
Latitudinal trends in plant-pollinator interactions: are tropical plants more specialised?

Jeff Ollerton and Louise Cranmer, School of Environmental Science, Univ. College Northampton, Park Campus, Northampton, NN2 7AL, UK (jeff.ollerton@northampton.ac.uk).

The increase in richness of species and higher taxa going from higher to lower latitudes is one of the most studied global biogeographical patterns. Latitudinal trends in the interactions between species have, in contrast, hardly been studied at all, probably because recording interactions is much less straightforward than counting species. We have assembled two independent data sets which suggest that plant-pollinator interactions are not more ecologically specialised in the tropics compared to temperate latitudes. This is in contrast to a prevailing view that tropical ecological interactions tend towards higher specificity than their temperate counterparts.

Latitudinal trends in biodiversity are well known for many groups of organisms, with taxon diversity being positively or negatively correlated with latitude (MacArthur 1972, Rohde 1992, Gaston and Williams 1996). In contrast, we know much less about latitudinal trends in the biodiversity of species interactions. For example, as one moves from temperate to tropical latitudes, do predator-prey, parasite-host or mutualistic interactions become more ecologically specialised (defined as the number of species involved in the interaction, as distinct from morphological or evolutionary specialisation; Waser et al. 1996, Armbruster et al. 2000)?

The proposal that resources are divided more finely amongst a greater number of species in the tropics, compared to temperate communities (MacArthur 1972, Janzen 1973), suggests that tropical organisms should indeed be more ecologically specialised. However, low species diversity in very high latitude areas may also lead to apparent ecological specialisation in species interactions. In this case, the resulting latitudinal trend would be hump-backed – high specificity of interactions in the tropics and towards polar regions, with much lower specificity (greater generalisation) at temperate latitudes. Interestingly, the extremes of the gradient would show greater specialisation in interactions for diametrically opposite reasons – the tropics because of high species

diversity and consequent finer division of resources, polar areas because of low species diversity and therefore a lack of opportunity for species to be more generalised. Are there any data for global patterns of species interactions which might support or refute this idea?

Few quantitative studies have explicitly addressed the question of how the specificity of species interactions varies with latitude. For example, Scriber (1973) and Price (1980) looked at specialisation in larval feeding in Lepidoptera, Beaver (1978) dealt with bark and ambrosia beetles, Hawkins (1990) and Porter and Hawkins (1998) studied global patterns of parasitoid numbers per insect host, whilst Rohde (1978) focused on latitudinal trends in fish parasites. Their findings will be considered later, but the question of tropical ecological specialisation remains largely unresolved for most categories of interaction and the functional groups involved in these relationships.

Despite their importance in most terrestrial ecosystems (Kearns and Inouye 1997), we possess an inadequate knowledge of the broad biogeographic patterns of plant-pollinator interactions and the underlying causes of any pattern (Johnson and Steiner 2000). An initial reading of the literature would suggest that there is a consensus amongst pollination biologists that tropical pollination systems are more ecologically specialised than temperate systems (Johnson and Steiner 2000) but there are almost no data to support this assertion, and only limited data to refute it (Kevan and Baker 1983).

The data sets

As a step towards understanding whether pollination systems show a significant latitudinal trend in specialisation, we have assembled two independent data sets at different taxonomic/ecological scales, full details of

which are given in Appendices 1 and 2. The first data set is at the scale of the plant community and comprises 27 published and unpublished surveys of plant-flower visitor interactions in 35 communities at different latitudes. From these studies we extracted information on the latitude at which the study was undertaken (decimalised for the purposes of analysis), mean number of species of flower visitors per plant species (most of these studies recorded flower visitors rather than pollinators per se; however, number of flower visitors is strongly correlated with number of pollinators and this should therefore be an appropriate proxy [Ollerton, unpubl.]), number of plant species studied and sampling effort (number of field days of observation). The latter variable was in some studies explicitly stated and in others was estimated from the published information.

The second data set consists of 103 published and unpublished studies of pollinators of species of asclepiads (subfamily Asclepiadoideae of the Apocynaceae sensu Endress and Bruyns 2000). This is part of the on-line ASCLEPOL database (<http://www.uni-bayreuth.de/departments/planta2/wgl/fsigrid2.html>). As in the first data set, we extracted information on latitude, number of pollinators per plant species (in this case, a much more straightforward variable as asclepiads possess aggregations of pollen (pollinia) that mechanically clip onto flower visitors, making identification of pollinators much easier – see Ollerton and Liede 1997) and number of days of observation, which was available for only 59 of the 103 studies.

