

Anthropogenic disturbance expands the climatic limits of annual plant dominance

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Abstract

Disturbance regimes and nutrient inputs are changing worldwide, with consequences for the structure and functioning of plant communities. Classical life-history theory predicts that disturbance should shift communities from long-lived perennials toward short-lived annuals, and that nutrient enrichment may amplify this shift. However, these predictions have not been tested experimentally across broad environmental gradients. Here, using a global coordinated grassland experiment spanning 37 sites, we tested how physical disturbance (vegetation removal and shallow soil tillage) and fertilisation reshape annual–perennial balance, and whether disturbance relaxes the climatic limits of annual dominance. Disturbance nearly doubled the proportion of annual species and more than doubled the relative cover of annuals, whereas fertilisation had little influence and did not interact with disturbance. The disturbance-driven shift arose through contrasting pathways: in graminoids and legumes, it reflected the loss of perennial cover, while in forbs, the expansion of annual cover. In the absence of disturbance, annual dominance was restricted to systems with extremely hot and dry summers, but disturbance nearly tripled the extent of climate space in which annuals dominated. By rapidly reassembling after disturbance, annuals may help maintain vegetation cover, but their expansion also signals loss of perennial cover and the long-term ecosystem functions associated with it.

1 Introduction

Land-use intensification is transforming grasslands worldwide through increased disturbances and nutrient inputs, with consequences for vegetation structure and ecosystem functioning^{1,2}. These changes may reorganize grassland communities by shifting the balance between annual and perennial life-history strategies. Annuals represent the short-lived extreme of plant life span, completing their life cycle within a year, while perennials persist for longer and often reproduce repeatedly³. Hence, annuals often allocate more to rapid aboveground growth and seed production, while perennials tend to invest more in storage organs and belowground structures⁴. Because perennials generally contribute more to long-term carbon storage, soil stabilisation, and hydrological regulation^{4,5}, shifts in annual–perennial balance can have important consequences for ecosystem functioning.

Annual species constitute $\sim 15\%$ of the world’s herbaceous flora, with substantially higher representation in hot, dry climates⁶. They also dominate many human-altered and agricultural systems⁷, suggesting that annual life histories confer advantages under frequent disturbance and sustained nutrient inputs. Classical life-history theory provides a demographic basis for this pattern: annuals should dominate when adult survival is low relative to juvenile survival^{8–12}. Disturbance can create these conditions by reducing survival of established individuals, particularly long-lived perennials, while opening recruitment windows for species that regenerate rapidly from seeds. Annuals are often over-represented in persistent soil seed banks¹³, may disperse seeds effectively¹⁴, and can benefit from litter removal and newly opened patches after disturbance^{12;15–17}.

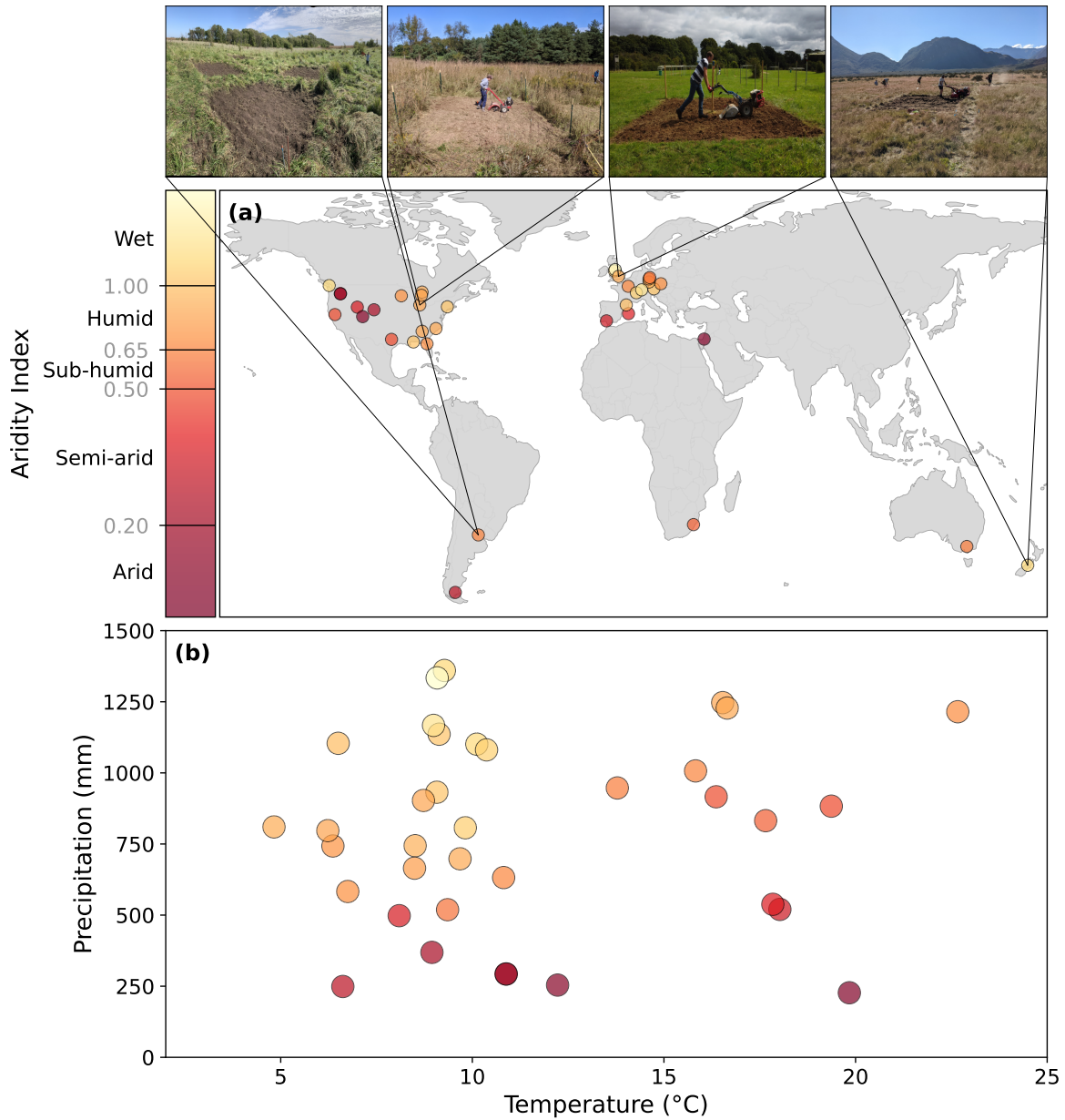


Figure 1: **Geographic and climatic distribution of the study sites.** The DRAG-Net experiment applied coordinated disturbance (vegetation removal and tilling) and fertilisation treatments across grassland sites spanning a broad climatic gradient. Photographs at the top show examples of DRAGNet grassland sites from different continents. **(A)** Geographical distribution of the 37 sites included in this study, colored by site aridity, with redder colors indicating more arid conditions. **(B)** Study sites plotted across mean annual temperature and annual precipitation. Photographs are shown from left to right: Argentina (San Claudio; photo credit: Pedro Tognetti), United States (Kellogg Biological Station; photo credit: Lars Brudvig), United Kingdom (Wytham Woods; photo credit: Roberto Salguero-Gomez), and New Zealand (Cass; photo credit: Andrew Barnes). Additional site information is provided in Table S1.

Fertilisation could also favor annuals, because they often exhibit traits associated with rapid resource acquisition, such as high specific leaf area and fast growth, potentially allowing them to complete their life cycle before subsequent disturbance or climatic stress reduces survival^{4;18}. Yet, any such advantage may be counterbalanced by the greater capacity of perennials to capture and retain resources through time, together with their vegetative growth capacity, which enables them to maintain dominance under high nutrient availability^{19;20}.

Local-scale experiments have compared annual and perennial species under contrasting environmental conditions, particularly during post-disturbance succession and community reassembly^{21–24}. At the other extreme, large scale observational studies have linked the global distribution of annual strategies to climatic gradients using species occurrence data^{6;25;26}. While these approaches have clarified biotic mechanisms at small scales and climatic correlates at broad scales, they have rarely been integrated. In particular, we still lack experimental tests of whether disturbance and fertilisation systematically alter annual–perennial balance across climate gradients, and whether such effects can expand the climatic conditions under which annuals dominate.

Here, we test how severe physical disturbance (vegetation removal and soil tillage), fertilisation, and their interaction shape the prevalence of annual plants, quantified as relative annual cover and annual species share (the proportion of species that are annual). We further ask whether these effects vary across climatic gradients and whether disturbance expands the climatic limits of annual dominance. To address these questions, we use the coordinated Disturbance and Recovery Across Global Grasslands Network (DRAGNet²⁷), which applies common experimental treatments and vegetation sampling protocols across 37 grassland sites (Fig. 1). Based on life-history theory, we expected disturbance to favor annuals over perennials, and fertilisation to have weaker and more context-dependent effects. If both drivers act jointly, nutrient addition could amplify disturbance-driven increases in annuals. We further expected disturbance to shift annual–perennial balance toward annuals within the major functional groups of grasslands (graminoids, legumes, and forbs). Finally, we expected climate to constrain baseline annual dominance, favoring annuals in hot, dry, and highly seasonal environments, and disturbance to relax those climatic constraints.

2 Results

Disturbance markedly increased the prevalence of annuals, raising relative annual cover from 19% to 43% and annual species share from 15% to 29% (Fig. 2A,B; Tables S2–S3).

These shifts were driven by declines in perennial cover and richness, accompanied by increases in annual cover and richness (Tables S4–S7). Disturbance increased annual prevalence in nearly all sites, although the magnitude of the response was highly variable (Fig. 2C,D). Part of this variation was associated with baseline annual values in control plots, with the largest proportional gains occurring where annuals were initially rare. Fertilisation, in contrast, had little influence on annual prevalence, did not interact with disturbance, and showed weak and inconsistent site-level effects (Fig. 2A,B; Appendix Fig. S2).

Within functional groups, disturbance shifted annual–perennial balance through different pathways (Fig. 3; Table S8–S13). In graminoids and legumes, the shift was driven mainly by reductions in perennial cover, although annual graminoid cover also increased modestly. In forbs, perennial cover showed no clear response to disturbance, while annual forb cover roughly doubled.

To link the experimental responses to climate, we modelled annual prevalence across the temperature–precipitation space represented by the network. Mean temperature and precipitation in the warmest quarter were the main climatic drivers of variation in annual prevalence (Tables S14–S22). Across the climatic space defined by these variables, annual dominance (defined as >50% species share or relative cover) was restricted to a narrow zone characterized by the highest temperatures and lowest warmest-quarter precipitation in the absence of disturbance (Fig. 4). However, disturbance markedly expanded this zone: the proportion of climatic space dominated by annuals increased from 11% to 29% when measured by species share, and from 12% to 34% when measured by relative cover (Fig. 4). Beyond this threshold shift, disturbance also reduced the extent of climate space with very low annual cover, indicating a broader upward shift in annual prevalence across the sampled gradients.

Disturbance effects were not uniform across climate space. The strongest increases in relative annual cover occurred in climates that were moderately favourable for annuals, rather than in the most favourable or most limiting conditions (Fig. 4C). Annual species share changed most strongly in hotter regions with intermediate warmest-quarter precipitation (Fig. 4F).

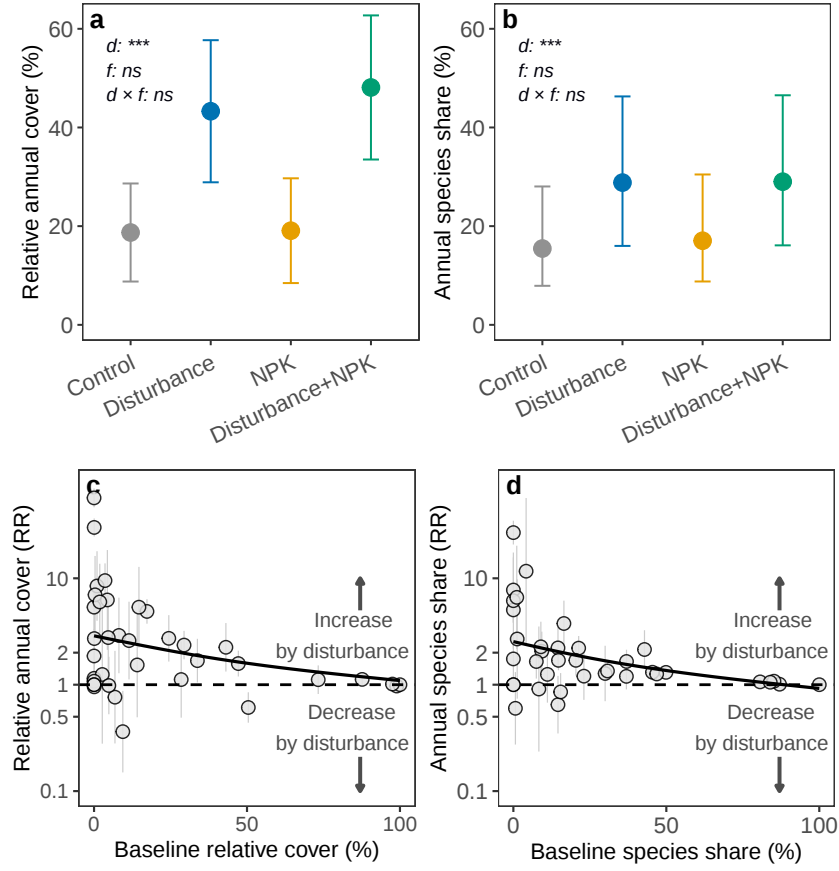


Figure 2: **Disturbance consistently increases the prevalence of annuals, whereas fertilisation has no effect. Panels A–B: network-level treatment effects.** (a) Relative annual cover, defined as the proportion of total vegetated cover contributed by annual species. (b) Annual species share, defined as the proportion of observed plant species that were annual. Points show estimated marginal means with 95% confidence intervals from mixed-effects models across four treatment groups. Relative annual cover was modelled using a zero-inflated beta regression, and annual species share using a binomial regression (Tables S2, S3). Annotations show planned factorial tests of the two experimental drivers and their interaction: d = disturbance, f = fertilisation, and $d \times f$ = disturbance $\times$ fertilisation interaction ($*** p < 0.001$; $ns p > 0.05$). $n = 1,444$. **Panels C–D: site-level disturbance effects.** (c) Relative annual cover. (d) Annual species share. Each point represents one site. Baseline values on the x-axis are site-level means in control plots. The y-axis shows the disturbance response ratio (RR, Disturbance/Control), calculated on a log scale and back-transformed for display. Solid lines show Gaussian GAM smoothers fitted to log response ratios using penalized thin-plate regression splines with the default basis dimension ($k = 10$) and generalized cross-validation. Approximate F-tests indicated non-zero smooth terms for relative annual cover ($p = 0.025$) and annual species share ($p = 0.008$). $n = 37$ sites.

