Transient and persistent species differ in germination rates, not establishment rates, across a grassland metacommunity.

John Guittar, Deborah Goldberg, Kari Klanderud, Astrid Berge, Marta Boixaderes, Eric Meineri, Joachim Topper, and Vigdis Vandvik.

Tables and Figures

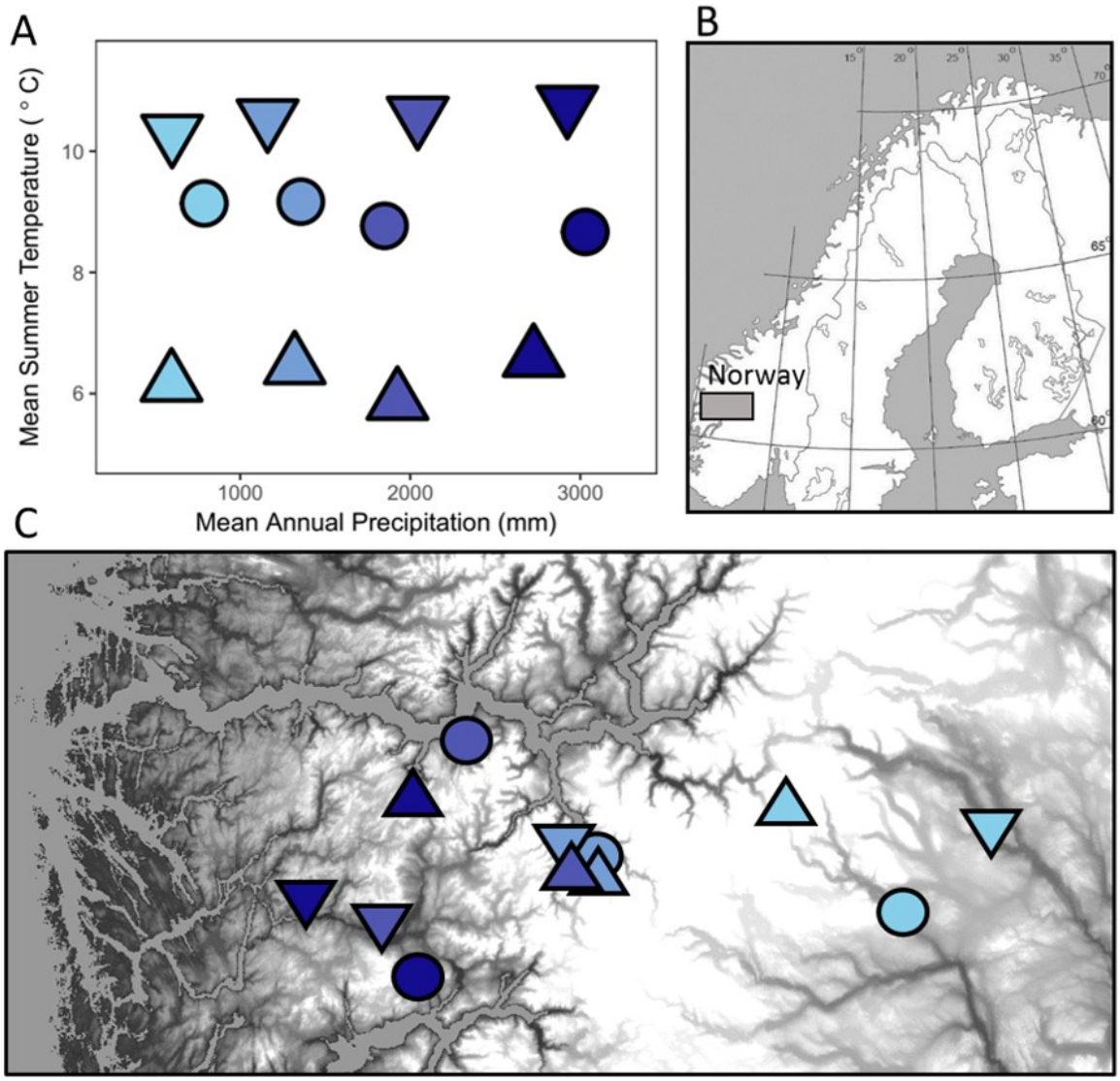

Figure 1. Panel A shows mean summer temperature and mean annual precipitation values at the twelve sites. Summer is defined as the warmest three months at each site. Panels B and C show site locations in southern Norway.

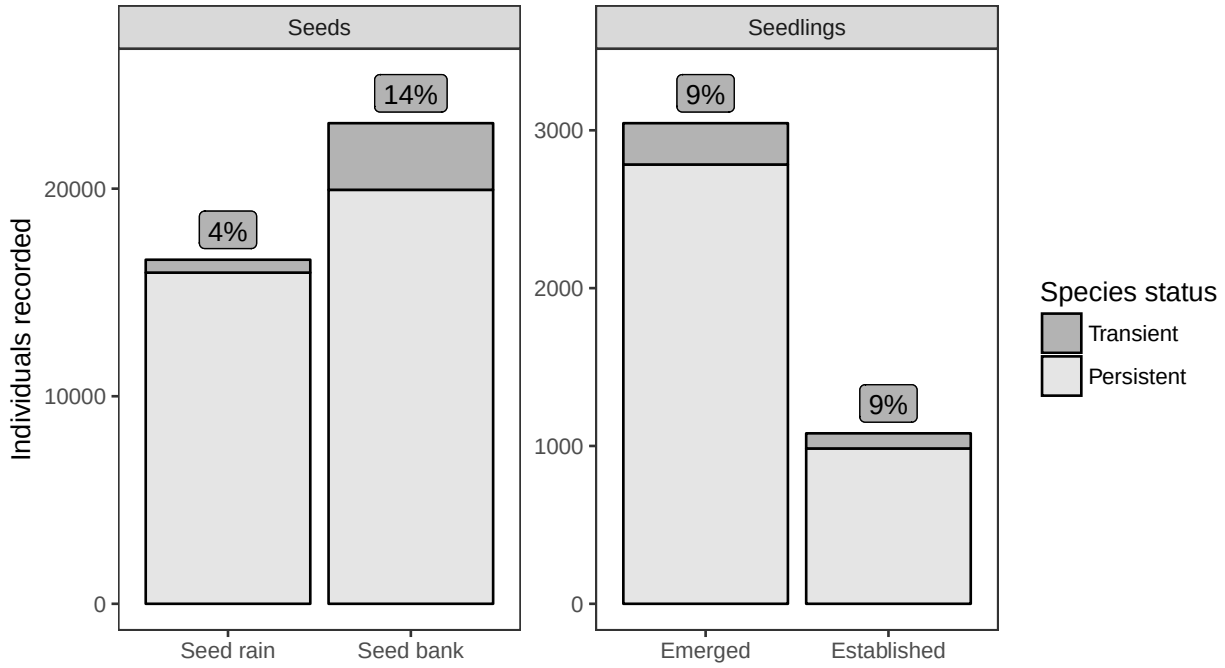

Figure 2. Numbers of individuals recorded in this study, grouped by life stage and shaded by local species status. "Persistent" species occur as adults in three or more of our four annual vegetation surveys, whereas "transient" seeds do not. Percentages are of transient species out of total life stage.

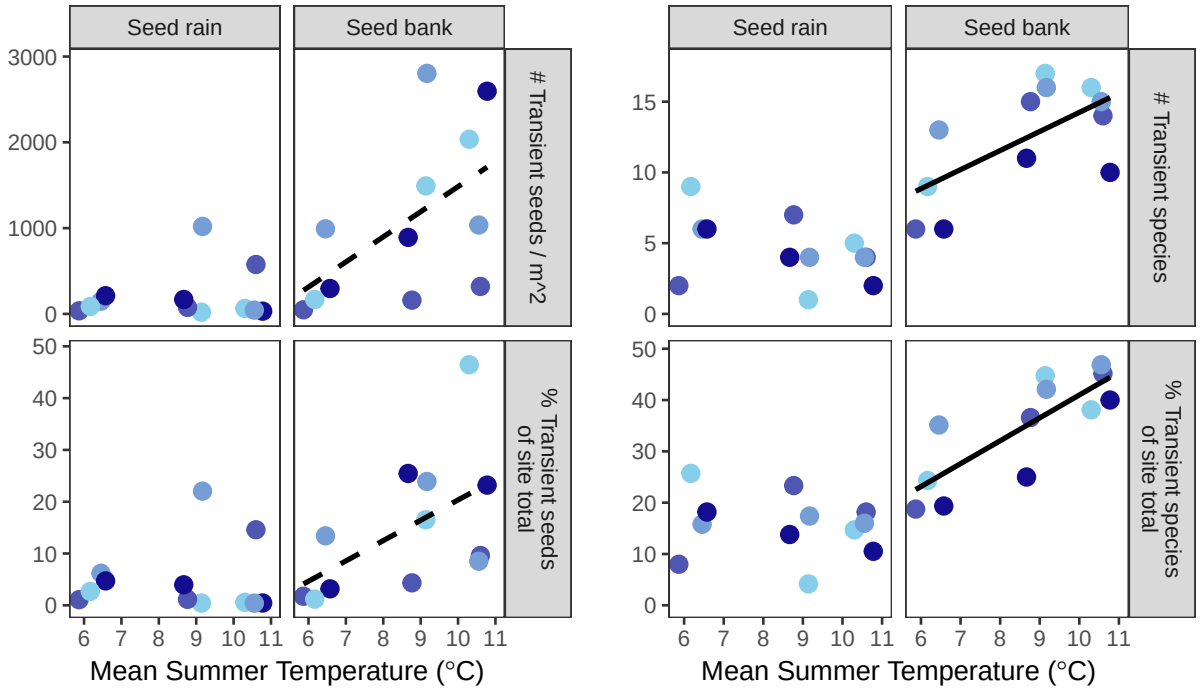

Figure 3. Seed density and richness of transient species by site, in raw numbers and as percentages of total seeds/species at each site, plotted by mean summer temperature. Summer is defined as the three warmest months at each site. Shape color is consistent with Fig. 1 and reflects mean annual precipitation values, from light blue to dark blue, of approximately 660 mm, 1300 mm, 2000 mm, and 2900 mm. Linear regression lines are solid when significant ($p < 0.05$) and dashed when marginally significant ($p < 0.1$). See Table S3 for linear regression summary statistics.

