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Supplementary Materials for

Seed predation increases from the Arctic to the Equator and from high to low elevations

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This PDF file includes:

Supplementary Materials

Supplementary Methods

Geographic variation in exposure to predation

Interaction strength depends on both interaction intensity (e.g. seed predation risk /day), and the duration individuals are exposed to the interaction (e.g. days seeds spend vulnerable to predation before germinating). For seeds that take a year or more to germinate, those at high-elevations and latitudes may benefit not only from lower predation intensity during snow-free months (as we show; main text), but also lower predation exposure during winter. Insects are inactive during winter and the few experimental assessments we found show that vertebrate seed predation drops by 60 to 70% under snow, though seems unaffected by cold (*35, 51*). While a robust assessment of geographic patterns in interaction strength (intensity × exposure) is beyond the scope of this study, we roughly assessed annual exposure and its potential effect on predation for long-lived seeds. First, we estimated the months each site is covered in >10 cm of snow based on personal field experience and/or online data bases. We then tested whether seed predation was correlated with annual snow duration, i.e. could decreased exposure via increased snow decouple gradients in interaction strength from gradients in interaction intensity. We used mean seed predation (averaged to 1 point/seed species/site as per SEMs) as the response, to match the precision of our snow cover estimates. We used a binomial GLM with snow duration, seed species, and their interaction as predictors. The importance of the interaction term was assessed using likelihood ratio tests (main text) and the interaction dropped if non-significant. Second, we estimated annual relative exposure to seed predation. We discounted the contribution of snow-covered months by either 100% (no predation under snow—the maximum effect snow cover could have on predation gradients) or 65% (reflecting the limited literature estimates (*35, 51*)). Thus a snow-free site would have 12 exposure months, while a site covered in snow for half the year would have either 6 (100% reduction) or 9.9 (65% reduction) exposure months. We then calculated a unit-less annual exposure as # exposure months / 12 months. Finally, we calculated an exposure-adjusted seed predation estimate by multiplying mean seed predation by the site's exposure fraction (both for 100% and 65% predation reduction).

We tested for geographic patterns using adjusted seed predation as the response and latitude, elevation, and seed species as interacting main effects, using binomial GLMs as above. To assess the effect of adjusting for snow cover, we compared the effect sizes to a GLM using unadjusted mean seed predation (this model differs from those in the main text by considering a single measure of seed predation/seed species/site). Results are presented in fig. S5.

Of course, estimating clines in annual exposure is only useful if seeds across ecosystems remain as seeds for a year or more; if most seeds germinate quickly the effect of winter is ecologically unimportant. A comprehensive review of latitudinal patterns in germination times is again beyond the scope of this study, but we surveyed the literature for community-level estimates of dormancy (time-to-germination under ideal lab conditions) and time-to-germination under field conditions. We found 16 studies that presented data for >3000 species in the tropics and temperate zone. While most latitudes and biomes had species that took >365 days to germinate under natural conditions, mean time-to-germination in the field was always <1 yr. Thus estimating latitudinal gradients in annual, exposure-adjusted predation is biologically relevant, but only for a subset of seeds.

Structural equation modelling

We first made a conceptual model, which was too complex to test with the collected data, but clarified our understanding about how predictors affect each other and seed predation and informed structural equation models (SEMs; fig. S5). Latitude and elevation are exogenous variables, whose values do not rely on values of other modelled variables. Climate variables were divided into a) a latent variable ‘Climate’ comprised of Temperature annual range, Annual precipitation, and Precipitation seasonality, and b) Mean annual temperature, modeled separately to allow temperature to directly affect seed predation via metabolic activity. Both Climate and Mean annual temperature are directly affected by latitude and elevation and directly affect productivity (*52*), and Mean annual temperature also directly affects seed predation (fig. S5). Productivity is modeled as a latent variable comprised of AET and NPP, which are correlated (fig. S5) but measure slightly different components of productivity (respiration vs. biomass, respectively). We assumed elevation’s effect on productivity was captured by its effect on climate and temperature, but that latitude could affect productivity directly via increasing irradiance (solar energy) toward the equator (*2*, *53*). Although productivity is positively correlated with species richness (fig. S4), global analyses suggest high productivity does not cause high richness or vice versa (*48, 54, 55*), so we modelled them as affected by climate but independent of each other. We let latitude affect species richness, as recolonization of high latitudes post glaciation has resulted in widespread migration lags (*56, 57*), which should reduce diversity at higher latitudes independent of modern climate (*55*). While high elevations were also glaciated, the shorter distances required to cross elevational gradients make migration lags negligible (*56, 57*). Higher seed predator populations could arise from more productive ecosystems (more food available) or more diverse predator assemblages (‘species packing’), so we modelled direct effects of productivity and species richness on seed predation. Finally, to account for effects not captured by other variables, we modelled a direct effect of latitude on seed predation intensity.

From this and results of an earlier analysis of climate and productivity vs. oat predation (*23*), we generated 15 simpler structural equation models (SEMs), which represented biologically-motivated simplifications of our conceptual model. These SEMs are illustrated in fig. S6, and the hypotheses they represent described fully below. For SEMs 3to8, which include productivity as one of several mechanistic predictors, we ran the model twice, once with productivity as AET (as in (*23*)) and again with productivity as NPP (modeling productivity as a latent variable comprised of AET and NPP increased the AIC of these models by >80, not shown).

SEM#) SEM name: Hypothesis

SEM1) Climate: seed predation intensity is best explained by climate plus any additional effects of latitude and elevation.

SEM2) Productivity: seed predation intensity is best explained by productivity (AET and NPP combined into a latent variable) plus any additional effects of latitude and elevation.