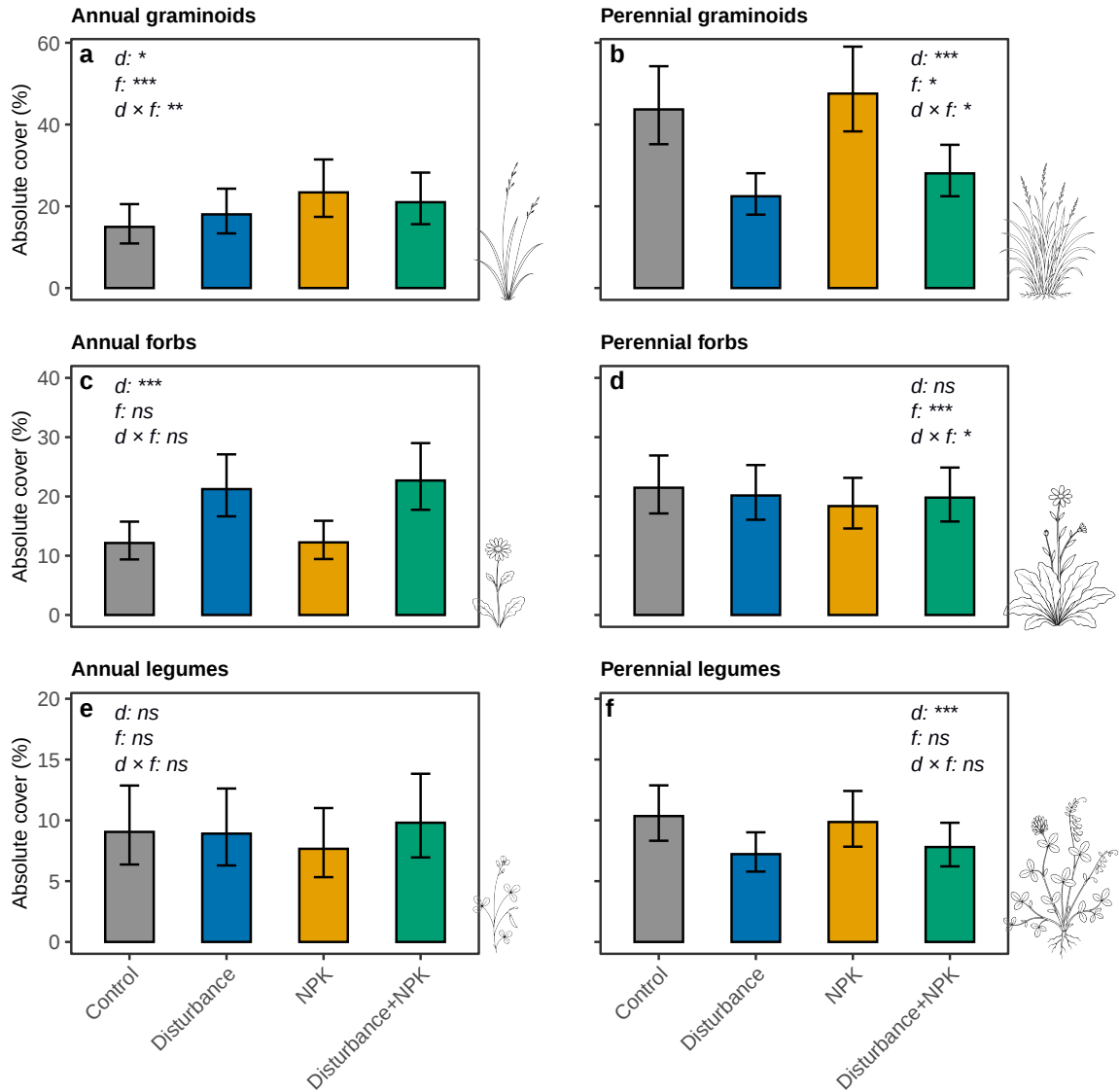


Figure 3: Disturbance shifts annual–perennial balance through different functional-group pathways. Bars show model-based marginal means of absolute cover with 95% confidence intervals, estimated from the continuous component of zero-inflated lognormal mixed-effects models; values therefore represent the percentage of plot area covered by each functional-group when present, i.e. conditional on non-zero cover. Panels show (a) annual graminoids, (b) perennial graminoids, (c) annual forbs, (d) perennial forbs, (e) annual legumes, and (f) perennial legumes. Note the different y-axis scales among panels. Annotations show planned factorial tests of the two experimental drivers and their interaction for the same model component: d = disturbance, f = fertilisation, and d × f = disturbance × fertilisation interaction (*** $p < 0.001$; * $p < 0.05$; ns $p > 0.05$). Full tests are reported in Tables S8–S13. $n = 1,425$.

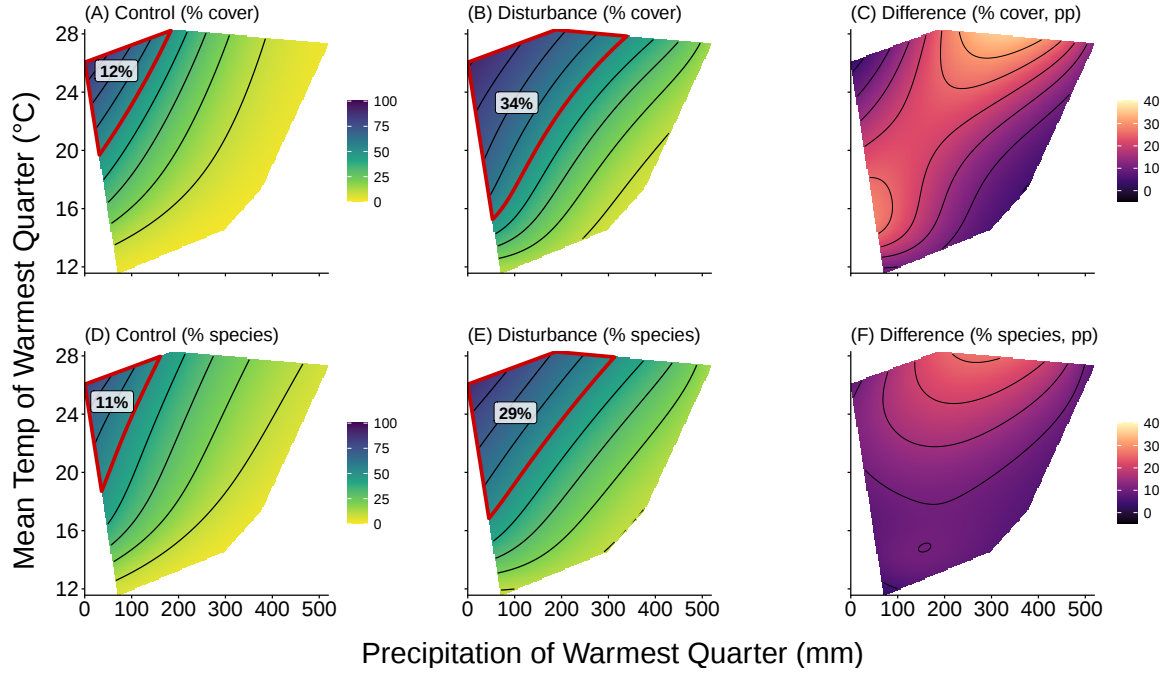


Figure 4: **Disturbance expands the climatic limits of annual plant dominance.** Panels show modeled annual prevalence across mean temperature ($^{\circ}\text{C}$) and precipitation (mm) of the warmest quarter (Q), based on zero-one-inflated beta regressions fitted separately for each disturbance treatment. Panels A–C show relative annual cover (% of cover), and panels D–F show annual species share (% species). In each case, the first two columns show predicted values under control and disturbance, with red solid lines marking the climatic limits of annual dominance (predicted values $> 50\%$). Labels inside the red boundary indicate the percentage of climate space occupied by the annual-dominance zone. Panels C and F show disturbance effects, expressed as disturbance minus control (percentage points, pp). White areas indicate unsampled climates. $n = 37$.

3 Discussion

Ecological theory predicts that disturbance shifts annual–perennial balance toward short-lived annual strategies^{8–12;28;29}. Consistent with this prediction, disturbance increased both annual species share and relative annual cover, while nutrient enrichment had minor and inconsistent effects.

Disturbance substantially expanded the climatic space in which annuals dominate, relaxing constraints that otherwise restrict annual dominance to sites with high temperatures and low precipitation during the warmest season. Together, these results identify disturbance as a key driver of annual dominance in grasslands, capable of

reshaping both community structure and the climatic geography of plant life-history strategies.

3.1 Disturbance favors annuals, whereas nutrient enrichment does not

The disturbance applied in this study removed nearly all aboveground biomass and disrupted shallow belowground structures, creating the severe reduction in adult persistence under which annual strategies are expected to gain an advantage. Under such conditions, reassembly likely depends primarily on colonization from outside the plot, supplemented by recruitment from seeds that survived the disturbance treatment. Annual plants are often more effective colonizers of newly opened patches^{15;16} and are disproportionately represented in persistent seed banks¹³. These traits allow annuals to exploit recruitment windows immediately following disturbance¹², while many perennials rely on vegetative persistence³⁰ that was largely eliminated by the disturbance treatment. Together, these processes favor annuals while disadvantaging perennials after disturbance.

In contrast, nutrient enrichment did not systematically favor annuals and did not interact with disturbance, providing no support for an amplifying effect of fertilisation by accelerating post-disturbance growth and competitive turnover, as predicted for fast, opportunistic strategies⁹. The absence of interaction suggests that, in this experiment, disturbance was the stronger short-term driver of community reassembly, shifting it toward processes that were only weakly limited by nutrients. Alternatively, fertilisation effects may emerge more slowly and develop over longer timescales than those captured here³¹.

Nonetheless, our results suggest that these drivers act through different mechanisms. Disturbance resets communities by removing established vegetation and shifting assembly toward recruitment by dispersal, whereas fertilisation influences resource acquisition during subsequent growth, where advantages of fast-growing annuals may be offset by the size, longevity, and clonal growth of perennials^{19;20}.

3.2 Consistency and heterogeneity across functional groups and sites

Disturbance consistently increased the relative cover of annuals within all functional groups, but the pathways underlying this shift varied. Forbs, the most diverse group in grasslands³², are widely known to increase following disturbance³³, yet our results

show that this response was driven mainly by annual forbs, while perennial forb cover remained relatively stable. In contrast, graminoids, which often dominate in the absence of disturbance³², showed a different response: disturbance reduced perennial, but not annual, graminoid cover. Perennial graminoids rely heavily on belowground organs for persistence and regrowth³⁴, which are particularly vulnerable to soil disruption.

We found that the prevalence of annuals generally increased under disturbance across the network, although the magnitude of this response varied with local conditions. Some of this variation is expected because annual prevalence is bounded between 0 and 100% leaving less scope for increase where annuals are already common. Yet differences among sites with similar baseline annual prevalence suggest that climate also modifies disturbance responses. In particular, species-share responses were stronger in hot regions with intermediate precipitation than in colder, drier sites (Fig. 5), suggesting that annuals may be constrained by abiotic stress in cold-dry environments, but by competitive exclusion from established perennials where warmer and wetter conditions otherwise permit rapid recruitment.

3.3 Disturbance expands the climatic limits of annual dominance

In the absence of disturbance, annual dominance was restricted to hot climates with very low precipitation during the warmest quarter. Previous biogeographic and evolutionary analyses established this climatic constraint for annual species share^{6;25;26}; here, we show that the same constraint also governs relative annual cover, the metric more directly linked to ecosystem functioning. If only species share had varied with climate, the pattern could reflect compositional turnover without dominance shifts; if only relative cover had varied, it could reflect dominance by only a few annual species. Their joint response therefore supports the interpretation that climate acts on the annual–perennial life-cycle axis itself.

Repeated physical disturbance markedly expanded the climate space in which annual dominance occurs, allowing annuals to dominate across a much broader range of temperature and precipitation conditions. This expansion likely reflects reduced competitive suppression and increased recruitment opportunities after disturbance, thereby relaxing the effective climatic limits on annual dominance.

3.4 Conclusions

Annual plants are often viewed as transient or subordinate components of grassland ecosystems^{12;19;24}. Our results instead show that disturbance can shift annual–perennial balance consistently across grasslands worldwide and expand the climatic conditions under which annual strategies dominate. In doing so, they highlight the central role of annuals in ecosystem resistance to perturbations under ongoing climate change. By rapidly reassembling from seed and sustaining vegetation cover and biomass production, annuals can buffer grasslands against repeated disturbance and increasing droughts, thereby preventing complete loss of plant cover and potentially maintaining basic ecosystem processes.

Perennial dominance and extensive belowground biomass are associated with many ecosystem services provided by grasslands, including long-term carbon storage, erosion control, and regulation of water runoff.^{4;5} As disturbance regimes intensify and climates become more favorable to annuals, the key risk is erosion of perennial dominance, with consequences for long-term ecosystem functioning. Our findings advance understanding of the broad range of conditions under which disturbance promotes annual dominance, helping to predict and manage grassland responses to global change.

Methods

Experimental design and vegetation sampling. These data were generated as part of the Disturbance and Recovery Across Global Grasslands Network (DRAGNet). DRAGNet is a recently established global experiment explicitly designed to test the effects of physical disturbance, alone and in combination with nutrient enrichment, across grassland ecosystems worldwide²⁷. DRAGNet sites span a broad climatic gradient, from mean annual temperatures of approximately -5 to 25°C and annual precipitation from roughly 200 to 1700 mm, and include both natural and semi-natural grasslands²⁷.

At each site, DRAGNet follows a randomized block design with 3–5 blocks. Each block contains one 5×5 , m plot assigned to each of four treatments used here: an unmanipulated Control, Disturbance, Nutrient Addition (NPK), and their combination (Disturbance + NPK). A fifth Nutrient Cessation treatment is part of the DRAGNet design but not analysed in this study. The Disturbance treatment is applied once per year for three consecutive years and is designed to create conditions for community reassembly by removing established vegetation and disrupting shallow belowground structures. Specifically, all standing biomass is removed, large visible stolons and rhizomes are extracted, and the soil is tilled to a target depth of 15 cm, or to rooting

depth or the rock layer in shallow soils. This treatment approximates severe physical land-use disturbances, such as tillage or mechanical vegetation removal, that remove established plants and open space for recolonization.

Within each 5×5 m plot, vegetation is sampled once per year during the growing season in a permanently marked 1 m^2 quadrat located at least 1 m inside the plot boundaries. For each vascular plant species, observers visually estimate percentage cover, allowing total cover to exceed 100% where canopies overlap. Vegetation is surveyed after plants have had time to re-establish following the annual disturbance; in disturbed plots, annual and perennial plants therefore establish either by dispersal or from below-ground organs and seeds that survived deeper than the tilled layer. We analysed the first three years after treatment initiation at each site, corresponding to the period during which the annual disturbance treatment was actively applied. Treatment effects therefore represent average differences between treated and control plots during this active treatment period, rather than responses to a single disturbance event. After applying a small set of a priori filters (Appendix S1), the dataset comprised 37 sites and 1,425–1,444 plot-year observations, depending on the analysis.