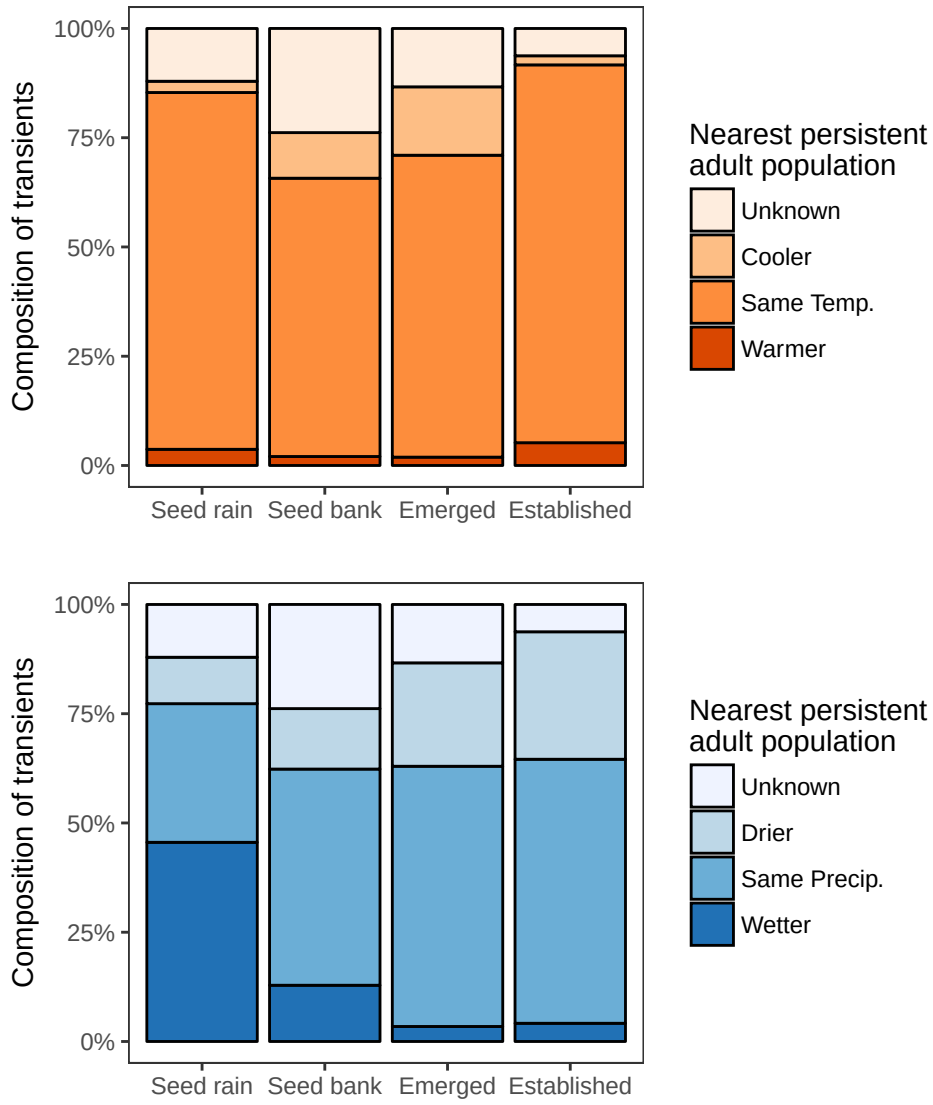

Figure 4. Putative climate origins of transient seeds by life stage. Seeds are assumed to originate from the nearest (i.e., most similar) climate at which persistent adult populations occur.

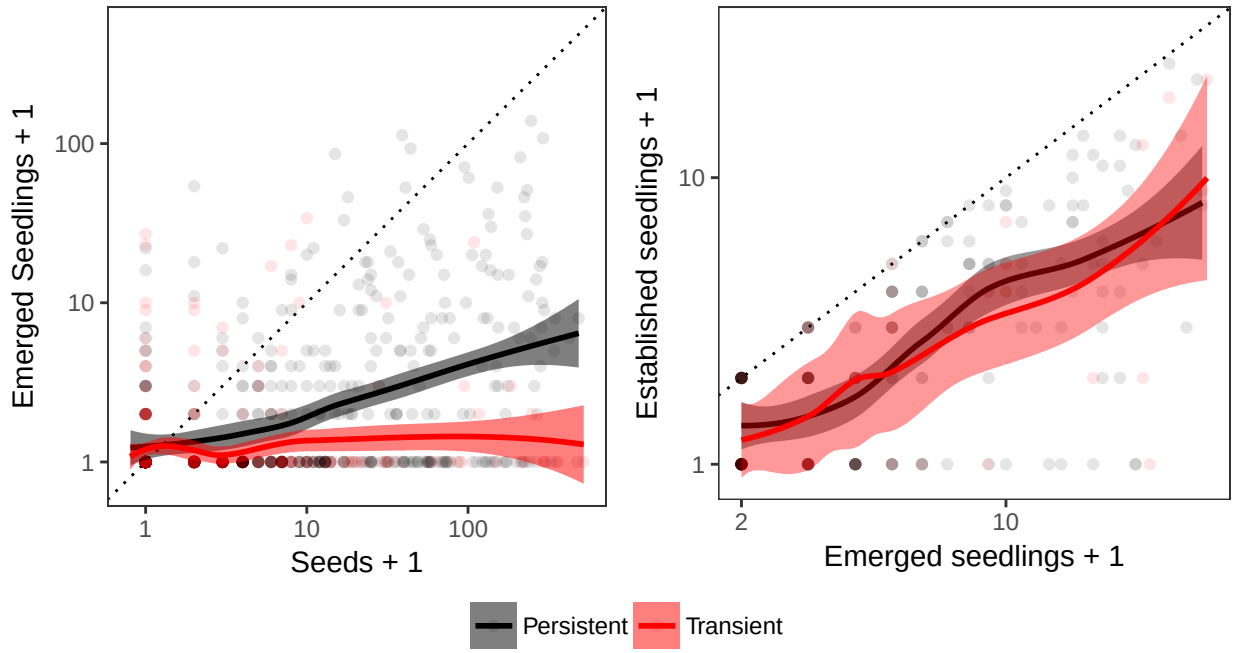

Figure 5. The abundances of emerged seedlings (left) and established seedlings (right) by species and site, colored by local species status. Each circle represents the presence/absence of one species at one site, and colored lines and shadings show LOESS smoothing functions and 95 % confidence intervals. Seed number is equal to the sum of seeds in the seed rain and seed bank. Abundances reflect the total number of individuals in four 0.25 m^2 subplots (i.e., 0.25 m^2) at each site. Count data are increased by one to enable plotting zeroes on a log scale. Panels only show data falling within the observed window of transient seed abundances (< 632 seeds) and transient seedling abundances (< 35 seedlings) in order to focus on the comparison of persistent and transient species.

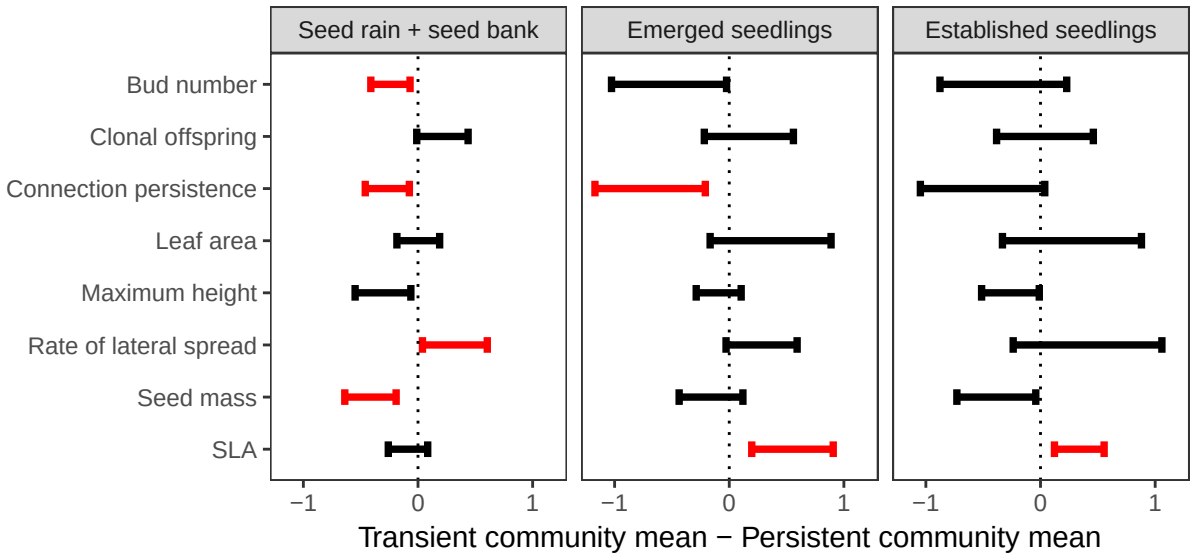

Figure 6. Community mean trait values of locally transient species relative to locally persistent species, calculated by site and life stage and summarized using error bars based on 95% confidence intervals. Values for each trait were scaled by their standard deviations to enable comparisons across traits. Values to the left of the dotted line (x = 0) denote sites where trait values of transient individuals were greater on average than the trait values of persistent individuals, and vice versa. Error bars are colored red when transient and persistent community weighted mean trait values differed significantly (paired t-test; $p < 0.05$).

	N	Null model	Local climate	Local climate + Local sp. status (P/T)	Local climate + Local sp. status (P/ST/C/Wa/U)	Local climate + Local sp. status (P/SP/D/We/U)
ΔAIC	-	0.00	-5.26	-19.38	-32.94	-41.55
General predictors						
Log(seed no.)	600	**7.41	**7.71	**5.46	**6.35	**6.68
Local temperature	600	-	*2.87	*2.29	*3.17	**3.32
Local precipitation	600	-	-0.83	-1.22	-1.39	-1.46
Transient/Persistent predictors						
Transient	209	-	-	**-4.89	-	-
Transient * Local temperature	209	-	-	*2.08	-	-
Transient * Local precipitation	209	-	-	1.47	-	-
Origin-based predictors						
Transient from similar temp.	103	-	-	-	-1.45	-
Transient from cooler climate	26	-	-	-	-1.48	-
Transient from warmer climate	20	-	-	-	*-3.02	-
Transient from similar precip.	82	-	-	-	-	-1.18
Transient from drier climate	34	-	-	-	-	-0.43
Transient from wetter climate	33	-	-	-	-	**-4.76
Transient from unknown climate	60	-	-	-	**-6.03	**-6.05

Table 1.

