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Factors affecting pollinator visitation rates: A biogeographic comparison

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Careful observations of flower visitors can provide estimates of pollinator visitation rates. Biological communities in varying biogeographic regions were compared using the same techniques. Bees were the predominant pollinators at low elevation sites, whereas flies were the most important pollinators at high elevations. Flower visitation rates varied by a factor of 10 across biological communities, suggesting that pollination activity may be limiting seed production in some places. Visitation rates were highly variable within communities, with temperature, wind speed, and time of the season explaining some of the variation. A picture emerges of relatively unspecialized relationships among the plants and animals involved in pollination, influenced by a variety of environmental and ecological factors.

CAREFUL observations of flowers and their visitors can yield information on the number of visits a flower receives in a certain time period, the *pollinator visitation rate*. Analysis of pollinator visitation rates can give valuable insight into the interaction between plants and their pollinators for those plants that require the services of pollinators to produce seeds. If visitation rates to such species are consistently low, the plants may have low seed production or even be threatened with extinction. Similarly, cultivated plants that need pollinators to produce a seed and fruit crop may have a low crop yield if pollinator visitation to the flowers is low. In the face of such strong selective pressure, flowering plants have evolved a variety of traits that help to attract pollinators, such as nectar production

and abundant pollen, or, in some cases, mechanisms for self-pollination and setting seeds in the absence of pollinators. Because most plant species do not grow in isolation, but in a community of potential competitors for the services of pollinators, visitation rates may serve as an indicator of their success in competing with other species for pollinators. Thus, comparisons of visitation rates among sites may shed light on differences in selective pressures among populations or species¹. Such comparisons can also highlight factors that limit plant reproduction in particular environments.

Another reason for measuring visitation rates is that they can provide insight about temporal variation in availability of pollinator species, either within or among seasons. Data on visitation rates can help in testing hypotheses such as, for instance, that visitation rates to flowers in the early spring are lower than visitation rates later in the growing season (e.g. ref. 2). Measurements of seed set may also provide similar information, but would not give any details about either the species of pollinators or mechanisms involved. Measurements of visitation rates can profitably identify the linkages among pollinators, plants, and subsequent seed set.

One potential pitfall in measurements of visitation rates is the fact that flower visitation may not necessarily translate into transfer of pollen onto the stigma of a flower. Careful observation or even microscopic examination may be required to confirm that a flower visitor is in fact a pollinator, although it is usually fairly obvious when species are foraging as to

which are nectar or pollen robbers with little chance of effecting pollination³. For some studies it may also be necessary to quantify the differences in effectiveness among different flower visitors. In this case, information on pollen removal or deposition per visit can be combined with visitation rate data to estimate pollen flow effected by different visitors⁴.

Visitation rates can be affected by the absolute or relative abundance of flower species, or of flower visitors⁵. These variables could potentially be assessed independently of measurements of visitation rates, by counting flowers or through insect censuses with malaise traps or trap nests. In addition, environmental variables are likely to affect visitation rates through effects on nectar production, pollen presentation, or the physiology of the flower visitor⁶. Thus, interpretation of visitation rates can be facilitated by simultaneous collection of data on environmental variables such as light levels, air temperature, relative humidity, and wind speed. Arroyo, Primack, and Armesto⁷ and Arroyo, Armesto, and Primack⁸ developed a protocol for making such measurements in conjunction with measurements of visitation rates in the Chilean Andes. These quantitative methods have since been used in additional studies in Australia⁹, South America¹⁰, North America, and Africa¹¹. A comparison and synthesis of these studies can demonstrate factors affecting pollination communities across biogeographic regions.

Experimental methodology

The method used for these studies involves 10-min observations in which the number of visitors to a known number of flowers is carefully recorded. The number of flowers watched can be adjusted so that an accurate count can be obtained, with more flowers being watched when visitation rates are low. To minimize the confusion between flower visitors and pollinators, only visitors that touch either the anthers or stigma are recorded. The observer's taxonomic skills will determine the level at which the insect visitors can be classified, but even observers with little entomological training can usually distinguish flies, bees, wasps, beetles, and Lepidoptera, while avian pollinators and particular common insects, such as honey bees, are often readily identified to species. Simultaneous with these observations, meteorological data are recorded with hand-held equipment. Wind speed is measured with an anemometer, incident light with a photographic light meter, and air temperature and relative humidity with a sling psychrometer.