Results and discussion

Initial analyses of these data sets suggests that pollination systems do indeed become more specialised moving from temperate latitudes towards the tropics (Fig. 1a and b). In both the community and asclepiad data sets there is a significant positive relationship between latitude and number of pollinators/flower visitors per plant species. This is also true if the data are separated into northern and southern hemispheres (data not presented). However, closer analysis reveals that this pattern is misleading. The various studies included within the community and asclepiad data sets varied considerably in the sampling effort undertaken to observe and record flower visitors. To take account of this we have used sampling effort per plant species together with latitude as independent variables in a multiple regression analysis of the community data set (Table 1).

Forty percent of the variation in mean number of flower visitors per plant species is explained by this stepwise multiple regression model. However, only 4% of this variation results from the latitude at which the study was conducted (and this is only significant at $p = 0.075$ for the t-ratio test). The remaining 36% of the

variance in this regression model is explained by differences in sampling effort between communities. Clearly tropical community pollination studies suffer from under sampling of the true diversity of flower visitors per plant species (though note that latitude and sampling effort are not directly correlated – Pearson's Product Moment Correlation: $r = 0.05$, $df = 33$, $p = 0.78$).

The distribution of the asclepiad data set is highly non-normal and untransformable and therefore violates the requirements of multiple regression analysis. To take account of sampling effort for these data we have corrected number of pollinators per plant species by dividing by number of days sampling for the subset of data where this is known (Fig. 1c). Correcting for sampling effort in this way removes any correlation between latitude and pollinator specialisation. Once again, the apparently more specialised tropical species suffer from under sampling of pollinators.

Two completely independent data sets, at two different taxonomic scales, show precisely the same result, that tropical plants are, on average, no more ecologically specialised in their pollination systems than temperate species. We conclude that the apparent trend towards more specialised pollination systems for tropical plants shown in Fig. 1a and b is an artefact of sampling bias and that there is no significant latitudinal trend in the specificity of plant-pollinator relationships.

How do our results compare to the previously published studies cited earlier. In particular, is there any evidence from other work that the humpbacked latitudinal trend may occur in some interactions? These studies have looked at a range of organisms and types of interaction and have uncovered a variety of relationships between latitude and ecological specificity. Scriber (1973) was probably the first worker to confront quantitatively the problem of temperate versus tropical specialisation, in a study of larval host plant use in Papilionidae (Lepidoptera). His analysis showed that a higher proportion of temperate species could be considered generalist compared to tropical species. Scriber's definition of generalist taxa was "...those species feeding on more than one taxonomic family of plants...". This may be considered a rather broad definition of "generalised" and, intriguingly, Price (1980) presented data that suggested that tropical butterflies tended to be no more host specific than temperate species. Rohde (1978) found that tropical taxa of marine plathyelminth fish parasites in the group Digenea were more host specific than temperate taxa, but that this was not so in the Monogenea. Beaver (1978) showed that bark and ambrosia beetles (Coleoptera: Scolytidae and Platypodidae) are actually less host specific in the tropics compared to temperate communities, a pattern that he considered may be explained by the low population densities of host trees in the tropics. Hawkins (1990) studied parasitoids of phytophagous insects with different feeding ecologies and showed that those parasitising

exposed hosts tended to be more host specific in the tropics, whilst no such pattern was apparent for parasitoids utilising hosts concealed in plant tissue. Clearly, different categories of species interaction and different groups of taxa may or may not show increased specialisation in tropical environments.

A literature review by Kevan and Baker (1983) concluded that "...from the arctic and alpine areas to the lowland tropics, it appears that the frequency of occurrence of specialised pollination syndromes is about the

same". This conclusion is confirmed by the data that we have presented in this paper. Tropical communities provide some of the best examples of close co-evolved plant-pollinator relationships and in absolute terms do contain a higher number of plants with specialised pollination systems. However, tropical plant assemblages are on average many times more species-rich than their temperate counterparts and so may not in fact possess disproportionately more ecologically specialised pollination systems than temperate assemblages.