Response variables We quantified the prevalence of annuals at the plot level using two complementary metrics: (i) the proportion of annual species out of total species richness (species share), and (ii) the proportion of total vegetated cover contributed by annuals (relative annual cover). Species share captures compositional shifts in the flora, while relative annual cover reflects changes in dominance (i.e., the contribution of annuals to total cover). In addition, we analysed richness and absolute cover (% cover) of annuals and perennials, and analogous responses within functional groups (graminoids, forbs, legumes), to understand which components of the community drive the aggregate patterns (Appendix S1).

Network-wide treatment effects. To estimate the average effects of disturbance and fertilisation across all sites, while accounting for spatial and temporal non-independence, we fitted generalized linear mixed models (GLMMs) to plot-level data. Because the experiment used a factorial 2×2 design, we modelled treatment effects as the planned factorial effects of Disturbance, NPK, and their interaction, rather than as a single four-level treatment factor. This parameterisation directly matches our biological questions: whether disturbance changes annual prevalence, whether nutrient addition changes annual prevalence, and whether nutrient addition modifies the disturbance response. All models also included random intercepts for site and for year nested within site, so that treatment effects were estimated after controlling for consistent differences among sites and repeated measurements through time.

Different responses were matched to appropriate non-Gaussian distributions and link functions (for example, binomial models for species share, zero-inflated Beta models for relative cover, negative-binomial models for richness, and zero-inflated lognormal models for absolute cover), chosen to respect the bounded or skewed nature of the data. In specific cases where model complexity impeded convergence, random effect structures were simplified. Full model specifications are given in Appendix S1.

For the main figures, we report treatment-wise estimated marginal means with 95% confidence intervals. Estimated marginal means provide a model-based summary of treatment contrasts for a “typical” site, defined as a site with random-effect values set to the network average on the model scale. These estimates therefore describe treatment differences after accounting for among-site and among-year variation, rather than simple averages that can be dominated by sites with extreme values or more observations.

For annual prevalence, estimated marginal means represent overall expected values on the response scale, combining the zero and positive-response components when zero-inflated models were used. For functional-group cover (Fig. 3), several groups were absent from most plots, especially annual graminoids, annual legumes and perennial legumes. In these cases, overall expected cover was strongly influenced by the high probability of zero cover (Tables S8, S12, S13) and was therefore less informative about changes in cover where the group occurred. We therefore visualised the continuous component of the zero-inflated lognormal models for the functional-group analyses, representing expected cover when the focal group was present. In all cases, full model results, including zero-inflation components, are reported in the Appendix.

Because the experiment was designed as a crossed manipulation of two drivers, statistical inference focused on the planned factorial contrasts for Disturbance, fertilisation, and their interaction, rather than on pairwise comparisons among the four treatment combinations.

Site-level variation in disturbance effects. Global averages do not reveal whether disturbance effects remain consistent across sites or vary with local context. We therefore estimated site-specific effects of Disturbance versus Control for annual species share and relative annual cover. To quantify proportional responses, we calculated log response ratios from site-level treatment means. To quantify absolute responses, we estimated additive differences in percentage points using simple models fitted separately within each site on the original response scale. We then tested whether site-level disturbance effects depended on initial community structure by relating log response ratios to baseline annual prevalence under Control using GAM smoothers.

Climatic space and climate–disturbance interactions. To examine how annual

prevalence and the impact of disturbance vary across climate, we aggregated plot-level data to site $\times$ treatment means for annual species share and relative annual cover, and related these site-level proportions to climate. We first compared models with different combinations of temperature and precipitation (or aridity) variables and identified mean temperature of the warmest quarter and precipitation in the warmest quarter as the best pair of climatic predictors (Table S22).

We then modeled annual prevalence as a function of mean temperature and precipitation in the warmest quarter, and their interaction in flexible regression models for proportional data that allow values of exactly 0 or 1. Fitting these models separately for each treatment (Control, Disturbance, NPK, Disturbance + NPK), we predicted the expected proportion of annuals across the observed climate space and visualised the resulting climatic surfaces with contour plots. Model checks based on predictive simulations confirmed that the fitted climate models reproduce the main gradients in our data (Table S22). Additional plots used to validate the figures in the paper, including additive effect size metric and diagnostic simulations for the climate model, can be found in Figures S3 – S9.

4 Acknowledgments

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5 Data availability

All data and code required to reproduce the analyses and results reported in this manuscript are publicly available from the Environmental Data Initiative repository at <https://doi.org/10.6073/pasta/65799ea6ae60abdf0590b35134a9ab43>.

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S1 Supporting Information

Appendix S1. Details on the statistical modelling and its rationale

Appendix S1 provides additional details supporting the analyses reported in the main text. We first describe the data filtering and site inclusion criteria, then list the DRAG-Net sites included in the study. We then provide the statistical details for the three main analytical components: network-level treatment effects, site-level variation in disturbance responses, and climate–disturbance models of annual prevalence. Because these analyses address different response variables and levels of aggregation, the sections below describe the model structure and rationale separately for each component.

Data cleaning and inclusion criteria

We applied a small set of a priori filters to focus on sites and plots with data suitable for estimating treatment effects. First, we retained only sites with at least two years of observations, on the assumption that a single year is unreliable for annual plants with high year-to-year variability. Second, because disturbance was only applied during the early phase of the experiment, we restricted the analysis to the first three years after the start of the manipulation at each site; later years, in which disturbance ceased, were excluded. Third, we removed plot–year combinations with zero total vegetated cover, for which the proportion of annual cover and the proportion of annual species are undefined. Records classified as biennial (852 observations, 3% of the filtered dataset) were excluded because they do not map unambiguously onto the annual–perennial dichotomy that is the focus of this study. After these filters, the dataset comprised 37 sites and 1,425–1,444 plot–year observations.

Study Sites

Table S1: Description of the 37 DRAGNet sites used in this study.

Site Name	Site Code	Country	Coordinates
Ainsdale Dune Slacks	ains_dn.uk	UK	53.59°N, 3.07°W
Agroscope Changins	chan_dn.ch	CH	46.40°N, 6.23°E
Algaida	alga_dn.es	ES	36.54°N, 6.20°W
Archbold Biological Station	arch_dn.us	US	27.17°N, 81.22°W
Bad Lauchstaedt	badlau_dn.de	DE	51.38°N, 11.88°E
Bayreuth DRAGNet	bayr_dn.de	DE	49.92°N, 11.58°E
Bladen Lakes State Forest	blsf_dn.us	US	34.72°N, 78.49°W
Caracoles	cara_dn.es	ES	37.07°N, 6.32°W
Cary IES	cary_dn.us	US	41.79°N, 73.74°W
Cass	cass_dn.nz	NZ	43.04°S, 171.75°E
Cedar Creek LTER	cedr_dn.us	US	45.40°N, 93.20°W
CEREEP – Ecotron IDF	cereep_dn.fr	FR	48.28°N, 2.67°E
Churning Rapids	chur_dn.us	US	47.18°N, 88.61°W
Cowichan	cowi_dn.ca	CA	48.81°N, 123.63°W
Dauphin Island	daup_dn.us	US	30.25°N, 88.20°W
Domaninek	doma_dn.cz	CZ	49.54°N, 16.25°E
Hazlerigg	lancaster_dn.uk	UK	54.01°N, 2.78°W
Jena	jena_dn.de	DE	50.94°N, 11.53°E
Kellogg Biological Station	kell_dn.us	US	42.42°N, 85.37°W
Kniezenberg	kzbg_dn.at	AT	46.96°N, 15.27°E
Meranges	mera_dn.es	ES	42.43°N, 1.78°E
Millville	mill_dn.us	US	41.65°N, 111.81°W
Nillahcootie	nilla_dn.au	AU	36.90°S, 146.01°E
Park Shaked	shak_dn.il	IL	31.27°N, 34.65°E
Piedmont Prairie	pied_dn.us	US	33.89°N, 83.36°W
Potrok Aike	potrok_dn.ar	AR	51.92°S, 70.41°W
San Claudio	sanc_dn.ar	AR	35.92°S, 61.16°W
Sandflats	sdft_dn.us	US	38.58°N, 109.49°W
Sierra Foothills REC	sier_dn.us	US	39.26°N, 121.32°W
Shortgrass Steppe LTER	sgs_dn.us	US	40.82°N, 104.77°W
Temple	temple_dn.us	US	31.10°N, 97.34°W
Ukulinga	ukul_dn.za	ZA	29.67°S, 30.40°E

Site Name	Site Code	Country	Coordinates
Univ. of Michigan Bio. Station	umbs_dn.us	US	45.56°N, 84.68°W
Wallula Gap – North Face	wgno_dn.us	US	46.00°N, 118.91°W
Wallula Gap – South Face	wgso_dn.us	US	46.00°N, 118.95°W
WSL	wald_dn.ch	CH	47.36°N, 8.46°E
Wytham Woods	wyth_dn.uk	UK	51.77°N, 1.33°W

(i) Network-level treatment effects

To estimate the overall effects of disturbance and fertilisation across the DRAGNet network, we fitted generalized linear mixed models (GLMMs) to plot-level data using the `glmmTMB` package. This framework allows us to combine non-Gaussian distributions (Beta, negative binomial, lognormal), zero-inflation components, and hierarchical random effects suitable for the multi-site, repeated-measures design.

For each response, we modelled the expected value at plot i in site j and year k as

$$g(\mu_{ijk}) = \mathbf{X}_{ijk}\boldsymbol{\beta} + b_j + u_{jk},$$

where $\mathbf{X}_{ijk}$ contains the fixed effects of the Disturbance $\times$ NPK factorial treatment (Disturbance and NPK coded as 0/1), $\boldsymbol{\beta}$ are fixed-effect coefficients, b_j is a random intercept for site, and u_{jk} is an additional random intercept for year nested within site. Here $g(\cdot)$ is the link function that maps the mean response μ_{ijk} to the linear predictor; the specific choice of link and response family depends on the outcome and is described below for each analysis.

We initially explored models with random slopes for Disturbance and NPK at the site level. These represent the most flexible structure in principle, but in practice they failed to converge, reflecting the limited replication of treatments within sites. We therefore retained a random-intercept structure as a stable and conservative choice that captures the dominant between-site heterogeneity without over-parameterizing treatment effects.

Year was treated as a random effect nested within site rather than as a fixed factor. This structure was chosen to account for shared annual conditions and repeated observations within each site, while keeping the focus on the overall Disturbance and NPK treatment contrasts across the network. Calendar years are not aligned across sites because treatment initiation occurred in different years, so a global fixed “year” effect would be difficult to interpret ecologically. Moreover, our goal was not to estimate a common temporal trajectory or the effect of each successive disturbance event, but

rather to estimate average treatment differences during the period of active treatment application.

Conceptually, the most natural repeated-measures structure would be a plot-level random effect, with plots nested within sites and years treated as repeated observations on the same plots. We initially fitted such plot-level random-effect structures, but these models failed to converge, likely because of the limited replication of plots, treatments, and years within sites. We therefore adopted a simpler structure in which year is treated as a site-specific random intercept. In this formulation, the year random effect absorbs among-year variation within each site, whereas the fixed treatment coefficients estimate average differences between treatment groups across the first three years of active treatment application. Thus, the treatment coefficients should be interpreted as average contrasts between disturbed, fertilised, combined, and control plots during the active treatment period, not as the response to a single disturbance event or as a year-by-year disturbance trajectory.

This structure still accounts for temporal non-independence within sites without imposing a shared time trajectory across sites with different start years. However, each site contributes only three treatment years, which is at the lower bound of what is usually recommended for estimating random effects. The models nevertheless converged reliably, and variance estimates indicated that within-site year-to-year variability was an order of magnitude smaller than among-site variability. Because random-effect estimates are partially pooled toward the site mean, this structure may slightly underestimate year-to-year variation. However, this limitation should mainly affect the estimated variance attributed to year, rather than biasing the fixed treatment effects, which are the focus of the paper.

Different responses required different distributions. Relative annual cover (proportion of total vegetated cover) is a proportion on $[0, 1]$ with roughly 30% exact zeros and a small number of exact ones. We modelled this response with a zero-inflated Beta GLMM with a logit link for the mean. The Beta component describes positive proportions in $(0, 1)$, while a zero-inflation component accounts for excess structural zeros. Because the Beta density in `glmmTMB` is defined only on $(0, 1)$, observations equal to 1 cannot be included directly. We therefore replaced the $\approx 8\%$ of observations equal to 1 with 0.9998675, the midpoint between 1 and the largest observed proportion below 1 ($0.999735 = 1 - 2.65 \times 10^{-4}$). This very small adjustment preserved the ordering of extreme values while avoiding numerical problems at the upper boundary. At the plot level, where we must also account for random effects, there is currently no implementation of a mixed-effects zero-one-inflated Beta model. This small adjustment is

therefore the most practical way to retain nearly all the information about plots that are fully dominated by annuals.

Annual species share (annual richness divided by total richness) is naturally expressed as a binomial outcome: “number of annual species out of total species”. We therefore used a binomial GLMM with a logit link, treating annual richness as the number of successes and total richness as the number of trials. Absolute richness of annuals and perennials is overdispersed count data, so we used negative-binomial GLMMs with a log link. Absolute cover of annuals and perennials, both at the whole-community level and within each functional group (graminoids, forbs, legumes), can be zero and can exceed 100% when overlapping canopies are summed. These responses are continuous, right-skewed, and contain frequent zeros, so we modelled them with zero-inflated lognormal GLMMs (with a log link), which handle the zeros and positive values separately.

Treatment effects in the main figures are reported as estimated marginal means from the fitted GLMMs, computed with the `emmeans` package. These estimates are model-based expectations for each treatment combination, evaluated at a “typical” site (random effects set to zero) on the linear predictor scale and back-transformed to the response scale. In a heterogeneous, unbalanced multi-site network, raw averages of plot-level data can be misleading because they are strongly influenced by sites with extreme values or many plots. Marginal means provide a more interpretable summary of the typical treatment contrast across the network, because they respect the link function and distributional assumptions and are not dominated by a small number of highly variable sites. For bounded indices such as proportions, averaging on the linear predictor (e.g. logit) scale and back-transforming typically yields values closer to the median than the simple arithmetic mean, which again aligns with the idea of a typical site.

Model adequacy for these GLMMs was checked using simulation-based diagnostics from the `DHARMa` package. We inspected quantile–quantile plots, residuals versus fitted values, and tests for dispersion and zero inflation, and did not detect systematic deviations that would compromise inference about the fixed-effects treatment contrasts.

(ii) Site-level comparison of effect size

The GLMMs described above quantify overall treatment contrasts across the network. To investigate how the effect of disturbance varies among individual sites, we also conducted site-specific analyses that focus on two complementary effect size metrics: the log response ratio and the additive difference in percentage points.