Comparison of z-scores from different GLM models (columns) predicting numbers of emerged seedlings by species and site. Abbreviations in column headers refer to the categories used in the model term denoting local species status, potentially including the putative climate origins of each transient species at each site: P = persistent, T = transient, ST = similar temperature (i.e., a transient from a site with a similar temperature), SP = similar precipitation, C = cooler, Wa = warmer, D = drier, We = wetter, or U = unknown climate. Data include all recorded seeds and seedlings that could be identified to species. N equals the number of unique species-by-site combinations for each category/predictor. Asterisks denote significance (*: $p < 0.05$, **: $p < 0.001$). Dashes indicate predictors that were not included in a given model. Including model terms for transient/persistent species status and then putative temperature and precipitation origins progressively improved model performance, as reflected in the reduction of AIC values relative to the null model that uses only local seed numbers as a predictor.

Supplementary Tables and Figures

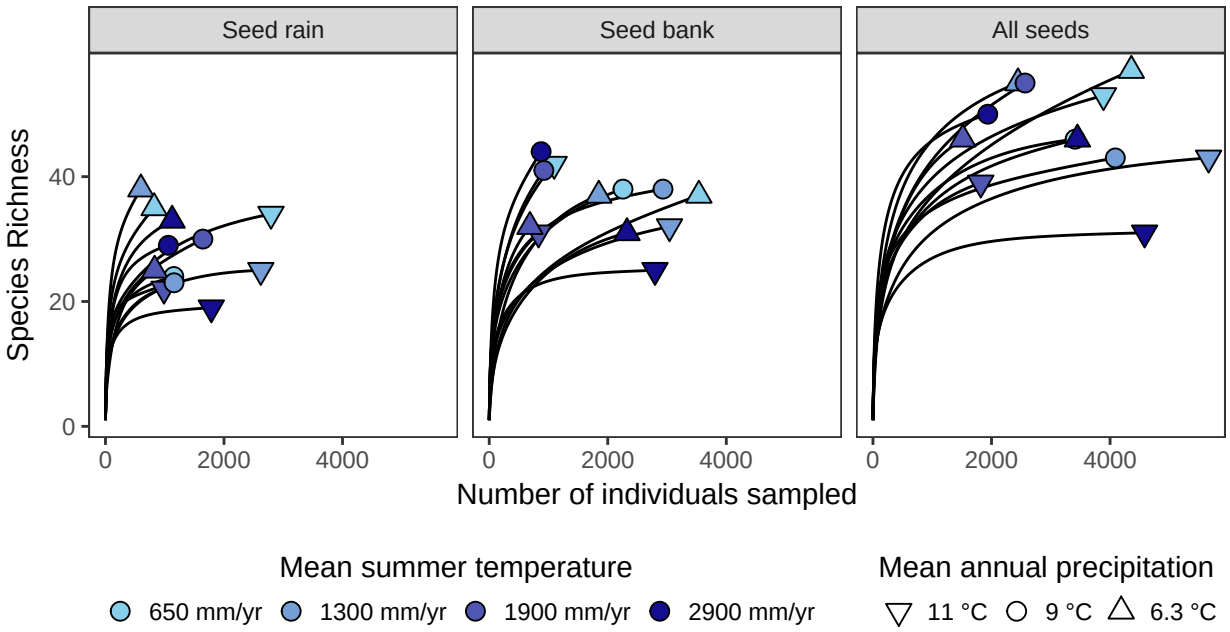

Figure S1. Rarefaction curves for seed sampling. Coloring and symbols are consistent with Figure 1.

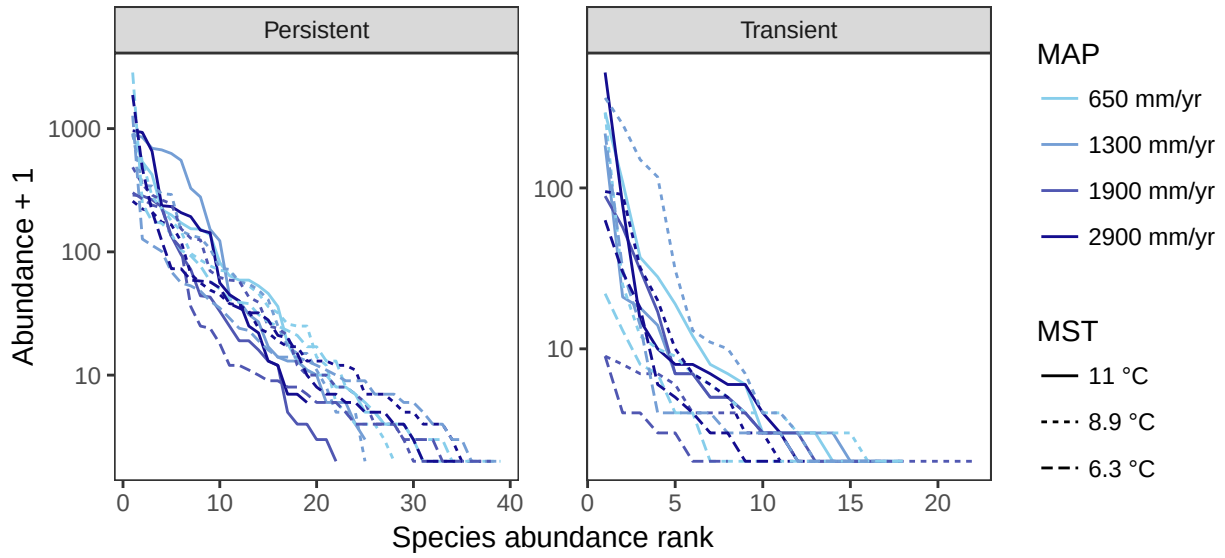

Figure S2. Whittaker rank abundance plots plotted by site. MST = Mean summer temperature, defined as the three warmest months at each site; MAP = Mean annual precipitation.

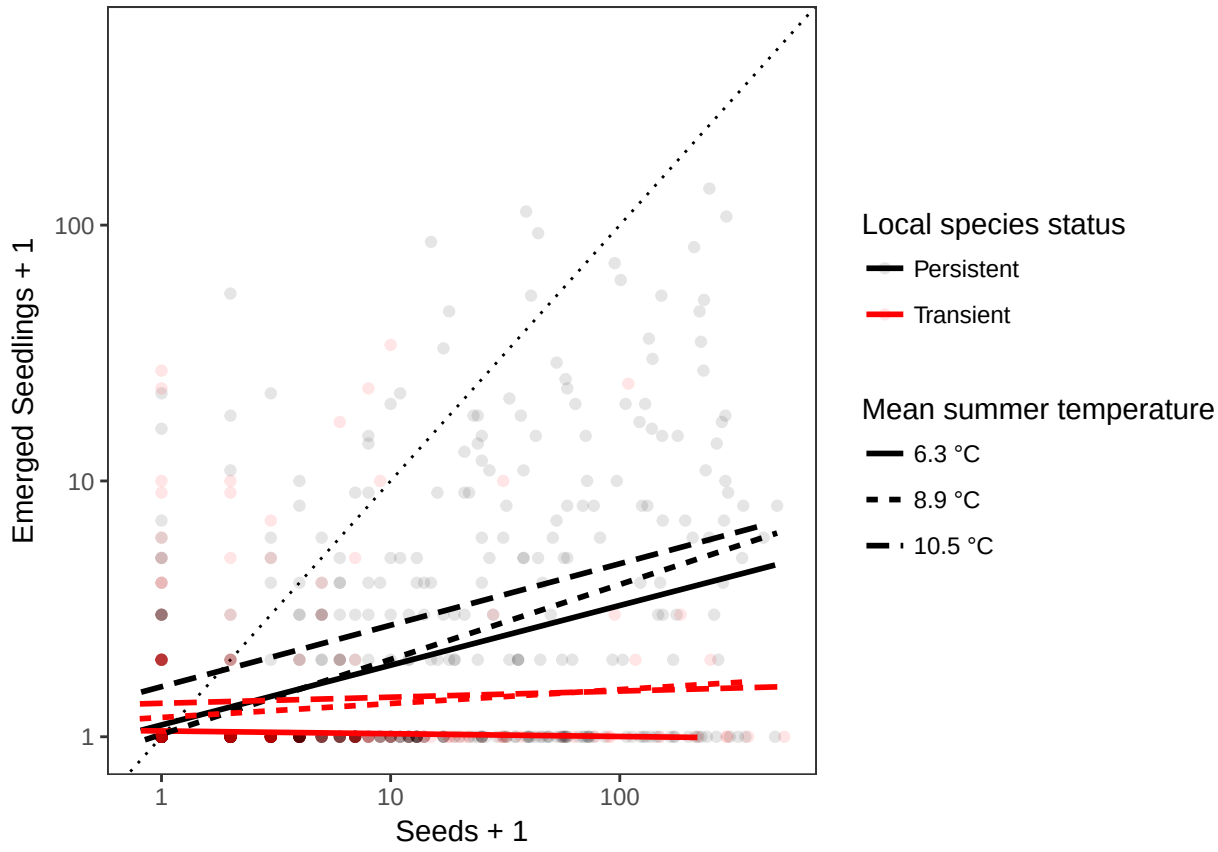

Figure S3. The abundances of emerged seedlings by species and site, colored by local species status. Each circle represents the abundance of one species at one site. Colored lines show linear regressions for data at the three temperature levels in our system; each temperature level includes data from four sites with different mean annual precipitations. Seed number is equal to the sum of seeds in the seed rain and seed bank. Abundances reflect the net number of individuals in four 0.25 m^2 subplots (i.e., 0.25 m^2) at each site. Count data are increased by one to enable plotting zeroes on a log scale. Panels only show data falling within the observed window of transient seed abundances (< 632 seeds) in order to focus on the comparison of persistent and transient species.