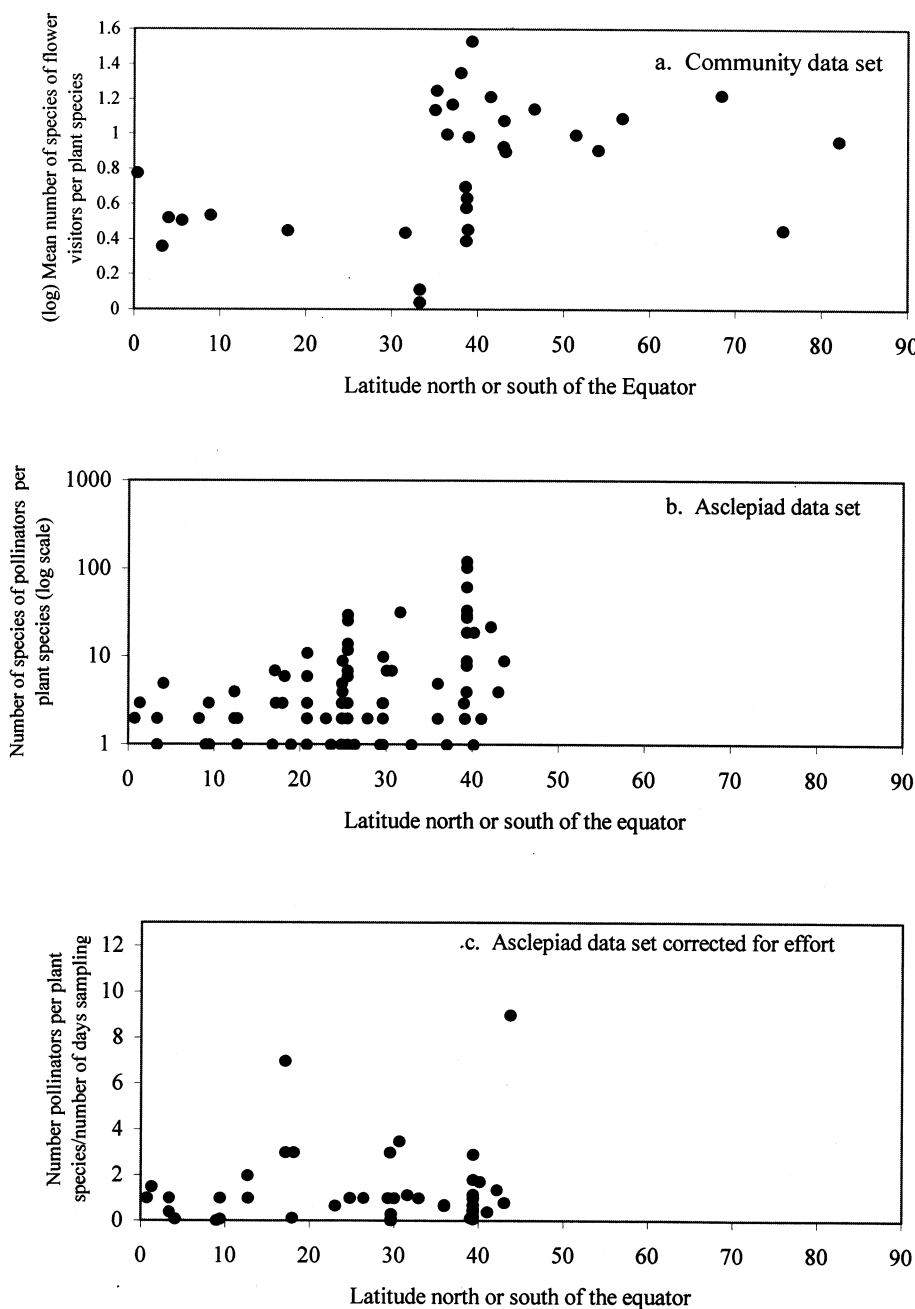


Fig. 1. Relationships between latitude and pollinator specialisation for the community survey and asclepiad data sets. a. Community surveys of plant-flower visitor relationships. Mean number of species of flower visitors per plant species has been log transformed. Pearson's product moment correlation: $r = 0.33$, $df = 33$, $p = 0.051$. b. Pollinators of asclepiads. Spearman rank correlation: $r = 0.33$, $n = 91$, $p = 0.002$. c. Pollinators of asclepiads, corrected for sampling effort. Spearman rank correlation: $r = 0.09$, $n = 59$, $p = 0.51$.

Table 1. Results of stepwise multiple regression on mean number of species of flower visitors per plant species for the community data set. All variables were natural log transformed.

Variable	Cumulative					
	r ² (adj.)	r ² (adj.)	F	Significance _F	t-ratio	Significance _t
Sampling effort	0.36	0.36	20.0	p < 0.0001	4.5	p < 0.0001
Latitude	0.04	0.40	12.4	p < 0.0001	1.8	p = 0.075

Problems with the data sets

The type of analysis that we have presented, in which largely pre-existing data are evaluated in relation to a question which they were not primarily collected to address, can be fraught with statistical problems. We have identified two possible causes for concern within the two data sets, which we detail below.

