The devil is in the detail: non-additive and context-dependent plant population responses to increasing temperature and precipitation

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Abstract

In climate-change ecology, simplistic research approaches may yield unrealistically simplistic answers to often more complicated problems. In particular, the complexity of vegetation responses to global climate change begs a better understanding of the impacts of concomitant changes in several climatic drivers, how these impacts vary across different climatic contexts, and of the demographic processes underlying population changes. Using a replicated, factorial, whole-community transplant experiment, we investigate regional variation in demographic responses of plant populations to increased temperature and/or precipitation. Across four perennial forb species and twelve sites, we found strong responses to both temperature and precipitation change. Changes in population growth rates were mainly due to changes in survival and clonality. In three of the four study species, the combined increase in temperature and precipitation reflected non-additive, antagonistic interactions of the single climatic changes for population growth rate and survival, while the interactions were additive and synergistic for clonality. This disparity affects the persistence of genotypes, but also suggests that the mechanisms behind the responses of the vital rates differ. In addition, survival effects varied systematically with climatic context, with wetter and warmer+wetter transplants showing less positive or more negative responses at warmer sites. The detailed demographic approach yields important mechanistic insights into how concomitant changes in temperature and precipitation affect plants, which makes our results generalizable beyond the four study species. Our comprehensive study design illustrates the power of replicated field experiments in disentangling the complex relationships and patterns that govern climate change impacts across real-world species and landscapes.

Introduction

The empirical evidence for climate change impacts on plants is rapidly accumulating, including range shifts (Gottfried et al., 2012; Grabherr, Gottfried, & Pauli, 1994; Lenoir, Gegout, Marquet, de Ruffray, & Brisse, 2008; Parmesan & Yohe, 2003; Pauli et al., 2012), increased productivity (Wu, Dijkstra, Koch, Peñuelas, & Hungate, 2011), phenological shifts (Oberbauer et al., 2013), and changes in biotic interactions (Alexander, Diez, & Levine, 2015). This list is by no means exhaustive, but illustrates that our understanding of the basic impacts of climate change on plant life is developing rapidly. Many climate-change impact studies measure responses at the community or ecosystem level (Elmendorf et al., 2012; Wu et al., 2011). While this is important for assessing effects and consequences for ecosystem functions and services, our mechanistic understanding of climate-change impacts is hampered by a lack of knowledge of the demographic processes behind changes in species abundance. It is, for instance, not trivial whether a population decline is driven by reductions in survival or reproduction, given the different implications that changes in these vital rates may have for population size, gene-pool size, selection processes, and spatial dynamics, as these rates differentially impact population extinction probabilities and hence biodiversity (Ehrlén & Morris, 2015; Pearson et al., 2014). Demographic studies can further such mechanistic insights into how specific climatic drivers affect local population dynamics. In addition to global warming, regionally varying changes in precipitation are predicted for significant areas across the globe (IPCC, 2014). The interplay between these two climatic changes is complex and may even vary across climatic gradients (Luo et al., 2008). For assessments of future vegetation changes, it is vital to know how plants respond to simultaneous changes in temperature and precipitation: can the single effects simply be added (additive interaction) or does the response to combined change deviate from that sum (non-additive interaction), either in an enforcing manner (synergistic interaction) or in a counteractive manner (antagonistic

interaction) (Darling & Côté, 2008)? However, as single-factor and local climate experiments still dominate the literature, we have only limited knowledge about the interaction effect of changes in temperature and precipitation (Barnett & Facey, 2016; Mundim & Bruna, 2016; Wu et al., 2011) and the climatic context-dependency (Dunne, Saleska, Fischer, & Harte, 2004; Root & Schneider, 1995; Rustad, 2008) of climate-change impacts, which can be expected to vary within a species' niche (Hampe & Petit, 2005).

Here we present the results of a turf transplant experiment in which we assess the effects of single and combined changes in temperature and precipitation on the population dynamics of four common forb species (*Viola biflora*, *Veronica alpina*, *Viola palustris*, *Veronica officinalis*) across broad bioclimatic gradients in Norway. Vegetation turfs were transplanted to sites that were warmer, wetter and warmer+wetter in accordance with global and regional climate-change projections (IPCC, 2014), as well as at 'home' for control. The experiment was replicated across a climatic grid of 12 sites arrayed in three levels of mean summer temperature (boreal ~10.5°C, sub-alpine ~8.5°C, and alpine ~6.5°C) and four levels of annual precipitation (ca. 600, 1200, 2000 and 2700 mm) (Figure 1). This experimental design allows us to disentangle the effects of concomitant changes in temperature and precipitation, and to assess how climate-change effects vary across climatic contexts. We followed all individuals of the target species in transplanted and control turfs over four years and parameterized size-structured population models for all species and treatments, yielding populations growth rates (λ) for all treatments and populations as well as vital rate contributions to differences in λ (Merow et al., 2014) based on spatially and temporally stochastic regression models. Uncertainty was assessed by bootstrapping the population datasets 10 000 times prior to model building. The climate-change effects were assessed by comparing transplants to controls at their 'home' sites. As a proxy for competitive interactions, we measured vegetation height in all turfs.

Materials and methods

Study area and species. The study was carried out over four years (2009 to 2012) as part of the SEEDCLIM climate change experiment performed in twelve grassland sites in Norway (Klanderud, Vandvik, & Goldberg, 2015). The sites were selected to fit within a systematic, orthogonal climate grid composed of three levels of summer temperature (boreal ~10.5°C, sub-alpine ~8.5°C, and alpine ~6.5°C) and four levels of annual precipitation (ca. 600, 1200, 2000 and 2700 mm) (Figure 1), where summer temperature (the mean of June to September) and annual precipitation are not correlated. The climate grid was based on long-term monthly means from the current 'normal period' 1961–1990 provided by the Norwegian Meteorological Institute (met.no). The sites were selected to be as similar as possible in all aspects other than climate (grazed, species-rich grasslands situated on south-facing, shallow slopes on calcareous bedrock).

For the demographic study, we selected two alpine and two lowland species: *Viola biflora* L, *Veronica alpina* L, *Viola palustris* L and *Veronica officinalis* L. All study species are perennial and reproduce sexually and clonally. The study species were common throughout the climate grid, although not all species occurred in all sites (Figure S1).

Experimental design. At each site, we established five experimental blocks, and in each block four 25 × 25 cm plots were placed semi-randomly to contain the study species. In September 2009, three plots from each block were transplanted to the sites one step warmer, wetter and warmer+wetter, respectively (Figure 1). This constituted a summer temperature increase of ca. 2–3 °C and an annual precipitation increase of ca. 700–800 mm, mimicking climate change projections for the study region (Intergovernmental Panel on Climate Change, 2014). The fourth plot was transplanted within the original site and block, as a control. The transplanted turfs measured 29 × 29 cm (i.e. the plot dimensions plus 2 cm at each side, to avoid edge effects)

and were 5–10 cm deep. As an estimate of competition, we measured overall vegetation height in all plots as the average of five measurements of the foliage height per plot in 2009, prior to transplanting, and in 2011, 2012 and 2013. To assess whether vegetation height changed in response to the climate transplant treatments, we analyzed the difference in vegetation height between transplant plots and controls from each block separately for each transplant treatment using linear mixed effects models with Gaussian error structure, year as fixed effect and random intercepts for site (n = 151, 171, and 118 for warmer, wetter, and warmer+wetter respectively).

Data collection. In July/August 2009, prior to transplanting, we tagged all ramets of the study species within each plot and recorded a selected set of vegetative and reproductive traits allowing estimation of dry biomass, our estimate of plant size (Meineri, Skarpaas, Spindelböck, Bargmann, & Vandvik, 2014), and fecundity. In the summers of 2010, 2011 and 2012, we recorded the survival of the previous years' ramets, tagged new clonal ramets and seedlings, and repeated the measures of vegetative and of reproductive traits for all live ramets (Methods S2). In total over the course of the experiment, we recorded 2501 ramets of *Viola palustris*, 2713 ramets of *Viola biflora*, 3920 ramets of *Veronica officinalis* and 897 ramets of *Veronica alpina*.