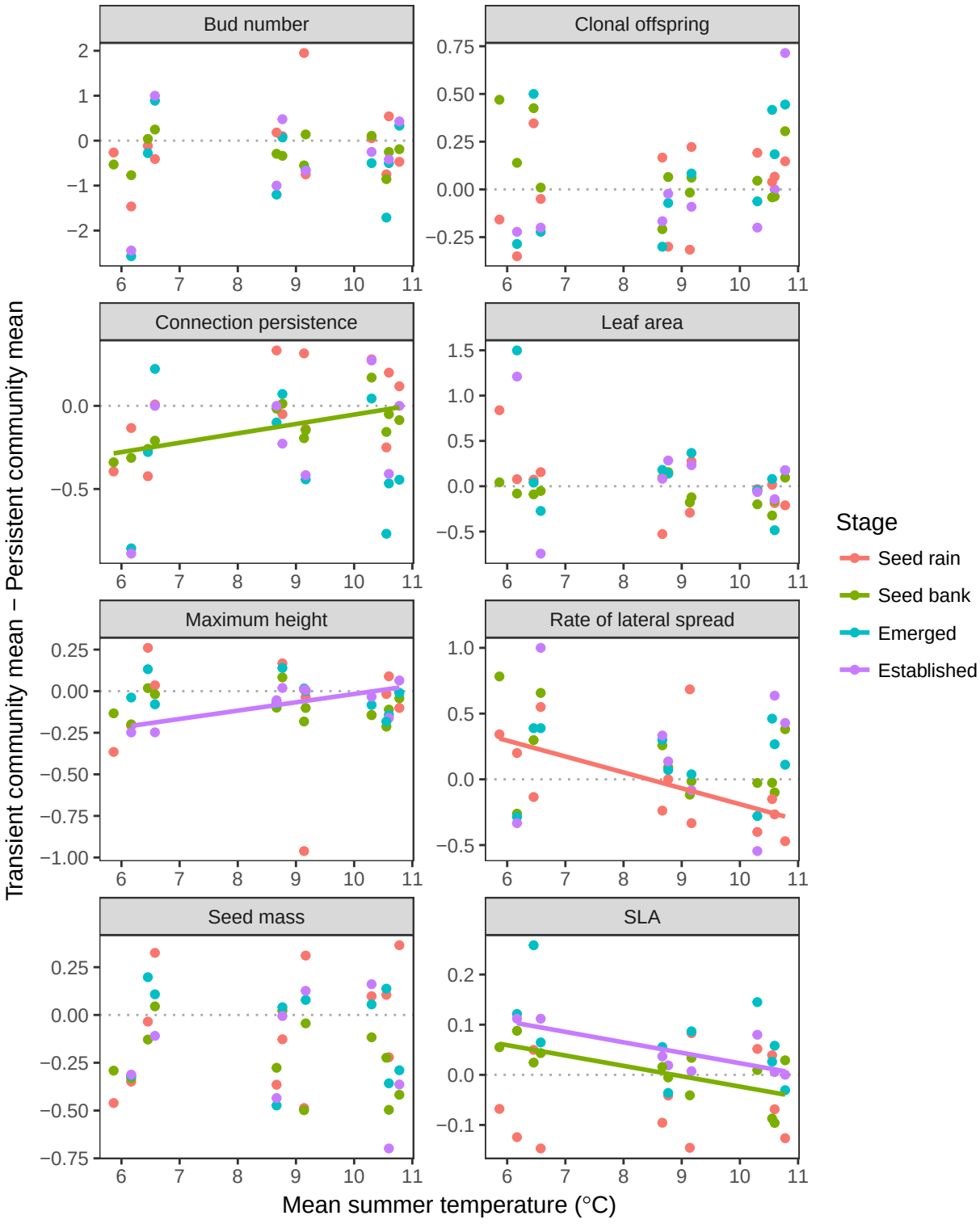

Figure S4. Community mean trait values of locally transient species relative to locally persistent species, grouped by site and life stage and plotted by mean summer temperature. Community means are calculated as the average trait value of all species present in the community. Values above the grey dotted line (y = 0) denote sites where the trait values of transient individuals were greater on average than the trait values of persistent individuals, and vice versa. Lines are shown only when linear regression is significant ($p < 0.05$).

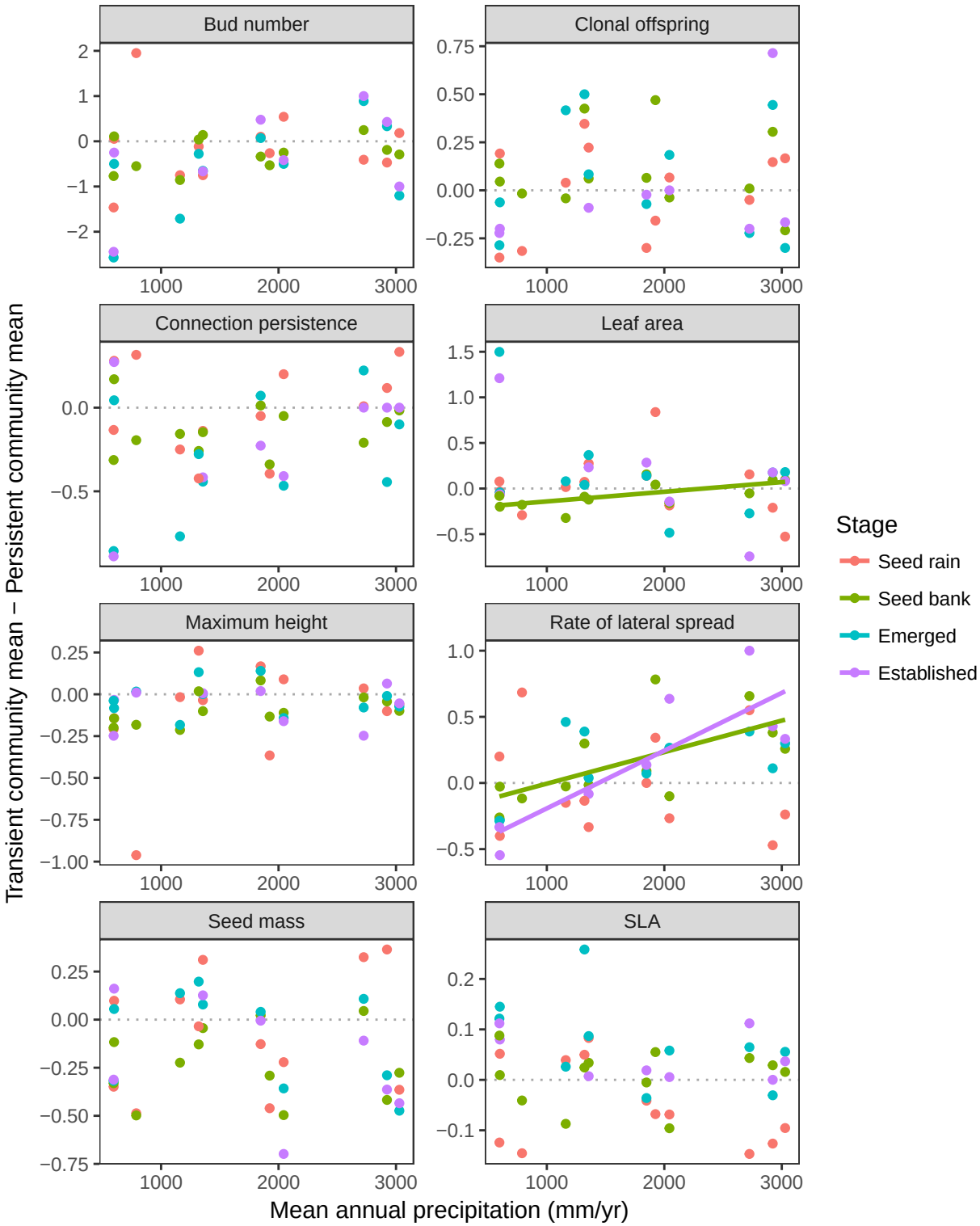

Figure S5. Community mean trait values of locally transient species relative to locally persistent species, grouped by site and life stage and plotted by mean annual precipitation. Community means are calculated as the average trait value of all species present in the community. Values above the grey dotted line (y = 0) denote sites where the trait values of transient individuals were greater on average than the trait values of persistent individuals, and vice versa. Lines are shown only when linear regression is significant ($p < 0.05$).

Stage	Density (per sq. m.)	Site richness	Regional richness
All Individuals			
Seed Rain	5611 ± 2885	28 ± 6	103
Seed Bank	7761 ± 4060	36 ± 6	113
All Seeds	13372 ± 5072	47 ± 8	141
Emerged Seedlings	1461 ± 612	20 ± 5	84
Established Seedlings	415 ± 206	14 ± 4	65
Seeds and Seedlings	15248 ± 5629	50 ± 7	144
Adults		56 ± 15	152
All Stages		68 ± 14	171
Transients Only			
Seed Rain	210 ± 302	4 ± 2	-
Seed Bank	1074 ± 976	12 ± 4	-
All Seeds	1284 ± 1113	16 ± 4	-
Emerged Seedlings	332 ± 418	4 ± 3	-
Established Seedlings	61 ± 94	2 ± 2	-
Seeds and Seedlings	1677 ± 1471	17 ± 5	-

Table S1.
Species richness within and across sites. The density of 'all individuals' includes unidentified seeds and seedlings. Regional richness is not shown for transient species because transient/persistent species status can vary by site.

Model/Variable	Coefficient	Std. Error	t-statistic	P-value
Seed rain seed density, all species				
Temperature	1036.2	349.3	2.967	**0.016**
Precipitation	-0.8	0.7	-1.032	0.329
Seed bank seed density, all species				
Temperature	4.4	698.9	0.006	0.995
Precipitation	-1.4	1.5	-0.903	0.390
Emerged seedling density, all species				
Temperature	116.4	50.5	2.305	**0.047**
Precipitation	-0.2	0.1	-2.102	*0.065*
Established seedling density, all species				
Temperature	44.5	25.6	1.737	0.116
Precipitation	0.0	0.1	-0.662	0.525
Seed rain richness, all species				
Temperature	-1.9	0.8	-2.319	**0.046**
Precipitation	0.0	0.0	-1.185	0.267
Seed bank richness, all species				
Temperature	-0.3	0.9	-0.286	0.781
Precipitation	0.0	0.0	-1.099	0.300
Emerged seedling richness, all species				
Temperature	1.0	0.7	1.351	0.210
Precipitation	0.0	0.0	-1.437	0.185
Established seedling richness, all species				
Temperature	0.7	0.6	1.289	0.230
Precipitation	0.0	0.0	-2.245	*0.051*
Adult vegetation richness, all species				
Temperature	-6.4	1.7	-3.786	**0.004**
Precipitation	0.0	0.0	0.350	0.734

Table S2.
Summary statistics for multiple linear regression models of total seed and seedling abundances, and total seed, seedling, and adult species richness across sites. Each set of rows (i.e., predictors) with a bold header is a model. In each model, a data point is a number of seeds, seedlings, percent cover units of adult vegetation, or species at a site; N = 12. P-values are bold when < 0.05, and italic when < 0.1. Temperature refers to mean summer temperature (°C), defined during the three warmest months of the year, and mean annual precipitation (mm/yr). Temperature and precipitation interaction terms were never significant (data not shown) and are not included here.