Descriptions of sites

Pollination studies have been conducted at a variety of localities:

Chile

This study site is on the western slope of the Andes in the Mediterranean section of Chile in the general latitude of Santiago. The area has an estimated 400–500 mm of annual precipitation, and generally clear summer days. Pollination observations were carried out at three distinct vegetation zones: I, Subandean Scrub (2200–2600 m elevation), a species-rich zone with shrubs, annuals and geophytes. II, Cushion Plant Community (2700–3100 m), dominated by dense cushion plants. III, Subnival Feldfield (3200–3600 m), a rocky area with scattered grasses, rosette herbs, and small cushion plants.

Australia

The study site is in the Snowy Mountains, Kosciusko National Park, New South Wales, in the vicinity of Charlotte's Pass. The area is montane habitat dominated by snow gums (*Eucalyptus pauciflora niphophila*) and alpine habitat, ranging from 1860 to 2040 m elevation.

Massachusetts

The lowland woodland-meadow site in Belmont, west of Boston, is dominated by deciduous plants of meadow and oak woodland. The summer climate is moderate.

New Hampshire

This alpine tundra site in the Presidential Range of the White Mountains has a short growing season, high winds, and rapid weather changes.

South Africa

The fynbos site is in the Cape Province of South Africa. This species-rich site is dominated by shrubs, but has other growth forms as well. The climate is Mediterranean, but moderate temperatures and scattered rainfall allow flowering and vegetative growth to take place throughout the year.

Types of pollinators: What are the predominant pollinators at these diverse communities?

Bees are the most common type of flower visitors at the low elevation sites in Massachusetts and South African fynbos, and at Site I in the Chilean Andes. However, at the high elevation sites in Australia, Colorado, Chile (II and III), and New Hampshire, flies are the most important pollinators. These results are seen most

strongly in the mountains of Chile, where the bee species dominate as pollinators at 2200 to 2600 m but become rare in the 3200 to 3600 m range (Figure 1). The abundance of flies remains relatively constant across the elevational gradient, with the result that flies dominate the upper elevation site with butterflies also being important.

These results confirm early observations elsewhere in the world. Müller¹² emphasized the increasing importance of lepidopterans at high elevations in the European Alps. Mani¹³ points out that bee-pollinated plants are not normally found above 4000 m in the Himalayas, with fly and butterfly plants being dominant at higher elevations. Similarly, flies and moths were found to be key pollinators in the New Zealand montane flora¹⁴.

Pollinator visitation rates: Which community has the most pollinator activity?

Pollinator visitation rates were quantified using 10 min observation intervals of known numbers of flowers. While this length of observation is convenient for recording data, it is not effective for presenting data, since researchers are generally concerned with the number of visits to a flower during one day or over the lifetime of the flower. For ease of understanding, the data will be presented as the number of visits to a flower during the course of a day, assuming for convenience that there are 400 min of pollinator activity per day.

At all sites, pollinator visitation rates were highly

variable with many periods of little or no visitation interspersed with a few periods of intense activity. Analysing and interpreting such highly skewed, non-normal data must be done cautiously. With these limitations in mind, the various sites had widely differing pollinator visitation rates. The highest visitation rates were at the woodland-meadow site in Massachusetts, with comparable rates in both years (Table 1). At this site, each flower would be predicted to receive an average of 13 to 14 visits per day, which seems more than sufficient to pollinate the flowers. Intermediate visitation rates in the range of 6 to 9 visits per flower per day were evident in the New Hampshire tundra, the South African fynbos, and the Australian mountains. Visitation rates were lowest in the Andean sites, and there was a distinct decrease in visitation rates at higher elevations. At the Andean sites I (2200–2600 m), II (2700–3100 m), and III (3200–3600 m), visitation rates were 2.8, 1.6, and 1.3 visits per flower per day respectively. The lower visitation rates at higher elevations may not translate to lower overall number of visits per flower because often the flowers of high elevation species last longer than the flowers of low elevation species¹⁵. Such a phenomenon would tend to equalize the total number of visits received per flower during its lifetime.