The first statistical problem concerns the phylogenetic relatedness of the plants and pollinators in the analysis. It is acknowledged (and debated) that possible phylogenetic biases must be taken into consideration in any comparative analysis (Harvey and Pagel 1991). However, the community survey data set spans such a wide range of plant and animal genera, orders and classes that a formal phylogenetically-corrected regression is not possible. Whether it is required for such a phylogenetically broad spread of taxa is arguable. In relation to the asclepiad data set, a robust molecular generic-level phylogeny of the group is not yet available. Therefore, whilst we recognise that the phylogenetic architecture of this data set may be a statistical problem (for example, the higher latitude data mainly come from North American *Asclepias* species) we cannot at the present time allow for this.

The second statistical problem specifically concerns the asclepiad data set. In order to correct for different sampling efforts across studies, for each plant the number of recorded pollinators was divided by the number of days of sampling. This correction assumes a linear relationship between sampling effort and number of pollinators per plant species. In reality the relationship is likely to be saturating, with records of new pollinators declining to zero at some point during the observation period. If the relationship between sampling effort and number of observed pollinators is indeed saturating, our simple correction would result in an under estimate of the number of pollinators per plant species expected from a given level of sampling effort. It is impossible to say what the exact sampling saturation point is as this information is never presented in studies of plant-pollinator interactions. In a recent survey of asclepiad pollinators at a site in South Africa, we had sampled all of the pollinators of some species in as little as 10 days, though for other species we were still recording new pollinators after 30 days (Ollerton et al. in prep.). Sampling saturation points (beyond which no new pollinators are recorded) are likely to vary between

plant species, localities and years and so there is no simple “rule of thumb” which would allow us to apply a simple correction. We have therefore opted to use a range of days of sampling effort to test how a saturating sampling function would affect our conclusions. We repeated the analysis of the asclepiad data set using sampling saturation points between 1 day and 60 days of sampling effort (Table 2). This covered the range of numbers of days of actual sampling effort undertaken by the various studies in Appendix 2. The analysis involved repeating the Spearman rank correlations between number of species of pollinator (corrected for sampling effort) and latitude and successively restricting the maximum number of days by which number of pollinators was corrected to 1, 2 ... 10 ... 20 ... up to 60 days. Low levels of maximum sampling effort (less than 10 days) yielded results not quantitatively different from that shown in Fig. 1b, with statistically significant relationships between latitude and number of species of pollinator. That is to say, correcting by a maximum of only a modest sampling effort is approximately similar to not correcting the data at all, a not unexpected result. The statistically significant correlation disappears when using more realistic saturation levels of

Table 2. Spearman rank correlations of latitude versus number of species of pollinators per plant species corrected by sampling effort for a range of sampling effort saturation points. N = 59 in all cases, except the uncorrected analysis, where N = 91.

Saturation point	Spearman's rho	p
Uncorrected	0.33	0.002
linear correction	0.09	0.51
1 day	0.46	0.0001
2 days	0.41	0.001
3 days	0.35	0.007
4 days	0.31	0.02
5 days	0.28	0.03
6 days	0.30	0.01
7 days	0.26	0.05
8 days	0.27	0.04
9 days	0.22	0.09
10 days	0.25	0.03
15 days	0.20	0.13
20 days	0.18	0.18
25 days	0.17	0.20
30 days	0.16	0.24
35 days	0.11	0.40
40 days	0.17	0.38
50 days	0.10	0.44
60 days	0.10	0.44

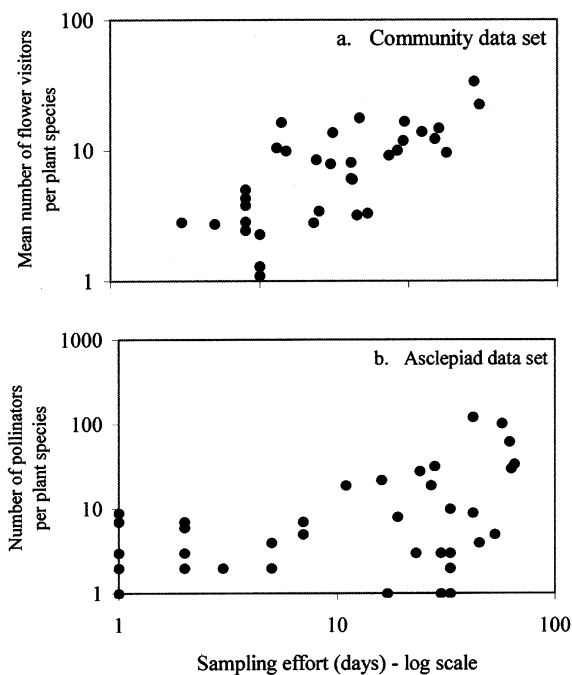


Fig. 2. The relationship between number of days sampling effort and the number of flower visitors/pollinators per plant species in (a) the community data set; and (b) the asclepiad data set. All axes are log scale.

greater than 10 days sampling (Table 2) and confirm the result obtained in Fig. 1c.