Model/Variable	Coefficient	Std. Error	t-statistic	P-value
Seed rain seed density, transient species only				
Temperature	26.13	52.57	0.497	0.631
Precipitation	0.01	0.11	0.086	0.933
Percent transient seeds in the seed rain				
Temperature	0.00	0.01	0.293	0.776
Precipitation	0.00	0.00	0.098	0.924
Seed bank seed density, transient species only				
Temperature	294.67	142.34	2.070	*0.068*
Precipitation	-0.12	0.30	-0.387	0.708
Percent transient seeds in the seed bank				
Temperature	0.04	0.02	2.020	*0.074*
Precipitation	0.00	0.00	-0.485	0.639
Seed rain richness, transient species only				
Temperature	-0.48	0.36	-1.324	0.218
Precipitation	0.00	0.00	-0.725	0.487
Percent transient species in the seed rain				
Temperature	-0.01	0.01	-0.486	0.638
Precipitation	0.00	0.00	-0.317	0.758
Seed bank richness, transient species only				
Temperature	1.39	0.37	3.755	**0.005**
Precipitation	-0.00241	0.00	-3.041	**0.014**
Percent transient species in the seed bank				
Temperature	0.05	0.01	5.453	**0.000**
Precipitation	-0.00004	0.00	-2.400	**0.040**

Table S3.
Summary statistics for multiple linear regression models of seed abundances and species richness of transient species across sites. Each set of rows (i.e., predictors) with a bold header is a model. In each model, a data point is a number of seeds or species at a site; N = 12. P-values are bold when < 0.05, and italic when < 0.1. Temperature refers to mean summer temperature (°C), defined as the three warmest months of the year, and mean annual precipitation (mm/yr). Temperature and precipitation interaction terms were never significant(data not shown) and are not included here.

	Seed rain		Seed bank		All seeds		Emerged		Established	
Species status	**No.**	**%**	**No.**	**%**	**No.**	**%**	**No.**	**%**	**No.**	**%**
All individuals	16575	100.0	23153	100.0	39728	100.0	3045	100.0	1080	100.0
Persistent	15954	96.3	19943	86.1	35897	90.4	2783	91.4	984	91.1
Transient	621	3.7	3210	13.9	3831	9.6	262	8.6	96	8.9
Temperature origins of transients										
Same	507	3.1	2044	8.8	2551	6.4	181	5.9	83	7.7
Cooler	16	0.1	335	1.4	351	0.9	41	1.3	2	0.2
Warmer	23	0.1	66	0.3	89	0.2	5	0.2	5	0.5
Unknown	75	0.5	765	3.3	840	2.1	35	1.1	6	0.6
Precipitation origins of transients										
Same	197	1.2	1588	6.9	1785	4.5	156	5.1	58	5.4
Drier	66	0.4	444	1.9	510	1.3	62	2.0	28	2.6
Wetter	283	1.7	413	1.8	696	1.8	9	0.3	4	0.4
Unknown	75	0.5	765	3.3	840	2.1	35	1.1	6	0.6

Table S4.
Numbers of individuals recorded, grouped by local status and putative climate origins. Percentages are of all individuals (top row). Individuals that could not be identified to species were not included.

	Seed bank	Emerged	Established	Mature vegetation
Seed rain	0.16	0.29	0.20	0.40
Seed bank		0.32	0.32	0.19
All seeds		0.39	0.35	0.32
Emerged			0.77	0.34
Established				0.35

Table S5.
Pearson correlations of species abundances across life stages, grouped by site (N = 814). Unidentified seeds and seedlings were not included.

	N	Null model	Local climate	Local climate + Local sp. status (P/T)	Local climate + Local sp. status (P/ST/C/Wa/U)	Local climate + Local sp. status (P/SP/D/We/U)
ΔAIC	-	0.00	3.57	0.03	0.33	10.25
General predictors						
Log(seedling no.)	243	**18.98	**18.81	**18.53	**18.55	**18.27
Local temperature	243	-	0.56	1.40	1.12	0.69
Local precipitation	243	-	-0.43	0.09	-0.15	-0.57
Transient/Persistent predictor						
Transient	46	-	-	0.83	-	-
Transient * Local temperature	46	-	-	*-2.96	-	-
Transient * Local precipitation	46	-	-	-1.50	-	-
Origin-based predictors						
Transient from similar temp.	28	-	-	-	-0.06	-
Transient from cooler climate	8	-	-	-	*-2.63	-
Transient from warmer climate	2	-	-	-	1.41	-
Transient from similar precip.	28	-	-	-	-	-0.85
Transient from drier climate	9	-	-	-	-	0.34
Transient from wetter climate	1	-	-	-	-	0.19
Transient from unknown climate	8	-	-	-	-0.70	-0.67

Table S6.
Comparison of z-scores from different GLM models (columns) predicting numbers of established seedlings by species and site. Abbreviations in column headers refer to the categories used in the model term denoting local species status, potentially including the putative climate origins of each transient species at each site: P = persistent, T = transient, ST = similar temperature (i.e., a transient from a site with a similar temperature), SP = similar precipitation, C = cooler, Wa = warmer, D = drier, We = wetter, or U = unknown climate. Data include all recorded seedlings that could be identified to species. Asterisks denote significance (*: $p < 0.05$, **: $p < 0.001$). Dashes indicate predictors that were not included in a given model. Including model terms for transient/persistent species status and then putative temperature and precipitation origins did not improve model performance, as reflected in the increase of AIC values relative to the null model based only on local numbers of emerged seedlings.

APPENDIX A

In addition to testing for performance differences between transient and persistent species using numbers of seeds and seedlings, we use generalized linear models (GLMs) to test for differences in the presence/absence of emerged seedlings and established seedlings by species at each site. In other words, we investigate the probability of transient species emerging and/or establishing at sites *at all*, rather than their rates of emergence and establishment. These models are structurally identical to the GLMs based on seedling abundance data, except that the response variable is binary (presence/absence) and therefore we use binomial error distributions and logit links. In this appendix, we compile results and figures that relate to this presence/absence analysis.

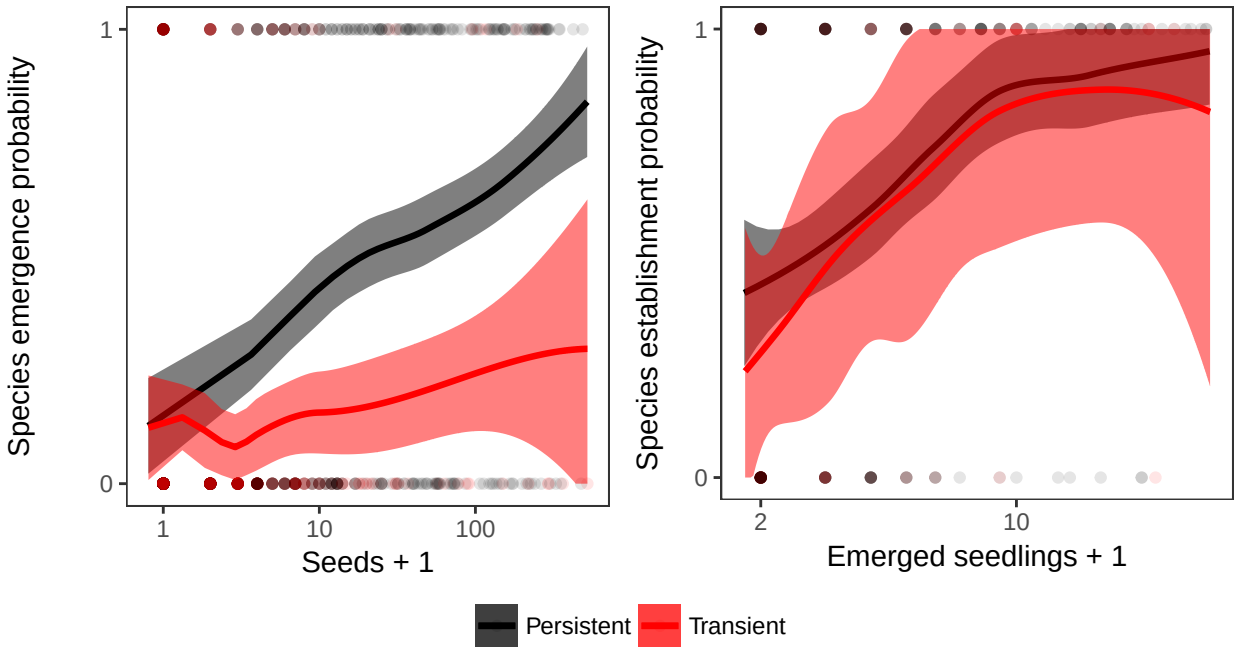

Figure A1-1. The presence/absence of emerged seedlings (left) and established seedlings (right) by species and site, colored by local species status. Each circle represents the presence/absence of one species at one site, and colored lines and shadings show LOESS smoothing functions and 95 % confidence intervals, respectively. Seed number is equal to the sum of seeds in the seed rain and seed bank. Presence/absence data are based on censuses in four 0.25 m^2 subplots (i.e., 0.25 m^2) at each site. Count data are increased by one to enable plotting zeroes on a log scale. Species emergence and species establishment denote whether any individuals of a given species emerged or established, respectively, at a given site. Plots only show data falling within the observed window of transient seed abundances (< 632 seeds) and transient seedling abundances (< 35 seedlings) in order to focus on the comparison of persistent and transient species.

