittent growth continues through February.

3. Subtropical rain forest. This formation, classified as complex notophyll vine forest (Webb 1959) was sampled in Dorrigo National Park at 760 m elevation. It is highly diverse in plant species composition and exhibits many features associated with tropical rain forests (e.g. lianes, tree ferns, buttresses and epiphytes). The canopy extends to 40 m and includes giant stinging tree (*Dendrocnide excelsa*), booyong (*Argyrodendron trifoliatum*), sassafras (*Doryphora sassafras*), red cedar (*Toona australis*), flame tree (*Brachychiton acerifolium*) and many others. The growing season is the most extensive of all three forest types, continuing from September through April. Individual species exhibit varying peaks of growth at different times, but the canopy overall maintains growth throughout 8 months.

Insect sampling techniques

Sweep net and light trap sampling were used to assess the seasonal changes in relative insect abundance and proportions of phytophagous types. The numbers of insects captured do not indicate the actual numbers within the entire community, but simply represent an index of temporal distribution. The nocturnal samples were not directly comparable to the sweeps since one was defined by air volume and the other by unit hours. The two methods together, however, gave overall assessment of the diurnal and nocturnal insects.

Sweep net sampling was carried out as described by Janzen & Schoener (1968), but with a 30 cm diameter net of 1.5 mm mesh. Species were identified to order and phytophages to family whenever possible (CSIRO 1970). Each sample consisted of 100 sweeps encompassing an area from ground level to 2 m conducted within mature rain forest. Sweep net sampling was repeated monthly in the subtropical and cool temperate rain forest sites, at approximately 1400 h during sunny intervals in order to minimize variation due to weather or diurnal rhythms of insects. Unlike Janzen (1968), I found it necessary to empty the net after every other sweep, to minimize loss of flying insects. Since moths and butterflies represent the adult form of herbivorous larvae, I decided to conduct fewer sweeps with greater retention per sweep, rather than to allocate time for more sweeps with less frequent emptying of the net.

Light trap sampling was conducted in all three rain forests at monthly intervals. The light trap, a funnel and box apparatus illuminated by a 6 V ultraviolet light, was set out on the forest floor under mature canopy for 10 h on rainless nights. When weather restricted the duration of trapping, I calculated the data for a 10 hour span. The light trap had no roof or cover in order to attract insects from the canopy as well as at ground level. All insects which fell through the funnel apparatus into the collecting box were sorted and identified to order, noting particularly the phytophagous types.

Results

The numbers obtained in sweep samples (Fig. 2) showed more diurnal insects in subtropical than in cool temperate rain forest (monthly means of 233 (s.e. = 21.6) and 165 (s.e. = 9.2) insects, respectively). The raw data are listed in Appendix 1. The