Population modeling and statistical analyses. To analyze population dynamics and estimate population growth rates (λ) of the different populations and treatments we used integral projection models (IPMs), which are based on regressions of vital rates (survival, growth, clonality, fecundity) against a continuous state variable describing each individuals' state (here plant size) (Easterling, Ellner, & Dixon, 2000). All regressions were performed separately for each species and treatment using generalized linear mixed effects models (Bates, Maechler, Bolker, & Walker, 2015) in R version 3.3.1 (R Development Core Team, 2016). This method

allows modeling of the temporal and spatial variability arising from the study design as stochastic by specifying site and annual transition as random effects. Using the fixed effects coefficients from these regressions we built IPMs for every species and treatment using the R-package 'IPMpack' (Metcalf, McMahon, Salguero-Gomez, & Jongejans, 2013). As the underlying mixed-effect models include random effects for site and annual transition, the 'deterministic' λs of our resulting IPMs account for temporal and spatial stochasticity. We calculated vital rates contributions to the differences in λ between the transplants and their respective controls through separate one-way life table response experiments (LTRE) for each treatment (Caswell, 2001). Uncertainties for λ and vital rate contributions were obtained by bootstrapping the original data (separately for every species and treatment) 10000 times (Manly, 1997): individual ramets were sampled with replacement to construct a resampled dataset containing the same number of observations as the original dataset. Regression modeling, construction of IPMs and calculation of λ were then repeated for each of the 10000 resampled datasets. To assess the effects of climatic context on the population responses to increased temperature and precipitation, we built site-specific IPMs based on the random site effects of the vital rate regressions for every bootstrap sample. We then regressed the differences in site-specific λ values between climate transplants and controls, and the respective vital rate contributions from the LTREs with site temperature and precipitation across all species 10000 times in linear mixed effects models. Here, we used a Gaussian error distribution with an identity link and specified summer temperature and precipitation (in two separate models) as fixed effects and species as a random intercept. For more detailed information on regressions, population models and their analyses please refer to Methods S2.

Results

All four species had stable or growing populations in the control turfs during the timeframe of the experiment. The transplants showed three principal response patterns in population growth rate (λ) to the climatic change treatments. In *Veronica alpina* and *Viola palustris* λ decreased in all three treatments, *Viola biflora* showed decreased λ in the wetter transplants, and in *Veronica officinalis* λ decreased in the wetter and warmer+wetter transplants (Figure 2a). The effect of the combined warmer+wetter transplant treatment on λ resembled the effect in the transplants that received warming only in *Viola biflora*, *Veronica alpina*, and *Viola palustris*, whereas it was comparable to the effect in the transplants with only higher precipitation in *Veronica officinalis* (Figure 2a, see Table S2 for the original λ values). The changes in λ in the climate transplant were mainly caused by reduced survival and reduced clonality, whereas growth and fecundity hardly changed (Figure 2b). In contrast, the height of the extant vegetation increased under warmer and warmer+wetter climates, though less so in the latter, while it stayed largely constant in the wetter transplants (Figure 3). When comparing the vital rate contributions to changes in λ from the added single treatments and the combined warmer+wetter treatment, we found negligible differences for clonality (indicating additivity) across all species but considerable differences for survival (indicating non-additivity) (Figure 4). The survival contributions in the combined treatments were generally less negative than expected in *Veronica alpina* and *Viola palustris*, and less positive than expected in *Viola biflora* (antagonistic effects). In *Veronica officinalis*, both clonality and survival contributions to changes in λ were additive. The magnitude of the decrease in λ and changes in all vital rates in response to warming was constant along the temperature gradient (Figure 5), as were the responses to increased precipitation along the precipitation gradient (not shown). However, the response to increased precipitation, whether it occurred alone or in combination with increased temperature, varied over the temperature gradient. In alpine populations,

increased precipitation generally had positive or neutral effects on λ and survival, whereas the effects became increasingly negative towards sub-alpine and boreal populations (Figure 5).

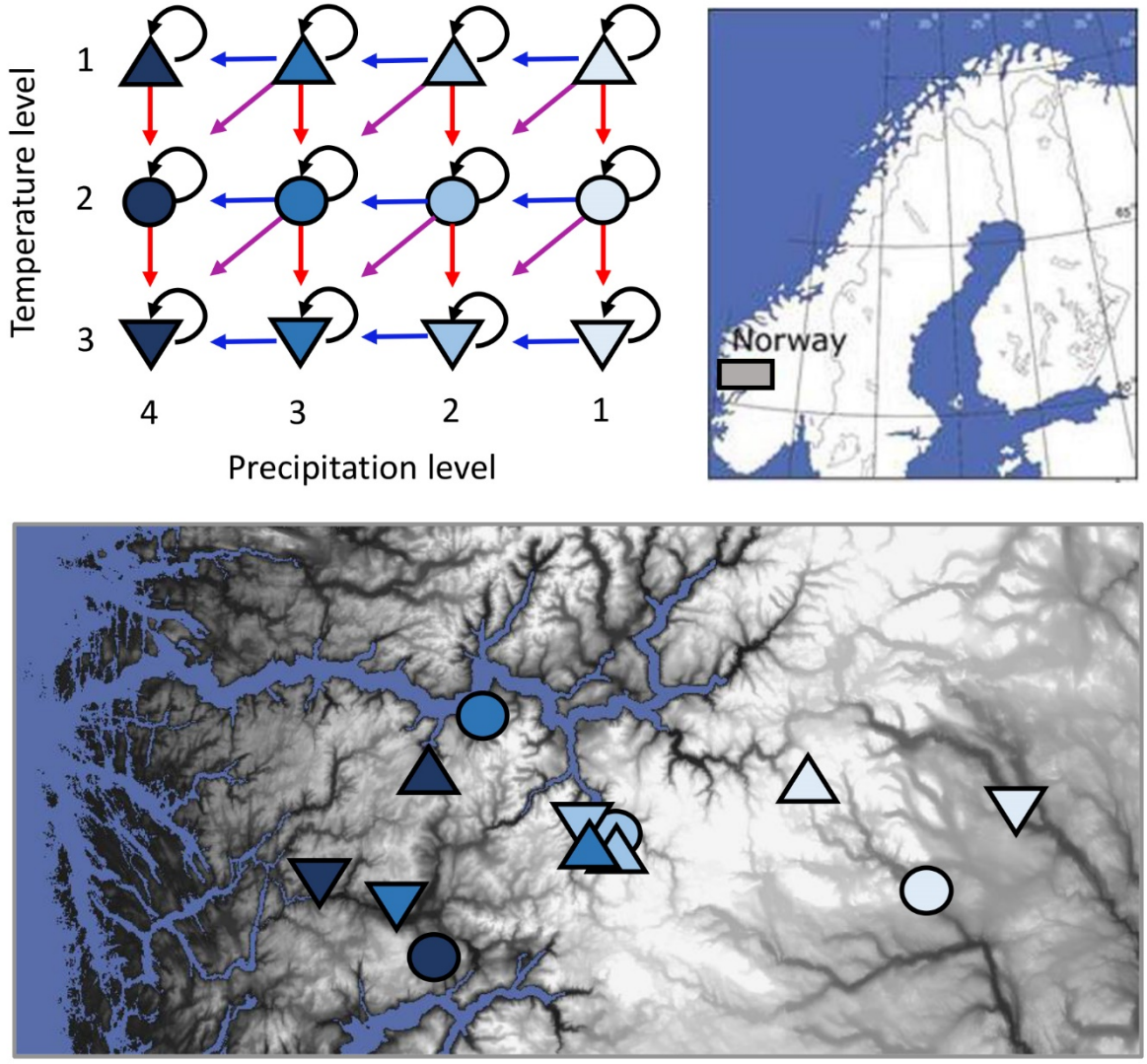

Figure 1. **Experimental design and geographical location of the study area and study sites.** Point-up triangles are alpine, circles are sub-alpine, and point-down triangles are boreal sites. Increasing precipitation level indicated by increasingly saturated blue. Colored arrows indicate direction of transplantation: red = warmer, blue = wetter, purple = warmer+wetter, black = control.