SEM3) Direct effects: seed predation intensity is best explained by the variables thought to influence it directly.

SEM4) Direct effects no richness: as for SEM3 but excluding species richness, assuming granivore diversity is unimportant or poorly captured by vertebrate richness.

SEM5) ‘Orrock’ structured: predation is best explained using the variables that explained granivory on oat seeds in temperate grasslands in the Americas (*23*). The effect of latitude is captured by its effects on climate and AET or NPP (*23*). Elevation can affect seed predation indirectly via an effect on AET/NPP; this represents the indirect effect of elevation on AET/NPP mediated by Mean annual temperature from the conceptual model. We let Annual temperature range affect seed predation directly, to represent the more direct potential effects of temperature vs. precipitation.

SEM6) 'Orrock' more linear: as for SEM5 but without the indirect effects of elevation and Annual temperature range via AET/NPP.

SEM7) 'Orrock' unstructured: as for SEM5 but climate and productivity variables are modelled independently rather than hierarchically.

SEM8) 'Orrock' direct only: including only variables identified as important in (*23*) for which direct effect can be reasonably hypothesized.

Finally, we compared the simplest possible model for each variable thought to have direct effects on seed predation intensity (SEM9-12) or that significantly affected predation in (*23*) (SEM13-14) to a model with latitude (SEM15). All models also included elevation, with both variables modelled as exogenous with the structure shown in fig. S6 SEM9.

SEM9) Mean annual temperature + elevation
SEM10) AET + elevation
SEM11) NPP + elevation
SEM12) Species richness + elevation
SEM13) Annual temperature range + elevation
SEM14) Annual precipitation + elevation
SEM15) Latitude + elevation

Supplementary Figures

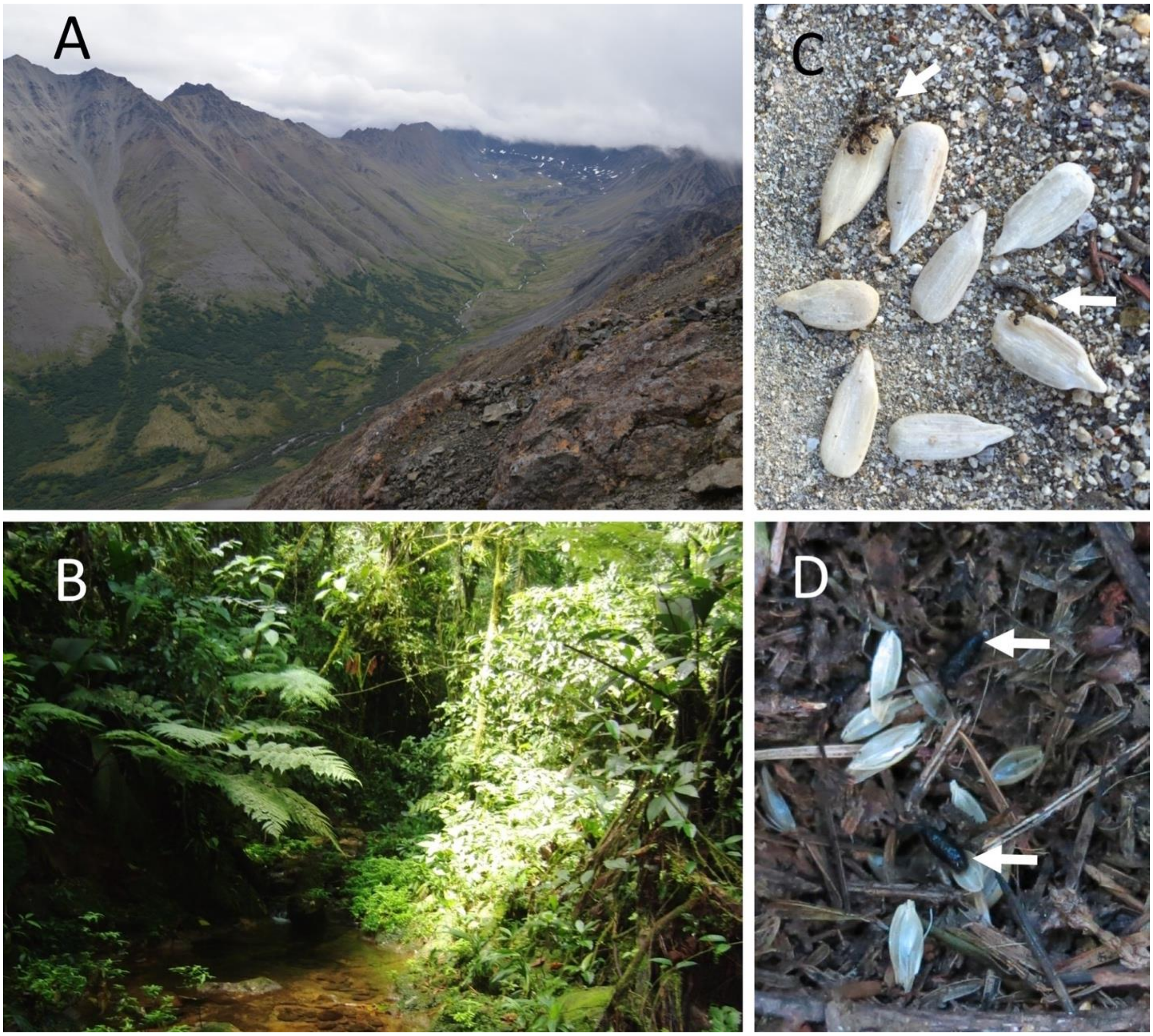

Fig. S1. Photos of field sites and seed predator signs. (**A**) Highest site at our most polar transect (1430 masl, Alaska, well above upper tree line), and (**B**) one of our lowland tropical sites at 700 masl in Costa Rica. (**C**) Sunflower depot with six intact and two partially consumed seeds still being eaten by ants (arrows). (**D**) Oat depot with no intact seeds—husks peeled from seeds and small mammal droppings (arrows) indicate mammal predation. Photo credits: (A) J. Brodie, University of Montana; (B) H. Slinn, University of Nevada, (C) S. Vanderplank, Botanical Research Institute of Texas; (D) A. Hargreaves (McGill University).