For the *log response ratio*, we worked with site-level summaries. For each site, the response (e.g. relative annual cover) was averaged across plots and years within each treatment (Control and Disturbance) to obtain site-level means $\bar{y}_C$ and $\bar{y}_D$. Before computing the log ratio, a constant of 1% was added to all means to yield the adjusted log response ratio $\log(\bar{y}_D + 1/\bar{y}_C + 1)$. This procedure ensures the ratio is well-defined at sites where $\bar{y} = 0$, preventing the exclusion of sites where annuals were absent. Additionally, the constant serves to stabilize the delta-method standard error approximation, which involves the squared mean in the denominator and would otherwise become poorly behaved as $\bar{y}$ approaches zero. The same adjusted means are utilized in the SE formula:

$$\text{SE} \left[\log \left(\frac{\bar{y}_D + 1}{\bar{y}_C + 1} \right) \right] \approx \sqrt{\frac{s_D^2}{n_D(\bar{y}_D + 1)^2} + \frac{s_C^2}{n_C(\bar{y}_C + 1)^2}},$$

assuming independence between treatments. Given that the constant is small relative to typical values (median control baseline $\approx 7\%$ for cover and $\approx 7\%$ for species share), its influence is negligible for sites with substantial annual presence while ensuring all sites contribute to the meta-analysis and forest plot. Repeating the analysis without adding the constant for the subset of sites with non-zero means in both treatments yielded the same overall qualitative pattern and very similar effect sizes for nearly all sites. The main discrepancies occurred only at sites with mean annual cover close to zero, where unadjusted log response ratios became extremely large and were likely driven by boundary sensitivity rather than biologically meaningful differences.

For the *additive effect* (Fig. S3, S4), we returned to the plot-level data. The goal here was to quantify the absolute change in percentage points between Disturbance and Control on the original response scale. By definition, such an additive contrast must be defined on the identity (response) scale. GLMMs with non-linear link functions (e.g. logit or log) are additive on the link scale and therefore imply multiplicative effects on the response scale; they cannot directly represent an additive difference in percentage points. We therefore estimated the additive effect using simple linear regression fitted separately within each site to the plot-level observations. In this formulation, the treatment coefficient corresponds directly to the additive treatment difference in percentage points for that site. To account for heteroscedasticity, we obtained heteroscedasticity-robust standard errors for these site-specific linear models using the `sandwich` package. Sites with zero variance (e.g., 0% of annuals across all plots and treatments) were assigned an additive effect of zero with a standard error of zero, reflecting the absence of any observed change rather than infinite precision.

The resulting log response ratios and additive effects, with their respective uncertainties, were displayed in forest plots to enable direct comparison of proportional and absolute disturbance effects across the network. To visualise how disturbance effects depend on baseline community structure, we related site-level effect sizes to the baseline annual proportion (under Control) using generalised additive models fitted with `mgcv`, allowing a smooth, data-driven relationship without imposing a specific functional form.

(iii) Climate niche and combined climate–disturbance models

The climate analyses address how annual prevalence varies across global climate gradients and how disturbance alters the climatic space of annual dominance. Because climate covariates such as temperature and precipitation are defined at the site level, we first aggregated the plot-level data to site $\times$ treatment means, so that each site contributes a single value per treatment for mean relative annual cover and mean annual species share (per square metre). After aggregation, these responses are continuous proportions on $[0, 1]$ that can take the values 0 and 1 exactly.

To model these site-level proportions as functions of climate, we used zero–one-inflated Beta regression (BEINF) implemented in the `gamlss` and `gamlss.dist` packages. Let Y denote the site-level proportion (either mean relative annual cover or mean annual species share). Under the BEINF model,

- $Y = 0$ with probability ν ,
- $Y = 1$ with probability τ , and
- conditional on $0 < Y < 1$, Y follows a Beta distribution with mean μ and dispersion σ .

We used logit links for μ and σ (with σ held constant with respect to climate) and log links for ν and τ , with linear predictors in the climate covariates. This formulation explicitly accommodates both intermediate proportions and sites that are entirely perennial ($Y = 0$) or entirely annual ($Y = 1$), without any ad-hoc transformation of 0 or 1. Conceptually, it is the site-level analogue of the plot-level zero-inflated Beta GLMM: at the site scale, we no longer need random effects, but we still need to model mass at both boundaries.

We first standardised all candidate climate variables by z -scoring within the network to improve numerical stability and make coefficients comparable. Our goal was to identify a pair of climate axes, one thermal and one moisture-related, that best explain variation in annual prevalence. Following the idea that plant performance is

jointly constrained by temperature and water availability, but without imposing *a priori* assumptions about which specific metrics matter most, we considered a broad set of temperature and precipitation variables, including annual means, ranges, and seasonal (quarter-based) indices. We also included the aridity index (precipitation / potential evapotranspiration). Although aridity is affected by temperature, we treated it as a “corrected precipitation” metric within our moisture-axis set. Monthly variables were not included because they are highly collinear with the quarter-based variables and harder to interpret ecologically. A complete list of candidate climate variables is given in Table S22.

For each response (relative annual cover and species share), we then fitted BEINF models for all combinations of one temperature variable and one precipitation (or aridity) variable, including their interaction in the linear predictors for μ , ν and τ . For each combination we calculated the Akaike Information Criterion (AIC). This structured search reflects the hypothesis that annual prevalence is primarily controlled by one temperature axis and one water-availability axis, while avoiding over-fitting and interpretational difficulties that would arise from including many correlated covariates in the same model. For both responses, mean temperature of the warmest quarter and precipitation of the warmest quarter emerged as the best predictors: the model with mean temperature and precipitation of the warmest quarter had the lowest AIC, and no alternative combination was within $\Delta\text{AIC} < 2$ (Table S22). We therefore focused on these two variables in the subsequent analyses and visualizations.

To examine how treatments alter the climatic niche of annuals, we next fitted BEINF models separately for each treatment (Control, Disturbance, NPK, NPK + Disturbance), using mean temperature of the warmest quarter (T_{warmQ}) and precipitation in the warmest quarter (P_{warmQ}) as predictors. For each treatment, the mean component took the form

$$\text{logit}(\mu) = \alpha_{\mu} + \beta_{\mu 1} T_{\text{warmQ}} + \beta_{\mu 2} P_{\text{warmQ}} + \beta_{\mu 3} T_{\text{warmQ}} \times P_{\text{warmQ}},$$

with analogous linear predictors for ν and τ (and σ modelled as a constant). Treatments were fitted separately rather than combined in a single Treatment $\times$ Climate model, to avoid imposing a restrictive parametric form on what are likely to be complex and treatment-specific interactions between climate and disturbance or fertilisation.

From each fitted BEINF model we computed the expected mixture mean,

$$E[Y] = (1 - \nu - \tau) \mu + \tau,$$

which is the expected proportion of annuals, including the contributions from excess 0s and 1s. We evaluated $E[Y]$ on a regular grid covering the convex hull of the observed

mean temperature in the warmest quarter $\times$ mean precipitation in the warmest quarter points, to avoid extrapolation beyond the sampled climate space. Contour plots of $\mathbb{E}[Y]$ were used to visualise the climatic surface of annual prevalence, and we highlighted regions where $\mathbb{E}[Y]$ exceeds 0.5, defining the climatic “dominance zone” of annuals in our network. To validate that these models do not distort the underlying data, we simulated predictive draws from each fitted BEINF model using `rBEINF` at climate points sampled uniformly within the same convex hull, and compared simulated and observed site-level responses on the same axes; the simulated clouds reproduced the main gradients and boundary cases. Fertilisation effects were weak across the network; their predictions are presented in the Supporting Information but are not emphasised in the main text. To highlight where disturbance has the strongest impact, we also mapped the difference in predicted annual prevalence between Disturbance and Control across the climate grid, expressed in percentage points.

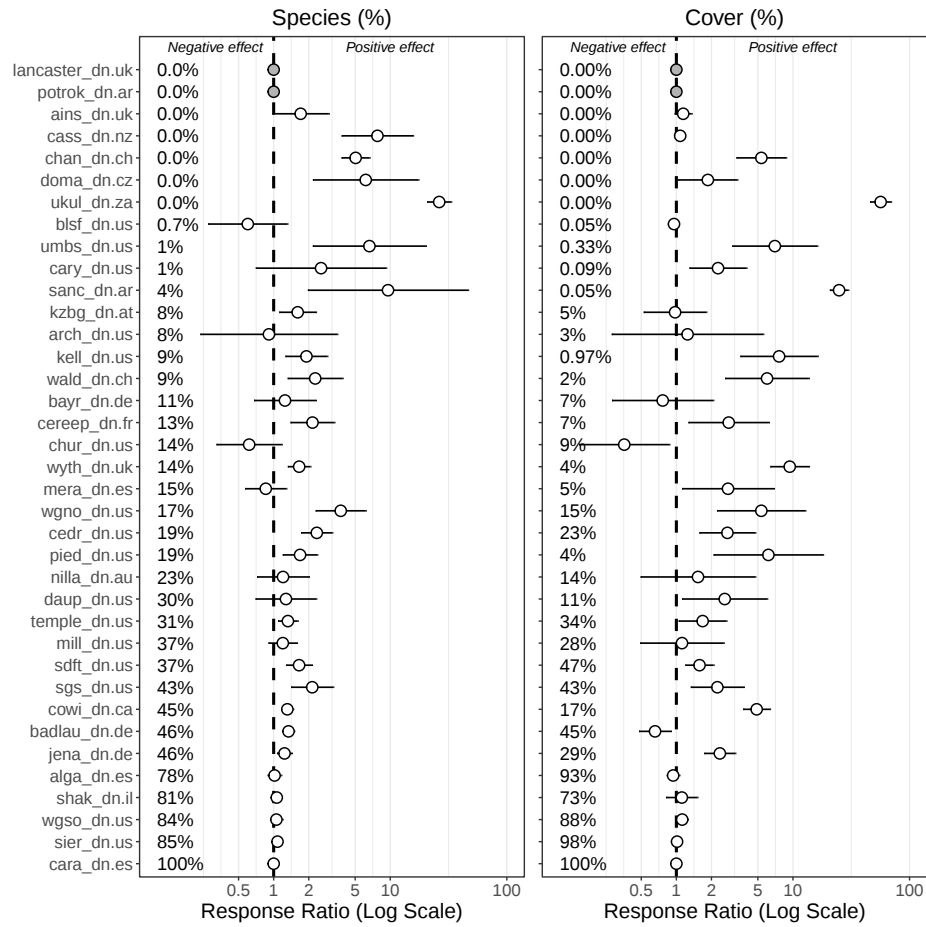


Figure S1: **Disturbance drives increases in annual prevalence across most sites.** The left panel shows effects of disturbance on annual species share (per plot), while the right panel shows the effects on relative annual cover. Axes show disturbance effects as response ratios, where values above 1 indicate higher annual prevalence in disturbed plots and values below 1 indicate lower annual prevalence. For statistical calculation, effect sizes were computed on the log scale as $\log(\text{Disturbance} / \text{Control})$ and then back-transformed for display. Sites are ordered (top to bottom) starting with sites with zero annual prevalence in both control and treatment plots (marked with grey circles), followed by the remaining sites ordered by baseline annual species share. Percent values shown beside each row indicate the baseline annual value for the response displayed in that panel: annual species share in the left panel and relative annual cover in the right panel. Uncertainty is shown by the 95% confidence intervals. See table S1 for additional site information.

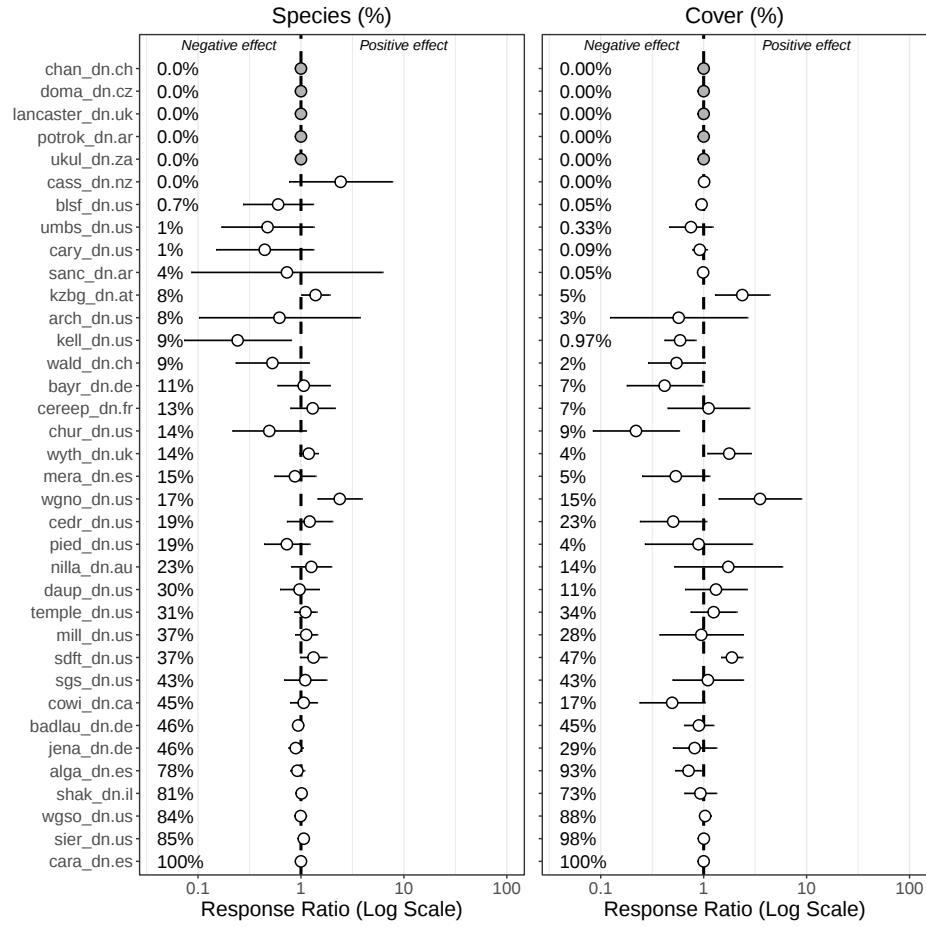


Figure S2: **Unlike disturbance, NPK addition elicits variable responses in annual prevalence, with no consistent directional trend.** Effect sizes were calculated as log response ratios; axes tick labels represent back-transformed response ratios. Horizontal error bars denote 95% confidence intervals. Sites are ordered (top to bottom) starting with sites that had zero annuals in both control and treatment plots (marked with grey circles), followed by the remaining sites ordered by baseline annual species share. Percent values shown beside each row indicate the baseline annual value for the response displayed in that panel: annual species share in the left panel and relative annual cover in the right panel. One site (ains dn.uk) was excluded from this analysis due to missing data for the NPK treatment. See table S1 for additional site information.