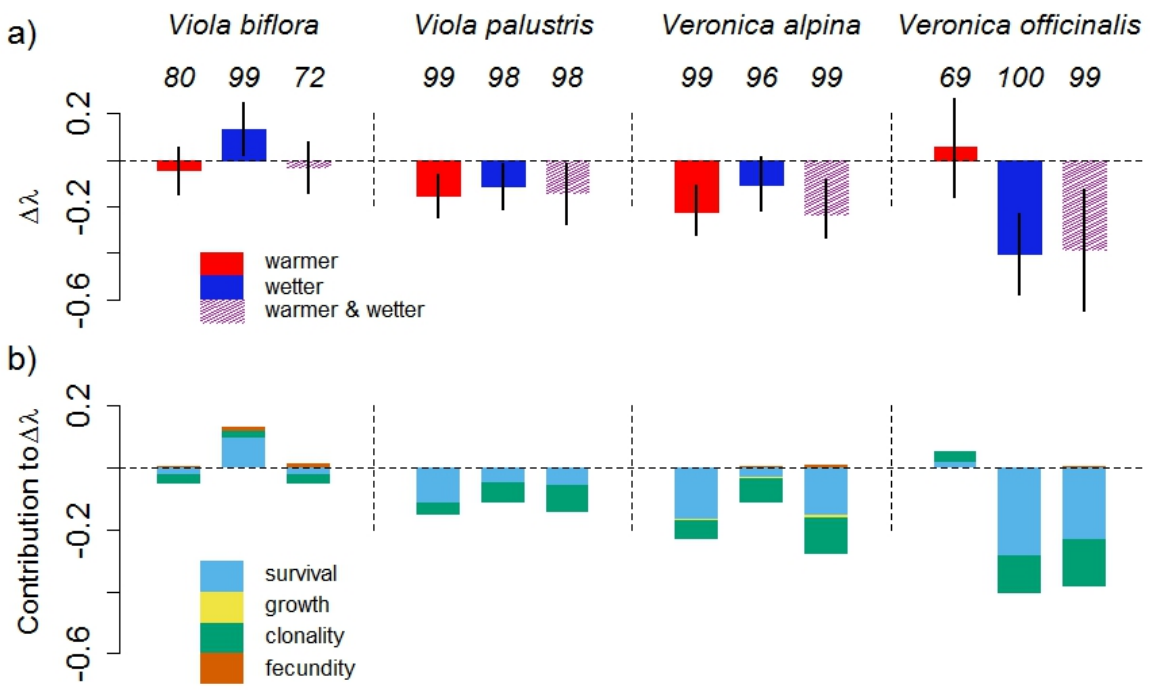

Figure 2. **Effects of increased temperature and precipitation on population growth rates (a) and vital rates (b).** Shown are (a) the median differences in population growth rates (Δλ) between climate transplants and controls and (b) the median vital rate contributions to Δλ for all species and treatments. Error bars in (a) indicate bootstrap confidence intervals (0.025 and 0.975 quantiles of 10 000 bootstrapped Δλ). Numbers in (a) indicate percentage of bootstrap Δλ values that are lower or higher (as indicated by the direction of the bar) than zero.

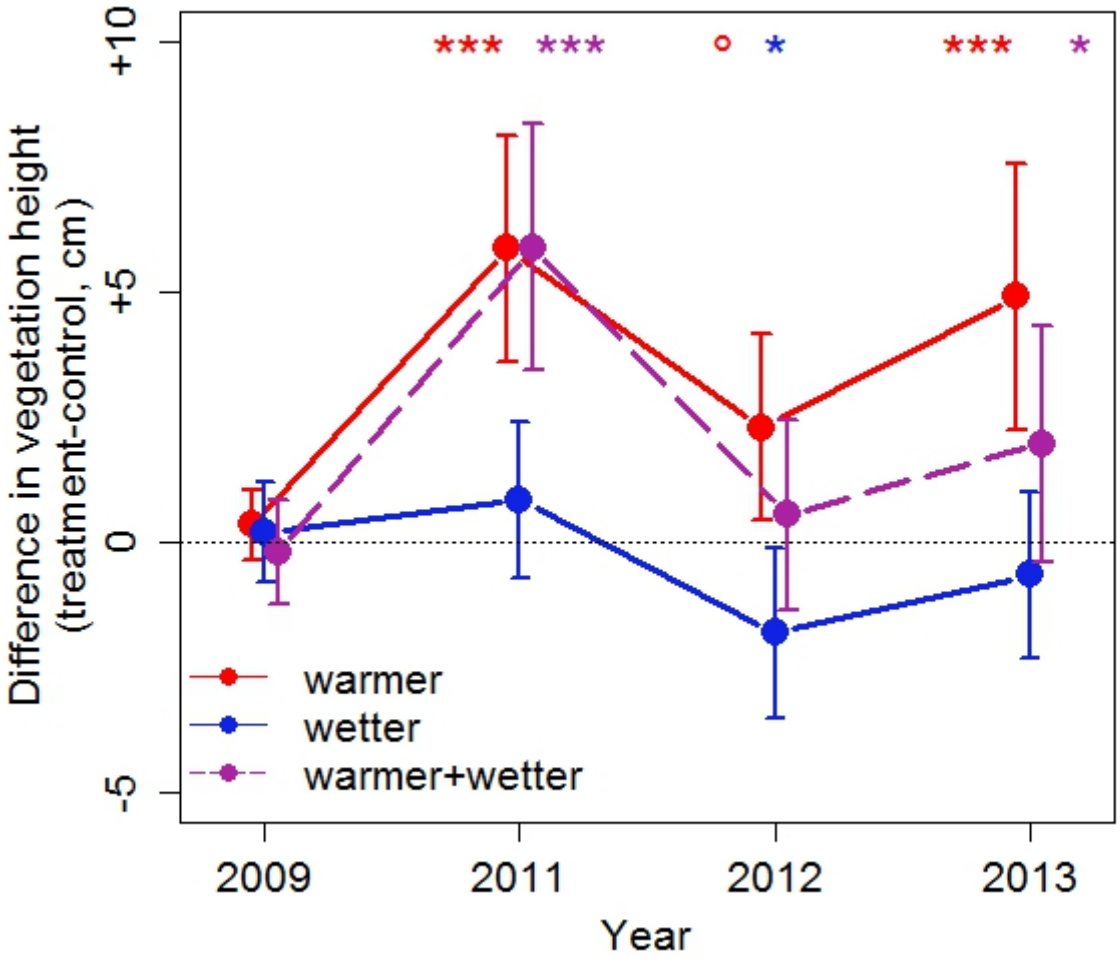

Figure 3. **Effects of increased temperature and precipitation on overall vegetation height.** Shown is the mean difference in overall vegetation height between the respective climate transplants and the home controls in each block. Error bars indicate 95% confidence intervals. Significant differences to values in 2009 indicated by stars: *** < 0.001 < ** < 0.01 < * < 0.05 < ° < 0.1.

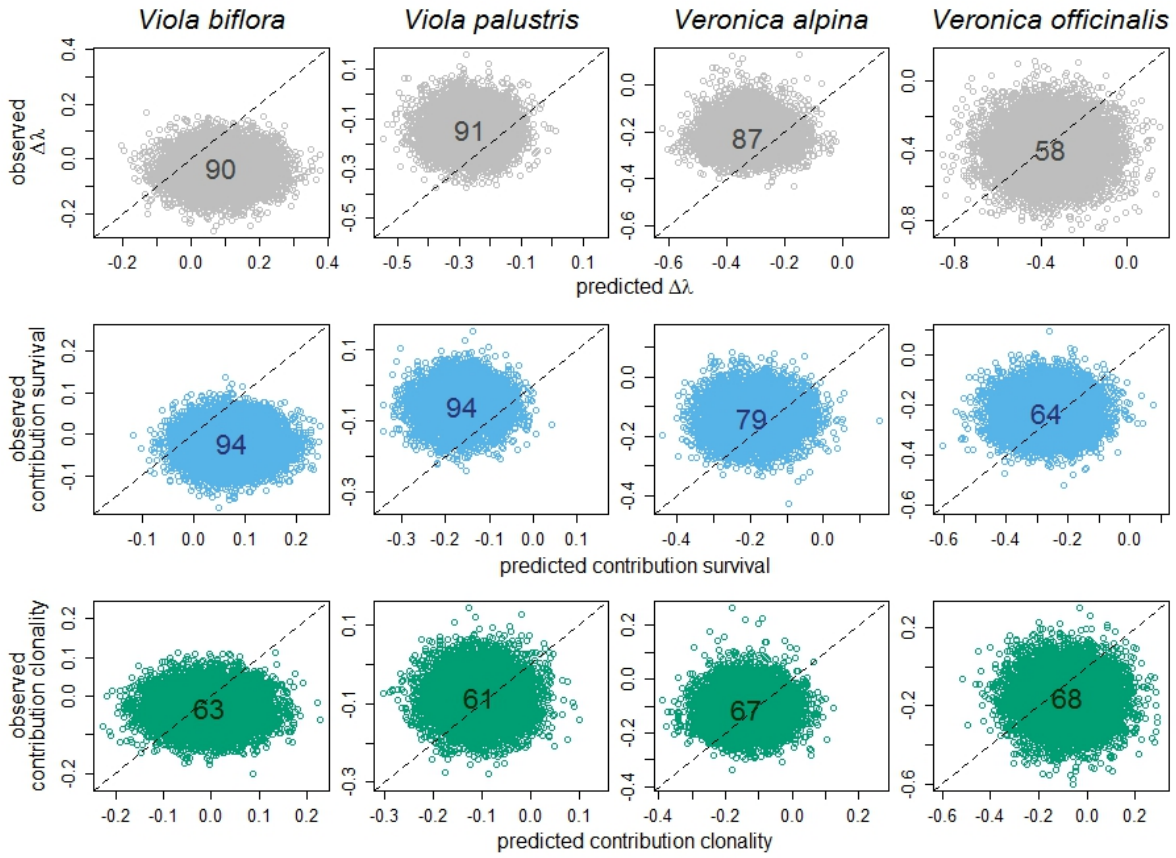

Figure 4. **Non-additivity vs. additivity of effects of increased temperature and precipitation.** Predicted values for changes in population growth rate (Δλ), survival, and clonality from added single treatment (x-axes) plotted against observed values from the combined treatment (y-axes) in all study species. The dashed line represents the perfect match between prediction and observation. Hence, a data cloud placed symmetrically on the dashed line indicates additivity, while non-symmetry indicates non-additivity. The area above the line indicates less negative (or more positive) effects than predicted, the area below the opposite. The numbers shown in the larger area (above or below the dashed line) of the respective data clouds indicate the percentage of 10 000 bootstraps lying in that area.

