Original Article

The macroecology of animal versus wind pollination: The macroecology of animal versus wind pollination: ecological factors are more important than historical climate stability

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Short running-title: The macroecology of pollination

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Abstract

Background: The relative frequency of wind and animal pollinated plants is non-randomly distributed across the globe and numerous hypotheses have been raised for the greater occurrence of wind pollination in some habitats and towards higher latitudes. To date, however, there has been no comprehensive global investigation of these hypotheses.

Aims: Investigating a range of hypotheses for the role of biotic and abiotic factors as determinants of the global variation in animal versus wind pollination.

Methods: We analysed 67 plant communities ranging from 70º North to 34º South. For these we determined habitat type, species richness, insularity, topographic heterogeneity, current climate and Late-Quaternary climate change. The predictive effects of these factors on the proportion of wind- and animal-pollinated plants were tested using correlations, ordinary least squares (OLS) and logistic regression analyses with information-theoretic model selection.

Results**:** The proportion of animal-pollinated plant species was positively associated with plant species richness and current temperature. Furthermore, in forest, animal pollination was positively related to precipitation. Historical climate was only weakly and idiosyncratically correlated with animal pollination.

Conclusion: Results were consistent with the hypothesised reduced chance for wind-transported pollen reaching conspecific flowers in species-rich communities, fewer constraints on nectar production in warm and wet habitats, and reduced relative effectiveness of wind dispersal in humid areas. There was little evidence of a legacy of historical climate change affecting these patterns.

Keywords: abiotic, biotic, community ecology, forest, mutualism, open vegetation, pollen dispersal, precipitation, species richness, temperature.

Introduction

Pollination is a fundamental ecological process that is crucial for the functioning of most terrestrial ecosystems (Kearns et al. 1998; Ollerton et al., 2011; Lever et al., 2014). Plants achieve pollen transfer among conspecifics using biotic (animal) and abiotic (wind and, rarely, water) pollen vectors. Wind pollination occurs in about 20% of angiosperm families and most groups of gymnosperms (Ackerman 2000), an estimated 12.5% of all angiosperm species are wind pollinated (Ollerton et al. 2011). Wind pollination is a derived condition that has evolved independently more than 60 times within otherwise animal-pollinated clades (Ackerman 2000; Friedman and Barrett 2009; Hu et al. 2012), with occasional reversions to biotic pollination (e.g. Wragg and Johnson 2011).

Wind pollination is currently understood to be a reproductive strategy that evolves when pollinators become unpredictable or unavailable (Barrett 1996; Culley et al. 2002; Friedman and Barrett 2009). Supporting this idea, the proportion of wind-pollinated plants is higher in the temperate zone (Culley et al. 2002; Ollerton et al. 2011), where climate is less stable seasonally (Cramer et al. 1999) and over longer glacial–interglacial time scales (Sandel et al. 2011). In temperate regions usually < 80% of the plant species within a community are animal pollinated, whereas animal pollination is more common in the tropics where on average ≥90 % of all co-occurring plants are pollinated by animals (Whitehead 1969; Regal 1982; Ollerton et al. 2011). Although this latitudinal pattern is already known, no study has quantitatively assessed the possible factors related to the global variation of community-level differences in wind *versus* animal pollination (Barrett 1996; Schemske et al. 2009; Ollerton et al. 2011).

The efficiency of wind and animal pollination may depend on the biotic and abiotic environment where plants occur. A number of testable hypotheses for geographic variation in wind *versus* animal pollination have been put forward (Whitehead 1969; Culley et al. 2002). For instance, extensive, dense and species-rich forests with high canopy and low wind speeds are supposed to be unfavourable places for wind pollination because the chance of wind transporting pollen to a conspecific should be rather low (Whitehead 1969; Regal 1982; Ollerton et al. 2006, 2011; Culley et al. 2002). Climate may also affect the efficiency of wind pollination. High humidity should make the cytoplasm of the pollen grains to collapse or become heavier and cause them to clump, reducing pollen dispersal distance (Whitehead 1969; Niklas 1985). Additionally, high temperature and precipitation may increase productivity and support more nectar production for animal pollination.

Thus, both mean annual temperature and precipitation should correlate positively with the proportion of animal pollination. On the other hand, high temperature and precipitation seasonality may promote wind pollination as pollinator abundances will fluctuate through the year, becoming less reliable pollen vectors (Regal 1982), unless pollination is in synchrony with these seasonal fluctuations in pollinator abundances, thereby causing no measurable effect on pollination mode (McKinney et al. 2012). Finally, in topographically flat environments such as coastal plains wind pollination could be favoured due to more constant and fast winds. Likewise wind pollination could be more frequent on islands because wind-pollinated plants are independent of pollinator colonisation to maintain reproduction (Kühn et al. 2006; Crawford et al. 2011).

Paleoclimate has been linked to contemporary ecological patterns, such as species distributions and endemism (Svenning and Skov 2007; Cárdenas et al. 2011; Sandel et al. 2011; Kissling et al. 2012), and the structure of interactions within communities of plants and pollinators (Dalsgaard et al., 2011, 2013; Groom et al., 2014). Past climatic instability may have broken up mutualistic associations between plant species and their pollinating animals (Dalsgaard et al., 2011, 2013, McKinney *et al*., 2012) that may have favoured wind pollination and could be related to the contemporary composition of plant communities.