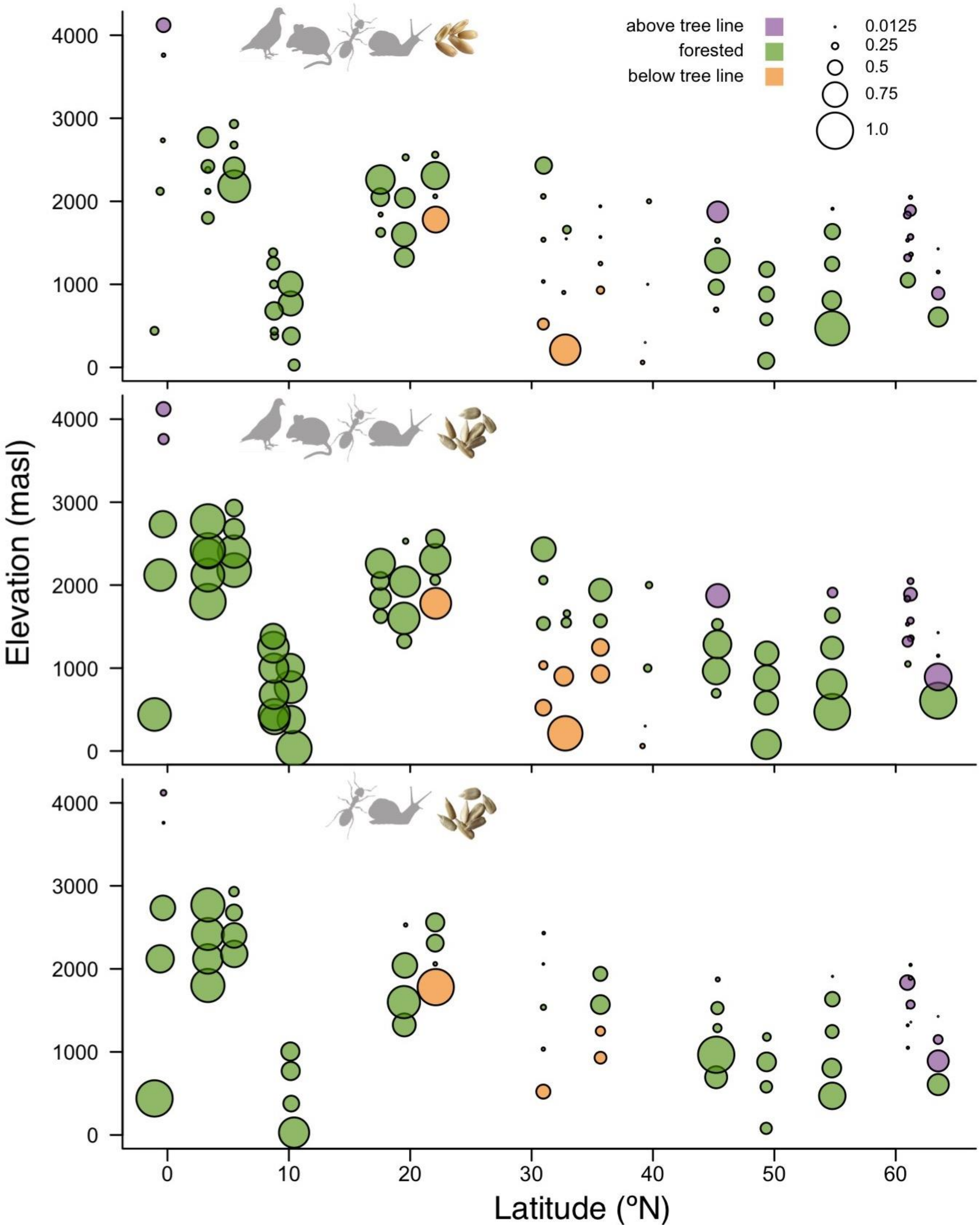

Fig. S2. Mean seed predation by site. Circle centre shows the latitudinal and elevational location of each site, size shows the mean fraction of predated seeds, averaged across depots and runs, colour shows site biome. From top, panels show total predation on oats, total predation on sunflower seeds, and invertebrate predation on sunflower seeds (i.e. depots caged to exclude vertebrates).