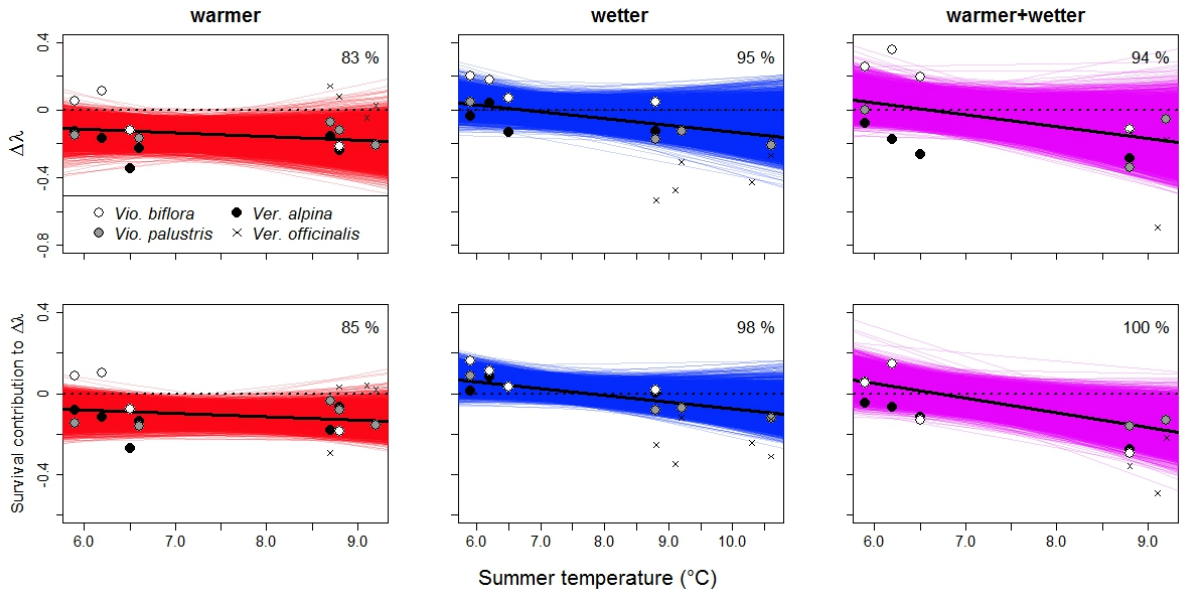

Figure 5. **Temperature context dependency.** Shown are the changes in population growth rate (Δλ) and survival in response to warming, increased precipitation and the combined treatment across *Viola biflora*, *Viola palustris* and *Veronica alpina*. The fourth study species, *Veronica officinalis*, was omitted from the analysis as it occurs at only one temperature level in the warmer and warmer+wetter climate transplants, but is indicated by '×'. The colored lines represent regression predictions from 10 000 linear mixed effect models with the bootstrapped Δλ or survival contribution per site as response variable, home site temperature as fixed effect explanatory variable and species identity as random effect. The bold black line represents the regression prediction based on the median Δλ or survival contribution per site. The number in the upper right corner indicates the percentage of negative bootstrap slopes.

Discussion

Three of the four study species showed non-additive effects of concomitant changes in temperature and precipitation on λ, illustrating that impacts of multiple global change drivers largely do not act independently (Parmesan & Hanley, 2015). In fact, our study mirrors the general pattern of non-additivity being more common than additive responses in factorial climate change experiments, with a ratio of occurrence at 3:1 (Darling & Côté, 2008). Interestingly, the underlying main contributors to the observed changes in λ, survival and clonality, responded in different ways. Whereas survival mirrored the antagonistic non-additivity seen in λ in *Viola biflora*, *Viola palustris* and *Veronica alpina*, the clonality effects were additive and synergistic in all species. This is important, as these antagonistic effects of temperature and precipitation increases on survival reduction translate into higher survival under the combined increase in temperature and precipitation relative to warming alone, while clonal reproduction is even more reduced due to synergistic negative effects on clonality. Together, this implies a higher retention of different genotypes and hence an improved chance of long-term population persistence (Morris & Doak, 2002) under a combined increase in temperature and precipitation, even though population growth rates and hence population size trajectories change similarly under warming alone.

In addition, non-additive effects on survival and additive effects on clonality suggest that there are differences in the mechanisms behind the effects of the tested climatic changes on these vital rates. In particular, for survival, the negative effects of warming for both *Viola palustris* and *Veronica alpina* likely relate to the observed simultaneous increase in competitive interactions in our experiment (Guittar, Goldberg, Klanderud, Telford, & Vandvik, 2016). This is supported by both these species being relatively weak competitors for light (Jensen & Meyer, 2001; Kollmann & Rasmussen, 2012; Olsen, Töpper, Skarpaas, Vandvik, & Klanderud, 2016) and by other studies that find changes in biotic interactions in

response to climate warming (Alexander et al., 2015). Reduced survival under increased precipitation might be a more direct, physiological response to excess water in an already humid study region (see also Schuur, 2003), although some species may benefit, as exemplified by *Viola biflora*, due to high moisture-affinity (Lenoir et al., 2010). Together, the weaker effects on survival in the warmer+wetter transplants might reflect the lower increase in vegetation height in this treatment compared to warming alone (cf. Figure 3), but also an alleviation of the excess-water effect through higher evapotranspiration in a warmer climate (Harte & Shaw, 1995). Therefore, the effects on the survival of our study species seem to be plastic realizations of the net-outcome of the concomitant climatic changes, acting either directly via soil moisture, indirectly via biotic interactions, or via a combination both. In contrast to survival, the largely additive effects on clonal growth suggest that increases in temperature and precipitation affect this vital rate independently of one another. The largest decreases in clonal growth in our study occurred under increased precipitation, which contrasts the general pattern of an increasing proportion of clonal plant species towards wetter habitats (Herben, Šerá, & Klimešová, 2015; Klimešová & Herben, 2015; Ye et al., 2014). This indicates that not precipitation *per se* but a related climatic factor might be the driving force behind the reduced clonality in our wetter transplants. For instance, transplants to more oceanic sites with higher rainfall would also experience an increase in cloudiness, and thus a decrease in light availability, which has been shown to reduce the production of clonal ramets (Guo et al., 2016; Méthy, Alpert, & Roy, 1990; M. T. Wang et al., 2008; P. Wang, Lei, Li, & Yu, 2012; Xie, Zhang, Zhao, Du, & He, 2014). Our experimental setup allows us to address this effect independent of any change in temperature, which otherwise may have masked this response.

While the net-effects of a warmer+wetter climate rather reflect the responses to warming alone in weak competitors as *Viola biflora*, *Viola palustris* and *Veronica alpina*,

species with higher competitive abilities could be expected to show a dominance of precipitation increase effects. *Veronica officinalis* exemplifies this in our study with a neutral effect of warming whereas the wetter and warmer+wetter treatments reduced λ, reflecting the species' low affinity to moisture (Mossberg & Stenberg, 2007). In contrast to the other species, the negative survival contribution to changes in λ was not reduced in the combined treatment. The consequent steep drops in population size under any wetter climate suggest a realistic risk of local extinctions in this species in the nearer future (Morris & Doak, 2002).