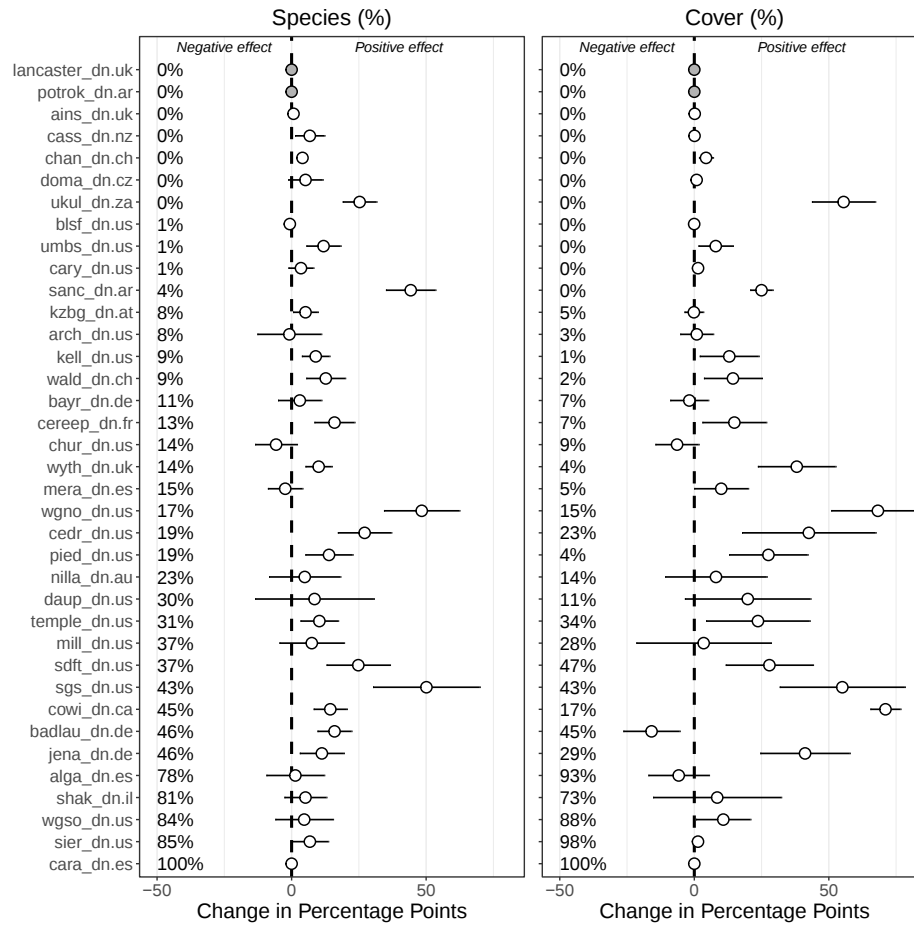


Figure S3: Disturbance drives absolute increases in the prevalence of annuals

The left panel shows the absolute difference in annual species share (per plot), while the right panel shows the difference in relative annual cover. Effect sizes were calculated as the difference in treatment means (Disturbance – Control). Sites are ordered (top to bottom) starting with sites that had zero annuals in both control and treatment plots (marked with grey circles), followed by the remaining sites ordered by baseline annual species share. Horizontal error bars represent 95% confidence intervals. Percent values shown beside each row indicate the baseline annual value for the response displayed in that panel: annual species share in the left panel and relative annual cover in the right panel. See table S1 for additional site information.

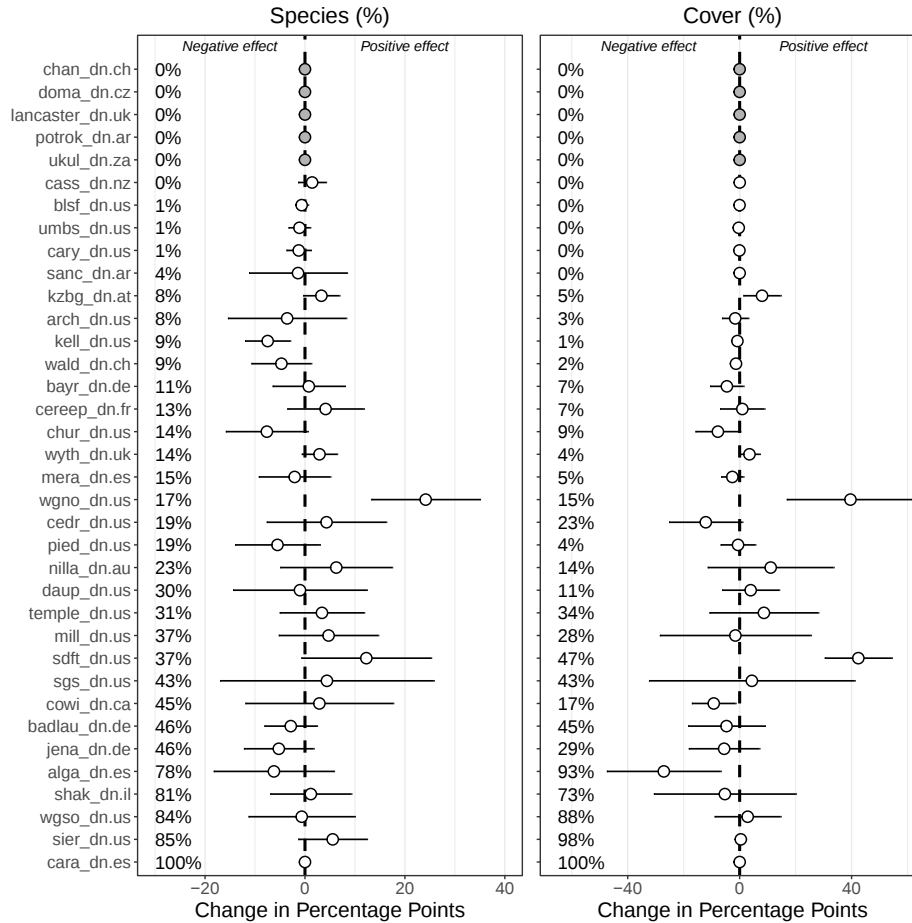


Figure S4: **NPK addition results in mixed absolute effects on annual prevalence, with substantial increases in cover observed at specific sites.** The panels display the absolute change in annual species share (left) and relative annual cover (right). Effect sizes represent the difference in means (NPK – Control). Horizontal error bars show 95% confidence intervals calculated using robust standard errors. Sites are ordered (top to bottom) starting with sites that had zero annuals in both control and treatment plots (marked with grey circles), followed by the remaining sites ordered by baseline annual species share. One site (ains dn.uk) was excluded from this analysis due to missing data for the NPK treatment. Percent values shown beside each row indicate the baseline annual value for the response displayed in that panel: annual species share in the left panel and relative annual cover in the right panel. See table S1 for additional site information.

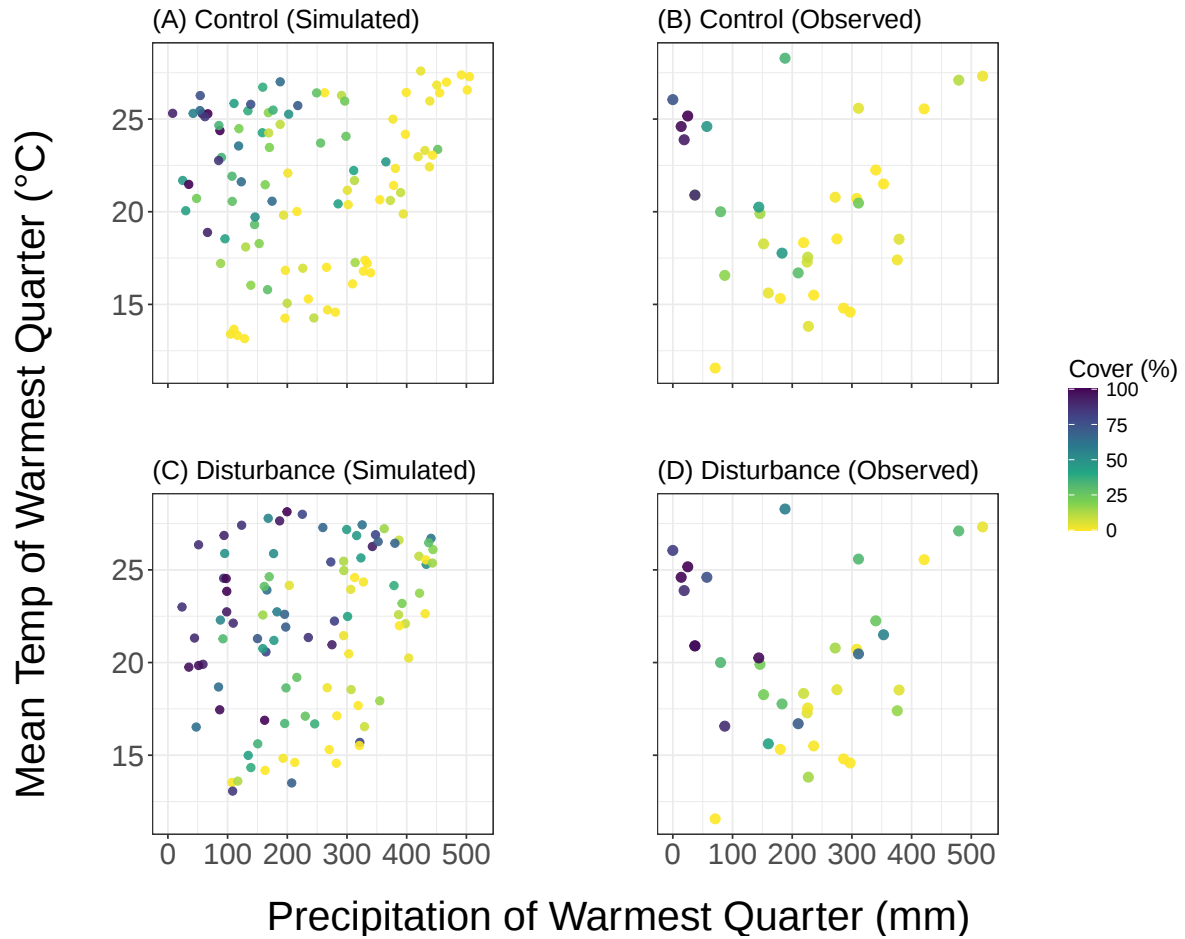


Figure S5: **The fitted models accurately reproduce the observed distribution of annual cover (unfertilised plots).** Comparison of simulated (left column) and observed (right column) annual plant cover across the climate space defined by annual temperature and precipitation in the warmest quarter. (A, C) Simulated datasets generated by drawing random climate locations uniformly within the convex hull of the study sites and sampling from the fitted zero-one-inflated beta (BEINF) models. (B, D) Empirical field observations from the control and disturbance treatments. The color scale indicates the percentage of total vegetation cover comprised of annuals. The structural similarity between the simulated predictive draws and the observed data demonstrates that the models adequately capture the climatic gradients and the distribution of proportion values (including zeros and ones).

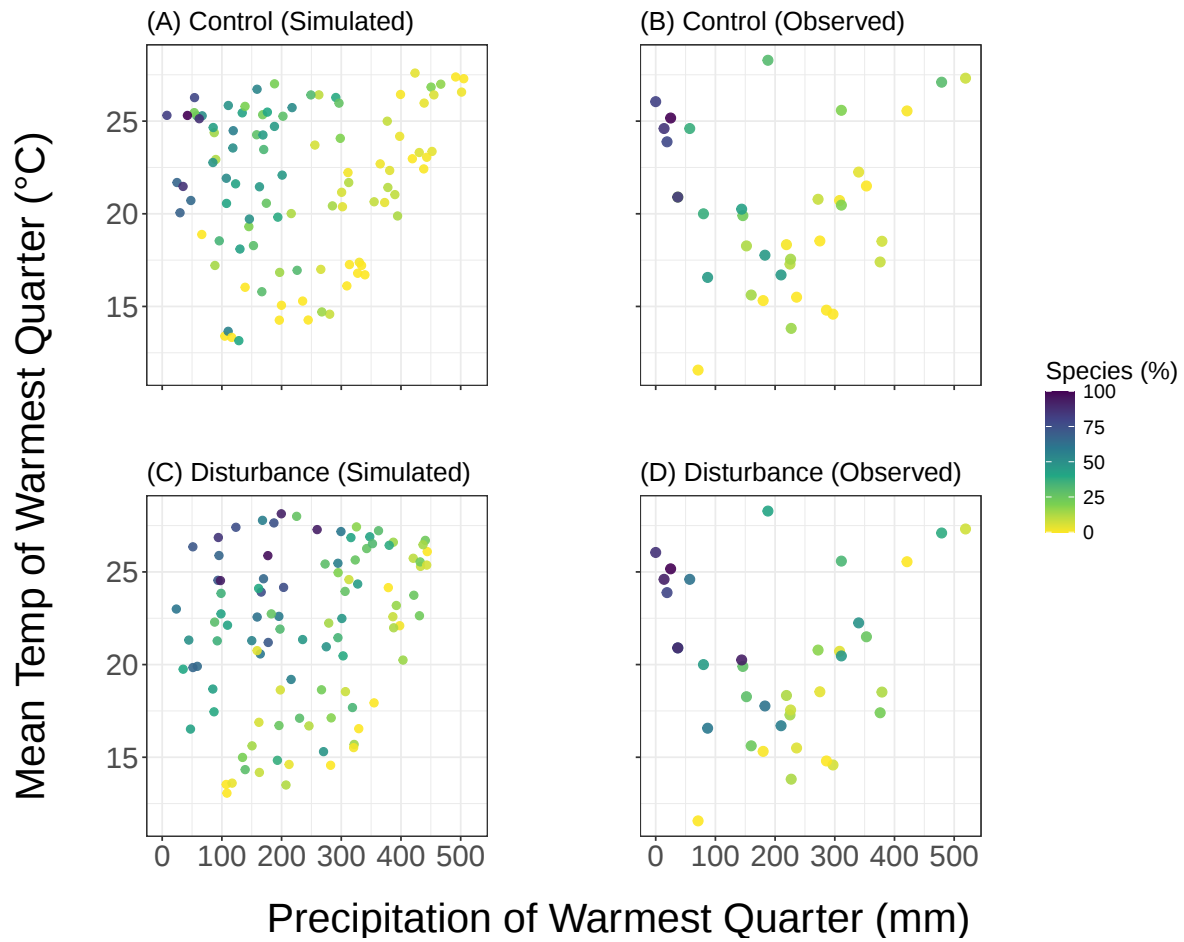


Figure S6: **The fitted models accurately reproduce the observed distribution of annual species share (unfertilised plots).** Comparison of simulated (left column) and observed (right column) annual species richness proportions across the climate space. (A, C) Simulated datasets generated from the fitted BEINF models using random climate draws within the climatic hull of the network. (B, D) Observed field data showing the proportion of total species richness identified as annuals at each site. Colors represent the percentage of annual species, from 0% (yellow) to 100% (dark purple). These diagnostics confirm that the fitted models successfully reproduce the observed patterns of species dominance, including the response to temperature and precipitation gradients under both control and disturbance conditions.