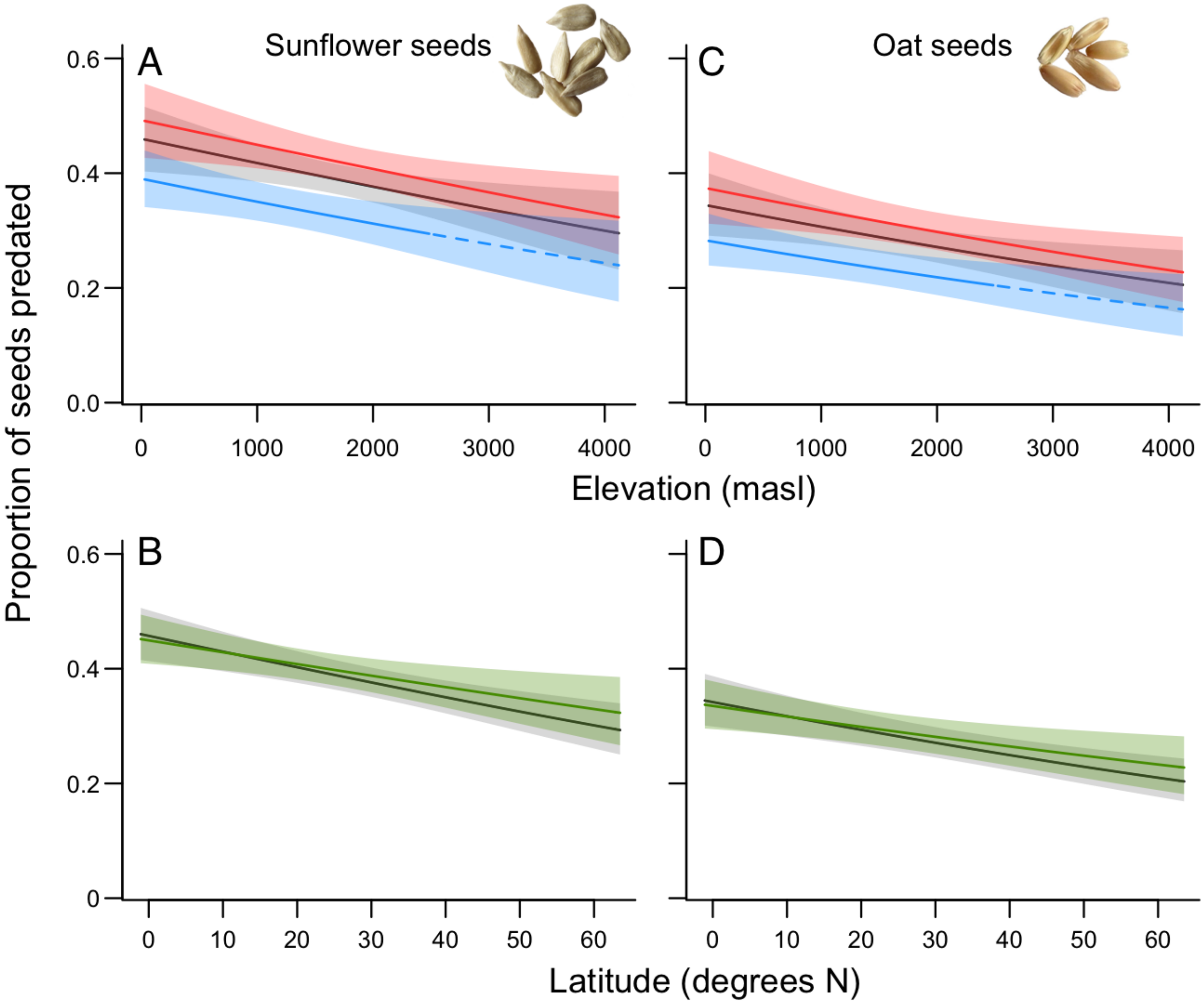

Fig. S3. Geographic trends in total predation on sunflower versus oat seeds. Lines and shading show trend line +/- 95% confidence intervals fitted by GLMMs (**A** and **B** correspond to Fig. 1D and E). All models include seed type as a factor; seed type was always significant, but never interacted with latitude or elevation, i.e. geographic patterns were consistent between sunflower (**A**, **B**) and oat seeds (**C**, **D**). Latitudinal trends (A, C) are shown for the median elevation (1500 m) across biomes (black; Model 2), and in forests (green; Model 5). Elevational trends (B, D) are shown at the median latitude (31°N; black), median tropical latitude (10.5°N; red), and median temperate latitude 47.7°N; blue, all Model 2). Dashed portion of the line shows trends extrapolated above 2500 m; we had no temperate sites above 2500 m because vegetation stops at lower elevations at higher latitudes. Total predation was 11% higher on sunflower vs. oat seeds across biomes (Model 2), and in forests specifically (Model 5). Full GLMM results are in Table 1.

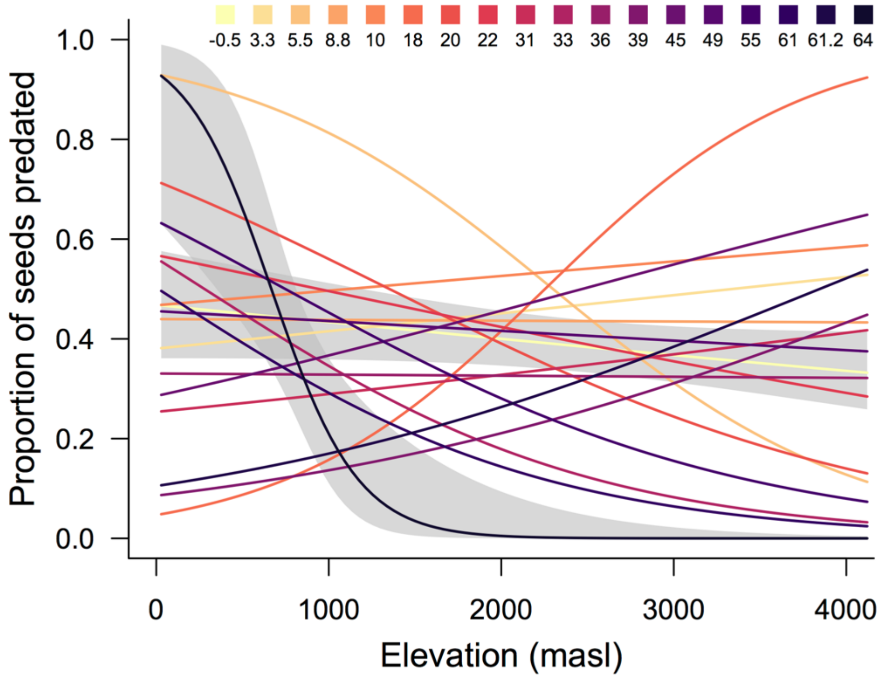

Fig. S4. Large-scale patterns emerged despite variation among the 18 transects. Trend lines show total predation on sunflower seeds and are for illustrative purposes only, taken from a binomial GLMM that considered transect latitude as a categorical variable with 18 levels, 1 per transect (seed predation ~ factorLatitude × elevation + seed.species). 95% confidence intervals are shown for the extreme latitudes only, otherwise their overlap obscures trend lines. Colour scale denotes the latitude of each transect in decimal degrees.