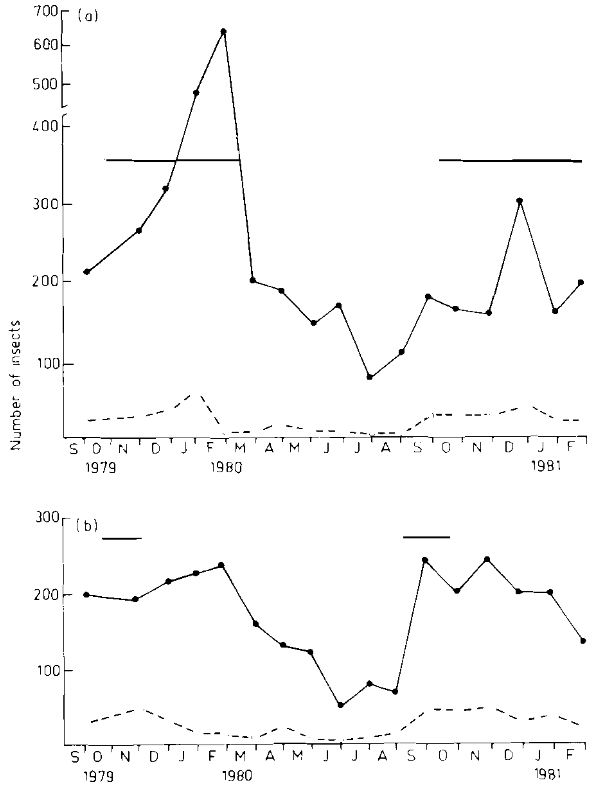

FIG. 2. Seasonal changes in NSW rain forest insect abundance, as reflected by sweep-net sampling. Points indicate total numbers caught per 100 sweeps: ● total, and ○ phytophagous. Bars indicate main leafing periods. (a) Indicates subtropical rain forest, (b) cool temperate rain forest.

difference between the two habitats was not significant, however, due perhaps to the large seasonal variability within each forest ($F_{1,28}$ = 3.01, $P >$ 0.05). The number of orders captured was consistently higher in the subtropical rain forest, although the cool temperate site had greater proportions of herbivores (monthly means of 12.9% versus 9.4%). The cool temperate herbivores were in greatest abundance during September–November which coincided with leaf flushing of Antarctic beech, the predominant canopy tree. The subtropical site had more phytophagous types during January–February, which marked the peak time of phenological activity for most subtropical trees.

Light trapping (Fig. 3) yielded slightly higher numbers of insects in the cool temperate than in the subtropical site, although the averages are affected by one dramatic peak during the cool temperate spring (monthly means of 217 versus 205 in 1980). The warm temperate site had the fewest insects, with an average of 121 individuals per catch. As with results for sweep sampling, there were no significant differences in the light trap catches among the three types of rain forest ($F_{2,51}$ = 1.35, $P>0.05$). The cool temperate catches were highly variable from month to month and exhibited sharp peaks just after the occurrence of leaf emergence of beech (November 1980 and September 1981). The lag was a consequence of the fact that the majority of nocturnal insects captured were adult Lepidoptera, and their larvae fed on young beech leaves during the previous month. The earlier peak during 1981 reflected an early budburst triggered by a spell of warm dry weather. The subtropical catches exhi-

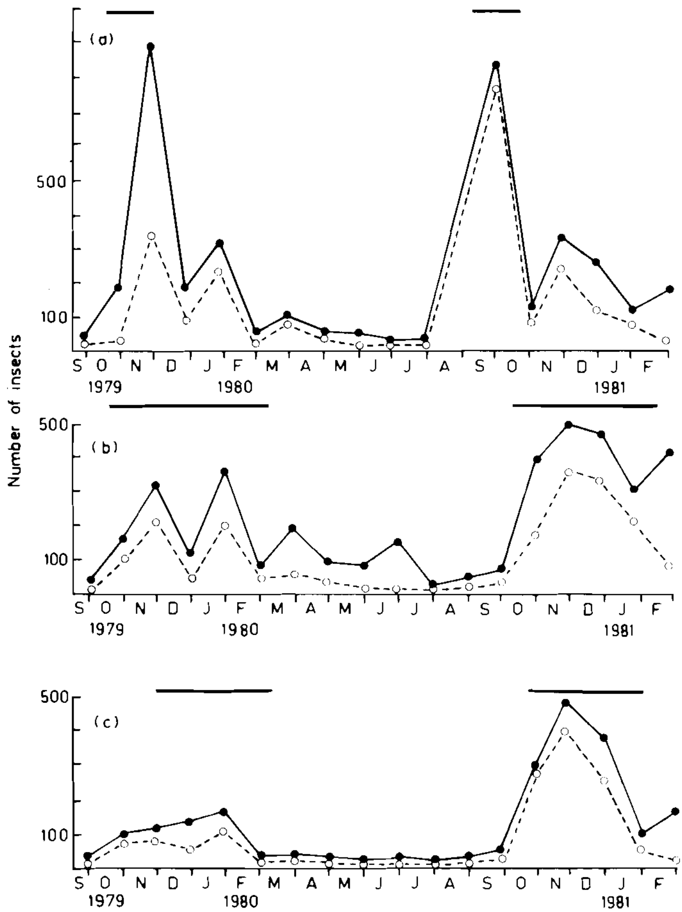

FIG. 3. Seasonal changes in NSW rain forest insect abundance, as reflected by light trap sampling. Points indicate total numbers captured per ten sampling hours: ● total, and ○ phytophagous. Bars indicate main leafing periods. (a) Indicates cool temperate rain forest, (b) subtropical rain forest and (c) warm temperate rain forest.

