Forum

Oikos 120: 321–326, 2011
doi: 10.1111/j.1600-0706.2010.18644.x

Subject Editor: Anna Traveset. Accepted 22 October 2010

How many flowering plants are pollinated by animals?

Jeff Ollerton, Rachael Winfree and Sam Tarrant

J. Ollerton (jeff.ollerton@northampton.ac.uk) and S. Tarrant, School of Science and Technology, Univ. of Northampton, Avenue Campus, Northampton, NN2 6JD, UK. Present address for ST: RSPB UK Headquarters, The Lodge, Sandy, Bedfordshire, SG19 2DL, UK. – R. Winfree, Dept of Entomology, Rutgers Univ., New Brunswick, NJ 08901, USA.

It is clear that the majority of flowering plants are pollinated by insects and other animals, with a minority utilising abiotic pollen vectors, mainly wind. However there is no accurate published calculation of the proportion of the ca 352 000 species of angiosperms that interact with pollinators. Widely cited figures range from 67% to 96% but these have not been based on firm data. We estimated the number and proportion of flowering plants that are pollinated by animals using published and unpublished community-level surveys of plant pollination systems that recorded whether each species present was pollinated by animals or wind. The proportion of animal-pollinated species rises from a mean of 78% in temperate-zone communities to 94% in tropical communities. By correcting for the latitudinal diversity trend in flowering plants, we estimate the global number and proportion of animal pollinated angiosperms as 308 006, which is 87.5% of the estimated species-level diversity of flowering plants. Given current concerns about the decline in pollinators and the possible resulting impacts on both natural communities and agricultural crops, such estimates are vital to both ecologists and policy makers. Further research is required to assess in detail the absolute dependency of these plants on their pollinators, and how this varies with latitude and community type, but there is no doubt that plant–pollinator interactions play a significant role in maintaining the functional integrity of most terrestrial ecosystems.

Plant–pollinator relationships may be one of the most ecologically important classes of animal–plant interaction: without pollinators, many plants could not set seed and reproduce; and without plants to provide pollen, nectar and other rewards, many animal populations would decline, with consequent knock-on effects for other species (Kearns et al. 1998). In addition, biotic pollination is thought to be a key factor in the diversification of some major groups of plants and animals (Dodd et al. 1999, Ollerton 1999). Human reliance on animal-pollinated crops demonstrates the value of the ecosystem services provided by pollinators: 75% of the world's leading food crops show increased fruit or seed set with animal pollination (Klein et al. 2007), with the economic value of this benefit being €153 billion annually, or 9.5% of the value of world agricultural production (Gallai et al. 2009).

In part because of the functional importance of biotic pollination, recent evidence for declines in native pollinator abundance and diversity has generated widespread concern (Biesmeijer et al. 2006, Kosior et al. 2007, Colla and Packer 2008, Grixti et al. 2009, Winfree et al. 2009, though see Ghazoul 2005). In response to these concerns, a number of national governments and organisations such as the Convention on Biological Diversity have instigated 'Pollinator initiatives' to protect pollinators. Most recently, the government of the UK, in consortia with the Wellcome Trust, has committed funding of £10 million (approximately $16.5 million) over the next five years for research aimed at halting pollinator declines.

Surprisingly, however, if a policy-maker or conservation planner were to ask an ecologist the straightforward question 'How many species of flowering plants are pollinated by animals?' the answer would be: 'We do not know'. There is no consensus nor even recent, evidence-based published estimate to which the questioner could be referred. Some of the most cited sources, whose estimates range from 67% to 96% of all angiosperm species being animal pollinated, are obscure as to how these figures have been calculated (Axelrod 1960, Renner 1996, Nabhan and Buchmann 1997). In contrast to the case for crop plants, which constitute $<$ 0.1% of all flowering plant species but have generated several recent reviews on animal pollination (Klein et al. 2007, Aizen et al. 2009, Gallai et al. 2009), there has been no systematic attempt to assess the fraction of the global flora that uses pollinators.

In order to provide an accurate estimate of the number and proportion of biotically pollinated flowering plant species worldwide, we compiled a data set of published and unpublished community-level surveys of plant–pollinator interactions that quantified the means of pollination, whether by animal or wind, for all plant species in the community. Our goals were to determine: (1) the variation in the proportion of animal pollinated flowering plants in terrestrial communities across latitudinal zones; (2) the global total number and proportion of flowering plants that use animals as pollinators.