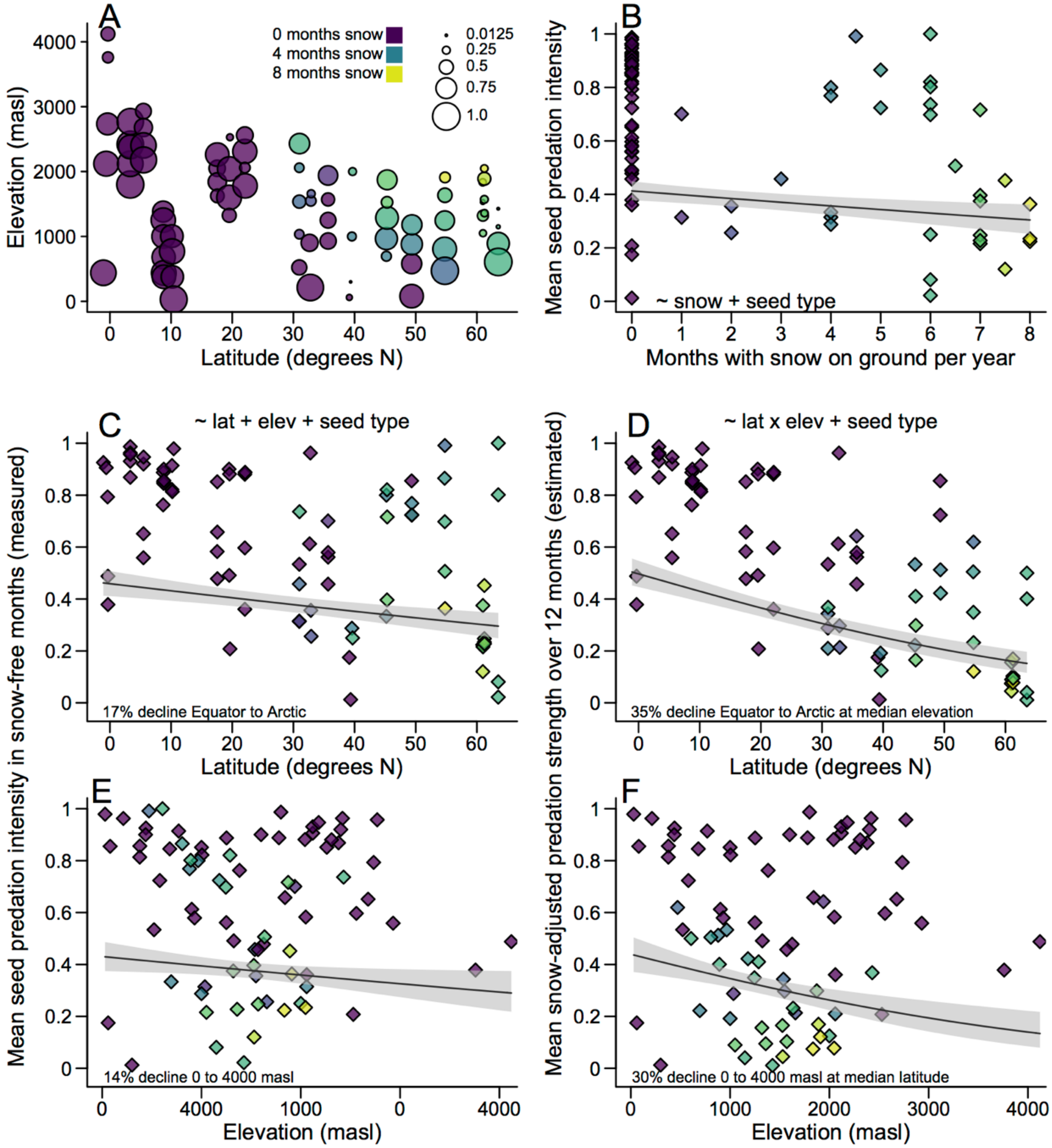

Fig. S5. Snow cover could steepen latitudinal and elevational interaction gradients. All plots show seed predation averaged to 1 data point/seed type/site as in SEMs, and annual duration of snow cover >10 cm (point colour). (**A**) Snow duration vs. latitude, elevation, and mean seed predation intensity during snow-free months (point size). Even high-elevation sites in the tropics are snow free, whereas snow duration increases with elevation and latitude in the temperate zone (North of 23.5°N). (**B**) Snow duration is weakly negatively related to snow-free seed predation intensity, such that snow is more likely to shelter seeds that already experience lower predation. Effect of snow: χ^2=9.9$_{df=1}$, *P*=0.0016. (**C&E**) Mean seed predation intensity with latitude and elevation, for comparison to D&F only (seed predation intensity results should be taken from models in main text that consider >1 data point/site). Points show raw means (i.e. points in C are unadjusted for elevation, points in E are unadjusted for latitude). Trend lines and 95% CI are from the minimum adequate binomial GLM shown in top text. (**D&F**) Estimated mean seed predation strength for seeds that take >1 yr to germinate: daily seed predation intensity from C&E × fraction of year at full predation intensity, assuming no predation under snow. Points & lines as in C/E; discounting for snow creates a latitude × elevation interaction, as no elevations have snow cover in the tropics whereas snow varies with elevation in the temperature zone (A). Accounting for reduced exposure under snow could double latitudinal (C vs. D) and elevational (E vs. F) clines in seed predation risk at median latitudes (the effect is less at low latitudes/elevations and greater at high latitudes/elevations). If one instead assumes that snow reduces seed predation by 65% rather than 100%, there is no longer a significant latitude × elevation interaction and the clines are more similar to those in predation intensity (C/E): 27% and 18%, across latitudes and elevations, respectively. Seed type never interacted with other main factors, so results are shown for predation on uncaged sunflower seeds only.