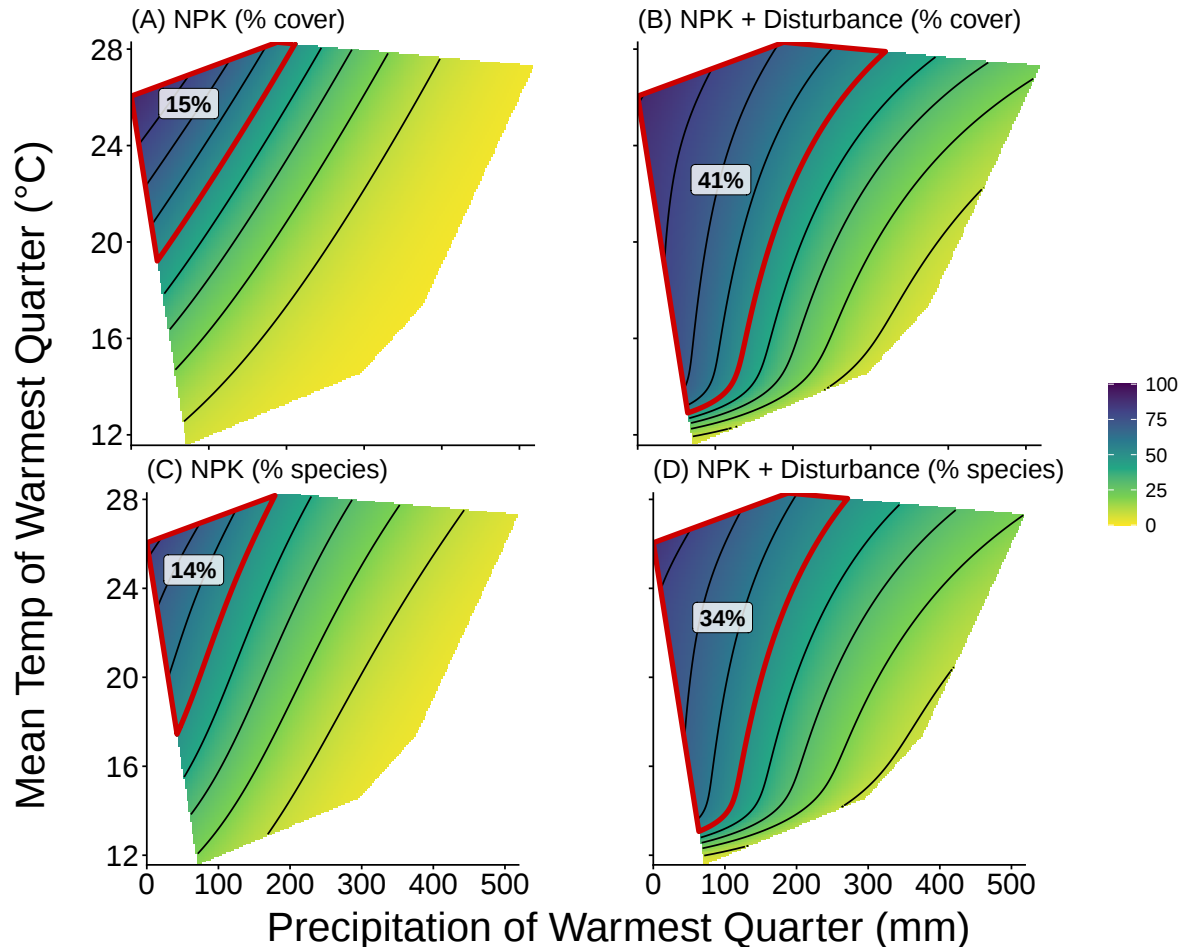


Figure S7: **Disturbance effects under fertilisations are similar to those in unfertilised plots.** Modelled annual prevalence across climate space under nutrient addition (NPK) and combined treatment (NPK + Disturbance). (A, B) Relative annual cover under fertilisation alone (A) versus fertilisation combined with disturbance (B). The red boundary marks the region of annual dominance (> 50% cover). (C, D) Annual species share under fertilisation alone (C) and combined with disturbance (D). Labels within the red boundaries indicate the percentage of the total climate hull occupied by annual-dominated communities. The number of sampled sites falling within these dominance zones are: (A) 6, (B) 11, (C) 6, and (D) 10. Comparing the top and bottom rows illustrates that while fertilisation alone constrains annual dominance to extreme climates, the addition of disturbance allows annuals to dominate in mesic and moderate-temperature regions.

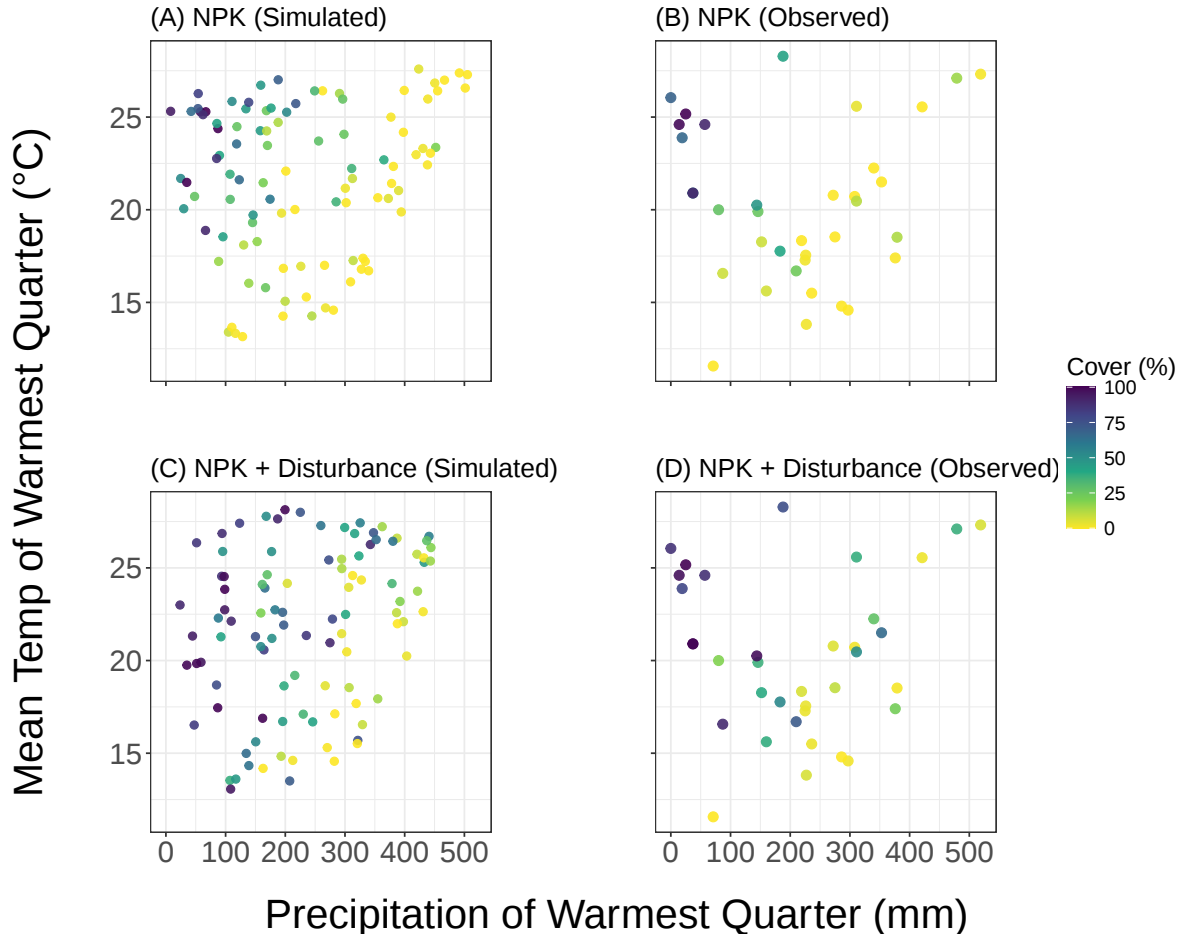


Figure S8: **The fitted models of fertilised plots accurately reproduce the observed distribution of annual cover.** Diagnostic comparison of simulated versus observed annual cover in fertilized treatments. (A, C) Simulated datasets generated from the fitted BEINF models for NPK (A) and NPK + Disturbance (C), created by drawing random coordinates within the climate hull and simulating responses. (B, D) Observed annual cover values from field sites subjected to NPK (B) and NPK + Disturbance (D). The color gradient represents the percentage of vegetation cover composed of annuals. The correspondence between the simulated clouds and observed data confirms the model's ability to replicate the expanded dominance of annuals in the combined treatment (C, D) compared to the more restricted distribution under fertilisation alone (A, B).

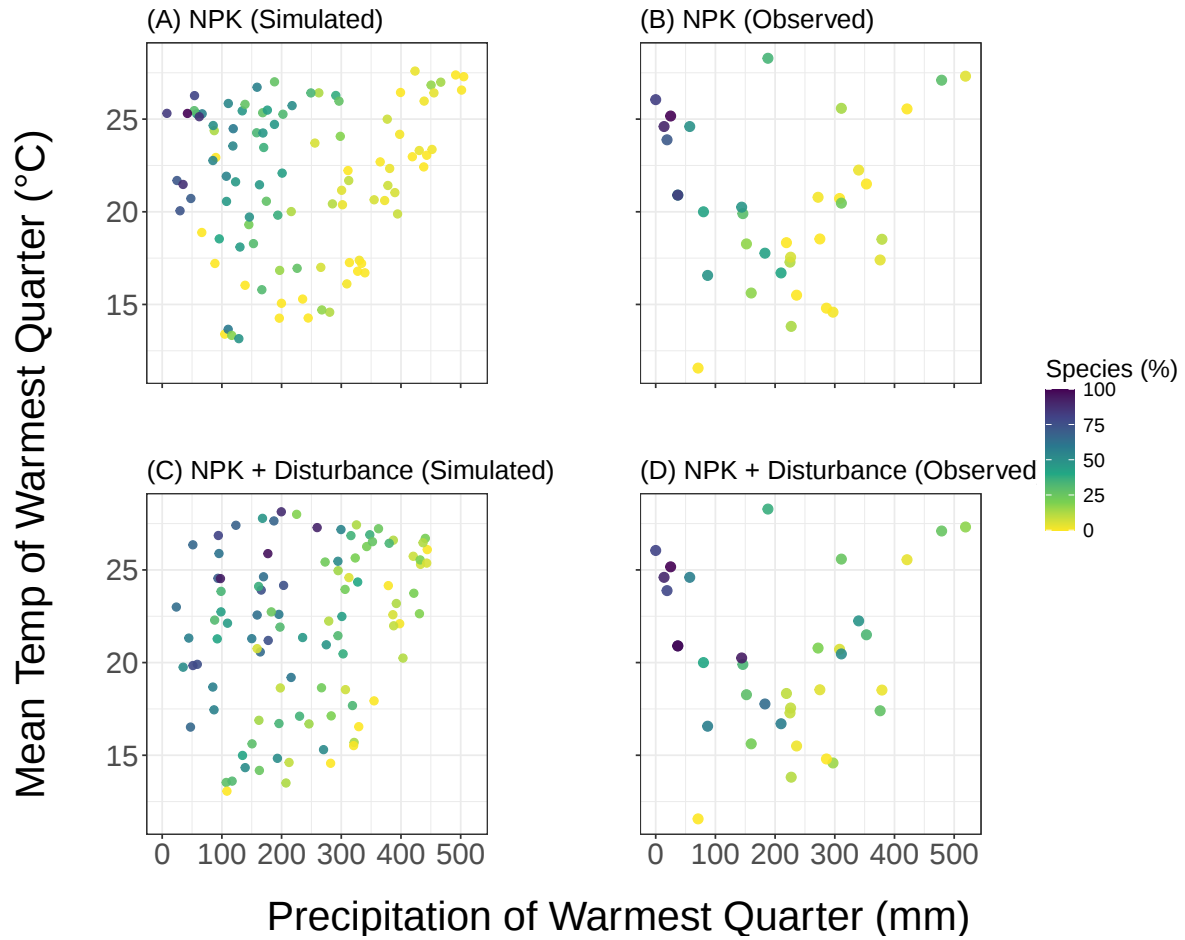


Figure S9: **The fitted models of fertilised plots accurately reproduce the observed distribution of annual species share.** Diagnostic comparison of simulated versus observed annual species richness proportions. (A, C) Simulated annual species proportions for NPK (A) and NPK + Disturbance (C) based on model predictions over a uniform climate grid. (B, D) Observed annual species proportions from experimental sites. Yellow points indicate perennial-dominated communities (0% annuals), while dark purple points indicate annual-dominated communities (100% annuals). The visual agreement between the simulated and observed patterns validates the fitted models, particularly in capturing the complex responses observed in the combined treatment (C, D).

Table S2: Zero-inflated beta GLMM for relative annual cover. The *Continuous Model* describes annual cover among plots where annual cover is present, whereas the *Zero-Inflated Model* describes the probability of zero annual cover. In each model component, the intercept describes the reference treatment (Control: no disturbance, no NPK): baseline annual cover among non-zero plots in the Continuous Model, and baseline odds of zero annual cover in the Zero-Inflated Model. Treatment coefficients describe multiplicative effects relative to this reference treatment. In the Continuous Model, values greater than 1 indicate higher annual cover and values below 1 indicate lower annual cover. In the Zero-Inflated Model, values greater than 1 indicate a higher probability of zero annual cover and values below 1 indicate a lower probability of zero annual cover. *Disturbance* and *NPK* test the main treatment effects, and *Disturbance* $\times$ *NPK* tests their interaction. Random-effect terms report variance components for site and site-by-year grouping structure; ICC is the intraclass correlation. $N_{\text{site}} = 37$.

relative annual cover			
<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
Continuous Model			
(Intercept)	0.29	0.16 – 0.53	< 0.001
Disturbance	2.71	2.26 – 3.26	< 0.001
NPK	1.11	0.92 – 1.32	0.274
Disturbance $\times$ NPK	1.10	0.87 – 1.40	0.435
Zero-Inflated Model			
(Intercept)	0.21	0.05 – 0.91	0.037
Disturbance	0.11	0.06 – 0.20	< 0.001
NPK	1.34	0.80 – 2.25	0.267
Disturbance $\times$ NPK	0.71	0.33 – 1.54	0.383
Random Effects			
σ^2	3.26		
τ_{00} site_name	2.99		
τ_{00} site_name:year_trt	0.19		
ICC	0.49		
N site_name	37		

Table S3: Binomial GLMM for annual species share, calculated as annual richness divided by total richness per plot. The intercept describes the reference treatment (Control: no disturbance, no NPK) and represents the baseline odds of a species being annual. Treatment coefficients describe multiplicative effects on these odds relative to the reference treatment. Values greater than 1 indicate a higher annual species share, whereas values below 1 indicate a lower annual species share. *Disturbance* and *NPK* test the main treatment effects, and *Disturbance* $\times$ *NPK* tests their interaction. Random-effect terms report variance components for site and site-by-year treatment grouping structure; ICC is the intraclass correlation. $N_{\text{site}} = 37$.

proportion of annual species			
<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	0.18	0.09 – 0.39	< 0.001
Disturbance	2.21	1.94 – 2.53	< 0.001
NPK	1.12	0.97 – 1.30	0.113
Disturbance $\times$ NPK	0.90	0.74 – 1.09	0.273
Random Effects			
σ^2	0.37		
τ_{00} site_name	5.27		
τ_{00} site_name:year_trt	0.03		
ICC	0.94		
N site_name	37		
N year_trt	3		