bited moderate fluctuations over both spring and summer months, reflecting the availability of food over a longer duration with the more extended growing season in this rain forest formation. The warm temperate site exhibited an intermediate pattern: a seasonal (or temperate) pattern with one peak period in spring and almost no insects during winter, but a more gradual surge of insects over a longer duration rather than one sharp peak period.

Insect abundance in NSW rain forests showed temporal variation, with numbers greater in the spring and summer than in the autumn or winter. When all three light trap catches were pooled as replicate monthly samples of rain forest habitat, time was statistically significant ($F_{11,24}$ = 3.23, P<0.01) despite the wide variability among the three sites during a given month. A similar test on diurnal insects showed a nonsignificant difference with time ($F_{11,12}$ = 1.99, P>0.05). This apparent anomaly may be due to the abundance of diurnal insects during winter months in the subtropical site. Daytime temperatures may be mild enough to allow insects to survive throughout the year, although the cool night-time temperatures cause a decline in nocturnal insect activity during winter.

Discussion

Light trapping and sweep net sampling, even if considered together, contribute only a partial assessment of the entire insect population. At best, the sampling methods provided a thorough survey of insects within a small spatial region of the rain forest: from ground level to approximately 3–4 m height. Insects restricted to upper canopy regions were probably not included by either method and particular orders were most certainly under-represented as an artifact of sampling (Blattodae or other nocturnal crawlers are not attracted to light, and Diptera or other day flying insects may have evaded the net). However, the repetition of a standard sampling regime, although not comprehensive in terms of assessment of absolute numbers and diversity, served to indicate the relative numbers and seasonality of insects which was the aim of this study.

The numbers of different orders were highly variable over time. Diptera was the most common diurnal group and usually comprised approximately half the total monthly sweep. Both Diptera and Lepidoptera had consistently high numbers in the nocturnal samples, as moths and gnats tended to swarm toward the light. The relative seasonality of these common orders can be assessed from this data whereas the appearance of other orders was less predictable (e.g. Ephemeroptera, Odonata and Thysanoptera). It is likely that these orders were generally less common in the rain forest, although the sampling methods may be too limited for their capture.

Phytophagous types, however, were well represented with the sampling: high proportions of Coleoptera, Lepidoptera, and Hemiptera were caught, as were some Phasmatodea. Although the moths (captured in the light trap) were not phytophagous as adults, their larvae were important herbivores, which justified their inclusion as herbivores in sampling tallies. In general, phytophagous insects were more abundant in the nocturnal samples, reflecting the behaviour of many Coleoptera and Lepidoptera. Herbivores in neotropical rain forest were more active at night (Elton 1973), and observations in these Australian rain forests confirm a similar behaviour. As Diptera were the most abundant dayflying order, their consistently high numbers resulted in relatively lower proportions of herbivores in diurnal samples.

Although diversity of species was not examined in this study, I continually observed a higher diversity of insects within orders in the subtropical samples. For example, the Coleoptera from the cool temperate site represented about 15 species over the entire year (mostly Chrysomelidae), whereas almost every individual in the subtropical catches was different. Specimens of Lepidoptera were retained from the nocturnal catches and are currently being identified (Australian Museum) to enable a more detailed discussion of diversity within this order in an upcoming publication.