It is important to realize that the fact that a plant species is pollinated by animals does not imply that all individual plants of that species require animal pollination in order to set seed at all times. Many species that use animal pollinators have a mixed mating system, meaning that individual plants can self-pollinate without the assistance of animals. However, at the species level, plants with mixed mating systems still require animal pollination because long-term selfing by all individuals would end inter-breeding among individuals of the same species. In addition, many plant species are either genetically self-incompatible or, although self-compatible, require animal pollinators to move pollen from the anthers to the stigma in order to self-pollinate. Lastly, a global meta-analysis of studies assessing pollen limitation in animal-pollinated plants suggests that individuals in many plant populations receive less pollen than is required for full seed set, particularly in regions with high plant diversity (Vamosi et al. 2006), which suggests that in general there is a high dependency of flowering plants on their pollinators.

Data set and methods

The data set of 42 surveys represents all of the available published studies that we could locate, plus eight unpublished surveys by ourselves and colleagues (Appendix 1). Studies were not included if they were restricted to particular life forms such as trees (Frankie 1980) or if they repeated similar studies in the same geographical area (Carpenter et al. 2003, cf. Kato and Kawakita 2004). We also excluded some potentially useful studies from Japan (Kato et al. 1993, Yamazaki and Kato 2003) because they were focussed mainly on animal pollinated species and excluded many species of wind pollinated plants, thereby biasing the community-scale estimates (M. Kato pers. comm. 2010). We took an ecological, community-level approach because we were interested in the ecological question of how many plant species in typical terrestrial communities are animal-pollinated, and how this fraction varies by latitude. An alternative approach, not taken here, would be phylogenetic, and would use the species rather than the plant community as the sampling unit. Such an approach is not feasible at present, however, given the fact that for most of the ca 352 000 species of flowering plants the mode of pollination is currently unknown, and that there have been repeated switches between wind and biotic pollination within some plant families (e.g. Asteraceae).

In each data set, researchers categorized plant species as either biotically pollinated (by insects and/or vertebrates) or wind pollinated based on observations of both flower visitors and the floral phenotype. A limitation of this approach is that it might misclassify plant species that are obligately self pollinating or non-sexually reproducing (e.g. seed production without fusion of gametes, such as apomixis), which, if flower visitors were observed, might be erroneously classified as biotically pollinated. Likewise, apparently wind pollinated taxa (e.g. some grasses) could also be obligate selfers or apomicts and would also be misclassified, which would serve to balance the relative proportions of biotically versus abiotically pollinated species. These errors should be small, however, because there are relatively few obligately apomictic and self-pollinating species and previous work suggests that these will be a small proportion of the total number of species within most terrestrial communities. For example, the studies by Moldenke in California and Chile estimated that between 1% and 9% of all species in each community were obligate selfers or apomicts, with up to 13% in Colorado communities (Moldenke 1979, Moldenke and Lincoln 1979). As the authors acknowledged even these estimates are likely to be too high due to low sampling effort for some species combined with infrequent insect visitation rates, resulting in some species being misclassified as obligate selfers when in fact they are animal pollinated (Moldenke and Lincoln 1979, p. 353). Therefore the inclusion of flowering plants that do not engage in out-crossing or sexual reproduction should not greatly affect the conclusions drawn from this analysis, though future analyses using more comprehensive data on plant breeding systems are certainly welcome.

The plant communities were classified according to latitudinal zone following Ollerton et al. (2006): temperate (64° to 40°), subtropical (39° to 30°), and tropical (29° to 0°). For the purposes of this paper, the arctic was not included as a zone as only one study meeting our criteria for inclusion could be found. Data were analysed using SPSS 17.0 for Windows.

Results and Discussion

The mean proportion of animal-pollinated plants increases from 78% of species in temperate-zone communities, to 94% in tropical communities (Fig. 1). This confirms the results of Regal (1982) who found that the proportion of wind pollinated trees and shrubs declined in tropical communities, for reasons that are still far from clear (Schemske et al. 2009). Our findings that there are significantly greater numbers of animal pollinated plants in tropical communities (regardless of life form) parallels the increase in the proportion of plants with functionally specialized pollination systems (i.e. pollinated by only a single functional group of animals, such as birds, hawkmoths, etc.) in tropical communities, as found by Ollerton et al. (2006). Whether these two patterns are directly associated is not known, but it is possible that the greater numbers of animal pollinated plants in the tropics has provided the impetus for the evolution of greater functional specialization (Schemske et al. 2009).