Here, we use a global dataset to describe (1) latitudinal patterns in pollination mode, and (2) the relationships between putative contemporary and historical factors, and the proportion of animal *versus* wind pollinated species in plant communities around the world. Specifically, following on from the discussion of abiotic and biotic factors that other authors have presented, we test the following hypotheses:

1. Wind pollination is less frequent in closed forest habitats compared to more open habitats, such as grasslands.

2. Animal pollination is more frequent in areas with higher mean annual temperature and precipitation.

3. Conversely, wind pollination is more frequent in regions with lower temperature and greater seasonality of precipitation.

4. Animal pollination is more frequent in communities with high plant species richness.

5. Wind pollination is more frequent in topographically flat environments.

6. Animal pollination is less frequent on islands.

7. Wind pollination is more frequent in those areas of the world that have experienced greater climatic instability during the Quaternary.

Materials and methods

Animal versus *wind pollination datasets*

The dataset was taken from 82 published and unpublished community-based assessments of the proportion of wind and animal pollinated species. These studies are censuses of all native angiosperm species in flower in a given community at a specific time. Gymnosperms were not considered by most of the published studies, hence we excluded gymnosperms from all communities. The latitudes ranged from 34° S to 70° N (Figure 1). When the same geographic coordinates were attributed to communities within the same vegetation type by the original authors, we pooled them together and used the mean of pollination mode proportion as a descriptor of the proportion of animal pollination for those coordinates. Doing this, we reduced the dataset to 67 data points for the spatial analysis (Appendix Table S1).

In some of the published community studies no species list was available, just data on the proportions of wind and animal pollinated species observed, preventing us from attributing genera or families to the data analysed by the original authors. For those studies having a species list, pollination mode at the species level was highly correlated with higher taxa, i.e. genera and families (Table 1). This does not mean that species within the same genus have always the same pollination mode. It implies that proportions are constant across taxonomic levels and therefore any level may be used in the analysis. For the published studies we followed the information provided by the original authors as to the pollination mode (wind or animal) of a given species. For our own field observations, flowers were assessed in terms of presence or absence of: mass pollen release when an inflorescence was shaken, reduced corolla, and feathery stigmas (wind pollination); or large and colourful flowers with scent or nectar, and the presence and behaviour of potential flower visitors (animal pollination) (Figure 2; see also Table 1 in Friedman and Barrett 2009). We paid particular attention to species with small, dull flowers, e.g. some tropical trees, where only the presence of scent, nectar, and/or insect visitation distinguished biotic from abiotic pollination.

The proportion of animal-pollinated plant species could be underestimated because some plant species that possess wind pollination traits can also be visited and sometimes pollinated by animals (Figueredo and Sazima 2000). There might also be cases of obligatory self-pollinating and non-sexually reproducing species coded as wind or animal pollinated, though this should be a relatively minor and not spatially structured bias and, hence, should not affect our results (Ollerton et al. 2011). Similarly to Ollerton et al. (2011), we took a community-level approach as we were interested in the ecological question of how large a proportion of plant species in terrestrial communities are animal or wind pollinated, and the possible factors related to these proportions. However, first, we measured the phylogenetic signal for pollination mode by means of Phylogenetic Eigenvector Regression (PVR) considering the species lists where plants were identified up to the species level (Diniz-Filho et al. 2012). Species lists were available for 56 plant communities, including 1689 genera. Phylogenetic information was extracted at genus level from Phylomatic (R20120829 stored tree, Webb and Donoghue 2005) and the tree generated by using Phylocom (Webb et al. 2008). PVR was calculated by using a principal coordinate analysis (PCoA) of the phylogenetic distance matrix and selecting the 50 first axes. Phylogenetic signal was obtained by the logistic regression coefficient (R^2) between the selected phylogenetic eigenvectors and the binomial pollination mode (Diniz-Filho et al. 2012). Phylogenetic signal significance was tested by measuring PVR on 1000 randomisations of the pollination mode in the phylogeny. The analysis was carried out by using the package PVR for R (Santos et al. 2013). Since phylogenetic signal of pollination mode was very low (PVR for 50 eigenvectors = 0.0411; $P = 0.47$; DF = 50; Deviance = 50.2) no taxonomic correction was required. The low phylogenetic signal probably came out of many independent origins of wind pollination and, due to many genera having one pollination mode also showing a minority of species possessing the other pollination mode.

Correlates of pollination mode

For each site, we extracted variables of contemporary and historical climate conditions hypothesised to affect the degree of wind *versus* animal pollination. Current climate descriptors included mean annual temperature (MAT), mean annual precipitation (MAP), temperature seasonality (MAT seasonality) and precipitation seasonality (MAP seasonality) extracted at 2.5 arc-minute resolution (approximately 16 km^2) from the WorldClim dataset (www.worldclim.org;

Hijmans et al. 2005). As different climate change metrics may capture different effects of climate change (Garcia et al. 2014), we considered two measures of historical climate stability: (1) the velocity of mean annual temperature (MAT velocity) and that of mean annual precipitation (MAP velocity) between the Last Glacial Maximum (LGM) and the present; and (2) the anomaly of mean annual temperature (MAT anomaly) and mean annual precipitation (MAP anomaly) between the LGM and the present (current minus LGM precipitation/temperature – i.e. positive values indicate wetter or warmer contemporary conditions, respectively). Velocities reflect the speed of climate change irrespective of the direction, integrating macroclimatic changes and local spatial topoclimate gradients (Loarie et al. 2009; Sandel et al. 2011), whereas anomalies reflect the direction of climate change. Paleoclimate estimates were obtained from the CCSM3 model (Collins et al. 2006; Otto-Bliesner et al. 2006), and statistically downscaled to 2.5 arc-minute resolution to match the current climate data (Hijmans et al. 2005).