In conclusion, correcting the data for sampling effort using a realistic saturating function (by which we consider that 10 days or less of observation is unlikely to identify all of the pollinators of even a moderately generalised species) does not affect the results obtained when a linear, non-saturating correction is applied. This raises quite a fundamental issue in relation to studying pollination ecology – when can we be sure that we have identified all of the pollinators of a plant? The annual fluctuations in pollinator abundances that are a feature of many plant-pollinator systems (see, amongst many potential examples, Pettersson 1991, Fishbein and Venable 1996, Lamborn and Ollerton 2000) suggests that a time scale of years to decades may be necessary before a complete list of pollinators is obtained for generalist pollination systems. This is reinforced by a crude analysis comparing sampling effort to number of identified pollinators in the community and asclepiad data sets presented here (Fig. 2a and b). In both of the data sets there is no suggestion of a levelling off of numbers of identified pollinators as sampling effort increases.

We have attempted to be honest about the limitations of our data sets and would argue that appreciation of these problems does not negate their value, nor the value of our analyses. For the purposes of

exploring latitudinal trends in plant-pollinator interactions, these data sets are as good as any that could be currently assembled. We hope that by publishing this study we will stimulate interest in the question of tropical versus temperate specialisation in ecological interactions and that future researchers will obtain grants large enough to allow dedicated data collection that will tackle this question. Until such time, these data sets must suffice.

Acknowledgements – The ideas presented in this paper have benefited from discussion with many colleagues. We would particularly like to thank Scott Armbruster, Kevin Gaston, David Inouye, Steve Johnson, Duncan McCollin, Jane Memmott, Paul Neal, Jens Olesen and Nick Waser and an anonymous reviewer. We also thank Steve Johnson, Sigrid Liede, Jane Memmott, Jens Olesen, Anton Pauw and Milene Vieira for providing us with unpublished data. We are grateful to the following organisations for providing funding which contributed to some the results in the paper: The Royal Society, The Leverhulme Trust, Church and Co. PLC, The Biodiversity Trust, The Percy Sladen Memorial Fund and The Royal Entomological Society.

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Appendix 1. Studies included in the community-level data set.