Using a global mean across all data sets, without accounting for the distribution of plant species in relation to latitude, we find that 85.0% of flowering plants are biotically pollinated; that is, 299 200 species, assuming a total figure of 352 000 species of angiosperms (Paton et al. 2008). However, a more accurate estimate will take into account the relative species richness of the different latitudinal zones, because the tropics have more angiosperm species than temperate and subtropical regions (Hillebrand 2004). Using the regional estimates of plant species richness from Kier et al. (2005),

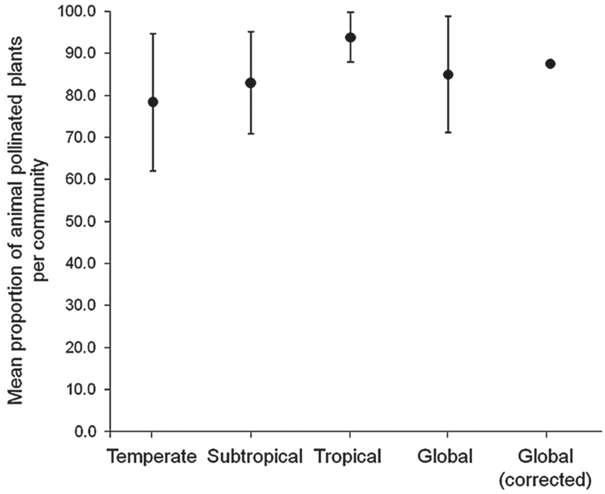

Figure 1. The mean (±SD) proportion of animal pollinated plant species found in terrestrial communities at different latitudes. The global average represents the mean of all studies used in the analysis. The global (corrected) average takes into account the relative distribution of plant diversity in the different zones. Data for the three latitudinal zones were analyzed with a one way ANOVA: $F_{2,39} = 5.9$, $p = 0.006$. LSD post-hoc test indicates that the only significant differences are between tropical and the other latitudinal zones.

we calculate that approximately 50.5% of angiosperm diversity is contained within the tropics, 27.7% in the subtropics and 21.8% the temperate regions. The number and proportion of biotically pollinated flowering plants can therefore be calculated as:

$$\Sigma(P_{zone} \times D \times B_{zone})$$

where: P_{zone} = the proportion of flowering plants in each of the three latitudinal zones; D = global angiosperm richness (estimated as 352 000 species by Paton et al. 2008); B_{zone} = the proportion of biotically pollinated flowering plants in each of the three latitudinal zones – Fig. 1.

Therefore the estimated number and proportion globally is: $(P_{tropics} \times D \times B_{tropics}) + (P_{subtropics} \times D \times B_{subtropics}) + (P_{temperate} \times D \times B_{temperate}) = (0.505 \times 352\,000 \times 0.939) + (0.277 \times 352\,000 \times 0.830) + (0.218 \times 352\,000 \times 0.784) = 308\,006$ species or 87.5% of all flowering plant species (Fig. 1).

Our estimates are based upon a sample of approximately 4000 flowering plant species, or slightly more than 1% of the estimated number of angiosperms, from a geographically non-random distribution of communities (Appendix 1). Nonetheless, this is the most comprehensive data set that can currently be assembled to answer the question of how many flowering plants are animal pollinated.

The high proportion of biotically pollinated flowering plants reinforces concerns about the potential consequences of pollinator losses for the world's flora. Although many plants are flexible as to their interactions with pollinators and there is significant substitutability in these communities (Alarcón et al. 2008), there is a point at which ecological redundancy is exhausted with continued pollinator species loss particularly in parts of the world where there is significantly greater ecological specialisation than is normally found, such as southern Africa (Johnson et al. 2009). If wild pollinator declines continue, we run the risk of losing a substantial proportion of the world's flora.