In addition, we determined potentially important non-climate descriptors of local conditions at each site, including whether the site was on the mainland (coded as 0) or on an island (1), topographic heterogeneity, regional proportion of tree cover, plant species richness, and whether the vegetation was forest (0; n = 16) or open vegetation type (1; grassland, scrubland, and other low and open vegetation types, n = 51). Topographic heterogeneity was calculated as the range of elevation values observed in a 0.2° × 0.2° window (ca. 20 km × 20 km) centered on the sampling location, using the WorldClim 1-km DEM (Farr et al. 2007). The regional proportion of tree cover was calculated as the average tree cover observed within a window of 64 km x 64 km around each site, based on the Vegetation Continuous Fields product applied to MODIS data (Hansen et al. 2003).

Statistical analyses

For all analyses, plant species richness, MAT anomaly, precipitation and temperature velocities were $\log_{10}$-transformed; contemporary mean annual precipitation and topography were square-root transformed; the proportion of regional tree cover was arcsine square-root transformed. The proportion of animal pollinated plant species in each community was arcsine square-root transformed for ordinary least squares (OLS) regression, but was left untransformed for logistic regression. All other variables were left untransformed.

First, the latitudinal pattern in pollination mode was tested with a quadratic regression between latitude and the proportion of animal pollination. Second, for all vegetation types, and separately for open vegetation types and forest, we tested the univariate associations between all predictor variables and between the proportion of animal pollinated plant species and all predictor variables (Appendix Table S2). This identified predictor variables that were strongly inter-correlated. For all further analyses, we excluded temperature seasonality as it was strongly correlated with mean annual temperature ($r = -0.73$, $P < 0.001$, $n = 67$), and we excluded the proportion of regional tree cover as it was unavailable for three island datasets and strongly correlated with contemporary precipitation ($r = 0.73$, $P < 0.001$, $n = 64$; see Appendix Table S2). Due to the strong positive relationship between precipitation and the proportion of regional tree cover, we adjusted our above hypothesis of a unidirectional positive effect of precipitation on animal pollination. For forest, we still expected a positive correlation between precipitation and the proportion of animal pollination. For open vegetation types, on the other hand, we expected a less strong (or even zero) effect of precipitation due to the possible opposite effects of increasing precipitation (favouring animal pollination) and associated increasing fragmentation of open vegetation communities surrounded by increasing amounts of forests as precipitation and regional tree cover coincide (increased fragmentation favouring wind pollination).

To test the study hypotheses, we used ordinary least squares (OLS) and logistic regression, conducting information-theoretic model selection, as outlined by Diniz-Filho et al. (2008). In doing so, we tested the effect of both measures of historical climate stability, i.e. temperature/precipitation velocity and anomaly; the anomaly models generally performed the best (highest R^2 and lowest AIC), so we focus the discussion on these models (but we also report models including velocity). First, we fitted models with all combinations of the explanatory variables: forest versus open vegetation, insularity, plant species richness, contemporary precipitation, contemporary temperature, precipitation seasonality, topography and historical climate stability as measured by temperature and precipitation anomaly. Furthermore, due to the possible different effect of precipitation in open and forest vegetation, we included an interaction term between precipitation and forest versus open vegetation. We then identified minimum adequate models (MAMs) among these as any model with $\Delta AIC_c < 2$ ($n = 67$, 1023 alternative models; Table 2). When using temperature and precipitation velocity as a measure of climate stability, we excluded topography as it is strongly correlated with velocities (Appendix S2), i.e. when using velocity as our historical climate variable we compared 511 models. We were unable to estimate velocities for one island data point, therefore in models using velocities there is one data point fewer.

Standardised regression coefficients are reported for both a multi-model average regression model based on weighted w_i and the MAMs (Diniz-Filho et al. 2008). We tested whether significant ($P < 0.05$) positive spatial autocorrelation remained in OLS model residuals, tested using 10 distance classes and applying a permutation test with 10,000 iterations. As no spatial autocorrelation was found in our anomaly models that performed the best, we did not use spatial models. All correlations and OLS regression analyses were conducted using Spatial Analysis in Macroecology 4.0 (Rangel et al. 2010). Logistic model selection analyses were carried out in R (R Development Core Team, 2014) using the ‘MuMIn’ package (Barton 2015).

Results

The proportion of animal-pollinated plants in a community decreased with latitude (Figure 1). This pattern appeared to be largely symmetrical across the Equator, though there was a geographical bias to the distribution of the studies, and more data from Africa and Asia, in particular, are needed to confirm the observed pattern.

The models to assess the relative importance of the factors tested as determinants of the proportion of animal pollination showed that overall the explanatory power was considerably higher for current climate variables (ca. $32\% < R^2 < 36\%$) than for species richness (ca. $4\% < R^2 < 5\%$) and historical climate variables (ca. $0\% < R^2 < 2\%$; Table 2 and Appendix S3). The proportion of animal pollination in both simple univariate correlations and in regression models was strongly and positively associated with current temperature and species richness (Figure 3; Table 2; Appendix S3). Furthermore, the interaction term between precipitation and vegetation type was included in the best-fit regression model (Table 2; Appendix S3), indicating that precipitation correlated strongly with the proportion of animal pollination in forest (Figure 3; Appendix S2). There were only weak associations with topography and temperature anomaly and velocity (Table 2, Appendix S2). In addition to explaining little variation in pollination mode, topography and historical temperature anomaly/velocity associated positively with animal pollination in regression models (Table 2), but were unrelated in simple univariate correlations (Table S1). In logistic, but not in OLS, regression islands were found to have a lower proportion of animal pollination. Seasonality, precipitation anomaly, and precipitation velocity were not statistically significant in simple univariate correlations nor were they included in any MAMs (Table 2 and Appendix S3).