	N	Null model	Local climate	Local climate + Local sp. status (P/T)	Local climate + Local sp. status (P/ST/C/Wa/U)	Local climate + Local sp. status (P/SP/D/We/U)
ΔAIC	-	0.00	-2.25	-32.03	-35.14	-46.62
General predictors						
Log(seed no.)	600	**6.01	**5.74	*3.29	*3.28	**3.43
Local temperature	600	-	*2.39	*2.46	*3.19	*3.20
Local precipitation	600	-	-0.75	-1.87	-0.97	-1.41
Transient/Persistent predictors						
Transient	209	-	-	**-5.41	-	-
Transient * Local temperature	209	-	-	1.32	-	-
Transient * Local precipitation	209	-	-	*2.08	-	-
Origin-based predictors						
Transient from similar temp.	103	-	-	-	**-3.54	-
Transient from cooler climate	26	-	-	-	-1.77	-
Transient from warmer climate	20	-	-	-	*-2.34	-
Transient from similar precip.	82	-	-	-	-	*-2.06
Transient from drier climate	34	-	-	-	-	-1.85
Transient from wetter climate	33	-	-	-	-	**-3.35
Transient from unknown climate	60	-	-	-	**-4.39	**-4.38

Table A1-1.

Comparison of z-scores from different GLM models (columns) predicting the presence/absence of emerged seedlings by species and site. Abbreviations in column headers refer to the categories used in the model term denoting local species status, potentially including the putative climate origins of each transient species at each site: P = persistent, T = transient, ST = similar temperature (i.e., a transient from a site with a similar temperature), SP = similar precipitation, C = cooler, Wa = warmer, D = drier, We = wetter, or U = unknown climate. Data include all recorded seedlings that could be identified to species. Asterisks denote significance (*: $p < 0.05$, **: $p < 0.001$). Dashes indicate predictors that were not included in a given model. Including model terms for transient/persistent species status and then putative temperature and precipitation origins improved model performance, as reflected in the reduction of AIC values relative to the null model using only local seed numbers as a predictor.

	N	Null model	Local climate	Local climate + Local sp. status (P/T)	Local climate + Local sp. status (P/ST/C/Wa/U)	Local climate + Local sp. status (P/SP/D/We/U)
ΔAIC	-	0.00	1.87	4.37	2.92	5.18
General predictors						
Log(seedling no.)	243	**6.26	**6.23	**6.04	**5.98	**5.92
Local temperature	243	-	-0.79	0.07	-0.25	-0.47
Local precipitation	243	-	-1.19	-1.28	-1.08	-1.38
Transient/Persistent predictor						
Transient	46	-	-	0.03	-	-
Transient * Local temperature	46	-	-	-1.53	-	-
Transient * Local precipitation	46	-	-	0.53	-	-
Origin-based predictors						
Transient from similar temp.	28	-	-	-	-0.10	-
Transient from cooler climate	8	-	-	-	-1.73	-
Transient from warmer climate	2	-	-	-	0.02	-
Transient from similar precip.	28	-	-	-	-	-1.27
Transient from drier climate	9	-	-	-	-	1.11
Transient from wetter climate	1	-	-	-	-	0.01
Transient from unknown climate	8	-	-	-	-1.01	-1.02

Table A1-2.

Comparison of z-scores from different GLM models (columns) predicting the presence/absence of established seedlings by species and site. Abbreviations in column headers refer to the categories used in the model term denoting local species status, potentially including the putative climate origins of each transient species at each site: P = persistent, T = transient, ST = similar temperature (i.e., a transient from a site with a similar temperature), SP = similar precipitation, C = cooler, Wa = warmer, D = drier, We = wetter, or U = unknown climate. Data include all recorded seedlings that could be identified to species. Asterisks denote significance (*: $p < 0.05$, **: $p < 0.001$). Dashes indicate predictors that were not included in a given model. Including model terms for transient/persistent species status and then putative temperature and precipitation origins did not improve model performance, as reflected in the increase of AIC values relative to the null model based only on local numbers of emerged seedlings.

APPENDIX B

List of species used in this study and their net abundances across stages. For adult plant data, the mean percent cover is calculated for each species at each site, and then summed over sites. Otherwise, abundance is the sum of all individuals collected or measured.

Species	Code	Rain	Bank	Emerged	Established	Adults
Achillea millefolium	Ach.mil	101	19	1	0	1574
Aconitum septentrionale	Aco.sep	0	0	0	0	1
Agrostis capillaris	Agr.cap	1079	2777	109	104	6181
Agrostis mertensii	Agr.mer	9	0	0	0	130
Ajuga pyramidalis	Aju.pyr	0	13	0	0	17
Alchemilla alpina	Alc.alp	182	195	189	68	1279
Alopecurus pratensis	Alo.pra	0	1	0	0	0
Anemone nemorosa	Ane.nem	0	19	6	0	150
Antennaria alpina	Ant.alp	27	6	0	0	0
Antennaria dioica	Ant.dio	45	0	0	0	575
Anthoxanthum odoratum	Ant.odo	1756	238	20	17	2478
Arabis alpina	Ara.alp	0	8	0	0	0
Arabis hirsuta	Ara.hir	0	3	0	0	0
Arctous alpinus	Arc.alp	3	0	0	0	2
Astragalus alpinus	Ast.alp	7	1	0	0	441
Avenella flexuosa	Ave.fle	84	15	2	1	352
Avenula pubescens	Ave.pub	0	0	0	0	17
Bartsia alpina	Bar.alp	0	0	0	0	7
Bistorta vivipara	Bis.viv	179	275	77	16	1576
Botrychium lunaria	Bot.lun	0	0	0	0	44
Calluna vulgaris	Cal.vul	0	304	2	0	81
Campanula rotundifolia	Cam.rot	271	1183	133	32	690
Carex atrata	Car.atr	0	1	0	0	37
Carex bigelowii	Car.big	56	10	0	0	228
Carex capillaris	Car.cap	60	35	1	0	626
Carex dioica	Car.dio	0	2	0	0	19
Carex echinata	Car.ech	31	1	0	0	6
Carex flava	Car.fla	0	0	0	0	35
Carex leporina	Car.lep	744	459	17	5	443
Carex nigra	Car.nig	5	17	1	1	117
Carex norvegica	Car.nor	6	82	0	0	152
Carex pallescens	Car.pal	229	930	13	4	198
Carex panicea	Car.pan	1	9	1	0	110
Carex pilulifera	Car.pil	220	187	14	6	404
Carex pulicaris	Car.pul	12	1	0	0	47
Carex rupestris	Car.rup	0	0	0	0	6
Carex saxatilis	Car.sax	0	0	0	0	2
Carex vaginata	Car.vag	3	22	0	0	614
Carum carvi	Caru.car	2	0	5	3	29
Cerastium alpinum	Cer.alp	0	0	1	0	22
Cerastium cerastoides	Cer.cer	7	3	2	1	32
Cerastium fontanum	Cer.fon	60	142	34	9	78
Cirsium palustre	Cir.pal	0	3	0	0	117
Coeloglossum viride	Coe.vir	0	0	0	0	7
Comastoma tenellum	Com.ten	1	0	0	0	6
Dactylis glomerata	Dac.glo	1	0	0	0	101

(continued)

Species	Code	Rain	Bank	Emerged	Established	Adults
Danthonia decumbens	Dan.dec	6	0	0	0	6
Deschampsia alpina	Des.alp	0	0	1	1	0
Deschampsia cespitosa	Des.ces	616	336	1	1	1232
Dianthus deltoides	Dia.del	30	87	26	7	101
Dryas octopetala	Dry.oct	0	1	0	0	12
Empetrum hermaphroditum	Emp.her	35	45	2	0	90
Epilobium sp	Epi.sp	1	308	14	3	135
Erigeron uniflorus	Eri.uni	0	1	0	0	20
Euphrasia sp	Eup.sp	276	0	152	40	326
Festuca ovina	Fes.ovi	236	2	2	0	467
Festuca rubra	Fes.rub	126	45	4	3	1183
Festuca vivipara	Fes.viv	0	0	0	0	16
Filipendula ulmaria	Fil.ulm	0	1	0	0	0
Fragaria vesca	Fra.ves	0	5	0	0	0
Galium boreale	Gal.bor	0	3	0	0	18
Galium saxatile	Gal.sax	9	7	4	0	52
Galium uliginosum	Gal.uli	0	5	5	3	50
Galium verum	Gal.ver	3	0	4	3	270
Gentiana nivalis	Gen.niv	30	0	0	0	35
Gentiana purpurea	Gen.pur	0	0	0	0	1
Gentianella amarella	Gen.ama	2	0	4	4	12
Gentianella campestris	Gen.cam	1	0	0	0	1
Geranium sylvaticum	Ger.syl	20	3	1	0	128
Geum rivale	Geu.riv	0	4	0	0	57
Hieracium alpinum	Hie.alp	0	0	0	0	23
Hieracium pilosella	Hie.pil	1060	252	157	5	1664
Hieracium vulgatum	Hie.vul	15	1	1	0	94
Huperzia selago	Hup.sel	0	0	0	0	4
Hypericum maculatum	Hype.mac	0	141	90	6	264
Hypochaeris maculata	Hypo.mac	4	8	0	0	53
Juncus alpinoarticulatus	Jun.alp	0	10	0	0	13
Juncus bufonius	Jun.buf	0	5	0	0	0
Juncus bulbosus	Jun.bul	0	1	0	0	0
Juncus filiformis	Jun.fil	0	101	0	0	0
Juncus trifidus	Jun.tri	37	0	0	0	7
Knautia arvensis	Kna.arv	24	1	8	3	566
Kobresia simpliciuscula	Kob.sim	0	0	0	0	11
Leontodon autumnalis	Leo.aut	813	37	127	33	566
Leucanthemum vulgare	Leu.vul	460	78	18	2	145
Loiseleuria procumbens	Loi.pro	16	0	0	0	4
Lotus corniculatus	Lot.cor	3	4	6	3	272
Luzula multiflora	Luz.mul	458	211	7	7	295
Luzula pilosa	Luz.pil	3	85	2	2	64
Luzula spicata	Luz.spi	8	1	0	0	57
Melampyrum pratense	Mel.pra	1	0	10	6	74
Minuartia biflora	Min.bif	0	0	0	0	19
Myosotis decumbens	Myo.dec	0	0	0	0	4
Nardus stricta	Nar.str	1144	105	0	0	1548
Noccaea caerulescens	Noc.cae	1	0	53	2	151
Omalotheca norvegica	Oma.nor	8	16	31	5	15
Omalotheca supina	Oma.sup	10	41	9	4	165