Acknowledgements – We would like to thank the authors of the published studies for their efforts, Nick Waser and Mary Price for supplying unpublished data, and Vince Tepedino and Makoto Kato for discussions. Thanks also to Linus Svensson and Anna Traveset for valuable comments that improved the manuscript.

References

Aizen, M. A. et al. 2009. How much does agriculture depend on pollinators? Lessons from long-term trends in crop production. – Ann. Bot. 103: 1579–1588.

Alarcón, R. et al. 2008. Year-to-year variation in the topology of a plant–pollinator interaction network. – Oikos 117: 1796–1807.

Axelrod, D. I. 1960. The evolution of flowering plants. – In: Tax, S. (ed.), Evolution after Darwin, Vol. I: The evolution of life. Univ. Chicago Press, pp. 227–305.

Biesmeijer, J. C. et al. 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. – Science 313: 351–354.

Carpenter, R. J. et al. 2003. Reproductive traits of tropical rainforest trees in New Caledonia. – J. Trop. Ecol. 19: 351–365.

Colla, S. R. and Packer, L. 2008. Evidence for decline in eastern North American bumblebees (Hymenoptera: Apidae), with special focus on *Bombus affinis* Cresson. – Biodiv. Conserv. 17: 1379–1391.

Dodd, M. E. et al. 1999. Phylogenetic analysis of trait evolution and species diversity variation among angiosperm families. – Evolution 53: 732–744.

Frankie, G. W. 1980. Tropical forest phenology and pollinator plant coevolution. – In: Gilbert, L. E. and Raven, P. H. (eds), Coevolution of animals and plants (revised edition). Univ. Texas Press, pp.192–209.

Gallai, N. et al. 2009. Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. – Ecol. Econ. 68: 810–821.

Ghazoul, J. 2005. Buzziness as usual? Questioning the global pollination crisis. – Trends Ecol. Evol. 20: 367–373.

Grixti, J. C. et al. 2009. Decline of bumble bees (*Bombus*) in the North American Midwest. – Biol. Conserv. 142: 75–84.

Hillebrand, H. 2004. On the generality of the latitudinal diversity gradient. – Am. Nat. 163: 192–211.

Johnson, S. D. et al. 2009. Advances in the pollination biology of South African plants. – S. Afr. J. Bot. 75: 625–629.

Kato, M. and Kawakita, A. 2004. Plant–pollinator interactions in New Caledonia influenced by introduced honey bees. – Am. J. Bot. 91: 1814–1827.

Kato, M. et al. 1993. Flowering phenology and anthophilous insect community in the cool-temperate subalpine forests and meadows at Mt. Kushigata in the central part of Japan. – Contrib. Biol. Lab. Kyoto Univ. 28: 119–172.

Kearns, C. A. et al. 1998. Endangered mutualisms: the conservation of plant–pollinator interactions. – Annu. Rev. Ecol. Syst. 29: 83–112.

Kier, G. et al. 2005. Global patterns of plant diversity and floristic knowledge. – J. Biogeogr. 32: 1107–1116.

Klein, A.-M. et al. 2007. Importance of pollinators in changing landscapes for world crops. – Proc. R. Soc. B. 274: 303–313.

Kosior, A. et al. 2007. The decline of the bumble bees and cuckoo bees (Hymenoptera: Apidae: Bombini) of western and central Europe. – Oryx 41: 79–88.

Moldenke, A. R. 1979. Pollination ecology as an assay for ecosystemic organization: convergent evolution in Chile and California. – Phytologia 42: 415–454.

Moldenke, A. R. and Lincoln, P. G. 1979. Pollination ecology in montane Colorado: a community analysis. – Phytologia 42: 349–379.

Nabhan, G. P. and Buchmann, S. L. 1997. Services provided by pollinators. – In: Daily, G. C. (ed.), Nature's services: societal dependence on natural ecosystems. Island Press, pp. 133–150.

Ollerton, J. 1999. The evolution of pollinator–plant relationships within the arthropods. – In: Melic, A. et al. (eds), Evolution and phylogeny of the arthropoda. Entomol. Soc. Aragon, Zaragoza, pp. 741–758.

Ollerton, J. et al. 2006. Geographical variation in diversity and specificity of pollination systems. – In: Waser, N. M. and Ollerton, J. (eds), Plant–pollinator interactions: from specialization to generalization. Univ. Chicago Press, pp. 283–308.