Discussion

The proportion of plant species using animal versus wind pollination in a given community is non-random with respect to latitude, animal pollination being especially dominant in the tropics (Figure 1), confirming previous studies, but with a much larger and geographically widespread data set. We found that differences in the proportion of animal pollinated species were associated mainly with current climate (Figure 3). Notably, temperature was overall positively related to the prevalence of animal pollination (partly supporting hypothesis 2), and in forests animal pollination was more frequent in areas with higher precipitation (supporting both hypothesis 1 and, in part, hypotheses 2 and 3). However, the 'more wind pollination with greater precipitation seasonality' aspect of hypothesis 3 was not supported, perhaps due to the different nature of seasonality in the lowland tropics (wet, dry) compared with the temperate or high altitude zones (cold and warm). In addition to current climate, we found that communities with greater local plant species richness have a higher proportion of animal pollination (supporting hypothesis 4). On the other hand, topography had little effect on frequency of pollination mode, not supporting hypothesis 5. Kühn et al. (2006) showed that wind pollination in Germany is more frequent in the flat landscapes of north relative to other parts of the country, although it increases also toward the southern Alpine uplands. This suggests that the effect of topography is scale- and context-dependent, which may explain its weak effect in our global analysis. Insularity also had only a minor influence on pollination-mode, with islands tending to have lower proportions of animal-pollination, but only when also taking climate into account (Table 2), which only partly supports hypothesis 6. In contrast to the strong associations with current factors (Table 2; Appendix S2), historical climate was associated only weakly and idiosyncratically with animal pollination, varying independently when using regression models or simple univariate correlations (Table 2 and Appendix S2), and therefore not supporting hypothesis 7. Overall, this suggests that the relative proportions of different pollination modes are more linked to current climate and ecological factors than to historical legacies.

Although these results support the greater influence of contemporary ecological factors over historical ones, it is not straightforward to determine the exact mechanism responsible for this pattern. For example, current precipitation was strongly related to the percentage of regional tree cover, hence, animal pollination is associated with both high precipitation and forest habitat. Wet forests clearly offer poor conditions for pollen dispersal, but it is difficult to disentangle whether this is because of mechanical restrictions imposed by dense vegetation or because air humidity decreases pollen dispersability, or both (Whitehead 1969; Niklas 1985). In open areas, especially in the tropics, the distribution of plant individuals tends to be sparse and floral resources less abundant. For example, an estimate of nectar energy available per hectare in the Atlantic rain forest in Brazil showed that forests produced twice as much floral energy as the nearby open ‘restinga’ (coastal scrub) vegetation (Fonseca 2013, Fonseca et al. 2015). Moreover, the distribution of an Andean plant species was associated with a progressive disruption of its animal pollination mutualism accompanied by the gradual decrease in precipitation (Chalcoff et al. 2012). This illustrates the potential role of vegetation structure and precipitation in determining the functioning of animal-dependent mutualisms, but disentangling the roles of correlated factors is a major challenge for macroecology.

Interestingly, current climate may play a similar role for seed dispersal as there is also a pattern of higher importance of animal dispersers in rain forests, whereas in dry forests wind and self-dispersal are more common (Howe and Smallwood 1982; Jordano 2000 and references therein). For instance, current precipitation patterns are largely correlated with proportion of endozoochory across the Atlantic forest of Brazil, animals being more important dispersers in the wetter areas (Almeida-Netto et al. 2008), although large-scale studies are not available to confirm this hypothesis. One tentative joint explanation for the lower frequency of animal-pollinated and animal-dispersed plants at drier sites could be the higher metabolic costs of producing nectar and fleshy fruit, as was originally proposed only for fruit (Wilson et al. 1989; Almeida-Neto et al. 2008). Associated with humidity, high temperature may also increase nectar production and therefore influence animal pollination, although, as temperature and temperature seasonality were found to be negatively correlated, we cannot rule out the possibility that seasonality promotes wind pollination (Regal 1982).

Another factor positively associated with animal pollination was plant species richness. Other trophic interactions between plants and animals respond to the bottom-up effect of plant species richness (Kissling et al. 2007; Scherber et al. 2010); for instance, in the Neotropics the diversity of pollinating birds and bats is associated with their food plant species richness (Fleming 2005; Kissling et al. 2007). Meanwhile, as plant species richness increases, the density of conspecifics per unit area tends to decrease (Comita et al. 2010), which may also reduce the efficiency of pollen dispersion by wind (Whitehead 1969; Regal 1982). Plant species richness may also play an important role in sustaining pollinator communities (Ebeling et al. 2008; Dorado and Vázquez 2014) via two main mechanisms: (1) more plant species per unit area may ensure a more predictable and diverse food supply through complementarity (Waser and Real 1979; Rathcke 1983; Blüthgen and Klein 2011; Yang et al. 2013); and (2) more plant species also increases species redundancy within functional groups ('biodiversity insurance effect'), reducing the extinction risk of functionally specialised interactions (Bartomeus et al. 2013; Fründ et al. 2013). For instance, manipulative experiments have shown that high functional diversity of plants enhances the number of pollinators, and the functional diversity of pollinators increases individual plant fitness and community persistence over time (Fontaine et al. 2006; Albrecht et al. 2012).