(continued)

Species	Code	Rain	Bank	Emerged	Established	Adults
Omalotheca sylvatica	Oma.syl	2	102	0	0	1
Oxalis acetosella	Oxa.ace	6	1	0	0	31
Oxyria digyna	Oxy.dig	0	0	0	0	36
Parnassia palustris	Par.pal	5	50	0	0	239
Phleum alpinum	Phl.alp	20	0	0	0	305
Phleum pratense	Phl.pra	77	0	0	0	8
Phyllodoce caerulea	Phy.cae	4	0	0	0	2
Pimpinella saxifraga	Pim.sax	422	4	5	1	215
Pinguicula vulgaris	Pin.vul	1	40	12	2	103
Plantago lanceolata	Pla.lan	57	15	9	7	202
Plantago major	Pla.maj	0	3	0	0	0
Plantago media	Pla.med	39	13	0	0	218
Poa alpina	Poa.alp	65	54	10	3	441
Poa annua	Poa.ann	0	0	0	0	1
Poa pratensis	Poa.pra	327	53	1	0	369
Polygonum aviculare	Pol.avi	0	1	0	0	0
Potentilla agrentea	Pot.arg	0	18	17	2	9
Potentilla crantzii	Pot.cra	4	6	7	2	196
Potentilla erecta	Pot.ere	503	737	105	28	2845
Primula skandinavica	Pri.ska	0	1	0	0	0
Prunella vulgaris	Pru.vul	236	165	73	34	676
Pyrola sp	Pyr.sp	0	0	2	0	102
Ranunculus acris	Ran.acr	139	337	46	18	497
Ranunculus auricomus	Ran.aur	0	1	1	0	88
Ranunculus repens	Ran.rep	0	0	0	0	23
Rhinanthus minor	Rhi.min	19	0	6	1	127
Rhodiola rosea	Rho.ros	0	0	0	0	8
Rubus idaeus	Rub.ida	12	0	0	0	61
Rumex acetosa	Rum.ace	683	144	28	4	796
Rumex acetosella	Rum.acl	529	632	171	128	385
Sagina sp	Sag.sp	148	6777	258	108	248
Salix herbacea	Sal.her	11	1	2	0	718
Salix reticulata	Sal.ret	20	0	0	0	22
Saussurea alpina	Sau.alp	0	1	0	0	132
Saxifraga aizoides	Sax.aiz	0	65	7	3	74
Saxifraga cespitosa	Sax.ces	0	2	0	0	0
Saxifraga oppositifolia	Sax.opp	0	1	0	0	4
Saxifraga rivularis	Sax.riv	0	2	0	0	0
Saxifraga stellaris	Sax.ste	1	2	0	0	0
Schedonorus pratensis	Sch.pra	0	12	0	0	0
Sedum acre	Sed.acr	0	0	0	0	17
Sedum annuum	Sed.ann	0	12	0	0	0
Selaginella selaginoides	Sel.sel	762	0	1	0	505
Sibbaldia procumbens	Sib.pro	3	180	213	64	650
Silene acaulis	Sil.aca	49	0	26	2	377
Silene vulgaris	Sil.vul	1	6	1	1	41
Solidago virgaurea	Sol.vir	2	0	0	0	80
Stellaria graminea	Ste.gra	163	5	40	21	228
Stellaria media	Ste.med	0	420	28	0	10
Succisa pratensis	Suc.pra	0	0	0	0	10
Taraxacum sp	Tar.sp	191	10	25	12	516

(continued)

Species	Code	Rain	Bank	Emerged	Established	Adults
Thalictrum alpinum	Tha.alp	29	46	1	0	1096
Tofieldia pusilla	Tof.pus	20	0	0	0	41
Trichophorum cespitosum	Tri.ces	0	0	0	0	9
Trientalis europaea	Tri.eur	0	0	0	0	6
Trifolium medium	Tri.med	0	0	0	0	116
Trifolium pratense	Tri.pra	229	9	6	3	481
Trifolium repens	Tri.rep	20	51	53	4	1321
Urtica diocia	Urt.dio	0	40	0	0	0
Vaccinium myrtillus	Vac.myr	0	7	3	1	127
Vaccinium vitis-idaea	Vac.vit	2	0	0	0	85
Valeria sambucifolia	Val.sam	0	0	0	0	2
Veronica alpina	Ver.alp	26	18	6	1	458
Veronica chamaedrys	Ver.cha	6	352	14	6	292
Veronica fruticans	Ver.fru	4	0	4	1	67
Veronica officinalis	Ver.off	910	1559	160	64	2878
Veronica serpyllifolia	Ver.ser	0	1297	116	48	98
Vicia cracca	Vic.cra	0	0	0	0	93
Vicia sepium	Vic.sep	0	0	0	0	1
Viola biflora	Vio.bif	30	57	15	0	538
Viola palustris	Vio.pal	111	486	30	14	1309
Viola riviniana	Vio.riv	41	163	69	28	358
Viola tricolor	Vio.tri	9	250	101	54	48
Viscaria vulgaris	Vis.vul	0	33	6	5	2

APPENDIX C

Species trait values used in this study. All values are $\log^{10}$transformed. Trait values for taxonomically unresolved genera (e.g., *Pyrola sp*, *Epilobium sp*) are means based on field data. Trait abbreviations (i.e., column headers) are defined as follows: LA: leaf area (mm^2); MH: maximum height (m); SM: seed mass (mg); SLA: specific leaf area (m^2/kg); CP: persistence of plant-offspring connections (0: fewer than two years; 1: two or more years); CO: number of offspring per parent per year (0: one or fewer offspring; 1: two or more offspring); LAT: rate of lateral spread (0: one cm/year; 1: more than one cm/year; BUDS: number of buds per ramet (an integer score ranging from one (few buds belowground and aboveground) to eight (many buds belowground and aboveground)). LA, MH, SM, and SLA values are log10-transformed.

Species	**LA**	**MH**	**SM**	**SLA**	**CP**	**CO**	**LAT**	**BUDS**
Achillea millefolium	2.70	-0.22	-0.89	1.26	1	1	1	5
Aconitum septentrionale	-	-	0.56	-	1	0	0	5
Agrostis capillaris	2.38	-0.10	-1.22	1.45	1	0	1	5
Agrostis mertensii	1.79	-0.52	-0.90	1.39	1	0	0	5
Ajuga pyramidalis	2.88	-0.60	0.19	1.24	1	0	0	4
Alchemilla alpina	2.58	-0.70	-0.54	1.15	1	0	0	4
Alopecurus pratensis	3.04	-	-0.18	1.40	1	0	0	5
Anemone nemorosa	3.48	-0.52	0.33	1.44	1	0	1	2
Antennaria alpina	-	-	-	-	-	-	-	-
Antennaria dioica	1.65	-0.60	-1.30	1.35	1	1	1	5
Anthoxanthum odoratum	2.45	-0.46	-0.31	1.45	1	1	0	5
Arabis alpina	-	-	-0.80	1.42	1	1	1	4
Arabis hirsuta	2.57	-	-1.03	1.45	1	1	1	5
Arctous alpinus	2.14	-1.30	0.38	1.06	-	-	-	-
Astragalus alpinus	2.70	-0.70	-	1.39	1	0	1	4
Avenella flexuosa	1.89	-0.15	-0.51	1.16	1	1	1	5
Avenula pubescens	2.93	0.08	0.28	1.32	1	0	1	5
Bartsia alpina	2.42	-0.52	-0.48	1.24	1	0	1	5
Bistorta vivipara	2.48	-0.52	0.26	1.28	-	-	-	-
Botrychium lunaria	2.62	-0.82	-	1.33	1	0	0	1
Calluna vulgaris	-0.01	-0.30	-1.61	1.07	1	1	1	8
Campanula rotundifolia	1.76	-0.30	-1.21	1.33	1	0	1	5
Carex atrata	2.68	-0.22	-0.21	1.32	1	0	0	2
Carex bigelowii	2.36	-0.40	-0.21	1.21	1	0	1	4
Carex capillaris	1.96	-0.60	-0.25	1.39	1	0	0	4
Carex dioica	1.53	-0.52	-0.26	1.10	1	0	0	3
Carex echinata	2.34	-0.52	-0.13	1.18	1	1	0	3
Carex flava	2.37	-0.30	-0.07	1.31	1	1	0	5
Carex leporina	2.55	-0.30	-0.21	1.35	1	0	0	4
Carex nigra	2.42	-0.30	-0.13	1.33	1	0	1	3
Carex norvegica	2.35	-0.40	-0.45	1.22	1	0	0	3
Carex pallescens	2.67	-0.22	0.10	1.40	1	1	0	5
Carex panicea	2.31	-0.30	0.37	1.25	1	1	0	3
Carex pilulifera	2.27	-0.40	0.09	1.33	1	1	0	3
Carex pulicaris	2.14	-0.70	0.17	0.97	1	0	0	4
Carex rupestris	1.49	-0.70	-	1.08	1	0	0	4
Carex saxatilis	2.55	-0.40	-0.10	1.08	1	0	1	3
Carex vaginata	2.67	-0.30	0.48	1.29	1	1	0	4
Carum carvi	3.10	-0.30	0.28	1.41	-	-	-	4
Cerastium alpinum	1.61	-0.70	-0.56	1.51	1	0	0	4
Cerastium cerastoides	1.15	-1.00	-0.83	1.39	1	0	1	5

(continued)