The sampling of insect populations at one time gives no indication of their seasonal variation. This study showed that, even in the case of subtropical rain forests, usually considered less seasonal than other Australian forest communities, there was considerable seasonal variation in numbers of insects, particularly those active at night. Nocturnal samples exhibited a marked seasonal variation in numbers, perhaps due to the stronger influence of temperature at night, and to the fact that night samples included a high proportion of adult Lepidoptera, which were very seasonal. In both nocturnal and diurnal samples, the insect numbers were greatest during times of vigorous vegetation growth. The cool temperate insect numbers peaked sharply during the spring when the trees exhibited their annual, synchronous leaf flush; and the subtropical insects fluctuated in moderate abundance over spring and summer, similar to the extended growing season observed there. These patterns of seasonality in insect populations are probably consistent from year to year, but would vary in amplitude with environmental factors such as temperature and rainfall.

The original hypothesis, examining the relationship between insect numbers and the phenology of the rain forest vegetation, is supported by the data. Insect numbers were not steady throughout the year, nor were their fluctuations consistent among the three sites. Rather, they varied with the periodicity of vegetation growth at each site. Insect fluctuations paralleled the phenology of the vegetation within a particular rain forest formation. The cool temperate forest had one major, rapid leaf flush and a similar surge in nocturnal insects (mainly herbivores). The subtropical insect numbers remained higher over a longer season, perhaps in response to the more extended plant growth season. The warm temperate insects exhibited an intermediate pattern with no single peak yet a well defined seasonality of insect numbers, and its growing season was intermediate between the cool temperate and subtropical vegetation.

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Appendix 1.

Raw data from insect sampling (1 = New England National Park; cool temperate rain forest; 2 = Dorrigo National Park; subtropical rain forest; 3 = Dorrigo National Park; warm temperate rain forest).

Order		S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F
(a) Sweep samples. Individuals collected in 100 sweep samples.																			
Apterygota	1	1	No					1	0	0		0		2					
	2	8						4	22	16		25		10					
Ephemeroptera	1				0			•					0						
	2				2								1						
Odonata	1					0									0		0		
	2					1									1		1		
Blathlodea	1	0			0	1	2							0			0		
	2	1			2	4	6							6			3		
Orthoptera	1	1		1		0	0	0	0					4			0	0	
	2	1		0		1	2	1	1					2			1	1	
Phasmatodea	1	5		7	4	6	4	5	7	4		2	3			1	8	18	4
	2	0		0	0	3	0	1	0	0		0	0			0	0	0	2
Hemiptera	1	8		7	2	2	4	1	3	0	0		1	26	6	20	4	2	
	2	7		11	0	6	4	1	11	4	2		5	2	3	9	6	3	
Thysanoptera	1					0		0						0					0
	2					2		9						4					10
Neuroptera	1	0							1								1		
	2	1							0								0		
Coleoptera (phytophagous)	1	12		21	4	6		0	2			2		6	16	16	14	12	6
	2	10		12	12	28		2	1			2		5	10	12	12	0	6
Coleoptera (Other)	1	12		7	15	10	2	0	10		0		3	8	8	24	12	8	4
	2	8		18	30	11	4	3	2		4		0	12	4	18	10	0	8
Diptera	1	55		51	93	92	171	38	5	19	14	16	32	40	28	54	83	60	70
	2	53		117	142	199	274	125	98	83	129	16	44	81	92	58	180	79	104
Lepidoptera	1	5		4	20	1	4	2	12	2	5	4	7	6	20	8	2	2	4
	2	7		7	26	23	4	5	6	2	0	2	2	18	12	6	18	14	12
Hymenoptera	1	12		8	17	18	6	22	1	8	0		1	26	2	50	8	19	8
	2	24		15	10	41	6	5	1	2	1		0	10	4	8	26	8	16

Appendix 1.(a) (cont'd)