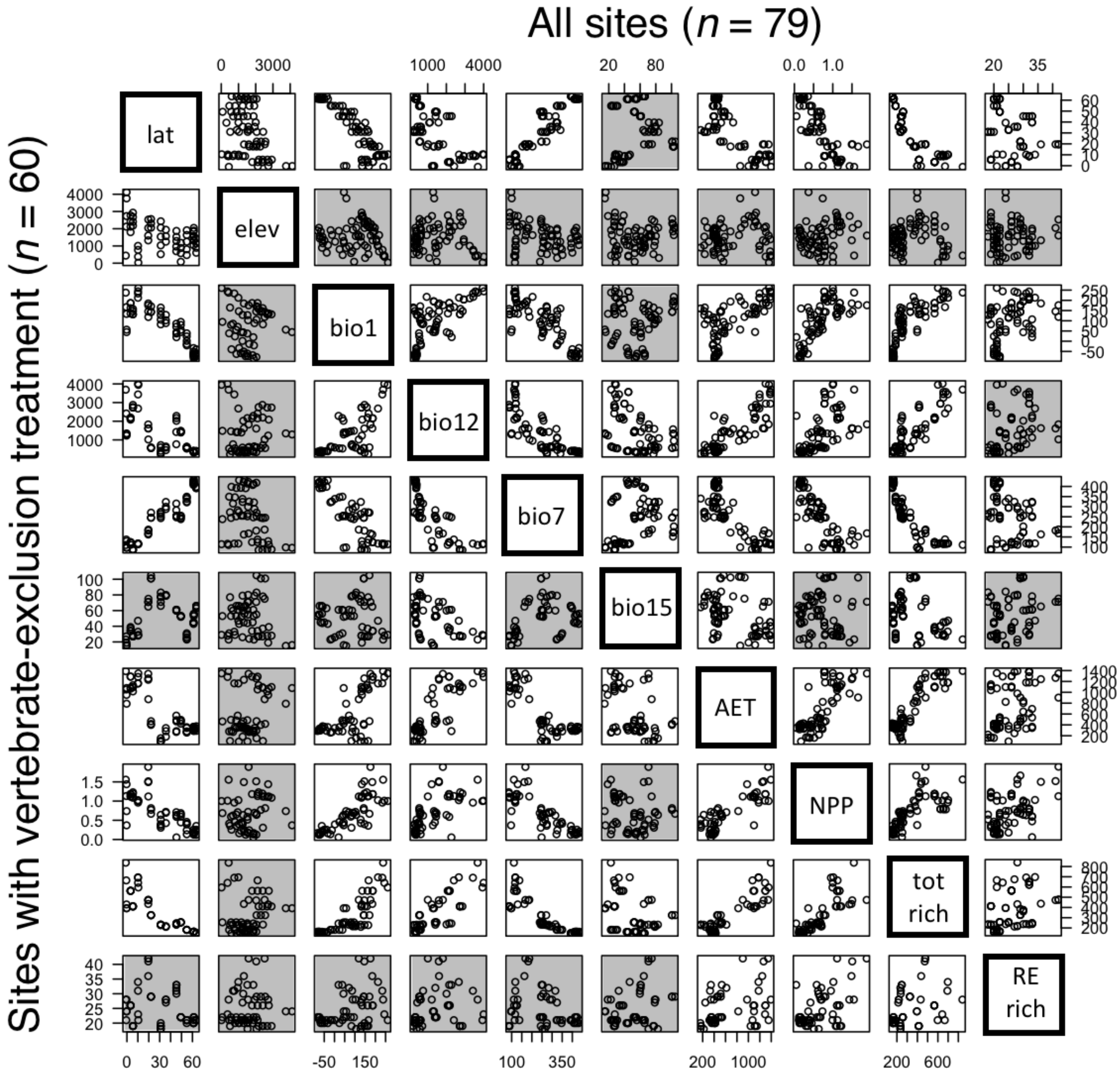

Fig. S6. Correlations between continuous environmental variables (latitude, elevation, mean annual temperature (bio1), mean annual precipitation (bio12), annual temperature range (bio7), seasonality of precipitation (bio15), actual annual evapotranspiration (AET), net primary productivity (NPP), total vertebrate species richness, and rodent and shrew richness. Plots above the diagonal show correlations among all 79 sites, plots below the diagonal show correlations among the 60 sites where the caging experiment was conducted. Grey background indicates correlations that are not significant after correcting for multiple comparisons.