Seasonal effects

All the three studies found strong seasonal effects. In Australia, visitation rates were 50% higher at the end of the flowering season than at the beginning. In Chile, pollination rates were low early in the growing season

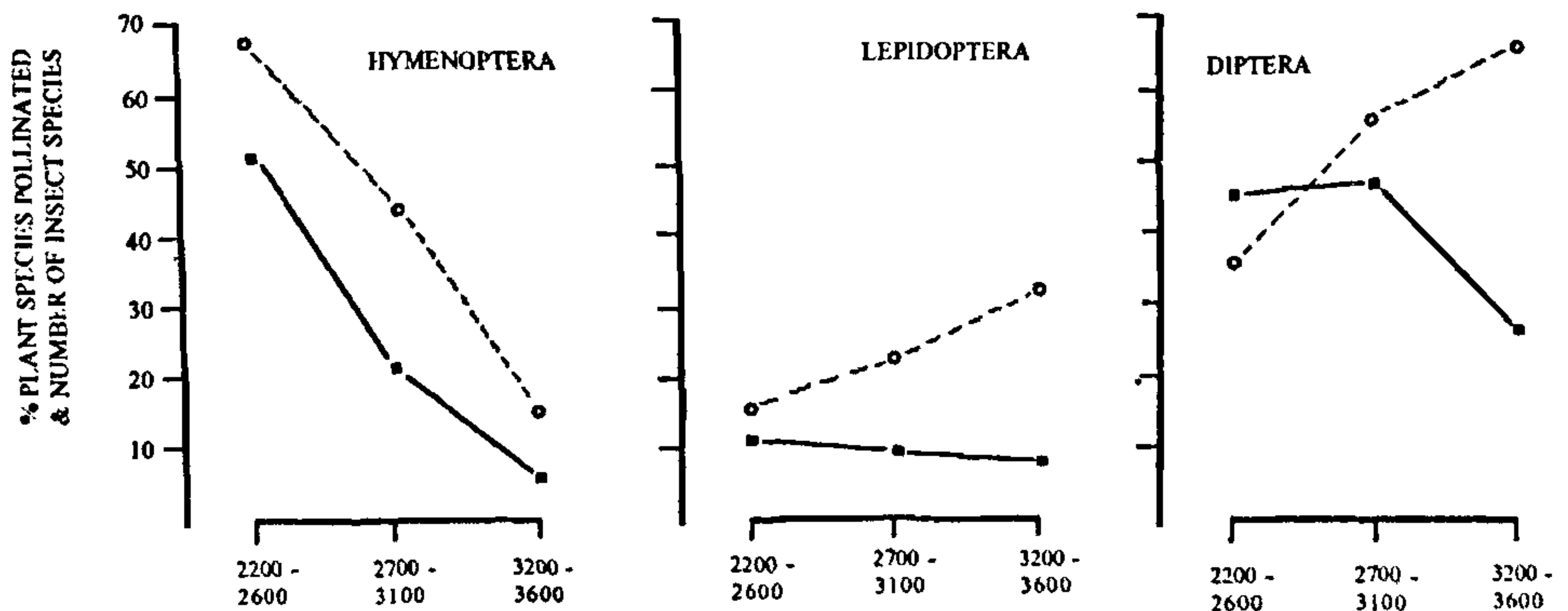


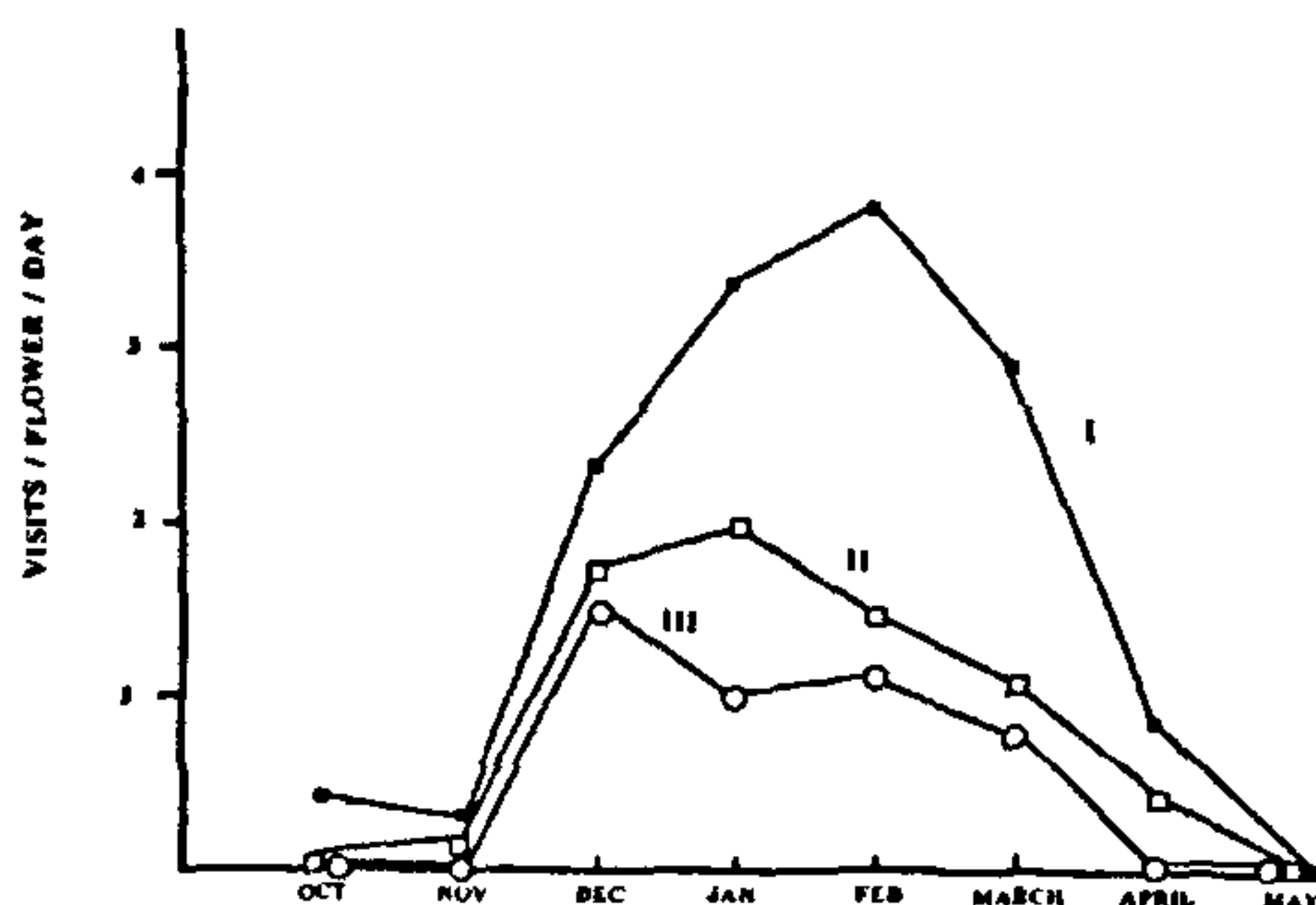
Figure 1. Percentage of plant species pollinated by bees and wasps (Hymenoptera), butterflies (Lepidoptera) and flies (Diptera), respectively, and insect species-richness at 3 sites with increasing elevation in the Central Andes. The total percentage exceeds 100, given that many species are pollinated by more than one kind of vector. Insect species-richness was determined from flower visitors collected throughout the entire flowering period. Circles: percentage of plant species pollinated by different types of insects. Squares: number of species of insect pollinators. From Arroyo et al.⁶.

Table 1. The mean frequency of insect visits to flowers (\pm SD) in contrasting communities, plus sample size

Site	Visitation rate (visits flower/400 minutes)	N
Woodland-meadow 1982	14.0 \pm 40.4	624
Woodland-meadow 1983	13.6 \pm 27.6	391
New Hampshire Tundra	8.8 \pm 22.8	319
South African Fynbos	7.2 \pm 23.2	472
Australian mountains	5.6 \pm 6.4	379
Andean sites		
I (2200–2600 m)	2.8	935
II (2700–3100 m)	1.6	891
III (3200–3600 m)	1.3	515

(October and November) and late in the season (March, April and May) in comparison with the middle of the growing season (December through March) (Figure 2). The peak month of flowering in Chile was progressively earlier at higher elevations; flowering took place during December at the highest site and February at the lowest site. Peak visitation rates occurred in the late summer at the Massachusetts woodland-meadow site, and during the late spring at the fynbos site. Overall, these results show that there is strong seasonal variation in visitation rates, but the pattern varies among different sites.