Non-additive synergistic effects of the individual climatic drivers (i.e. stronger than predicted from summed single effects) did not occur in our experiment, which likely is due to inherent counteractive effects of warming and increased precipitation (Luo et al., 2008; Wu et al., 2011). Thus, quantitative predictions based on single effects would at least not have underestimated the impacts of the combined climatic change. However, such non-additive synergistic effects are anything than rare, occurring about as regularly as antagonistic effects (Darling & Côté, 2008). This highlights that factorial experiments are vital for reasonably precise quantitative predictions of combined climate change responses (Barnett & Facey, 2016; Darling & Côté, 2008), even when well-known biotic and abiotic affinities of the focal species may tempt to make predictions based on single factor effects, as is commonly done in the literature (Mundim & Bruna, 2016; Wu et al., 2011).

Plant population responses to climate change have been hypothesized to vary across different climatic contexts throughout the species' range and realized bioclimatic niches (Grime et al., 2000; Holub, Fabsicova, Tuma, Zahora, & Fiala, 2013), but this has rarely been tested empirically (Ehrlén & Morris, 2015; Ehrlen, Morris, von Euler, & Dahlgren, 2016). From niche theory, we expected stronger negative responses of our alpine species to climate warming in the sub-alpine sites, which are near the 'rear edge' of the species' temperature niche (Hampe & Petit, 2005), as well as generally more negative (or less positive) effects of

increased precipitation towards the wettest sites (Schuur, 2003). Our experiment did not support these expectations. However, our study documents less negative effects of increased precipitation, with and without increased temperature, on λ and survival towards lower ambient temperatures in *Viola biflora*, *Viola palustris* and *Veronica alpina* (Figure 4). A possible reason why increased precipitation did not result in negative effects in the alpine could be that a large amount of the precipitation in the alpine falls as snow during the winter. In *Viola biflora*, a snowbed species, λ and survival increased under wetter conditions in the alpine, which might reflect a competitive advantage relative to other species under prolonged snow cover (Reinhardt, Odland, & Pedersen, 2013). In addition, poorly developed alpine soil types, with typically low water retention and high runoff, could buffer against higher precipitation and explain weaker impacts than in the warmer sites with better developed and stronger water-retaining soils (Rawls, Pachepsky, Ritchie, Sobecki, & Bloodworth, 2003).

In summary, our results illustrate important benefits of choosing a more complex experimental design and measuring responses at a more detailed level. The demographic approach allowed us to identify which vital rates were most responsive to the tested climatic changes, the factorial experiment separated non-additive from additive effects, and both approaches together revealed that the mechanisms behind the effects of the climatic changes varied between the vital rates. This illustrates that the links between a changing environmental variable and an affected species rarely are simple and *uni-causal*, which also can be generalized to communities or ecosystems (Emmett et al., 2004; Parmesan & Yohe, 2003). We also demonstrate that including context dependency in the design of a climate change study, is a strong approach for achieving results that are both precise and ecologically generalizable (Borer et al., 2014; De Boeck et al., 2015; Fraser et al., 2013; Parmesan & Hanley, 2015), which is important for the development of good spatial predictions for future environmental changes.

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517

Supporting information:

The devil is in the detail: non-additive and context-dependent plant population responses to increasing temperature and precipitation

J. P. Töpper, E. Meineri, S. L. Olsen, K. Rydgren, O. Skarpaas & V. Vandvik

In this document, we provide additional information on:

- Study species occurrence in the experimental sites (Figure S1; page 23)
- Details of demographic study and population modelling (Methods S2; pages 24-43)
- Population growth rates in controls and treatments (Table S3; page 44)

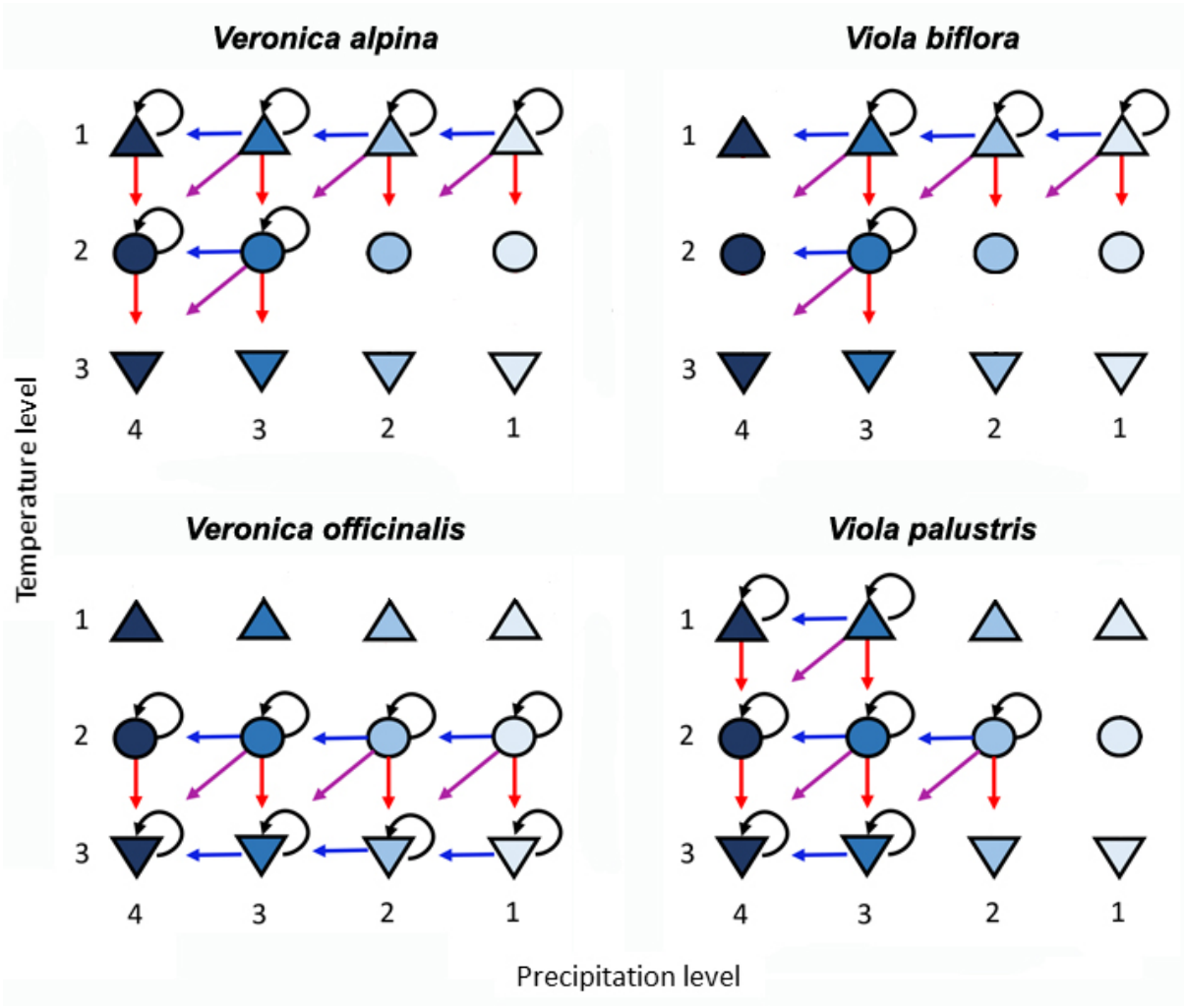

Figure S1. **Illustration of the transplant experiment by species.** The four species occurred naturally in those sites where the arrows originate. Point-up triangles are alpine, circles are sub-alpine, and point-down triangles are boreal sites. Increasing precipitation level indicated by increasingly saturated blue. Colored arrows indicate direction of transplantation: red = warmer, blue = wetter, purple = warmer+wetter, black = control.

Methods S2. **Detailed description of demographic data collection and population modeling.**

The methods described in this section for "demographic data collection", "population modelling", and "analysis of population models" are mostly similar to the methods described in Olsen, Töpper, Skarpaas, Vandvik, and Klanderud (2016), another study performed in the SEEDCLIM climate grid, and co-authored by four of the six authors of the paper at hand.