Table S4: Negative binomial GLMM for annual species richness, calculated as the number of annual species per plot. The intercept describes the reference treatment (Control: no disturbance, no NPK) and represents the baseline expected annual species richness. Treatment coefficients describe multiplicative effects relative to this reference treatment. Values greater than 1 indicate higher annual species richness, whereas values below 1 indicate lower annual species richness. The negative binomial family was used to accommodate overdispersion in count data, as supported by DHARMA diagnostics. *Disturbance* and *NPK* test the main effects; *Disturbance* $\times$ *NPK* tests their interaction. Random Effects (τ_{00}) report between-site and between-year variance; ICC is the intraclass correlation. $N_{\text{site}} = 37$.

annual species richness			
<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	1.12	0.68 – 1.83	0.654
Disturbance	1.42	1.30 – 1.55	< 0.001
NPK	0.91	0.83 – 1.00	0.050
Disturbance $\times$ NPK	1.06	0.93 – 1.20	0.379
Random Effects			
σ^2	0.22		
τ_{00} site_name	2.19		
τ_{00} site_name:year_trt	0.04		
ICC	0.91		
N site_name	37		
N year_trt	3		

Table S5: Negative binomial GLMM for perennial species richness, calculated as the number of perennial species per plot. Model structure and interpretation follow Table S4. The intercept represents the baseline expected perennial species richness in the reference treatment (Control: no disturbance, no NPK). Treatment coefficients describe multiplicative effects relative to this reference treatment. Values greater than 1 indicate higher perennial species richness, whereas values below 1 indicate lower perennial species richness.

perennial species richness			
<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	5.31	3.84 – 7.34	< 0.001
Disturbance	0.80	0.76 – 0.85	< 0.001
NPK	0.81	0.76 – 0.85	< 0.001
Disturbance × NPK	1.19	1.09 – 1.29	< 0.001
Random Effects			
σ^2	0.13		
τ_{00} site_name	0.98		
τ_{00} site_name;year_trt	0.03		
ICC	0.89		
N site_name	37		
N year_trt	3		
Observations	1444		

Table S6: Zero-inflated lognormal GLMM for absolute annual cover. The *Continuous Model* describes annual cover among plots where annual cover is present, whereas the *Zero-Inflated Model* describes the probability of zero annual cover. In each model component, the intercept describes the reference treatment (Control: no disturbance, no NPK): the baseline geometric mean annual cover among non-zero plots in the Continuous Model, and the baseline odds of zero annual cover in the Zero-Inflated Model. Treatment coefficients describe multiplicative effects relative to this reference treatment. In the Continuous Model, values greater than 1 indicate higher annual cover and values below 1 indicate lower annual cover. In the Zero-Inflated Model, values greater than 1 indicate a higher probability of zero annual cover and values below 1 indicate a lower probability of zero annual cover. *Disturbance* and *NPK* test the main effects; *Disturbance* $\times$ *NPK* tests their interaction. $N_{\text{site}} = 37$.

annual cover			
<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
Continuous Model			
(Intercept)	19.68	15.00 – 25.84	< 0.001
Disturbance	1.43	1.29 – 1.60	< 0.001
NPK	1.15	1.03 – 1.28	0.011
Disturbance $\times$ NPK	0.99	0.87 – 1.13	0.889
Zero-Inflated Model			
(Intercept)	0.21	0.05 – 0.91	0.037
Disturbance	0.11	0.06 – 0.20	< 0.001
NPK	1.34	0.80 – 2.25	0.267
Disturbance $\times$ NPK	0.71	0.33 – 1.54	0.383
Random Effects			
σ^2	43.32		
τ_{00} site_name	0.51		
τ_{00} site_name:year_trt	0.12		
ICC	0.01		
N site_name	37		
N year_trt	3		
Observations	1444		

Table S7: Zero-inflated lognormal GLMM for absolute perennial cover. Model structure and interpretation follow Table S6.

perennial cover			
<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
Continuous Model			
(Intercept)	66.35	51.57 – 85.38	< 0.001
Disturbance	0.59	0.56 – 0.63	< 0.001
NPK	1.03	0.99 – 1.08	0.151
Disturbance $\times$ NPK	1.13	1.04 – 1.22	0.003
Zero-Inflated Model			
(Intercept)	0.00	0.00 – 0.00	< 0.001
Disturbance	3.61	1.57 – 8.31	0.002
NPK	1.21	0.50 – 2.96	0.675
Disturbance $\times$ NPK	1.45	0.47 – 4.51	0.521
Random Effects			
σ^2	35.27		
τ_{00} site_name	0.57		
τ_{00} site_name:year_trt	0.03		
ICC	0.02		
N site_name	37		
N year_trt	3		
Observations	1444		

Table S8: Zero-inflated lognormal GLMM for absolute annual graminoid cover (%). Model structure and interpretation follow Table S6.

Annual graminoid cover (%)			
<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
Continuous Model			
(Intercept)	14.96	10.91 – 20.53	< 0.001
Disturbance	1.20	1.02 – 1.43	0.032
NPK	1.56	1.33 – 1.84	< 0.001
Disturbance $\times$ NPK	0.74	0.61 – 0.91	0.005
Zero-Inflated Model			
(Intercept)	52.71	2.03 – 1370.07	0.017
Disturbance	0.55	0.29 – 1.06	0.073
NPK	1.05	0.55 – 1.99	0.883
Disturbance $\times$ NPK	0.68	0.27 – 1.70	0.410
Random Effects			
σ^2	41.10		
τ_{00} site_name	0.27		
τ_{00} site_name:year_trt	0.17		
ICC	0.01		
N site_name	37		
N year_trt	3		
Observations	1425		

Table S9: Zero-inflated lognormal GLMM for absolute perennial graminoid cover (%). Model structure and interpretation follow Table S6.

Perennial graminoid cover (%)			
<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
Continuous Model			
(Intercept)	43.69	35.18 – 54.26	< 0.001
Disturbance	0.51	0.47 – 0.56	< 0.001
NPK	1.09	1.02 – 1.16	0.012
Disturbance × NPK	1.15	1.02 – 1.29	0.019
Zero-Inflated Model			
(Intercept)	0.01	0.00 – 0.06	< 0.001
Disturbance	4.55	2.29 – 9.07	< 0.001
NPK	1.05	0.49 – 2.27	0.902
Disturbance × NPK	1.30	0.51 – 3.33	0.589
Random Effects			
σ^2	35.84		
τ_{00} site_name	0.35		
τ_{00} site_name:year_trt	0.05		
ICC	0.01		
N site_name	37		
N year_trt	3		
Observations	1425		

Table S10: Zero-inflated lognormal GLMM for absolute annual forb cover (%). Model structure and interpretation follow Table S6.

Annual forb cover (%)			
<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
Continuous Model			
(Intercept)	12.15	9.37 – 15.75	< 0.001
Disturbance	1.75	1.54 – 1.99	< 0.001
NPK	1.01	0.88 – 1.16	0.909
Disturbance $\times$ NPK	1.06	0.90 – 1.25	0.496
Zero-Inflated Model			
(Intercept)	0.79	0.23 – 2.80	0.721
Disturbance	0.12	0.07 – 0.20	< 0.001
NPK	1.38	0.86 – 2.19	0.179
Disturbance $\times$ NPK	1.01	0.51 – 1.99	0.978
Random Effects			
σ^2	36.80		
τ_{00} site_name	0.39		
τ_{00} site_name:year_trt	0.08		
ICC	0.01		
N site_name	37		
N year_trt	3		
Observations	1425		

Table S11: Zero-inflated lognormal GLMM for absolute perennial forb cover (%). Model structure and interpretation follow Table S6.

Perennial forb cover (%)			
<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
Continuous Model			
(Intercept)	21.47	17.13 – 26.91	< 0.001
Disturbance	0.94	0.86 – 1.02	0.156
NPK	0.86	0.78 – 0.93	0.001
Disturbance × NPK	1.15	1.02 – 1.30	0.028
Zero-Inflated Model			
(Intercept)	0.02	0.01 – 0.09	< 0.001
Disturbance	1.64	1.00 – 2.70	0.051
NPK	2.70	1.65 – 4.42	< 0.001
Disturbance × NPK	0.36	0.18 – 0.72	0.004
Random Effects			
σ^2	28.54		
τ_{00} site_name	0.39		
τ_{00} site_name:year_trt	0.06		
ICC	0.02		
N site_name	37		
N year_trt	3		
Observations	1425		

Table S12: Zero-inflated lognormal GLMM for absolute annual legume cover (%). Model structure and interpretation follow Table S6.

Annual legume cover (%)			
<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
Continuous Model			
(Intercept)	9.05	6.37 – 12.86	< 0.001
Disturbance	0.98	0.81 – 1.20	0.877
NPK	0.85	0.70 – 1.02	0.083
Disturbance $\times$ NPK	1.30	0.99 – 1.71	0.058
Zero-Inflated Model			
(Intercept)	10697.27	463.77 – 246741.66	< 0.001
Disturbance	1.14	0.60 – 2.17	0.694
NPK	1.39	0.73 – 2.64	0.319
Disturbance $\times$ NPK	0.84	0.34 – 2.07	0.700
Random Effects			
σ^2	21.90		
τ_{00} site_name	0.27		
τ_{00} site_name:year_trt	0.02		
ICC	0.01		
N site_name	37		
N year_trt	3		
Observations	1425		

Note: the odds-ratio scale (463.77–246741.66), this corresponds to an estimated zero-inflation probability between 0.998 and 0.999996.

Table S13: Zero-inflated lognormal GLMM for absolute perennial legume cover (%). Model structure and interpretation follow Table S6.

Perennial legume cover (%)			
<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
Continuous Model			
(Intercept)	10.35	8.32 – 12.88	< 0.001
Disturbance	0.70	0.60 – 0.82	< 0.001
NPK	0.95	0.81 – 1.13	0.569
Disturbance $\times$ NPK	1.13	0.90 – 1.42	0.275
Zero-Inflated Model			
(Intercept)	5.95	1.82 – 19.39	0.003
Disturbance	0.81	0.51 – 1.27	0.351
NPK	1.59	1.00 – 2.54	0.050
Disturbance $\times$ NPK	0.99	0.52 – 1.90	0.979
Random Effects			
σ^2	18.77		
τ_{00} site_name	0.12		
τ_{00} site_name;year_trt	0.04		
ICC	0.01		
N site_name	37		
N year_trt	3		
Observations	1425		

Table S14: Zero-one-inflated Beta regression (BEINF) for mean relative annual cover in the **Control** treatment, as a function of mean temperature and precipitation of the warmest quarter (both z-scored; $n = 37$ sites). The table has four row groups: *Mu* (*Mean*) — logit-scale coefficients for the Beta mean (expected cover where $0 < Y < 1$); *Sigma* (*Precision*) — held constant (intercept only); *Nu* (*Zero-Inflation*) — log-scale probability of a site having no annual cover ($Y = 0$); *Tau* (*One-Inflation*) — log-scale probability of a site being fully dominated by annuals ($Y = 1$). The (Intercept) in each submodel gives the expected value at mean climate. Positive Mu coefficients indicate higher expected annual cover.

<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
Mu (Mean)			
(Intercept)	−1.56	−1.94 – −1.19	< 0.001
Precipitation of Warmest Q (mm)	−1.21	−1.66 – −0.76	< 0.001
Mean Temp of Warmest Q (°C)	0.57	0.17 – 0.97	0.009
Precipitation of Warmest Q (mm) × Mean Temp of Warmest Q (°C)	−0.13	−0.60 – 0.34	0.593
Sigma (Precision)			
(Intercept)	−0.28	−0.59 – 0.03	0.082
Nu (Zero-Inflation)			
(Intercept)	−3.43	−5.92 – −0.94	0.011
Precipitation of Warmest Q (mm)	1.75	−0.54 – 4.04	0.144
Mean Temp of Warmest Q (°C)	−2.78	−5.03 – −0.54	0.021
Precipitation of Warmest Q (mm) × Mean Temp of Warmest Q (°C)	0.53	−0.97 – 2.03	0.494
Tau (One-Inflation)			
(Intercept)	−6.85	−24.99 – 11.29	0.464
Precipitation of Warmest Q (mm)	−1.79	−16.16 – 12.57	0.808
Mean Temp of Warmest Q (°C)	1.57	−11.39 – 14.54	0.814
Precipitation of Warmest Q (mm) × Mean Temp of Warmest Q (°C)	−0.78	−12.14 – 10.59	0.894
N = 37; AIC = −10.3			

Table S15: Zero-one-inflated Beta regression (BEINF) for mean relative annual cover in the **Disturbance** treatment. Model structure and column definitions are identical to Table S14 (Control).

<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
Mu (Mean)			
(Intercept)	−0.60	−0.97 – −0.23	0.003
Precipitation of Warmest Q (mm)	−1.12	−1.58 – −0.66	<0.001
Mean Temp of Warmest Q (°C)	0.76	0.35 – 1.17	<0.001
Precipitation of Warmest Q (mm) × Mean Temp of Warmest Q (°C)	0.20	−0.28 – 0.68	0.411
Sigma (Precision)			
(Intercept)	0.11	−0.20 – 0.41	0.487
Nu (Zero-Inflation)			
(Intercept)	−4.71	−8.63 – −0.79	0.025
Precipitation of Warmest Q (mm)	1.86	−1.40 – 5.11	0.272
Mean Temp of Warmest Q (°C)	−2.27	−5.32 – 0.77	0.153
Precipitation of Warmest Q (mm) × Mean Temp of Warmest Q (°C)	1.28	−0.12 – 2.68	0.082
Tau (One-Inflation)			
(Intercept)	−6.95	−24.73 – 10.82	0.449
Precipitation of Warmest Q (mm)	−1.87	−15.95 – 12.22	0.797
Mean Temp of Warmest Q (°C)	1.64	−11.00 – 14.28	0.801
Precipitation of Warmest Q (mm) × Mean Temp of Warmest Q (°C)	−0.72	−11.85 – 10.40	0.899
N = 37; AIC = 5.3			

Table S16: Zero-one-inflated Beta regression (BEINF) for mean relative annual cover in the **NPK** treatment. Model structure and column definitions are identical to Table S14 (Control).

<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
Mu (Mean)			
(Intercept)	−1.59	−1.97 – −1.22	< 0.001
Precipitation of Warmest Q (mm)	−1.40	−1.84 – −0.97	< 0.001
Mean Temp of Warmest Q (°C)	0.80	0.42 – 1.18	< 0.001
Precipitation of Warmest Q (mm) × Mean Temp of Warmest Q (°C)	−0.01	−0.45 – 0.44	0.980
Sigma (Precision)			
(Intercept)	−0.42	−0.74 – −0.11	0.012
Nu (Zero-Inflation)			
Precipitation of Warmest Q (mm)	1.01	−0.35 – 2.36	0.154
Mean Temp of Warmest Q (°C)	−1.12	−2.42 – 0.18	0.100
Precipitation of Warmest Q (mm) × Mean Temp of Warmest Q (°C)	0.38	−0.56 – 1.31	0.435
Tau (One-Inflation)			
(Intercept)	−6.76	−24.66 – 11.13	0.464
Precipitation of Warmest Q (mm)	−1.75	−15.91 – 12.40	0.810
Mean Temp of Warmest Q (°C)	1.53	−11.22 – 14.28	0.815
Precipitation of Warmest Q (mm) × Mean Temp of Warmest Q (°C)	−0.79	−11.97 – 10.39	0.891
N = 36; AIC = −3.3			

Table S17: Zero-one-inflated Beta regression (BEINF) for mean relative annual cover in the **NPK + Disturbance** treatment. Model structure and column definitions are identical to Table S14 (Control).