Seasonal variation is undoubtedly the rule in temperate habitats, and probably in most tropical ones too. For example, colonies of social bees, such as bumblebees, are annual colonies, with populations consisting of a single queen at the beginning of the season and increasing numbers of workers during the summer. Early species of flowers may bloom before flies or Lepidoptera emerge for the summer, with consequent low visitation rates. Many species of pollinators may only occur for limited parts of the flowering season. Even species of pollinators that are present during all of the flowering season, such as hummingbirds at high

**Figure 2.** Seasonal variation in visitation rates at three altitudinal levels in the high Andes of central Chile. Site I = ■, Site II = □, Site III = ○ (modified from Arroyo *et al.*⁸).

elevations in temperate North America, may vary in abundance, as young are born and as individuals vary in arrival time in the spring and departure time in the late summer. Data derived from monitoring methods such as malaise traps may provide insight into seasonal and annual patterns of insect abundance that are likely to be reflected in visitation rates⁴.

Weather and diurnal effects

Weather and diurnal effects affect visitation rates, but the patterns are characteristic to each site.

Wind speed

In the New Hampshire and Australian mountains, visitation rates were highest in calm weather, but the fynbos had the highest rates in moderately windy weather.

Temperature and light

At the fynbos, Australian, and woodland-meadow sites, visitation rates increased substantially at higher light levels and higher temperature (Table 2). At the Chilean sites, temperature was a major factor in determining visitation rates, with peak pollinator activity at 15–24°C for the high elevation site (3200–3600 m), whereas the lower elevation site (2200–2600) had peak visitation rates in the 20–34°C range (Figure 3).

Humidity

High humidity appeared to depress visitation rates in the fynbos.

Table 2. Summary of the effects of environmental variables on visitation rates at the Snowy Mountains, Australia site

Temperature	<10°C	10–15°C	>15°C
mean	2.1	5.4	6.7
S.D.	3.2	6.7	9.6
n	19	103	255
Wind speed	<2.5 m/s	2.5–3.0 m/s	>3.0 m/s
mean	7.2	6.6	4.4
S.D.	8.9	11.1	6.9
n	177	65	135
Light level	0–4 × 10 ⁴ lux	>4 × 10 ⁴ lux	
mean	4.6	7.2	
S.D.	7.0	9.7	
n	161	216	
Date	Dec–Jan	Feb–Mar	
mean	4.8	8.1	
S.D.	7.6	10.0	
n	231	146	

Differences among the classes are statistically significant for each variable. Visitation rates are expressed as the predicted mean number of visits to a flower over a 400-min day, standard deviation and sample size.