Species	LA	MH	SM	SLA	CP	CO	LAT	BUDS
Cerastium fontanum	2.26	-0.40	-0.85	1.44	1	0	0	3
Cirsium palustre	-	-	0.19	1.26	0	0	0	4
Coeloglossum viride	2.63	-0.52	-	1.34	0	0	0	2
Comastoma tenellum	-	-1.00	-	-	-	-	-	-
Dactylis glomerata	3.38	0.08	-0.04	1.31	1	1	0	5
Danthonia decumbens	2.58	-0.40	0.16	1.23	1	1	0	5
Deschampsia alpina	-	-0.30	-	-	-	-	-	-
Deschampsia cespitosa	2.64	0.00	-0.68	1.16	1	1	0	5
Dianthus deltoides	1.43	-0.60	-0.70	1.31	1	1	1	5
Dryas octopetala	2.34	-1.00	-0.13	1.01	1	1	1	5
Empetrum hermaphroditum	1.04	-0.70	0.01	0.92	-	-	-	-
Epilobium sp	1.97	-0.82	-1.23	1.39	-	-	-	-
Erigeron uniflorus	-	-0.82	-0.64	1.27	1	0	0	4
Euphrasia sp	1.57	-	-0.60	1.49	-	-	-	-
Festuca ovina	1.71	-0.40	-0.36	1.16	1	0	0	3
Festuca rubra	2.13	-0.15	-0.04	1.20	1	1	0	5
Festuca vivipara	1.62	-0.52	-	1.04	-	-	-	-
Filipendula ulmaria	-	0.18	-0.13	1.39	1	0	1	5
Fragaria vesca	3.38	-0.70	-0.50	1.36	1	0	0	5
Galium boreale	1.69	-0.40	-0.15	1.29	1	1	1	5
Galium saxatile	0.70	-0.70	-0.22	1.38	-	-	-	-
Galium uliginosum	1.11	-0.40	-0.40	1.52	1	-	0	5
Galium verum	1.23	-0.22	-0.30	1.20	1	0	1	5
Gentiana nivalis	1.00	-0.70	-1.82	1.60	0	1	0	2
Gentiana purpurea	-	-0.10	-0.32	-	1	0	0	5
Gentianella amarella	3.54	-0.60	-0.85	1.45	0	0	0	2
Gentianella campestris	2.24	-0.52	-0.71	1.48	-	-	-	3
Geranium sylvaticum	3.59	-0.10	0.78	1.32	1	0	0	5
Geum rivale	3.54	-0.28	0.16	1.45	1	0	1	5
Hieracium alpinum	-	-0.70	0.00	1.50	1	0	0	3
Hieracium pilosella	2.74	-0.52	-0.62	1.45	0	0	0	4
Hieracium vulgatum	3.24	-0.10	-0.35	1.54	-	-	-	-
Huperzia selago	0.85	-0.60	-	1.14	1	0	0	4
Hypericum maculatum	2.45	0.00	-0.78	1.46	1	1	1	5
Hypochaeris maculata	3.38	-0.31	0.01	1.32	-	-	-	-
Juncus alpinoarticulatus	-	-0.40	-	-	1	0	1	5
Juncus bufonius	1.91	-	-1.64	1.25	0	1	0	2
Juncus bulbosus	1.41	-	-1.73	1.28	1	1	0	6
Juncus filiformis	2.79	-	-1.62	0.99	1	0	0	3
Juncus trifidus	2.18	-0.60	-0.88	1.20	1	0	1	3
Knautia arvensis	3.10	-0.10	0.62	1.28	1	0	0	5
Kobresia simpliciuscula	-	-0.52	-0.32	-	-	-	-	-
Leontodon autumnalis	2.41	-0.40	-0.10	1.43	0	0	0	3
Leucanthemum vulgare	2.19	-0.15	-0.59	1.29	1	0	1	5
Loiseleuria procumbens	0.95	-1.00	-1.77	0.65	1	0	1	6
Lotus corniculatus	2.22	-0.52	0.15	1.31	1	1	0	5
Luzula multiflora	2.31	-0.40	-0.40	1.42	1	0	0	5
Luzula pilosa	2.84	-0.60	-0.01	1.42	1	0	1	5
Luzula spicata	1.42	-0.60	-0.51	1.06	1	0	0	5
Melampyrum pratense	2.48	-0.40	0.78	1.52	-	-	-	1
Minuartia biflora	-	-1.00	-	-	1	0	0	4

(continued)

Species	LA	MH	SM	SLA	CP	CO	LAT	BUDS
Myosotis decumbens	-	-0.40	-	-	1	0	0	4
Nardus stricta	1.95	-0.52	-0.45	0.94	1	0	1	4
Noccaea caerulescens	2.59	-0.40	-0.58	1.45	-	-	-	-
Omalotheca norvegica	2.54	-0.52	-1.05	1.32	-	-	-	-
Omalotheca supina	1.54	-0.82	-1.08	1.48	-	-	-	-
Omalotheca sylvatica	-	-0.40	-1.34	1.38	-	-	-	-
Oxalis acetosella	2.61	-1.00	-0.02	1.56	0	1	1	4
Oxyria digyna	2.69	-0.52	-0.14	1.36	1	0	0	5
Parnassia palustris	2.29	-0.60	-1.48	1.43	0	0	0	4
Phleum alpinum	2.29	-0.52	-0.41	1.36	1	0	0	5
Phleum pratense	2.58	0.00	-0.23	1.39	1	0	0	4
Phyllodoce caerulea	0.93	-0.82	-1.68	1.01	-	-	-	-
Pimpinella saxifraga	2.52	-0.30	0.06	1.17	1	0	0	5
Pinguicula vulgaris	2.42	-0.70	-1.74	1.70	0	0	0	1
Plantago lanceolata	3.41	-0.30	0.21	1.28	1	0	0	3
Plantago major	-	-0.52	-0.58	1.32	1	0	0	3
Plantago media	3.53	-0.30	-0.42	1.25	1	0	0	3
Poa alpina	2.17	-0.40	-0.37	1.30	1	1	0	6
Poa annua	2.14	-0.60	-0.66	1.56	0	1	0	3
Poa pratensis	2.53	0.00	-0.57	1.32	1	0	1	5
Polygonum aviculare	2.56	-	0.26	1.46	-	-	-	2
Potentilla agrentea	-	-	-	-	-	-	-	-
Potentilla crantzii	2.51	-0.60	-0.20	1.28	1	0	0	4
Potentilla erecta	2.33	-0.52	-0.32	1.37	1	0	0	5
Primula skandinavica	-	-	-	-	-	-	-	-
Prunella vulgaris	2.26	-0.60	-0.16	1.42	0	1	1	4
Pyrola sp	2.76	-0.65	-2.68	1.16	-	-	-	-
Ranunculus acris	2.68	-0.12	0.24	1.37	0	0	0	5
Ranunculus auricomus	3.11	-0.30	0.37	1.50	1	0	0	2
Ranunculus repens	3.27	-0.40	0.35	1.41	0	1	1	5
Rhinanthus minor	2.06	-0.40	0.43	1.27	-	-	-	1
Rhodiola rosea	2.06	-0.52	-0.51	1.38	1	0	0	5
Rubus idaeus	3.46	0.18	0.31	1.32	1	0	1	6
Rumex acetosa	3.09	-0.10	0.04	1.51	1	0	0	5
Rumex acetosella	2.33	-0.30	-0.45	1.43	1	1	1	5
Sagina sp	1.85	-	-1.20	1.14	-	-	-	-
Salix herbacea	2.18	-1.30	-0.71	1.23	1	0	1	6
Salix reticulata	2.32	-1.30	-0.82	0.98	1	0	1	6
Saussurea alpina	2.80	-0.30	0.24	1.22	1	0	1	5
Saxifraga aizoides	1.14	-0.82	-1.31	1.05	1	0	0	6
Saxifraga cespitosa	-	-0.82	-1.30	-	1	1	0	4
Saxifraga oppositifolia	-	-1.30	-0.96	1.17	1	1	1	4
Saxifraga rivularis	-	-	-1.52	-	0	1	1	5
Saxifraga stellaris	1.50	-	-1.59	1.36	0	0	0	3
Schedonorus pratensis	-	-	-	-	-	-	-	-
Sedum acre	-	-1.00	-1.47	1.04	1	1	1	3
Sedum annuum	1.07	-	-2.00	1.26	-	-	-	2
Selaginella selaginoides	0.09	-1.00	-	1.39	1	0	0	4
Sibbaldia procumbens	2.41	-1.00	-0.30	1.28	1	0	0	3
Silene acaulis	1.15	-1.30	-0.51	1.21	1	0	0	6
Silene vulgaris	2.44	-0.15	-0.03	1.47	1	0	0	5

(continued)

Species	LA	MH	SM	SLA	CP	CO	LAT	BUDS
Solidago virgaurea	2.68	0.00	-0.22	1.34	1	0	0	5
Stellaria graminea	1.62	-0.52	-0.48	1.37	0	-	1	6
Stellaria media	2.69	-0.52	-0.42	1.73	0	1	1	3
Succisa pratensis	3.12	-0.22	0.13	1.47	0	0	0	5
Taraxacum sp	-	-	-	-	-	-	-	-
Thalictrum alpinum	2.20	-0.70	-0.07	1.23	1	0	0	2
Tofieldia pusilla	1.84	-0.70	-1.44	1.16	1	0	0	3
Trichophorum cespitosum	-	-0.40	-	-	-	-	-	-
Trientalis europaea	2.35	-0.70	-0.20	1.68	0	1	1	4
Trifolium medium	3.16	-0.30	0.33	1.31	1	1	1	5
Trifolium pratense	2.78	-0.30	0.20	1.34	1	0	0	4
Trifolium repens	2.55	-0.40	-0.23	1.46	0	1	1	2
Urtica diocia	-	-	-	-	-	-	-	-
Vaccinium myrtillus	2.07	-0.30	-0.57	1.20	1	0	1	7
Vaccinium vitis-idaea	1.81	-0.52	-0.55	0.85	0	0	1	7
Valeria sambucifolia	-	-	-	-	-	-	-	-
Veronica alpina	1.88	-0.82	-1.09	1.36	1	0	0	5
Veronica chamaedrys	2.34	-0.52	-0.69	1.44	0	0	1	4
Veronica fruticans	1.24	-1.00	-0.86	1.23	1	1	0	4
Veronica officinalis	2.30	-0.52	-0.92	1.22	0	0	1	3
Veronica serpyllifolia	2.27	-0.70	-1.35	1.36	0	0	1	3
Vicia cracca	2.80	-0.10	1.21	1.31	1	1	1	5
Vicia sepium	3.09	-0.22	1.36	1.60	1	0	1	6
Viola biflora	2.60	-0.82	-0.13	1.60	0	0	0	4
Viola palustris	2.80	-1.00	-0.17	1.47	0	0	0	3
Viola riviniana	2.47	-0.70	0.08	1.39	1	0	0	4
Viola tricolor	2.64	-0.52	-0.10	1.43	1	0	0	3
Viscaria vulgaris	-	-0.40	-	-	-	-	-	-