Conclusions

We tested a range of previously proposed hypotheses and found that a subset of contemporary climate and ecological processes are the factors more strongly related to the global pattern of animal than to wind pollination at the community level. The deduced limited influence of historical climate instability on the contemporary prevalence of animal and wind pollination is in contrast with previous findings of high importance of historical factors on the structuring of plant-pollinator interaction networks (Dalsgaard et al., 2011, 2013; Martín González et al. 2015) and the distribution of animal and plant life on earth (Svenning and Skov 2007; Cárdenas et al. 2011; Sandel et al. 2011; Kissling et al. 2012), but is in accordance with studies of the organisation of plant-frugivore interaction networks (Schleuning et al. 2014). In future studies, it would be interesting to examine if other measures of historical processes, e.g. geological differences or historical measures of plant migration rates, influence plant reproduction. The large scale drivers of plant reproductive ecology will be better understood with similar studies examining also the role of both historical and contemporary factors on other processes, such as plant reproduction via autogamy and seed dispersal. In addition, to improve the certainties of the conclusions presented here will require additional sampling effort in Africa, Asia, Russia and oceanic islands, where so few data have been collected on plant reproductive ecology at the community level.

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Supporting information

Appendix Table S1. Site descriptions
Appendix Table S2. Correlations between predictor variables
Appendix Table S3. Contemporary and historical determinants of the pollination mode

Table and Figures

Table 1. Correlations among the proportion of units in different taxonomic categories regarding pollination mode (animal *versus* wind pollination).

Taxa	Pearson correlation	t-value	Degrees of freedom	*P*-value
Species and Genera	0.971	31.2131	59	< 0.001
Species and Families	0.776	9.4789	59	< 0.001
Genera and Families	0.836	11.7435	59	< 0.001

Table 2. Contemporary and historical correlates (precipitation and temperature anomalies) of the proportion of animal-pollinated plant species in plant communities worldwide (n=67). The standardised regression coefficients are reported both for ordinary least square (OLS) and logistic regression, and reported for both an averaged model based on weighted *wi* and minimum adequate models (MAMs), as in Diniz-Filho et al. (2008). For all MAMs based on OLS, we give AIC_c, Condition Number, Moran's I, and coefficients of determination (R^2). Finally, "$R^2_{\text{species richness}}$", "$R^2_{\text{topography}}$", "$R^2_{\text{current climate}}$" and "$R^2_{\text{historical climate}}$" reflect the unique variation explained by species richness, topography, current climate and historical climate, respectively. Note that historical climate stability is represented by temperature and precipitation anomaly between 21,000 years ago and the present (current minus Last Glacial Maximum - LGM precipitation/temperature, i.e. positive values reflect areas having been drier or colder at LGM than at present). See Appendix Table 2 for similar calculations when using temperature and precipitation velocities as historical climate stability measures.

	OLS			Logistic		
	Σw_i	Averaged	MAM[†]	Σw_i	Averaged	MAM [¶]
Insularity	0.22	+0.02		0.96	-0.33	-0.33
Topography	0.84	+0.28	+0.28	1.00	+0.45	+0.42
Plant species richness	0.83	+0.23	+0.22	0.93	+0.24	+0.25

Open vegetation vs. forest	0.42	-0.22		1.00	+0.27	+0.29
MAP x Open vegetation vs forest	0.64	+0.37	+0.18	1.00	+1.18	+1.23
MAP (Mean Annual Precipitation)	0.25	-0.05		1.00	+0.13	+0.18
MAT (Mean Annual Temperature)	1.00	+0.69	+0.74	1.00	+1.42	+1.34
MAP seasonality	0.31	-0.11		0.48	-0.17	
MAT anomaly	0.70	+0.25	+0.25	1.00	+0.84	+0.85
MAP anomaly	0.24	+0.00		0.51	+0.18	
AIC (Akaike Information Criteria$_c$)			-73.29			668.9
Moran's Index			$\leq 0.08^{NS}$			
Condition Number			2.6			
R^2			0.49			
$R^2_{\text{species richness}}$			0.04			

$R^2_{\text{topography}}$	0.01
$R^2_{\text{current climate}}$	0.36
$R^2_{\text{historical climate}}$	0.02

**, $P < 0.01$; *, $P < 0.05$; ^{NS}, non-significant. [†] three models were equally fit (i.e. $\Delta AIC_c \leq 2$) containing the following variables, 1) Open vegetation vs forest, plant species richness, MAT, MAP x Open vegetation versus forest, topography, MAT anomaly; 2) plant species richness, MAT, topography, MAT anomaly; 3) Open vegetation vs forest, plant species richness, MAT, topography, MAT anomaly. [¶] three other models were equally fit (i.e. $\Delta AIC_c \leq 2$) containing the following variables, 1) Open vegetation vs forest, insularity, plant species richness, MAT, MAP, MAP x Open vegetation versus forest, MAP seasonality, topography, MAT anomaly, MAP anomaly ; 2) Open vegetation vs forest, insularity, plant species richness, MAT, MAP, MAP x Open vegetation versus forest, MAP seasonality, topography, MAT anomaly; 3) Open vegetation vs forest, insularity, plant species richness, MAT, MAP, MAP x Open vegetation versus forest, topography, MAT anomaly, MAP anomaly.

Figure 1. Geographic patterns of animal pollination in 67 communities surveyed across the world. Fitted curves are second order polynomials; $r^2 = 0.28$, $F_{2,47}$, 13.85, $P < 0.001$. On the map, dots were separated slightly within a small range to reduce the overlap of nearby sites.