Study	Habitat	Locality	Latitude N or S (decimalised)	Mean species of flower visitors	Sampling effort (days)	Number of plant species	Days sampling per plant species
Barrett and Helenurm (1987)	Boreal forest	nr Doaktown, Canada	46.55	13.9	123	12	10.3
Ramirez and Brito (1992)	Palm swamp	nr Calabozo, Venezuela	8.93	3.4	25	34	0.7
Percival (1974)	Coastal scrub	Morant Point, Jamaica	17.92	2.8	23	36	0.6
Robertson (1928)	Grassland and woodland	Carlinville, USA	39.28	33.5	275	278	1.0
Clements and Long (1923)	Montane conifer forest and grassland	Pikes Peak, USA	38.88	9.6	180	95	1.9
Herrera (1988)	Coastal scrub	Donana National Park, Spain	37.02	14.8	160	26	6.2
Burkill (1897)	Coastal grassland and woodland	Yorkshire, UK	54.00	8.1	41	37	1.1
Ramirez (1989)	Tropical shrubland	Guyana Highlands, Venezuela	5.58	3.2	45	46	1.0
Arroyo et al. (1982)	Alpine grass/scrub land	Andes, Chile					
		– low altitude	33.28	1.3	10	83	0.1
		– mid altitude	33.28	1.3	10	43	0.2
		– high altitude	33.28	1.1	10	36	0.3
Primack (1983)	Alpine grass/scrub land	New Zealand					
		– Cass	43.03	11.9	92	30	3.1
		– Mount Cook National Park	42.95	8.5	24	28	0.9
		– Craigieburn	43.20	7.9	30	49	0.6
Elberling and Olesen (1999)	Subarctic alpine tundra	Latnjajaure, Sweden	68.35	16.7	94	23	4.1
Willis and Burkill (1903–1908)	Subalpine grass/shrubland	Clova, Scotland	56.83	12.3	150	172	0.9
Momose et al. (1998)	Tropical rainforest	Sarawak, Malaysia	4.03	3.3	53	269	0.2
Inouye and Pike (1988)	Alpine grass/scrubland	Kosciusko National Park, Australia	36.42	10.0	84	40	2.1
Bosch et al. (1997)	Mediterranean grassland	Canet de Mar, Spain	41.42	16.4	14	17	0.8
Memmott (1999)	Temperate meadow	Bristol, UK	51.42	9.9	15	26	0.6
Moldenke and Lincoln (1979)	Alpine tundra	Colorado, USA	38.68	3.8	8	84	0.1
	Montane fescue grassland		38.52	5.0	8	100	0.1
	Montane spruce-fir forest		38.87	2.8	8	80	0.1
	Montane aspen forest		38.63	2.5	8	72	0.1
	Montane sagebrush		38.72	4.3	8	66	0.1
Struck (1995)	Semi-arid succulent vegetation	Knervslakte, South Africa	31.58	2.7	5	32	0.2
Mosquin and Martin (1967)	Arctic tundra	Melville Island, Canada	75.50	2.8	3	16	0.2
Kato et al. (1990)	Primary beech forest	Ashu, Japan	35.03	13.7	31	83	0.4
Inoue et al. (1990)	Temperate deciduous forest	Kibune, Japan	35.17	17.7	47	101	0.5
Ollerton et al. (unpubl.)	Tropical rainforest/savannah in- terface	Kumu, Guyana	3.25	2.3	10	18	0.6
Kanstrup and Olesen (2000)	Tropical rainforest canopy	Bilsa, Ecuador	0.35	6.0	42	47	0.9
Kevan (1970)	Arctic tundra	Hazen Camp, Canada	81.82	9.2	74	86	0.9
Petanidou (1991)	Mediterranean shrubland	Daphni, Greece	38.00	22.4	300	661	0.5
Small (1976)	Temperate peat bog	Mer Bleue, Ottawa	45.37	10.5	13	13	1.0
Hocking (1968)	Arctic tundra	Hazen Camp, Canada	81.82	6.5	41	37	1.1

Appendix 2. Studies used in the asclepiad data set. Note that data for sampling effort are not available for all studies.