Order		S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F
Collembola	1	0		0	0	0	0	0	6	0			0				0		
	2	17		21	40	111	264	10	1	2			6				10		
Arachnida	1	90		89	62	89	42	94	99	94	30	64	28	125	120	70	68	76	44
	2	70		63	46	50	68	35	47	38	32	32	45	32	36	46	46	50	36
Total number	1	201		195	217	225	235	163	136	127	49	88	75	243	200	243	200	200	140
	2	206		265	308	480	632	201	190	147	168	77	104	182	162	157	300	155	194
Number herbivores	1	31(12)		40(21)	30(14)	15(7)	12(5)	8(5)	24(13)	6(5)	5(10)	8(9)	11(15)	42(17)	42(21)	45(19)	28(19)	35(18)	14(10)
(% phytophagous)	2	25(12)		30(11)	38(12)	61(13)	8(1)	9(4)	19(10)	6(4)	6(4)	4(5)	7(7)	27(15)	25(15)	27(17)	36(12)	17(11)	20(10)
(b) Light trapping (total mean numbers). Individuals collected per 10 hours' trapping monthly.																			
Blatlodea	1	2						0						3	0	0			
	2	1						1						0	0	1			
	3	1						1						0	1	1			
Orthoptera	1			0	0									0		0		0	
	2			2	0									1		2		1	
	3			0	10									0		4		1	
Phasmatodea	1																		
	2																		
	3																		
Hemiptera	1													1	0	0		1	
	2													0	0	3		4	
	3													0	1	6		0	
Thysanoptera	1		50	0		0													
	2		0	2		5													
	3		0	0		0													
Neuroptera	1	1				0		1						1	0	1		2	
	2	1				1		0						0	1	3		0	
	3	1				0		0						1	0	0		0	
Coleoptera (phytophagous)	1	2	0	345	20	28	0	1	0	0				0	2	35		12	
	2	2	7	28	3	8	11	1	1	2				3	5	28		5	
	3	0	3	30	0	27	6	0	0	0				0	20	41		12	

Appendix 1.(b) (cont'd)

Order		S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F
Coleoptera (Other)	1	8	2			0								10	0	2		0	3
	2	1	0			12								0	1	10		8	0
	3	5	5			0								1	1	10		0	1
Diptera	1	20	88	149	66	23	19	15	15	38	9	3		62	15	13		24	152
	2	28	70	128	80	71	34	135	54	75	140	9		36	210	97		58	346
	3	12	20	38	80	46	17	13	11	10	20	8		30	36	48		45	150
Lepidoptera	1	2	20	329	60	200	16	69	27	4	1	3		742	59	229		56	47
	2	1	79	186	29	193	19	54	34	1	3	0		21	167	332		151	78
	3	1	63	43	50	80	6	21	11	3	7	1		15	236	380		54	28
Hymenoptera	1	2	20	374	18	67	5	2						4	27	62		26	2
	2	0	0	0	2	70	8	0						4	2	3		29	0
	3	0	0	0	0	13	1	0						3	2	5		1	1
Arachnida	1		5	2			0												
	2		0	0			0												
	3		0	0			1												
Total number	1	37	180	873	174	316	40	88	42	42	10	6	261	823	104	343	250	121	204
	2	34	156	346	114	360	72	190	90	78	143	9	28	61	387	480	460	256	424
	3	20	90	111	140	166	30	35	22	14	27	8	26	50	297	495	360	115	180
Number herbivores	1	4(11)	20(11)	345(40)	80(46)	228(72)	16(40)	70(80)	27(69)	4(10)	1(10)	3(50)	89(34)	742(90)	61(59)	264(77)	115(46)	69(57)	47(23)
(% phytophagous)	2	3(9)	86(59)	214(62)	32(29)	201(56)	40(56)	55(29)	35(39)	3(4)	3(2)	0(0)	11(39)	24(39)	72(19)	363(76)	330(72)	161(63)	78(18)
	3	1(5)	65(72)	73(66)	50(36)	107(69)	12(46)	21(60)	11(50)	3(21)	7(26)	1(13)	8(31)	15(30)	257(87)	431(87)	270(75)	66(57)	29(16)