Figure 2. Examples of species having traits representing wind (A-D) and animal (E-G) pollination used to classify plant species according to pollination mode in this study. A, *Ambrosia artemisiifolia* L. (Asteraceae) a diclinous wind pollinated plant with minute flowers that produce a large amount of pollen (Photo by Andrew Butko via Wiki images), B, *Mercurialis annua* L. (Euphorbiaceae) a dioecious wind-pollinated plant species; the circle highlights the female flower and, in detail at the right side of the image, we show the inflorescence of a male individual (Photo by Hasan Yldirin), C, *Olyra ciliatifolia* Raddi (Poaceae) female flower with feathery stigmas (Photo by Pedro Viana), D, *Paspalum notatum* Flüggé (Poaceae) showing the flexible white filaments; the arrow is pointing to the wide anther aperture (Photo by Pedro Viana), E, *Turnera ulmifolia* L. (Passifloraceae) a 3D heterostyle species and a butterfly, one of its animal pollinators, F, *Couroupita guianensis* Aubl. (Lecythidaceae) with food (colourful) and pollination (white) specialised stamens (Photo by Hipolito Neto), G, *Gongora bufonia* Lindl. (Orchidaceae) being pollinated by a male euglossine bee (*Eufrisea violacea*) when collecting scented oil from its labellum (Photo by Carlos Eduardo Coquinho).

Figure 3. The relationship between the proportion of animal pollinated plant species per community and the most important and consistent predictors, a) plant richness; b) temperature; c) precipitation. Open symbols illustrate open vegetation types whereas filled symbols

illustrate forest communities. All relationships significant in simple univariate correlations are shown: all vegetation types (n = 67; dashed line); open vegetation types (n = 51, dotted line); and forest (n = 16, full line). See Table 2 and Tables S1-S2 for statistics.

Appendix Table S1. Site descriptions for each community analysed in the study: “The macroecology of animal *versus* wind pollination”. Each number in the first column corresponds to a reference below.

Nº	Study site	Mainland = 0 Island = 1	Forest: 1 Other = 0	Total plants:	Nº wind pol. species	% animal pollination	Latitude Decimalised	Longitude Decimalised
1	Juan Fernandez Islands, Chile	1	0	149	70	53.02	-33.64	-78.84
2	Coastal scrub, UK	1	0	37	9	75.68	54.40	-0.51
3	Degraded tropical scrub/secondary	0	1	82	3	96.34	22.28	114.2
4	Serra da Bocaina - Grassland	0	0	179	55	69.27	-22.73	-44.61
5	Cerrado, Brazil	0	0	294	52	82.31	-22.87	-48.49
6	semi-arid scrub - Spain	0	0	31	6	80.65	37.01	-6.55
7	Amami Island, Japan	1	0	103	6	94.17	28.32	129.42
8	All habitats across New Caledonia	1	0	97	3	96.91	-21.17	165.25
9	La Selva, Costa Rica	0	1	283	13	95.41	10.45	-84.00
10	Caatinga, Brazil	0	0	147	3	97.96	-8.45	-36.76
11	various localities, Faroe Islands	1	0	70	19	72.86	62.00	6.783
12	Guyana Highlands, Venezuela	0	0	55	6	89.09	5.58	-61.71
13	Rainforest, Malaysia	1	1	262	0	100.00	4.20	114.5
14	Alpine pavement plain, California	0	0	17	4	76.47	34.30	-116.86
15	Woodland, USA	0	1	208	57	72.60	42.1	-111.59
16	various localities, St Kilda	1	0	92	39	57.61	57.81	-8.58
17	Palm swamp, Venezuela	0	1	33	5	84.85	8.93	-67.25
18	Prairie, Illinois	0	0	409	14	96.58	39.46	-89.90
19	Flooded/Upland Rainforest, Colombia	0	1	90	2	98.51	-0.61	-72.33
20	Lower alpine, Scotland	1	0	153	8	94.77	56.50	-3.11
21	Serra do Cipo	0	0	64	5	92.19	-23.336667	-45.14
22	Botucatu	0	0	34	3	91.18	-22.844167	-48.68
23	Santa Virginia	0	1	70	8	88.57	-19.334722	-43.58

24	Picinguaba - restinga	0	0	47	5	89.36	-23.358056	-44.85
25	Picinguaba - Atlantic forest	0	1	43	2	95.35	-23.338611	-44.83
26	La Floresta - Canelones - Uruguay -	0	0	24	10	58.33	-34.760706	-55.69
27	Quebrada de los Cuervos - Uruguay -	0	0	42	14	66.67	-32.935091	-54.46
28	Kumu - Guyana - rainforest	0	1	59	3	94.92	3.266667	-59.75
29	Kumu - Guyana - savannah	0	0	43	6	86.05	3.266667	-59.77
30	Wahroonga - South Africa	0	0	73	4	94.52	-29.616667	30.13
31	Mantanay - Peru	0	0	148	6	95.95	-13.2	-72.08
32	Scrub Field - Northampton - UK	1	0	162	35	78.40	52.26	-0.88
33	Bahia de Patano - Venezuela	0	0	78	12	84.62	10.466667	-67.75
34	Guimar Badlands, Tenerife	1	0	18	2	88.89	28.33	-16.42
35	Mean JasperRidge Plant Covariates -	0	0	109	24	78.98	37.417	-122.19
36	Mean JasperRidge Plant Covariates –	0	1	78	16	77.85	37.417	-122.19
37	JasperRidge Plant Covariates –	1	0	16	7	56.25	37.701067	-123.00
38	MatherPlantCovariatesPUPPLEEsEt –	0	0	92	31	66.30	37.8774	-119.25
39	MatherPlantCovariatesPUPPLEEsEt –	0	0	58	6	89.66	37.8374	-120.30
40	MatherPlantCovariatesPUPPLEEsEt –	0	1	132	19	85.61	37.8774	-119.29
41	MatherPlantCovariatesPUPPLEEsEt –	0	0	134	33	75.37	38.0095	-123.00
42	TimberlinePlantDataPurple – Dore	0	0	60	19	68.33	37.9683	-119.30
43	TimberlinePlantDataPurple –	0	0	95	47	50.53	37.9382	-119.25
44	TimberlinePlantDataPurple –	0	1	91	34	62.64	37.9612	-119.29
45	TimberlinePlantDataPurple – Talus	0	0	126	38	69.84	37.9462	-119.25
46	Virginia Basin (Colorado)	0	0	64	6	90.63	38.98	-106.966667
47	Mean Hangklip, South Africa	0	0	124	41	65.55	-34.25	18.75
48	Brattnesdalen, Norway	0	0	18	8	55.56	70.25	22.07
49	Fjorddalen, Norway	0	0	31	10	67.74	70.19	22.10
50	various localities, Australia	0	1	148	8	94.59	-19.18	146.75
51	Torrey Pines - California	0	0	85	21	75.29	32.89	-117.24
52	Japatul Valley - California	0	0	91	15	83.52	32.78	-116.68
53	Echo Valley - California	0	0	56	4	92.86	32.89	-116.65