Paton, A. J. et al. 2008. Towards target 1 of the global strategy for plant conservation: a working list of all known plant species – progress and prospects. – Taxon 57: 602–611.

Renner, S. S. 1996. Effects of habitat fragmentation on plant–pollinator interactions in the tropics. – In: Newbery, D. M. et al. (eds), Dynamics of tropical communities. Blackwell, pp. 339–360.

Schemske, D. et al. 2009. Is there a latitudinal gradient in the importance of biotic interactions? – Annu. Rev. Ecol. Evol. Syst. 40: 245–269.

Winfree, R. et al. 2009. A meta-analysis of bees' responses to anthropogenic disturbance. – Ecology 90: 2068–2076.

Vamosi, J. C. et al. 2006. Pollination decays in biodiversity hotspots. – Proc. Natl Acad. Sci. USA 103: 956–961.

Yamazaki, K. and Kato, M. 2003. Flowering phenology and anthophilous insect community in a grassland ecosystem at Mt. Yufu, western Japan. – Contrib. Biol. Lab. Kyoto Univ. 29: 255–318.

Appendix 1. Studies used in the analysis.

Reference	Study site	No. of flowering plant species	Percentage of wind pollinated species	Percentage of biotically pollinated species	Latitudinal zone
Kress and Beach 1994	La Selva, Costa Rica	277	2.5	97.5	tropical
Burkill 1897	coastal scrub, UK	37	24.3	75.7	temperate
van Dulmen 2001	upland rainforest, Colombia	86	0.0	100.0	tropical
van Dulmen 2001	flooded rainforest, Colombia	101	2.0	98.0	tropical
Corlett 2001	scrub/secondary forest, Hong Kong.	83	0.0	100.0	tropical
O'Brien 1980	alpine pavement plain, California	15	13.3	86.7	subtropical
Robertson 1928	prairie, Illinois	391	3.8	96.2	temperate
Willis and Burkill 1895, 1903a, b,1908	lower alpine, Scotland	143	4.9	95.1	temperate
Bernadello et al. 2001	Juan Fernandez Islands, Chile	42	54.8	45.2	subtropical
Ramirez and Brito 1992	palm swamp, Venezuela	33	15.2	84.8	tropical
Momose et al. 1998	rainforest, Malaysia	129	0.0	100.0	tropical
Herrera 1988	semi-arid scrub, Spain	26	19.2	80.8	subtropical
Pojar 1974	salt marsh, Canada	18	66.7	33.3	temperate
	Sphagnum bog, Canada	34	41.2	58.8	temperate
	subalpine meadow, Canada	45	24.4	75.6	temperate
Waser and Price unpubl.	grassland, Virginia Basin, Colorado	64	9.4	90.6	temperate
Ollerton unpubl.	rainforest, Kumu, Guyana	59	5.1	94.9	tropical
	savannah, Kumu, Guyana	43	14.0	86.0	tropical
	grassland, Wahroonga, South Africa	74	6.8	93.2	temperate
	scrub/grassland, Mantanay, Peru	148	4.1	95.9	tropical
	scrub/grassland, Northampton - UK	162	20.4	79.6	temperate
	coastal scrub, Bahia de Patano, Venezuela	78	15.4	84.6	tropical
	xerophytic scrub, Güimar Badlands, Tenerife	18	11.1	88.9	subtropical
Ostler and Harper 1978	woodland, USA	125	36.0	64.0	temperate
Machado and Lopes 2004	Caatinga, Brazil	147	2.0	98.0	tropical
Gottsberger and Gottsberger 2006	Cerrado, Brazil	301	13.0	87.0	tropical
Moldenke and Lincoln 1979	alpine, montane Colorado	not given	17.0	83.0	temperate
	Aspen, montane Colorado	not given	21.0	79.0	temperate
	sage, montane Colorado	not given	12.0	88.0	temperate
	grassland, montane Colorado	not given	17.0	83.0	temperate
	spruce-fir woodland, montane Colorado	not given	19.0	81.0	temperate
Kato and Kawakita 2004	all habitats, New Caledonia	95	3.2	96.4	tropical
Kato 2000	all habitats, Amami Island, Japan	54	9.3	90.7	tropical
Moldenke 1979	coastal scrub, Torrey Pines, California	140	15.0	85.0	subtropical
	chaparral, Japatul Valley, California	157	11.0	89.0	subtropical
	chaparral, Echo Valley, California	72	10.0	90.0	subtropical
	oak-pine forest, Mount Laguna, California	84	20.0	80.0	subtropical
	desert scrub, Ocotillo, California	140	11.0	89.0	subtropical
	Papudo, Chile	154	17	83	subtropical
	Fundo Santa, Chile	158	21	79	subtropical
	Cero Porterillo, Chile	105	10	90	subtropical
	El Tofo, Chile	80	7	93	subtropical