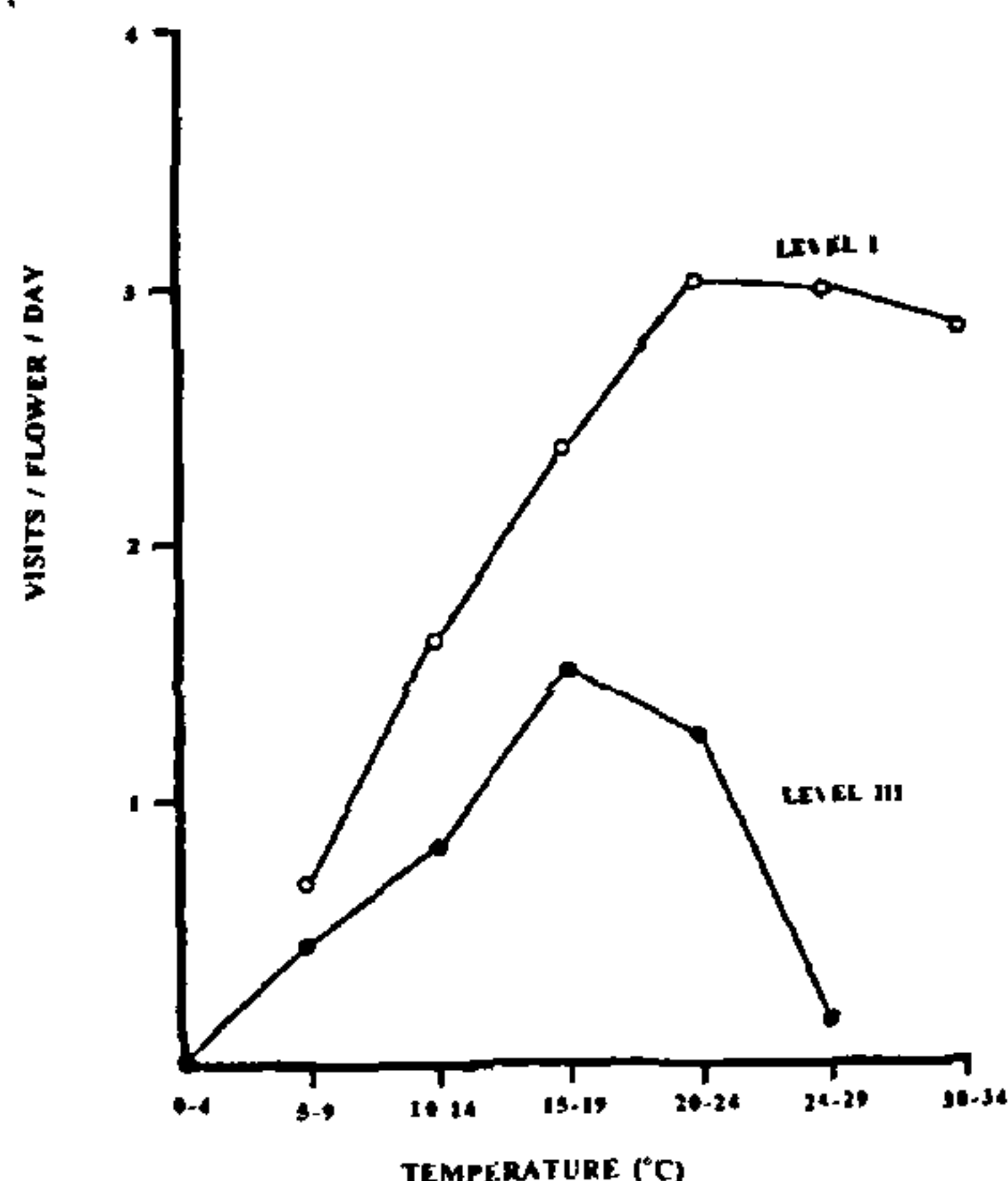


Figure 3. Comparison of the mean visitation rate at different temperatures in Level I (2200–2600 m s.m.) and Level III (3200–3600 m s.m). From Arroyo *et al.*⁸.

Time of day

High visitation rates were found in the middle of the day at the woodland-meadow site, but early in the day at the fynbos site.

These results indicate that environmental and seasonal variables are important in explaining variation in visitation rates. However, the relative importance of these factors varies dramatically among sites, with certain factors being important or unimportant at different sites. Discerning the key environmental variables is complicated by the fact that the variables are inter-correlated among themselves; for example, high temperatures tend to be associated with high light levels. In general, at any one site, seasonality, temperature and light levels to be closely linked to visitation rates, and are probably the most important factors to monitor.

Conclusion

The frequency of insect visits varied substantially among the five research sites, with the woodland-meadow having more than 10 times the visitation rates of the Andean sites. This result was unexpected because flowering in the Andes generally occurs in dry, sunny weather and the Andes have a high diversity of bee species. Also, the relatively high visitation rates observed in the New Hampshire alpine site were surprising, considering the windy, cold, and often cloudy conditions that frequently occur. These surprising results need to be verified at other sites. It also needs to be determined whether variation among sites

is due to differences in the abundance of pollinators, differences in the abundance of flowers, or differences in the relative activity of the pollinators. In any case, the results suggest that at certain sites, pollinator activity may be so low as to limit fruit set and seed set. The veracity of this suggestion needs to be determined by further experiments involving adding extra pollen to stigmas to test for increased reproductive output.

These results confirm earlier observations that pollinator communities vary considerably across environmental gradients and among biogeographic regions. A particularly critical variable identified here is elevation. Bees predominate as pollinators at low elevations, whereas flies and to some extent lepidopterans become important at higher elevations.