54	Mount Laguna - California	0	1	65	15	76.92	32.86	-116.41
55	Ocotillo - California	0	0	80	14	82.50	32.74	-115.99
56	Papudo - Chile	0	0	95	23	75.79	-32.55	-71.44
57	Fundo Santa Laura - Chile	0	0	106	18	83.02	-33.26	-70.85
58	Cerro Potrerillo - Chile	0	0	47	11	76.60	-30.29	-70.57
59	El Tofo - Chile	0	0	44	5	88.64	-29.88	-71.20
60	Alpine - montane Colorado	0	0	68	17	75.00	38.68	-107.115532
61	Aspen - montane Colorado	0	1	56	15	73.21	38.73	-106.772653
62	Sage - montane Colorado	0	0	45	9	80.00	38.73	-106.823376
63	Grassland - montane Colorado	0	0	103	24	76.70	38.95	-106.988824
64	Spruce-fir - montane Colorado	0	1	50	11	78.00	38.86	-107.101081
65	Salt marsh, Canada	0	0	18	6	66.67	49.08	-125.85
66	Sphagnum bog, Canada	0	0	33	13	60.61	49.08	-125.86
67	Subalpine meadow, Canada	0	0	45	11	75.56	49.11	-120.84

Appendix Table S1 - References

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Appendix Table S2. Correlations between the proportion of animal pollinated plant species and all predictor variables for all vegetation types (n = 67, except for velocities which had one data point less as we were unable to extract it for St Kilda Island, Scotland) above the diagonal, and separately for open vegetation types (n = 51, except for velocities which had one data point less as we were unable to extract it for St Kilda Island, Scotland) below the diagonal.

	% animal pollinated	Plant richness	MAT	MAP	MAP seasonality	Topography	MAT anomaly	MAP anomaly	MAT velocity	MAP velocity
% animal pollinated		**+0.32****	**+0.57***	**+0.29**†	+0.09$^{\text{NS}}$	-0.11$^{\text{NS}}$	-0.14$^{\text{NS}}$	+0.03$^{\text{NS}}$	+0.07$^{\text{NS}}$	+0.13$^{\text{NS}}$
Plant richness	+**0.28***		+0.11$^{\text{NS}}$	+0.11$^{\text{NS}}$	-0.05$^{\text{NS}}$	-0.11$^{\text{NS}}$	+0.06$^{\text{NS}}$	+0.23$^{\text{NS}}$	+0.16$^{\text{NS}}$	+0.05$^{\text{NS}}$
MAT (Mean Annual Temperature)	+**0.42***	+0.09$^{\text{NS}}$		**+0.44***	**+0.35***	**-0.45****	**-0.50***	+0.01$^{\text{NS}}$	+0.05$^{\text{NS}}$	**+0.37****
MAP (Mean Annual Precipitation)	-0.02$^{\text{NS}}$	-0.04$^{\text{NS}}$	+0.24$^{\text{NS}}$		-0.17$^{\text{NS}}$	**-0.25**†	-0.20$^{\text{NS}}$	+**0.33****	+0.14$^{\text{NS}}$	+**0.25***
MAP seasonality	+0.14$^{\text{NS}}$	+0.02$^{\text{NS}}$	**+0.39***	**-0.18***		+0.12$^{\text{NS}}$	**-0.53***	-0.05$^{\text{NS}}$	**-0.36**†	+0.20$^{\text{NS}}$
Topography	+0.04$^{\text{NS}}$	-0.08$^{\text{NS}}$	**-0.36****	-0.17$^{\text{NS}}$	+0.19$^{\text{NS}}$		-0.04$^{\text{NS}}$	-0.16$^{\text{NS}}$	**-0.71****	**-0.47****
MAT anomaly	-0.08$^{\text{NS}}$	+0.12$^{\text{NS}}$	**-0.51***	-0.10$^{\text{NS}}$	**-0.60****	-0.13$^{\text{NS}}$		-0.17$^{\text{NS}}$	**+0.50****	-0.21$^{\text{NS}}$
MAP anomaly	-0.22$^{\text{NS}}$	+0.08$^{\text{NS}}$	-0.17$^{\text{NS}}$	+0.22$^{\text{NS}}$	+0.06$^{\text{NS}}$	-0.01$^{\text{NS}}$	-0.13$^{\text{NS}}$		+0.16$^{\text{NS}}$	+0.10$^{\text{NS}}$
MAT velocity	+0.01$^{\text{NS}}$	+0.16$^{\text{NS}}$	-0.04$^{\text{NS}}$	+0.10$^{\text{NS}}$	**-0.41***	**-0.70****	**+0.58****	+0.05$^{\text{NS}}$		**+0.40***
MAP velocity	+0.02$^{\text{NS}}$	-0.01$^{\text{NS}}$	**+0.29****	+0.14$^{\text{NS}}$	+0.17$^{\text{NS}}$	**-0.42****	-0.15$^{\text{NS}}$	-0.05$^{\text{NS}}$	**+0.43***	