Demographic data collection. In July/August 2009, prior to transplanting, we non-destructively tagged all ramets of the study species within each plot with plastic rings (*Veronica officinalis*) or toothpicks with plastic beads (the other species), measured a selected set of vegetative traits and counted the number of floral buds, flowers and capsules. In the summers of 2010, 2011 and 2012 we recorded the survival of the previous years' ramets, tagged new clonal ramets and seedlings, and repeated the measures of vegetative and reproductive traits for all live ramets. The vegetative traits measured differed between species and were selected for each species to allow estimation of plant biomass (Meineri, Skarpaas, Spindelböck, Bargmann, & Vandvik, 2014). For the *Veronica* species the measured vegetative traits were shoot height, number of leaves, length of the longest leaf, and width of the broadest leaf. For the *Viola* species we measured number of leaves, length of the longest leaf (*Viola palustris*) and width of the broadest leaf (*Viola biflora*). For *Veronica alpina* each ramet could include several shoots, hence we took the measurements for every shoot separately, calculated shoot biomass and summed them to obtain ramet biomass. As far as possible we also determined the clonal branching structure of the species in order to assign 'mother ramets' to new clonal offspring. When this was not possible, a clone was assigned to the closest potential parent ramet (present in the previous year, not a seedling). The two *Viola*s and *Veronica alpina* exhibit prolonged vegetative dormancy. Since ramets in these species can resprout after having been dormant for

565 at least two, sometimes three, years (Evju, Halvorsen, Rydgren, Austrheim, & Mysterud, 2010;
566 Spindelböck & Olsen, 2013), the limited time frame of the study does not allow disentangling
567 mortality from 'going dormant' and clonality from 'resprouting'. We hence regarded all newly
568 emerged non-seedling ramets as new clonal offspring and all disappearing ramets as 'dead'.
569 By destructive sampling outside the demography plots we obtained numbers of seeds
570 per capsule for 30 plants covering the size range of reproductive individuals in each site and for
571 each species. Probability of germination and seedling establishment until the end of the growing
572 season were tested in a field sowing experiment in which seeds of our target species were sown
573 in 12.5 × 25 cm plots in the sites where the respective species naturally occurred. We sowed 50
574 seeds per plot in the *Veronica* species and 30 seeds per plot in the *Viola* species in 5 replicate
575 sowing plots with an adjacent control plot each (no seeds sown, to control for natural seed
576 dispersal and germination) per site and species (Meineri, Spindelböck, & Vandvik, 2013). Non-
577 germinating seeds of all four species were assumed to enter the soil seed bank, and we
578 calculated the proportion of seeds entering the seed bank by multiplying the number of non-
579 germinated seeds from the field sowing experiment by their probability of surviving in the seed
580 bank for at least one year. To obtain the probability of seed survival in the seed bank we buried
581 five replicate batches of 50 seeds in nylon stockings for each species in each site for 18 months.
582 The unburied seeds that had not disintegrated were germinated in the laboratory, and non-
583 germinated seeds were checked for viability using a tetrazolium test (Association of Official
584 Seed Analysts and the Society of Commercial Seed Technologists, 2010).
585
586 **Population modeling.** To analyze population dynamics and estimate population growth rates
587 (λ) of the different populations and treatments we used integral projection models (IPMs),
588 which are based on regressions of vital rates (survival, growth, clonality, fecundity) against a
589 continuous state variable (size, weight, age, etc.) describing each individuals' state (Easterling,

590 Ellner, & Dixon, 2000). All analyses were performed separately for each species and treatment
591 using R (R Development Core Team, 2016).

592 We examined the effects of plant size on survival, growth, probability of producing
593 clonal offspring, number of clonal offspring produced, size of clonal offspring, flowering
594 probability and number of flowers produced separately for each treatment and their respective
595 controls across all sites. For each climate treatment, we used the control plots at the home sites
596 as control level (home sites = sites from which the transplanted plots came from). Because of
597 the nested design (blocks within sites) and repeated measures on the same plants (three annual
598 transitions from 2009–2012), we used generalized linear mixed effects models (GLMM) for all
599 analyses (Bates, Maechler, Bolker, & Walker, 2015). This method allows for modeling of the
600 temporal and spatial variability arising from the study design as stochastic by specifying the
601 data structure (site and annual transition) as random effects alongside the predictor arguments
602 (fixed effects). All vital rate models were first fitted with linear and quadratic terms for size in
603 the fixed effects and random intercepts and slopes for block nested in site and random intercepts
604 for transition. The appropriate minimum model structure for both fixed and random effects was
605 found in a backward selection procedure using likelihood ratio tests (significance level 0.05).
606 The random intercepts for “site” and “transition” were always kept as the minimum random
607 structure. For the models of probability of survival, clonal reproduction and flower production
608 we used a binomial error distribution with logit link, for the models of number of clonal
609 offspring and flowers we used a Poisson error distribution with a log link, and for the models
610 of growth and size of clonal offspring we used a Gaussian error distribution with an identity
611 link. Where necessary, over-dispersion in the binomial and Poisson models was accounted for
612 by extending the error structure with an observation-level random effect (Maindonald & Braun,
613 2010). The dependency of the number of seeds per flower on plant size was tested using
614 GLMMs with a Poisson error distribution and a log link with site as a random factor. Since no

significant relationship was found for any of the study species, we used the mean number of seeds per capsule as a constant in the population models. Seed and seedling vital rates, including the probabilities for seedling establishment, the probabilities for entering and staying in the seed bank, and seedling size, could not be related to the size of their unknown mother plants and were therefore also represented by constants in the population models. All model coefficients and constants are documented in Supplementary Methods Table 1 and model figures are shown in Supplementary Methods Figures 1-12.

Using the R-package IPMpack (Metcalf, McMahon, Salguero-Gomez, & Jongejans, 2013) we built integral projection models (IPMs) from the regression models and fecundity constants for the vital rates growth, survival, clonality (probability of producing clonal offspring, number of clonal offspring produced and size of clonal offspring) and fecundity (flowering probability, number of flowers produced, number of seeds per flower, the probabilities of seed germination, seedling establishment and entering the seed bank, as well as the mean size of seedlings). The seed bank is a discrete stage in an otherwise continuous population model, and was represented by a model describing transitions between the continuous distribution of plant sizes and the discrete seed bank (probability of staying in the seed bank, leaving the seed bank with subsequent seedling establishment and leaving the seed bank with subsequent seedling establishment failure) (Metcalf et al., 2013). These vital rates models were then used to construct matrices for growth-survival, clonality and fecundity (the discrete transition seed bank model goes into the growth-survival matrix) with size ranges from the observed minimum and maximum sizes minus / plus a small increment of 1% of the minimum / maximum size as described in Metcalf et al. (2013) (Metcalf et al., 2013). The matrices were of the bin dimensions 101 × 101 with the first bin representing the seedbank transitions and the bins 2-101 representing the continuous part of the size range. Finally, these matrices were combined into a full IPM. Following this procedure, separate IPMs were

constructed for a) each overall transplant treatment and its respective control (based on the fixed effects estimates from the mixed effects models), and b) each site-specific transplant treatment and its respective control at every site (based on the random effects estimates from the mixed effects models).

Analyses of population models. For each IPM we obtained the dominant eigenvalue λ, representing population growth rate (Caswell, 2001). As the underlying mixed-effect models already include random effects for transition period and site, the 'deterministic' λs of our resulting IPMs account for temporal and spatial stochasticity and thus resemble the stochastic λs issued from separate IPMs that are based on standard glm-regressions for every site and transition (tested, not shown). We estimated the uncertainty of the IPM models by bootstrapping (Manly, 1997). Individual ramets were sampled with replacement to construct a resampled dataset containing the same number of observations as the original dataset. Regression modeling, construction of IPMs and calculation of λ were then repeated as described above using the resampled dataset. Performing this procedure 10000 times generated a set of 10000 bootstrap λ and vital rates estimates. Pairwise independent transplant and control bootstrap λ samples were subtracted from each other (control-treatment) resulting in 10000 Δλ values.

We used life table response experiments (LTRE) to calculate how much every vital rate contributed to the differences in λ between the transplants and their respective controls. The use of a two-way LTRE for factorial experiments (Caswell, 2001) was problematic to implement here since every treatment had its own control group (the controls used for each treatment and species comprise data from control plots in different sets of sites, see Supplementary Figure 1), hence we performed separate one-way LTREs for each treatment. The contribution of a given vital rate was calculated as the sum of the differences between the vital rate matrices of the transplant and control treatments multiplied by the sensitivity of a matrix midway between the

full IPM matrices of the two treatments (i.e. transplant and control) (Caswell, 2001). We separated growth and survival, which together make up the P-matrix, by setting the probability of survival to 1 for all sizes. The contribution of growth alone could then be calculated using the method outlined above. By subtracting the contribution of growth from the total growth-survival contribution, we found the contribution from survival alone. The LTREs were performed both for the overall population models and for the site-specific ones.