References

Bernadello, G. et al. 2001. A survey of floral traits, breeding systems, floral visitors, and pollination systems of the angiosperms of the Juan Fernandez Islands (Chile). – Bot. Rev. 67: 255–308.

Burkill, I. H. 1897. Fertilization of some spring flowers on the Yorkshire coast. – J. Bot. 35: 92–189.

Corlett, R. T. 2001. Pollination in a degraded tropical landscape: a Hong Kong case study. – J. Trop. Ecol. 17: 155–161.

Gottsberger, G. and Silberbauer-Gottsberger, I. 2006. Life in the Cerrado. – Reta Verlag.

Herrera, J. 1988. Pollination relationships in southern Spanish mediterranean shrublands. – J. Ecol. 76: 274–287.

Kato, M. and Kawakita, A. 2004. Plant–pollinator interactions in New Caledonia influenced by introduced honey bees. – Am. J. Bot. 91: 1814–1827.

Kato, M. 2000. Anthophilous insect community and plant–pollinator interactions on Amami Islands in the Ryukyu Archipelago, Japan. – Contrib. Biol. Lab. Kyoto Univ. 29: 157–252.

Kress, W. J. and Beach, J. H. 1994. Flowering plant reproductive systems. – In: McDade, L. A. et al. (eds), La Selva: ecology and natural history of a neotropical rainforest. Univ. Chicago Press, pp. 161–182.

Machado, I. C. and Lopes, A. V. 2004. Floral traits and pollination systems in the caatinga, a Brazilian tropical dry forest. – Ann. Bot. 94: 365–376.
Moldenke, A. R. 1979. Pollination ecology as an assay for ecosystemic organization: convergent evolution in Chile and California. – Phytologia 42: 415–454.
Moldenke, A. R. and Lincoln, P. G. 1979. Pollination ecology in montane Colorado: a community analysis. – Phytologia 42: 349–379.
Momose, K. et al. 1998. Pollination biology in a lowland dipterocarp forest in Sarawak, Malaysia. Characteristics of the plant–pollinator community in a lowland dipterocarp forest. - Am. J. Bot. 85: 1477–1501.
O'Brien, M. H. 1980. The pollination biology of a pavement plain: pollinator visitation patterns. – Oecologia 47: 213–218.
Ostler, W. K. and Harper, K. T. 1978. Floral ecology in relation to plant species diversity in the Wasatch Mountains of Utah and Idaho. – Ecology 59:848–861.
Pojar, J. 1974. Reproductive dynamics of four plant communities of southwestern British Columbia. – Can. J. Bot. 52: 1819–1834.
Ramirez, N. and Brito, Y. 1992. Pollination biology in a palm swamp community in the Venezuelan Central Plains. - Bot. J. Linn. Soc. 110: 277–302.
Robertson, C. 1928. Flowers and insects: lists of visitors of four hundred and fifty-three flowers. – Privately published, Carlinville, Illinois.
van Dulmen, A. 2001. Pollination and phenology of flowers in the canopy of two contrasting rain forest types in Amazonia, Colombia. – Plant Ecol. 153: 73–85.
Willis, J. C. and Burkill, I. H. 1895. Flowers and insects in Great Britain. Part I. – Ann. Bot. 9: 227–273.
Willis, J. C. and Burkill, I. H. 1903a. Flowers and insects in Great Britain. Part II. – Ann. Bot. 17: 313–349.
Willis, J. C. and Burkill, I. H. 1903b. Flowers and insects in Great Britain. Part III. – Ann. Bot. 17: 539–570.
Willis, J. C. and Burkill, I. H. 1908. Flowers and insects in Great Britain. Part IV. – Ann. Bot. 22: 603–649.