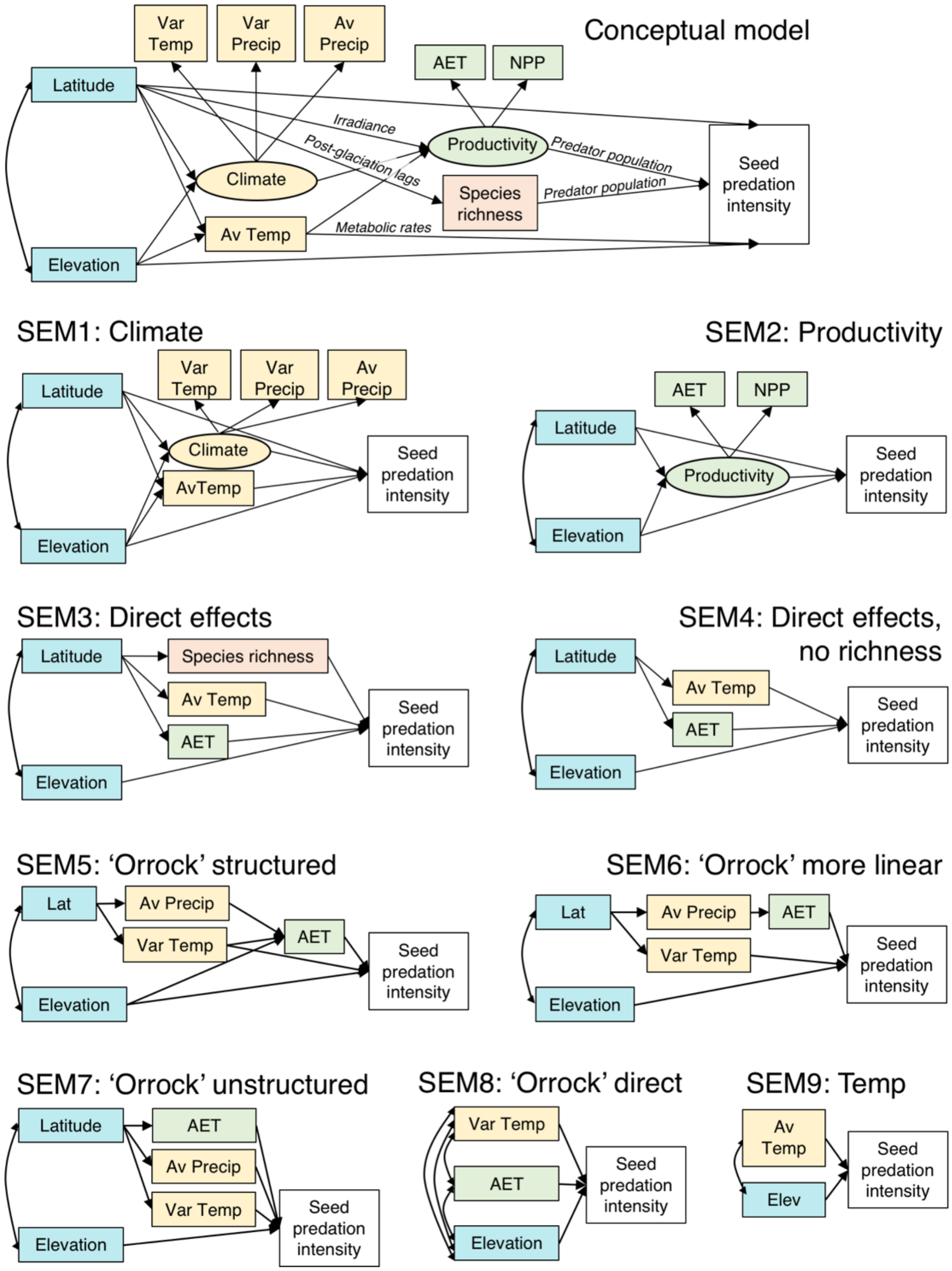

Fig. S7. Path diagrams of SEM1 to SEM9. Manifest variables are boxes, latent variables are ovals, straight arrows denote regression effects and curved double-headed arrows denote correlations. Climate variables (yellow) are Mean annual temperature (Av Temp), Annual temperature range (Var Temp), Annual precipitation (Av Precip), and Precipitation seasonality (Var Precip). Productivity variables (green) are Annual Evapotranspiration (AET) and Net primary productivity (NPP). Italics along conceptual model arrows give the hypothesized reason for these effects. For 'Species richness', models of predation on sunflower seeds use total vertebrate richness, whereas models of predation on oat seeds use the total richness of rodents and shrews. Models 10 to 15 have the same structure as SEM9.

Supplementary Tables

Table S1. Transect details.

Country	Latitude (decimal °)	Transect elevation (m)			Tree line elevation (m)	
		Min	Max	Total	Upper	Lower
USA	63.5	605	1430	825	640	–
Canada[2]	61.2	1050	1835	1000[1]	1200	–
Canada	61.2	1360	2050	1000[1]	1200	–
Canada	54.8	470	1910	1440	1650	–
Canada	49.4	80	1180	1100	1350	–
USA	45.4	695	1875	1180	1850	630
USA	39.9	60	2000	1940	2200	100
USA	35.7	930	1940	1010	3100	1550
USA	33.0	210	1660	1450	3100	1350
Mexico	31.0	520	2430	1910	3000	1500
Mexico	22.1	1780	2560	780	2600	1800
Mexico[3]	19.6	1325	2530	1205	4000	–
Mexico	17.2	1625	2265	640	3600	–
Costa Rica	10.4	25	1005	980	2700	–
Panama[2]	8.8	380	1380	1000	3100	–
Colombia	5.5	2180	2930	750	3750	–
Colombia[2,3]	3.3	1800	2770	970	3700	–
Ecuador[3]	-0.7	440	4120	3680	3750	–

[1] Total elevation combined over the two transects at this latitude (Yukon, Canada)

[2] Location of one or two sites were adjusted between runs of the experiment. Thus the transect had four sites each run but five (or six, for Panama) sites in total.