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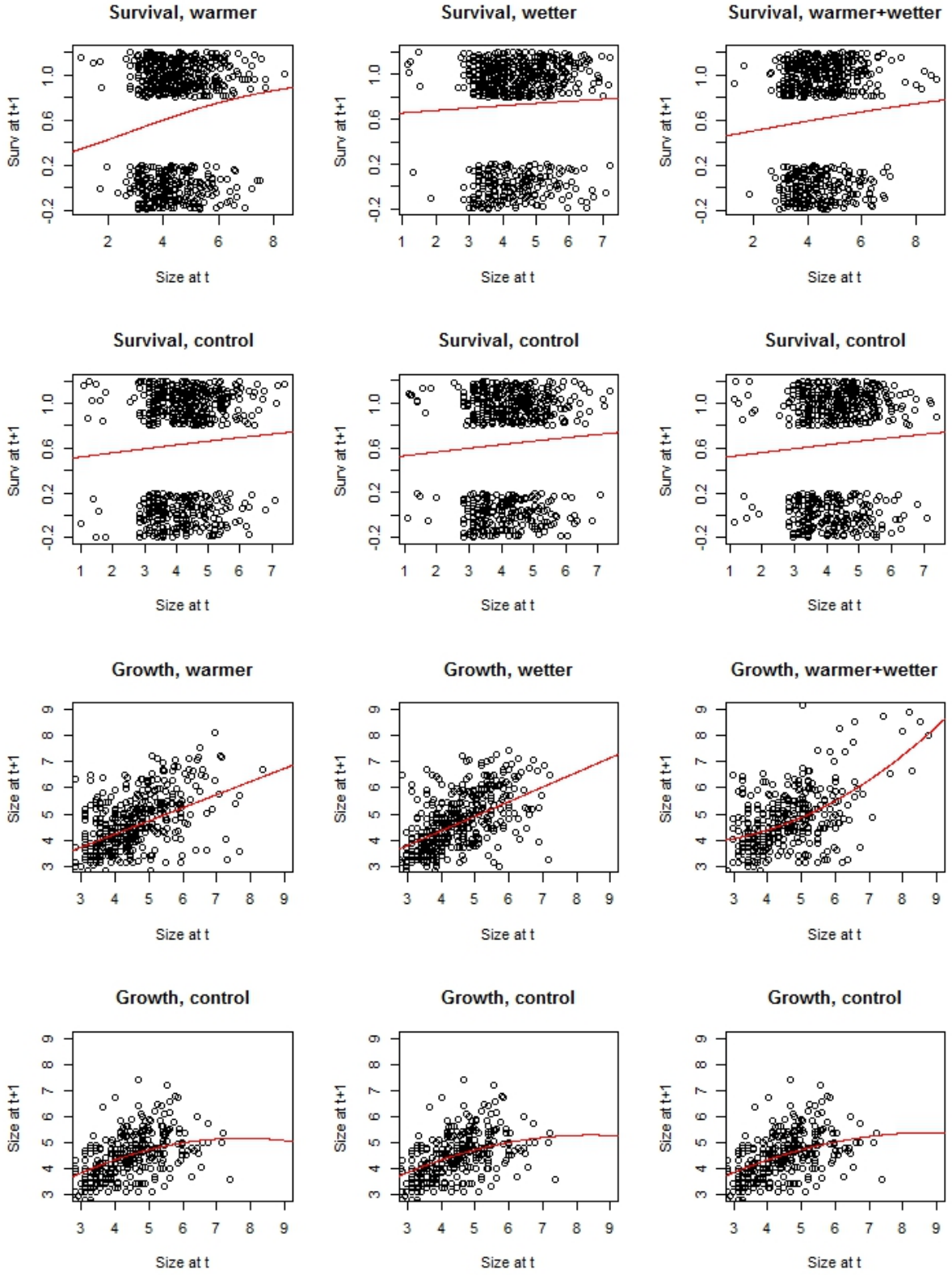
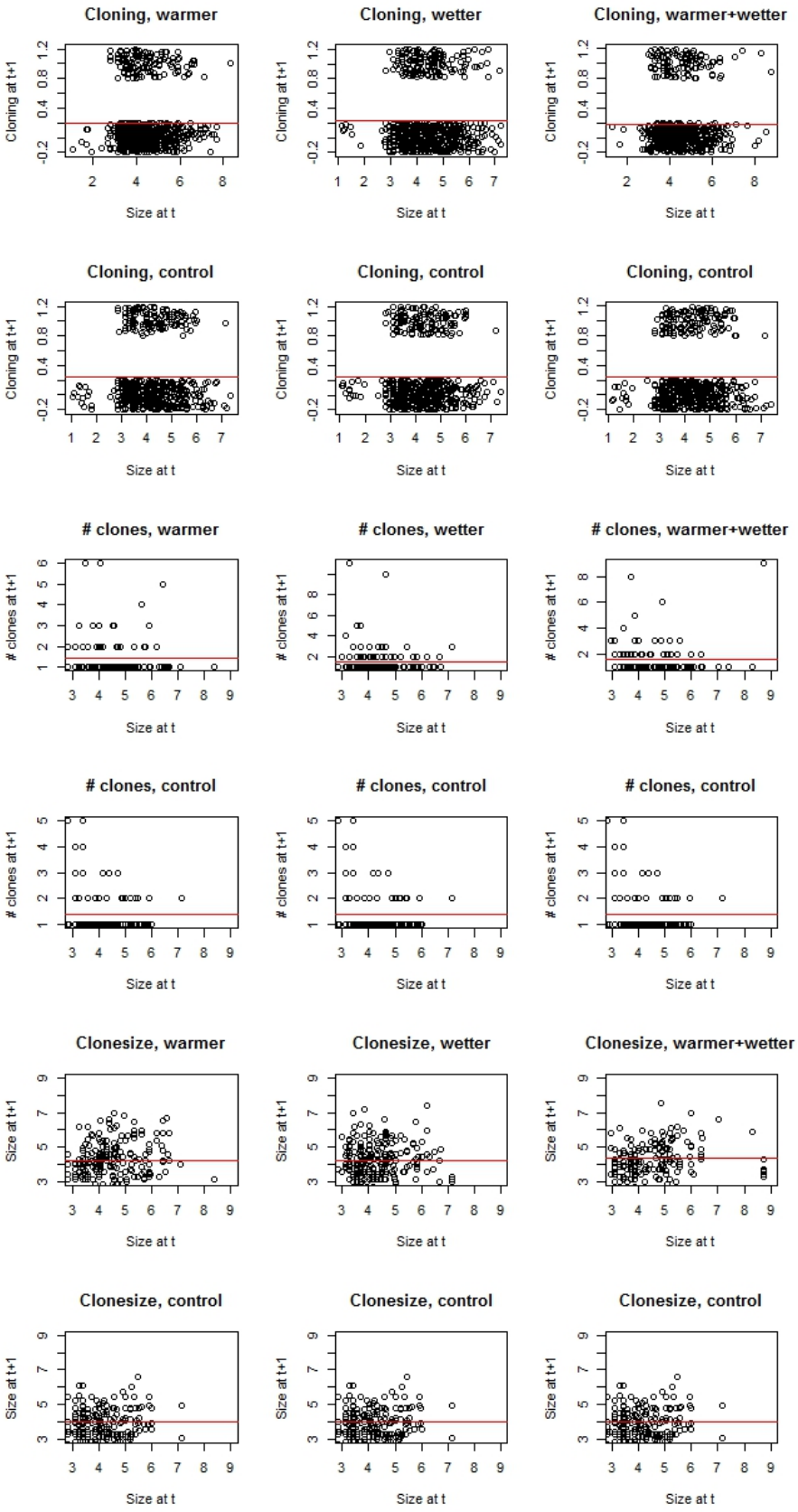
Supporting Methods Table 1. **Fixed-effects model coefficients for the different vital rates of the study species.** Shown are the fixed effects model structures that were found significant ($p<0.05$) in likelihood ratio tests and the fixed effects coefficients. The number of seeds per capsule, the probabilities of seeds entering and staying in the seed bank, seed germinating and seedling establishment are given as constants (mean), as well as seedling size (mean±SD).