	Latitude N or S (decimalised)	Number of species of pollinators	Sampling effort (days)	Number of pollinators/ sampling effort	Locality	Reference
<i>Asclepias cornuti</i>	39.28	28	24	1.17	Carlinville, Illinois	Robertson (1891)
<i>Asclepias cryptoceras</i>	37.00	1			SW Colorado	Payson (1916)
<i>Asclepias curassavica</i>	17.92	3	23	0.13	Morant Point, Jamaica	Percival (1974)
<i>Asclepias exaltata</i>	43.00	4	5	0.80	Devil's Lake, Wisconsin	Betz et al. (1994)
<i>Asclepias floridana</i>	39.28	9	42	0.21	Carlinville, Illinois	Robertson (1928)
<i>Asclepias hirtella</i>	41.00	2	5	0.40	NE Illinois/ NW Indiana, USA	Betz et al. (1994)
<i>Asclepias incarnata</i>	39.28	122	42	2.90	Carlinville, Illinois	Robertson (1891 and 1928)
<i>Asclepias incarnata</i>	43.64	9	1	9.00	SE Wisconsin	Macior (1965)
<i>Aclepias lanuginosa</i>	41.00	2	5	0.40	NE Illinois/ NW Indiana, USA	Betz et al. (1994)
<i>Asclepias longifolia</i>	39.28	8	19	0.42	Carlinville, Illinois	Robertson (1891)
<i>Asclepias meadii</i>	39.00	3	23	0.13	W. Missouri/ NE Kansas, USA	Betz et al. (1994)
<i>Asclepias purpurascens</i>	39.28	19	27	0.70	Carlinville, Illinois	Robertson (1891 and 1928)
<i>Asclepias quadrifolia</i>	42.11	22	16	1.38	Missouri, USA	Chaplin and Walker (1982)
<i>Asclepias solanoana</i>	40.13	1			Tehama County	Lynch (1977)
<i>Asclepias solanoana</i>	39.09	2			Lake County	Lynch (1977)
<i>Asclepias sullivantii</i>	39.28	30	63	0.48	Carlinville, Illinois	Robertson (1891 and 1928)
<i>Asclepias syriaca</i>	39.28	62	62	1.00	Carlinville, Illinois	Robertson (1928)
<i>Asclepias tuberosa</i>	39.28	34	65	0.52	Carlinville, Illinois	Robertson (1891 and 1928)
<i>Asclepias tuberosa</i>	31.56	32	28	1.14	Canelo Hills	Fishbein and Venable (1996)
<i>Asclepias verticillata</i>	40.10	19	11	1.73	Urbana, Champaign County	Willson et al. (1979)
<i>Asclepias verticillata</i>	39.28	103	57	1.81	Carlinville, Illinois	Robertson (1891 and 1928)
<i>Asclepias viridiflora</i>	39.28	4	45	0.09	Carlinville, Illinois	Robertson (1887 and 1928)
<i>Asclepias woodii</i>	29.60	2	33	0.06	KwaZulu-Natal, South Africa	Ollerton et al. (unpubl.)
<i>Aspidonepsis diploglossa</i>	29.60	3	33	0.09	KwaZulu-Natal, South Africa	Ollerton et al. (unpubl.)
<i>Calotropis gigantea</i>	8.98	1	30	0.03	Mannar, Sri Lanka	Wanntorp (1974)
<i>Calotropis gigantea</i>	12.30	2			Mysore and Srinivasapur	Ramakrishna and Arekal (1979)
<i>Calotropis gigantea</i>	8.20	2			Bandung, Java	Van der Pijl (1954)
<i>Calotropis procera</i>	25.45	6			Allahabad, India	Pant et al. (1982)
<i>Calotropis procera</i>	25.50	12			India	Bhatnagar (1986)
<i>Calotropis procera</i>	16.80	1			Timbuctu, Mali	Hagerup (1932)
<i>Calotropis procera</i>	24.90	4			Pakistan	Ali (1994)
<i>Caralluma arabica</i>	23.00	2	3	0.67	Oman	Jonkers (1990, 1993)
<i>Ceropegia albisepta</i>	18.90	1			Mandraka, Madagascar	Sabrosky (1987)
<i>Ceropegia bulbosa</i>	25.50	1			India	Bhatnagar (1986)
<i>Ceropegia bulbosa</i>	24.80	1			Pakistan	Ali (1994)
<i>Ceropegia lushii</i> var. <i>acuminata</i>	25.50	1			India	Bhatnagar (1986)
<i>Cosmostigma racemosum</i>	25.50	30			India	Bhatnagar (1986)
<i>Cynanchum adeladinae</i>	0.73	2	2	1.00	Gabon	Ollerton (unpubl.)
<i>Duvalia pubescens</i>	29.52	3	1	3.00	Concordia, South Africa	Meve and Liede (1994)
<i>Fischeria funebris</i>	9.37	3	30	0.10	El General, Costa Rica	Skutch (1988)
<i>Funastrum arenarium</i>	24.78	1	1	1.00	San Carlos, Baja California Sur	Liede (1994)
<i>Funastrum clausum</i>	17.05	7	1	7.00	Oaxaca, Mexico	Kunze and Liede (1991)
<i>Funastrum panosum</i>	18.13	6	2	3.00	Puebla, Mexico	Kunze and Liede (1991)
<i>Glossonema varians</i>	24.8	5			Pakistan	Ali (1994)
<i>Gomphocarpus physocarpus</i>	30.58	7	2	3.50	Vernon Crooks, South Africa	Johnson (unpubl.)