[3] These transects were less accessible, so instead of setting up all sites on one day and checking them all the following day, sites were split into two groups and tested consecutively (ie the experiment was run over 4 days)

Table S2. Relative performance of SEMs. Performance of all SEMs (fig. S7) in explaining the intensity of total invertebrate seed predation. Models 3–8 were run twice, once with productivity given by AET and again with productivity given by NPP (modeling productivity as a latent variable in SEM3–8 increased AICs by >80, not shown). Top model(s) for each data set (lowest AIC) are in bold. Annual temperature range best explained total predation intensity on sunflower seeds, while annual temperature range and latitude equally explained total predation intensity on oats. We did not find support for the predicted stronger role of temperature on invertebrate predation, which was best explained by a non-mechanistic model including only elevation and latitude. Simpler models preformed the best, and additional complexity via indirect effects, latent variables, or more than two predictors increased AIC values and resulted in poor model fits. We assessed model goodness-of-fit using the Tucker-Lewis Index (<0.9 indicates poor fit, *74*) and Root Mean Square Error of Approximation (>0.1 indicates poor fit, *75*)*.

	Total predation sunflower		Total predation oat		Invert predation sunflower	
Structural Equation Model	ΔAIC	TLI, RMSEA	ΔAIC	TLI, RMSEA	ΔAIC	TLI, RMSEA
SEM1: Climate	475	0.46, 0.45	470	0.44, 0.45	361	0.56, 0.40
SEM2: Productivity	301	1, 0	298	1, 0	195	1.0, 0
SEM3: Direct effects AET	420	0.14, 0.61	511	0.05, 0.51	313	0.34, 0.51
SEM3: Direct effects NPP	423	0.33, 0.49	514	0.25, 0.42	304	0.21, 0.58
SEM4: Direct effects no richness AET	296	0.09, 0.60	292	0.02, 0.60	217	0.17, 0.59
SEM4: Direct effects no richness NPP	303	0.22, 0.52	295	0.02, 0.50	207	0.30, 0.54
SEM5: Orrock structured AET	392	0.33, 0.51	391	0.26, 0.52	314	0.32, 0.51
SEM5: Orrock structured NPP	448	0.23, 0.51	448	0.15, 0.52	324	0.32, 0.50
SEM6: Orrock more linear AET	362	0.61, 0.38	362	0.57, 0.40	294	0.59, 0.39
SEM6: Orrock more linear NPP	437	0.47, 0.42	436	0.41, 0.43	320	0.50, 0.42
SEM7: Orrock unstructured AET	405	0.36, 0.49	404	0.30, 0.50	309	0.44, 0.46
SEM7: Orrock unstructured NPP	408	0.56, 0.38	408	0.50, 0.40	298	0.58, 0.39
SEM8: Orrock direct only AET	129	—	129	—	115	—
SEM8: Orrock direct only NPP	154	—	154	—	108	—
SEM9: Mean Temperature	21	—	10	—	18	—
SEM10: AET	16	—	7.6	—	14	—
SEM11: NPP	15	—	4.5		4.3	
SEM12: Species richness	13	—	12	—	17	—
SEM13: Temperature range	**0** (AIC = 638.2)	**—**	**0** (AIC = 666.6)	—	10	—
SEM14: Mean Precipitation	16	—	8.9	—	26	—
SEM15: Latitude	4.2	**—**	**1.4**	**—**	**0** (AIC = 476.4)	**—**

* TLI = 1 and RMSEA = 0 for SEM9 to SEM15, in which all predictors directly affect the response.

Table S3. Multispecies surveys of time to germination under natural field conditions (exposure to post-dispersal seed predation) and ideal lab or greenhouse conditions (dormancy). Days to germinate are species means, so ‘Mean’ is the across-species average.

Study Ref	Country	Latitude zone	Biome	N spp	Days to germinate Mean	Min	Max
Time to germinate in field							
(*58*)	Brazil	Tropics	Forest	319	36	4	450
	India	Tropics	Forest	90	17	8	45
	Ivory Coast	Tropics	Forest	277	48	7	810
	Malaysia	Tropics	Forest	114	72	9	669
	Panama	Tropics	Forest	237	55	5	404
(*59*)	Panama	Tropics	Forest	100	36	4	450
(*60*)	Mexico	Tropics	Forest	10	102	49	434
(*61*)	China	Tropics	Forest	4	21	5	139
(*62*)	Ghana	Tropics	Forest	18	40	20	110
(*63*)	Australian	Tropics	Grassland	6	175	160	196
(*64*)	USA (CA)	Temperate	Grassland	6*	23	14	26
(*65*)	USA (IL)	Temperate	Grassland	31	21**	4	—
(*66*)	Tibet	Temperate	Alpine	265	225***	—	—
(*67*)	Canada (NWT)	Temperate	Forest	10	301	2	—
Time to germinate in lab (dormancy)							
(*68*)	Panama	Tropics	Forest	4	—	10	45
(*62*)	Ghana	Tropics	Forest	16	25	7	65
(*69*)	Tibet	Temperate	Alpine	134	—	5	28
(*70*)	Tibet	Temperate	Alpine	633	14	0	53
(*71*)	China	Temperate	All	726	18	—	—
		Temperate	Forest	393	29	—	—
(*72*)	Argentina	Temperate	Forest & Grassland	17	12	8	—
(*73*)	USA (CO)	Temperate	Alpine	16	15	2	>30

*all native, annual species. Mean is days to reach 50% emergence.

**germination only followed for 28 d, 31/32 species had some seeds germinate in <28d. Mean is estimated assuming seeds that did not germinate in 28 d would have taken 30 d

***seeds were only followed for 1 year