$^{**}P < 0.01$; $^{*}P < 0.05$ when P-values based on degrees of freedom corrected for spatial autocorrelation using Dutilleul's (1993) method;

†significant when using traditional non-spatial statistics, but non-significant when corrected for spatial autocorrelation; ^{NS}non-significant.

Appendix Table S2, continued. Correlations between predictor variables separately for forest (n = 16).

	% animal pollinated	Plant richness	MAT	MAP	MAP seasonality	Topography	MAT anomaly	MAP anomaly	MAT velocity	MAP velocity
% animal pol.		+0.30^{NS}	**+0.82**†	**+0.84***	-0.01^{NS}	**-0.59**†	-0.46^{NS}	+0.37^{NS}	+0.32^{NS}	**+0.50**†
Plant richness			+0.05^{NS}	+0.38^{NS}	-0.29^{NS}	-0.22^{NS}	-0.29^{NS}	**+0.57***	+0.21^{NS}	+0.26^{NS}
MAT (Mean Annual Temperature)				+0.74†	+0.32^{NS}	**-0.73**†	**-0.67**†	+0.19^{NS}	+0.34^{NS}	**+0.58**†
MAP (Mean Annual Precipitation)					-0.13^{NS}	**-0.52**†	**-0.70***	+0.42^{NS}	+0.33^{NS}	**+0.58**†
MAP seasonality						-0.14^{NS}	-0.26^{NS}	-0.30^{NS}	-0.13^{NS}	+0.26^{NS}
Topography							+0.55†	**-0.56***	**-0.78***	**-0.61**†
MAT anomaly								-0.41^{NS}	-0.17^{NS}	**-0.64***
MAP anomaly									**+0.56***	+0.44^{NS}
MAT velocity										+0.36^{NS}
MAP velocity										

**P < 0.01; *P < 0.05 when P-values based on degrees of freedom corrected for spatial autocorrelation using Dutilleul's (1993) method; †significant when using traditional non-spatial statistics, but non-significant when corrected for spatial autocorrelation; ^{NS}non-significant.

Appendix Table S3. Contemporary and historical determinants (precipitation and temperature velocities) of the proportion of animal-pollinated plant species in plant communities worldwide (n=66). The standardized regression coefficients are reported both for ordinary least square (OLS) and logistic regression, and reported for both an averaged model based on weighted *wi* and minimum adequate models (MAMs), as in Diniz-Filho *et al*. (2008). For all MAMs based on OLS, we give AIC$_c$, Condition Number, Moran's I, and coefficients of determination (R^2). Finally, "$R^2_{\text{species richness}}$", "$R^2_{\text{current climate}}$" and "$R^2_{\text{historical climate}}$" reflect the unique variation explained by species richness, current climate and historical climate, respectively. Notice that historical climate stability is represented by temperature and precipitation velocity between 21000 years ago and now, and that topography is not included as strongly correlated with velocities. See Table 2 for similar calculations using precipitation and temperature anomalies as historical climate stability measures.

	OLS			Logistic		
	Σw_i	Averaged	MAM[†]	Σw_i	Averaged	MAM
Insularity	0.25	+0.05		0.75	-0.24	-0.25
Plant species richness	0.85	+0.24	+0.24	0.85	+0.21	+0.20
Open vegetation vs forest	0.44	-0.24		1.00	+0.31	+0.29
MAP x Open vegetation vs forest	0.67	+0.39	+0.20	1.00	+1.22	+1.23
MAP (Mean Annual Precipitation)	0.27	-0.07		1.00	+0.03	+0.02
MAT (Mean Annual Temperature)	1.00	+0.50	+0.47	1.00	+0.82	+0.84

MAP seasonality	0.31	-0.10		0.87	-0.26	-0.27
MAT velocity	0.23	-0.00		1.00	+0.42	+0.40
MAP velocity	0.29	-0.09		0.22	-0.01	
Akaike Information Criteria$_c$			-69.94			675.9
Moran’s Index			$\leq 0.14^{*}$			
Condition Number			1.5			
R^2			0.43			
$R^2_{\text{species richness}}$			0.05			
$R^2_{\text{current climate}}$			0.32			
$R^2_{\text{historical climate}}$			0.00			

$^{**}P < 0.01$; $^{*}P < 0.05$; ^{NS}non-significant. † five other models were equally fit (i.e. $\Delta AIC_c \leq 2$) containing the following variables, 1) Open vegetation vs forest, plant species richness, MAT, MAP x Open vegetation versus forest; 2) plant species richness, MAT; 3) plant species richness, MAT, MAP x Open vegetation versus forest, MAP velocity; 4) plant species richness, MAT, MAP x Open vegetation versus forest, MAP seasonality; 5) Open vegetation vs forest, plant species richness, MAT.