	Latitude N or S (decimalised)	Number of species of pollinators	Sampling effort (days)	Number of pollinators/ sampling effort	Locality	Reference
<i>Gongronema</i> sp.	4.03	5	53	0.09	Sarawak, Malaysia	Momose et al. (1998)
<i>Blepharodon nitidum</i>	3.33	2	5	0.40	Kumu, Guyana	Ollerton et al. (unpubl.)
<i>Gymanthera nitida</i> (?)	9.38	1	1	1.00	Torres Strait, Australia	Piper et al. (1991) and Forster (1991)
<i>Gymanthera nitida</i> (?)	12.70	1	1	1.00	Jabiru, Australia	Piper et al. (1991) and Forster (1991)
<i>Gymnema sylvestre</i>	25.50	7			India	Bhatnagar (1986)
<i>Holostemma annulare</i>	25.50	2			India	Bhatnagar (1986)
<i>Hoodia namaquensis</i>	29.28	1	1	1.00	Anenouspass, South Africa	Meve and Liede (1994)
<i>Leptadenia pyrotechnica</i>	24.90	9			Pakistan	Ali (1994)
<i>Leptadenia reticulata</i>	25.45	3			Allahabad, India	Pant et al. (1982)
<i>Marsdenia cymulosa</i>	12.65	2	1	2.00	Weipa, Australia	Forster (1992)
<i>Marsdenia fraseri</i>	26.33	1	1	1.00	Noosa National Park, Australia	Forster (1989)
<i>Marsdenia tenacissima</i>	25.50	7			India	Bhatnagar (1986)
<i>Matelea argentinensis</i>	24.80	1	1	1.00	Salta, Argentina	Liede (unpubl.)
<i>Matelea carolinensis</i>	35.93	2	3	0.67	North Carolina, USA	Drapalik (1969)
<i>Matelea carolinensis decipens</i>	35.93	5	7	0.71	North Carolina, USA	Drapalik (1969)
<i>Matelea reticulata</i>	17.15	3	1	3.00	Santa Cruz Etlá, Oaxaca	Liede (1994)
<i>Microloma sagittatum</i>	29.60	1	17	0.06	South Africa	Pauw (1998)
<i>Miraglossum verticillare</i>	29.60	1	33	0.03	KwaZulu-Natal, South Africa	Ollerton et al. (unpubl.)
<i>Morrenia odorata</i>	32.90	1	1	1.00	Mendoza, Argentina	Liede (unpubl.)
<i>Orthanthera albida</i>	23.55	1			Namibia	Nel (1995)
<i>Oxypetalum alpinum</i> var. <i>alpinum</i>	20.75	3			Vicosa, Brazil	Vieira and Shepherd (1999)
<i>Oxypetalum appendiculatum</i>	20.75	3			Vicosa, Brazil	Vieira and Shepherd (1999)
<i>Oxypetalum banksii</i> subsp. <i>banksii</i>	20.75	11			Vicosa, Brazil	Vieira and Shepherd (1999)
<i>Oxypetalum jacobinae</i>	20.75	2			Vicosa, Brazil	Vieira and Shepherd (1999)
<i>Oxypetalum mexiae</i>	20.75	1			Vicosa, Brazil	Vieira and Shepherd (1999)
<i>Oxypetalum pachyglossum</i>	20.75	3			Vicosa, Brazil	Vieira and Shepherd (1999)
<i>Oxypetalum capitatum</i>	3.33	1	1	1.00	Kumu, Guyana	Ollerton et al. (unpubl.)
<i>Oxypetalum subriparium</i>	20.75	6			Vicosa, Brazil	Vieira and Shepherd (1999)
<i>Oxystelma esculentum</i>	24.80	3			Vicosa, Brazil	Vieira and Shepherd (1999)
<i>Oxystelma secamone</i>	25.45	3			Allahabad, India	Pant et al. (1982)
<i>Pachycarpus natalensis</i>	29.60	1	33	0.03	KwaZulu-Natal, South Africa	Ollerton et al. (unpubl.)
<i>Pentarrhinum insipidum</i>	1.30	3	2	1.50	Kenyatta, Kenya	Liede (unpubl.)
<i>Pentatropis nivalis</i>	24.80	2			Pakistan	Ali (1994)
<i>Pergularia daemia</i>	12.30	4			Mysore, India	Ramakrishna and Arekal (1982–83)
<i>Pergularia daemia</i>	25.50	26			India	Bhatnagar (1986)
<i>Pergularia daemia</i>	25.45	1			Allahabad, India	Chaturvedi and Pant (1986)
<i>Pergularia daemia</i>	24.80	5			Pakistan	Ali (1994)
<i>Pergularia tomentosa</i>	27.80	2			Pakistan	Ali (1994)
<i>Philibertia gilliesii</i>	32.90	1	1	1.00	Mendoza, Argentina	Liede (unpubl.)
<i>Sarcostemma viminalis</i>	30.00	7	7	1.00	South Africa	Liede and Whitehead (1991)
<i>Sisyranthus trichostomus</i>	29.60	3	33	0.09	KwaZulu-Natal, South Africa	Ollerton et al. (unpubl.)
<i>Stapelia</i> sp.	25.50	7			India	Bhatnagar (1986)
<i>Telosma palida</i>	25.50	14			India	Bhatnagar (1986)

Appendix 2. (Continued).

	Latitude N or S (decimalised)	Number of species of pollinators	Sampling effort (days)	Number of pollinators/ sampling effort	Locality	Reference
<i>Wattakaka volubilis</i>	25.45	3			Allahabad, India	Pant et al. (1982)
<i>Xysmalobium gerrardii</i>	29.60	10	33	0.30	KwaZulu-Natal, South Africa	Ollerton et al. (unpubl.)
<i>Xysmalobium imolucratum</i>	29.60	2	33	0.06	KwaZulu-Natal, South Africa	Ollerton et al. (unpubl.)

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