<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
Mu (Mean)			
(Intercept)	−0.53	−0.89 – −0.18	0.006
Precipitation of Warmest Q (mm)	−1.35	−1.80 – −0.90	<0.001
Mean Temp of Warmest Q (°C)	0.62	0.22 – 1.02	0.004
Precipitation of Warmest Q (mm) × Mean Temp of Warmest Q (°C)	0.37	−0.10 – 0.84	0.131
Sigma (Precision)			
(Intercept)	0.00	−0.30 – 0.31	0.979
Nu (Zero-Inflation)			
(Intercept)	−14.28	−46.04 – 17.47	0.384
Precipitation of Warmest Q (mm)	6.56	−15.62 – 28.73	0.566
Mean Temp of Warmest Q (°C)	−8.72	−28.60 – 11.16	0.396
Precipitation of Warmest Q (mm) × Mean Temp of Warmest Q (°C)	2.56	−5.66 – 10.78	0.546
Tau (One-Inflation)			
(Intercept)	−6.96	−24.74 – 10.82	0.449
Precipitation of Warmest Q (mm)	−1.87	−15.94 – 12.20	0.796
Mean Temp of Warmest Q (°C)	1.64	−11.03 – 14.31	0.801
Precipitation of Warmest Q (mm) × Mean Temp of Warmest Q (°C)	−0.72	−11.85 – 10.40	0.899
N = 36; AIC = −1.2			

Table S18: Zero-one-inflated Beta regression (BEINF) for mean annual species share in the **Control** treatment. Model structure and column definitions are identical to Table S14, with annual species share (proportion of species that are annual) as the response instead of relative annual cover.

<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
Mu (Mean)			
(Intercept)	−1.25	−1.59 – −0.92	< 0.001
Precipitation of Warmest Q (mm)	−1.00	−1.40 – −0.60	< 0.001
Mean Temp of Warmest Q (°C)	0.40	0.04 – 0.75	0.035
Precipitation of Warmest Q (mm) × Mean Temp of Warmest Q (°C)	0.06	−0.36 – 0.48	0.784
Sigma (Precision)			
(Intercept)	−0.54	−0.86 – −0.23	0.002
Nu (Zero-Inflation)			
(Intercept)	−3.43	−5.92 – −0.94	0.011
Precipitation of Warmest Q (mm)	1.75	−0.54 – 4.04	0.144
Mean Temp of Warmest Q (°C)	−2.78	−5.03 – −0.54	0.021
Precipitation of Warmest Q (mm) × Mean Temp of Warmest Q (°C)	0.53	−0.97 – 2.03	0.494
Tau (One-Inflation)			
(Intercept)	−6.85	−24.99 – 11.29	0.464
Precipitation of Warmest Q (mm)	−1.79	−16.16 – 12.57	0.808
Mean Temp of Warmest Q (°C)	1.57	−11.39 – 14.54	0.814
Precipitation of Warmest Q (mm) × Mean Temp of Warmest Q (°C)	−0.78	−12.14 – 10.59	0.894
N = 37; AIC = 14.2			

Table S19: Zero-one-inflated Beta regression (BEINF) for mean annual species share in the **Disturbance** treatment. Model structure and column definitions are identical to Table S18 (Control).

<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
Mu (Mean)			
(Intercept)	−0.63	−0.94 – −0.31	< 0.001
Precipitation of Warmest Q (mm)	−0.88	−1.27 – −0.49	< 0.001
Mean Temp of Warmest Q (°C)	0.66	0.32 – 1.01	< 0.001
Precipitation of Warmest Q (mm) × Mean Temp of Warmest Q (°C)	0.07	−0.34 – 0.47	0.754
Sigma (Precision)			
(Intercept)	−0.36	−0.66 – −0.06	0.024
Nu (Zero-Inflation)			
(Intercept)	−4.71	−8.63 – −0.79	0.025
Precipitation of Warmest Q (mm)	1.86	−1.40 – 5.11	0.272
Mean Temp of Warmest Q (°C)	−2.27	−5.32 – 0.77	0.153
Precipitation of Warmest Q (mm) × Mean Temp of Warmest Q (°C)	1.28	−0.12 – 2.68	0.082
Tau (One-Inflation)			
(Intercept)	−6.95	−24.73 – 10.82	0.449
Precipitation of Warmest Q (mm)	−1.87	−15.95 – 12.22	0.797
Mean Temp of Warmest Q (°C)	1.64	−11.00 – 14.28	0.801
Precipitation of Warmest Q (mm) × Mean Temp of Warmest Q (°C)	−0.72	−11.85 – 10.40	0.899
N = 37; AIC = 14.5			

Table S20: Zero-one-inflated Beta regression (BEINF) for mean annual species share in the **NPK** treatment. Model structure and column definitions are identical to Table S18 (Control).

<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
Mu (Mean)			
(Intercept)	−1.25	−1.55 – −0.94	< 0.001
Precipitation of Warmest Q (mm)	−1.23	−1.59 – −0.87	< 0.001
Mean Temp of Warmest Q (°C)	0.49	0.18 – 0.79	0.004
Precipitation of Warmest Q (mm) × Mean Temp of Warmest Q (°C)	0.20	−0.17 – 0.56	0.300
Sigma (Precision)			
(Intercept)	−0.82	−1.14 – −0.50	< 0.001
Nu (Zero-Inflation)			
Precipitation of Warmest Q (mm)	1.01	−0.35 – 2.36	0.154
Mean Temp of Warmest Q (°C)	−1.12	−2.42 – 0.18	0.100
Precipitation of Warmest Q (mm) × Mean Temp of Warmest Q (°C)	0.38	−0.56 – 1.31	0.435
Tau (One-Inflation)			
(Intercept)	−6.76	−24.66 – 11.13	0.464
Precipitation of Warmest Q (mm)	−1.75	−15.91 – 12.40	0.810
Mean Temp of Warmest Q (°C)	1.53	−11.22 – 14.28	0.815
Precipitation of Warmest Q (mm) × Mean Temp of Warmest Q (°C)	−0.79	−11.97 – 10.39	0.891
N = 36; AIC = 18.9			

Table S21: Zero-one-inflated Beta regression (BEINF) for mean annual species share in the **NPK + Disturbance** treatment. Model structure and column definitions are identical to Table S18 (Control).

<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
Mu (Mean)			
(Intercept)	−0.62	−0.94 – −0.31	< 0.001
Precipitation of Warmest Q (mm)	−1.13	−1.54 – −0.73	< 0.001
Mean Temp of Warmest Q (°C)	0.49	0.13 – 0.84	0.011
Precipitation of Warmest Q (mm) × Mean Temp of Warmest Q (°C)	0.28	−0.15 – 0.70	0.209
Sigma (Precision)			
(Intercept)	−0.30	−0.60 – 0.01	0.064
Nu (Zero-Inflation)			
(Intercept)	−14.28	−46.05 – 17.48	0.385
Precipitation of Warmest Q (mm)	6.56	−15.63 – 28.74	0.566
Mean Temp of Warmest Q (°C)	−8.72	−28.60 – 11.17	0.397
Precipitation of Warmest Q (mm) × Mean Temp of Warmest Q (°C)	2.56	−5.66 – 10.78	0.546
Tau (One-Inflation)			
(Intercept)	−6.96	−24.75 – 10.83	0.449
Precipitation of Warmest Q (mm)	−1.87	−15.95 – 12.21	0.796
Mean Temp of Warmest Q (°C)	1.64	−11.03 – 14.32	0.801
Precipitation of Warmest Q (mm) × Mean Temp of Warmest Q (°C)	−0.72	−11.85 – 10.41	0.899
N = 36; AIC = 6.6			

Table S22: Model selection for climate predictors using zero-one-inflated Beta (BEINF) regression. Each row is one combination of a temperature variable and a precipitation (or aridity) variable, fitted for both mean relative annual cover and mean annual species share across sites ($n = 37$). All predictors were z-scored before fitting. Models include a temperature $\times$ precipitation interaction in μ , ν , and τ ; precision (σ) was held constant. ΔAIC is the difference from the lowest AIC within each response column; values < 2 indicate similar fit. Mean temperature of the warmest quarter (TEMP_WARM_Q) and precipitation of the warmest quarter (MAP_WARM_Q) achieved the lowest AIC for both responses and were used in all subsequent analyses (Tables S14–S21). Abbreviations: MAT = mean annual temperature; ISO = isothermality; AI = aridity index; PET = potential evapotranspiration; Q = climatic quarter (3-month period).

<i>Temperature</i>	<i>Precipitation</i>	AIC_{cov}	AIC_{sp}	ΔAIC_{cov}	ΔAIC_{sp}
TEMP_WARM_Q	MAP_WARM_Q	−44.5	9.6	0.0	0.0
TEMP_DRY_Q	AI	−30.6	20.5	13.9	10.9
TEMP_DRY_Q	MAP_DRY_Q	−26.7	19.0	17.8	9.4
TEMP_DRY_Q	MAP_WARM_Q	−25.0	23.3	19.6	13.7
TEMP_DRY_Q	MAP	−24.8	24.7	19.8	15.1
TEMP_WET_Q	MAP_WARM_Q	−23.8	26.0	20.7	16.4
MAT	MAP_WARM_Q	−20.1	30.4	24.4	20.7
TEMP_WARM_Q	MAP_DRY_Q	−14.6	37.3	29.9	27.7
TEMP_WARM_Q	AI	−10.4	43.6	34.2	33.9
TEMP_VAR	MAP_WARM_Q	−7.6	44.6	36.9	35.0
TEMP_WARM_Q	MAP	−6.2	53.0	38.3	43.4
TEMP_COLD_Q	MAP_WARM_Q	−5.4	44.0	39.1	34.4
TEMP_WET_Q	MAP_DRY_Q	−5.2	43.5	39.3	33.9
MAT_RANGE	MAP_WARM_Q	−4.5	45.9	40.0	36.3
TEMP_VAR	AI	−4.2	48.4	40.3	38.8
MAT_RANGE	PET	−3.4	54.8	41.1	45.2
ANN_TEMP_RANGE	MAP_WARM_Q	−3.0	50.3	41.6	40.7
MIN_TEMP	MAP_WARM_Q	−2.4	48.2	42.1	38.6
ANN_TEMP_RANGE	AI	−1.8	50.4	42.7	40.8
MAT_RANGE	AI	−1.7	53.3	42.8	43.7
TEMP_WET_Q	AI	−1.0	49.5	43.5	39.9
MAT	AI	−1.0	52.6	43.5	43.0

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Table S22 continued

<i>Temperature</i>	<i>Precipitation</i>	AIC_{cov}	AIC_{sp}	ΔAIC_{cov}	ΔAIC_{sp}
MIN_TEMP	AI	-0.9	52.2	43.7	42.6
TEMP_COLD_Q	AI	0.2	53.3	44.8	43.7
TEMP_VAR	MAP_DRY_Q	0.5	50.5	45.1	41.0
TEMP_DRY_Q	PET	1.7	56.0	46.3	46.4
MAT	MAP_DRY_Q	2.3	53.3	46.9	43.7
MIN_TEMP	MAP_DRY_Q	2.7	53.4	47.3	43.8
ANN_TEMP_RANGE	MAP_DRY_Q	3.9	55.3	48.4	45.6
TEMP_DRY_Q	MAP_VAR	4.4	51.5	48.9	41.9
TEMP_COLD_Q	MAP_DRY_Q	4.6	54.6	49.1	45.0
TEMP_WET_Q	PET	6.4	52.3	50.9	42.7
MAT_RANGE	MAP_DRY_Q	7.8	61.3	52.3	51.7
TEMP_DRY_Q	MAP_COLD_Q	8.1	55.6	52.7	46.0
MAT	MAP	10.0	66.6	54.6	57.0
TEMP_WET_Q	MAP_VAR	15.7	60.3	60.2	50.7
TEMP_COLD_Q	MAP	16.4	72.1	60.9	62.5
TEMP_DRY_Q	MAP_WET_Q	18.5	70.0	63.0	60.4
MIN_TEMP	MAP	18.9	75.7	63.4	66.1
TEMP_VAR	PET	21.1	80.9	65.7	71.3
TEMP_WARM_Q	MAP_WET_Q	21.7	83.5	66.3	73.9
TEMP_VAR	MAP_VAR	22.5	74.3	67.1	64.7
TEMP_VAR	MAP	22.5	79.6	67.1	70.0
TEMP_WARM_Q	MAP_VAR	23.2	75.9	67.8	66.3
TEMP_WARM_Q	PET	24.7	76.2	69.2	66.6
ANN_TEMP_RANGE	PET	25.0	84.6	69.6	74.9
TEMP_COLD_Q	PET	25.7	83.0	70.3	73.3
MIN_TEMP	PET	26.0	84.0	70.6	74.3
ANN_TEMP_RANGE	MAP_VAR	27.0	79.9	71.5	70.3
MAT	PET	28.6	83.8	73.2	74.2
ANN_TEMP_RANGE	MAP	29.3	88.2	73.9	78.6
MIN_TEMP	MAP_VAR	31.5	84.0	76.0	74.4
MAT	MAP_VAR	32.5	84.7	77.0	75.1
TEMP_COLD_Q	MAP_VAR	32.9	84.8	77.4	75.1

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Table S22 continued

<i>Temperature</i>	<i>Precipitation</i>	AIC_{cov}	AIC_{sp}	ΔAIC_{cov}	ΔAIC_{sp}
MAT_RANGE	MAP	33.3	93.0	77.9	83.4
TEMP_WET_Q	MAP	33.6	91.5	78.1	81.9
MAT_RANGE	MAP_VAR	36.2	87.3	80.7	77.7
MAT	MAP_WET_Q	37.6	96.6	82.2	87.0
TEMP_COLD_Q	MAP_WET_Q	45.0	103.4	89.5	93.8
TEMP_COLD_Q	MAP_COLD_Q	45.4	107.6	89.9	98.0
TEMP_WARM_Q	MAP_COLD_Q	48.5	112.0	93.0	102.4
MIN_TEMP	MAP_WET_Q	48.9	108.8	93.5	99.2
MIN_TEMP	MAP_COLD_Q	50.7	113.2	95.2	103.6
TEMP_VAR	MAP_WET_Q	51.5	112.0	96.0	102.4
MAT	MAP_COLD_Q	56.2	119.8	100.7	110.2
ANN_TEMP_RANGE	MAP_WET_Q	57.0	118.4	101.5	108.8
MAT_RANGE	MAP_WET_Q	61.6	123.1	106.1	113.5
TEMP_WET_Q	MAP_WET_Q	64.9	124.9	109.4	115.2
TEMP_VAR	MAP_COLD_Q	65.0	125.1	109.5	115.5
ANN_TEMP_RANGE	MAP_COLD_Q	66.8	128.8	111.4	119.2
TEMP_WET_Q	MAP_COLD_Q	70.2	130.4	114.8	120.8
MAT_RANGE	MAP_COLD_Q	71.5	132.9	116.1	123.3