All five sites reported here are characterized by relatively unspecialized relationships between plants and the insects that visit their flowers. The highly specialized species relationships so frequently described in the literature, whereby one plant species is pollinated exclusively by one animal species¹⁶, appear to be relatively uncommon in nature. Rather, the flowers of large numbers of plant species are visited by an array of animals that are not specialized for any plant species¹⁷. Flower shape and color give some idea of the type of pollinators that might be expected to visit a particular species, but many other pollinators may visit the flower as well. Weather variables similarly have some degree of predictive power in explaining pollinator visitation rates. An independent measure of insect abundance, perhaps by using malaise traps (which are particularly effective for flies), might also help to decipher the significance of differences in abundance of pollinators. However, the percentage of overall variation explained within one habitat using these methods is slight, and the predictions may even run in opposite directions at different sites. These results show that pollination communities should often be considered highly variable and unspecialized. A new perspective that takes into account this loose association of plant species and flower visitors might lead to a more realistic picture of these guilds of species.

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The role of thrips in pollination

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The article reviews the role of thrips in the pollination of members of Asteraceae, Solanaceae and Fabaceae. Several features such as the highly synchronized phenology of flowering with the life cycle of thrips, modification of flowers to facilitate pollen transfer by thrips and definite pattern of host succession that help maintain the population of thrips are reported. We argue that these features represent strategies in plants favouring a strong association between the thrips and the plants.

THE efficiency of thrips-flower association for pollination depends on the dynamics of pollen transfer through thrips. Thus availability of pollen and nectar as reward, pollen-stigma interaction, pollen wall architecture, mechanism of pollen attachment to thrips are the critical factors in thrips-flower interactions. Synchronization of anthesis and nectar availability with the development of the pollinator as well as behavioural aspects of thrips, play an essential role¹. Generally thrips are considered as pure pollinators because unlike bees and butterflies they carry pollen grains of only one plant species. Active involvement of thrips in pollination is well documented by Anand² and Billes³ on cacao, Odland and Porter⁴ on *Capsicum annum*, Hagerup⁵ and Carlson⁶ on onion, Syed⁷ on oil palm, Appanah and Chen⁸ on *Dipterocarpus* and Kirk⁹ on *Echium plantagineum*. Indian work on thrips pollination biology was initiated at the Entomology Research Institute, Madras and are documented in the contributions of Ananthakrishnan and coworkers¹⁰⁻¹², Velayudhan and Annadurai^{13,14} and Gopinathan and Varatharajan¹⁵ on a few species of Asteraceae, Solanaceae and Fabaceae.

Asteraceae

Synchronization of flowering periodicity with the developmental phase of the pollinating thrips appears to be controlled by the population build-up of thrips, eventually leading to dispersal. This is established in

our studies on thrips pollination of *Tridax procumbens*, *Wedelia chinensis*, *Synedrella nodiflora*, *Vernonia cinerea*, *Ageratum conyzoides* and *Cosmos bipinnatus* (all Asteraceae). Our studies have also established the relation between the host succession, population build-up of thrips and possible implications for their associated evolution.

For instance, the succession patterns of the host plants *Wedelia*, *Synedrella* and *Ageratum* and their flowering periodicities enable *Microcephalothrips abdominalis* to maintain their populations throughout the year. The continued availability of hosts with ample intra-floral resources facilitates thrips to build their populations.

The adaptive nature of the pollinator to the flower appears impressive in *M. abdominalis* which has a 9-12 day life cycle. Oviposition in this species coincides with the emergence of the petals of the disc florets of *W. chinensis* in its late bud stage, so that the larval emergence, anthesis and nectar production in the flowers are all synchronized. The disc florets of Asteraceae are protandrous and when their stigmas emerge through the staminal columns they carry pollen grains also on their lower surfaces. The nectary is located at the base of the style with minute stomata-like apparatuses, which are distributed diversely in different species, with the guard-cells containing plenty of starch grains¹⁵. Nectar secretion coincides with pollen maturation, maximal secretion occurring when the stigmas are receptive, providing an opportunity for fertilization by the foraging insects with mature pollen on their bodies. Pollen loads were heavy with *Frankliniella schultzei* carrying 120-180 grains. Pollen loads of different species range from 25 to 200 in the adults and the larvae, the adults having an increased load due to greater surface area such as wing fringes, abdominal setae, as well as the antenna.

Incidentally, a limitation of the food reward in the flowers encourages the foragers to visit other plants. Species living in the heterogamous capitula spend lesser energy for their migration due to corymbose arrange-