		Viola biflora	*Veronica alpina*	*Viola palustris*	*Veronica officinalis*
Survival probability					
warmer	control	-0.06 + 0.15×size	-0.95 + 0.68×size	-0.21 + 0.28×size	-9.21 + 2.55×size + -0.16×size^2
	transplant	-1.02 + 0.35×size	-0.69 + 0.26×size	-0.61 + 0.24×size	-7.99 + 2.08×size + -0.12×size^2
wetter	control	-0.02 + 0.14×size	-3.18 + 1.45×size	-0.8 + 0.36×size	-6.93 + 1.68×size + -0.09×size^2
	transplant	0.55 + 0.1×size	0.28 + 0.24×size	-1.1 + 0.38×size	-4.57 + 1.01×size + -0.07×size^2
warmer+wetter	control	-0.05 + 0.14×size	-3.18 + 1.45×size	-1.37 + 0.49×size	-9.58 + 2.65×size + -0.17×size^2
	transplant	-0.34 + 0.18×size	26.57	-2.35 + 0.61×size	-5.45 + 1.15×size + -0.06×size^2
Growth					
warmer	control	1.64 + 0.91×size + -0.06×size^2	5.38 + 0.38×size	2.1 + 0.62×size	1.84 + 1.12×size + -0.05×size^2
	transplant	2.23 + 0.5×size	4.4 + 0.43×size	0.17 + 1.56×size + -0.1×size^2	1.37 + 1.33×size + -0.07×size^2
wetter	control	1.83 + 0.82×size + -0.05×size^2	6.71 + 0.26×size	0.3 + 1.37×size + -0.07×size^2	4.42 + 0.41×size
	transplant	2.13 + 0.56×size	5.18 + 0.34×size	1.37 + 1.09×size + -0.06×size^2	3.85 + 0.49×size
warmer+wetter	control	1.91 + 0.78×size + -0.04×size^2	6.71 + 0.26×size	0.44 + 1.27×size + -0.06×size^2	4.08 + 0.45×size
	transplant	4.01 + -0.22×size + 0.08×size^2	3.08 + 0.56×size	3.35 + 0.42×size	4.55 + 0.41×size
Cloning probability					
warmer	control	-1.15	-1.86	-1.11	-11.97 + 2.52×size + -0.13×size^2
	transplant	-1.41	-2.1	-1.34	-16.99 + 4.1×size + -0.25×size^2
wetter	control	-1.15	-1.83	-0.96	-10.79 + 2.21×size + -0.11×size^2
	transplant	-1.24	-2.25	-1.26	-16.43 + 3.61×size + -0.2×size^2
warmer+wetter	control	-1.15	-1.83	-1.01	-11.22 + 2.34×size + -0.12×size^2
	transplant	-1.48	-2.94	-1.49	-16.67 + 4.18×size + -0.28×size^2
No. of clones					
warmer	control	0.31	0.4	0.21	-0.25 + 0.14×size
	transplant	0.36	0.34	0.26	-0.39 + 0.14×size
wetter	control	0.31	0.3	0.21	-0.26 + 0.13×size
	transplant	0.43	0.3	0.28	0.73

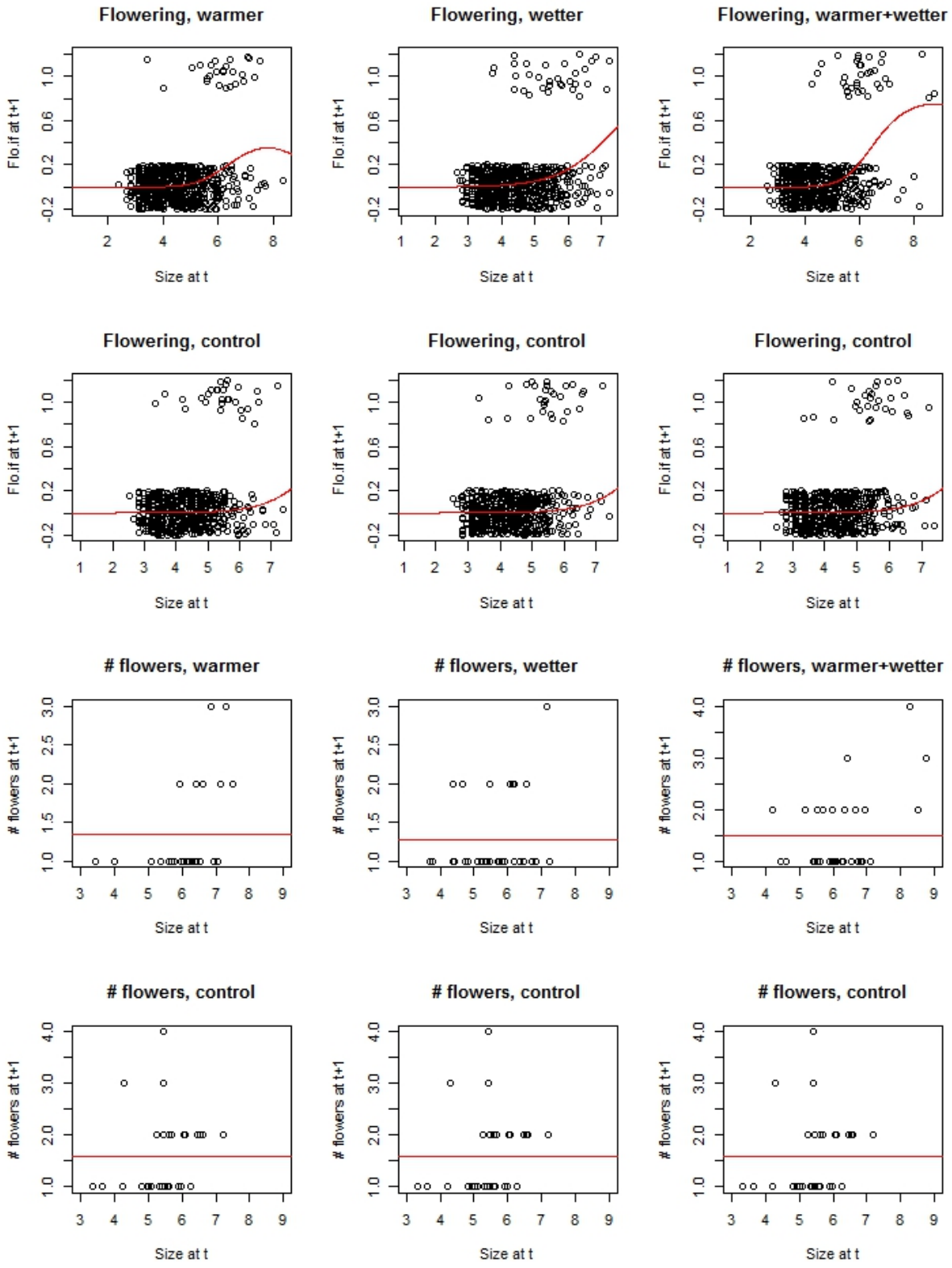
warmer+wetter	control	0.31	0.3	0.22	-0.14 + 0.13×size
	transplant	0.44	0.13	0.3	0.62
Clone size					
warmer	control	3.97	5.18	5.11	3.55 + 0.24×size
	transplant	4.24	4.93	5.21	4.99 + 0.12×size
wetter	control	3.97	5.37	5.57	4.29 + 0.21×size
	transplant	4.24	6.15	5.23	3.03 + 0.4×size
warmer+wetter	control	3.97	5.37	5.43	3.52 + 0.27×size
	transplant	4.37	5.25	5.32	3.34 + 0.37×size
Flowering probability					
warmer	control	-11.07 + 1.28×size	-5.75 + 0.48×size + -	-15.39 + 1.92×size	-18.63 + 3.9×size + -0.22×size^2
	transplant	-23.26 + 5.81×size + -0.37×size^2	-4.17 + 0.19×size	-14.9 + 1.52×size	-18.05 + 3.33×size + -0.15×size^2
wetter	control	-11.07 + 1.28×size	-5.53 + 0.47×size + -	-12.07 + 1.39×size	-19.02 + 4.12×size + -0.22×size^2
	transplant	-8.98 + 1.22×size	-2.61 + 0.12×size	-11.53 + 1.31×size	-15.52 + 2.79×size + -0.11×size^2
warmer+wetter	control	-11.07 + 1.28×size	-5.53 + 0.47×size + -	-13.01 + 1.62×size	-17.18 + 3.62×size + -0.2×size^2
	transplant	-12.23 + 1.78×size	-5.57 + 0.73×size + -	-41.08 + 11.25×size + -0.81×size^2	-9.69 + 1.16×size
No. of flowers					
warmer	control	0.46	1.4	0.14	-3.56 + 1.34×size + -0.07×size^2
	transplant	0.3	1.4	0	0.54 + 0.28×size
wetter	control	0.46	1.55	0.13	0.55 + 0.27×size
	transplant	0.25	1.55	0.07	0.23 + 0.3×size
warmer+wetter	control	0.46	1.55	0.15	0.91 + 0.22×size
	transplant	0.4	0.52 + 0.11×size	0	0.63 + 0.22×size
No. seeds per capsule		7.1	6.5	32.6	20.0
Prob. Seed going into seed bank		0.16	0.28	0.67	0.61
Prob. Seed staying in seed bank		0.17	0.27	0.67	0.61
Prob. Seedling establishment		0.03	0.003	0.01	0.01
Seedling size		2.17±0.45	2.15±0.33	3.57±0.60	4.56±0.59



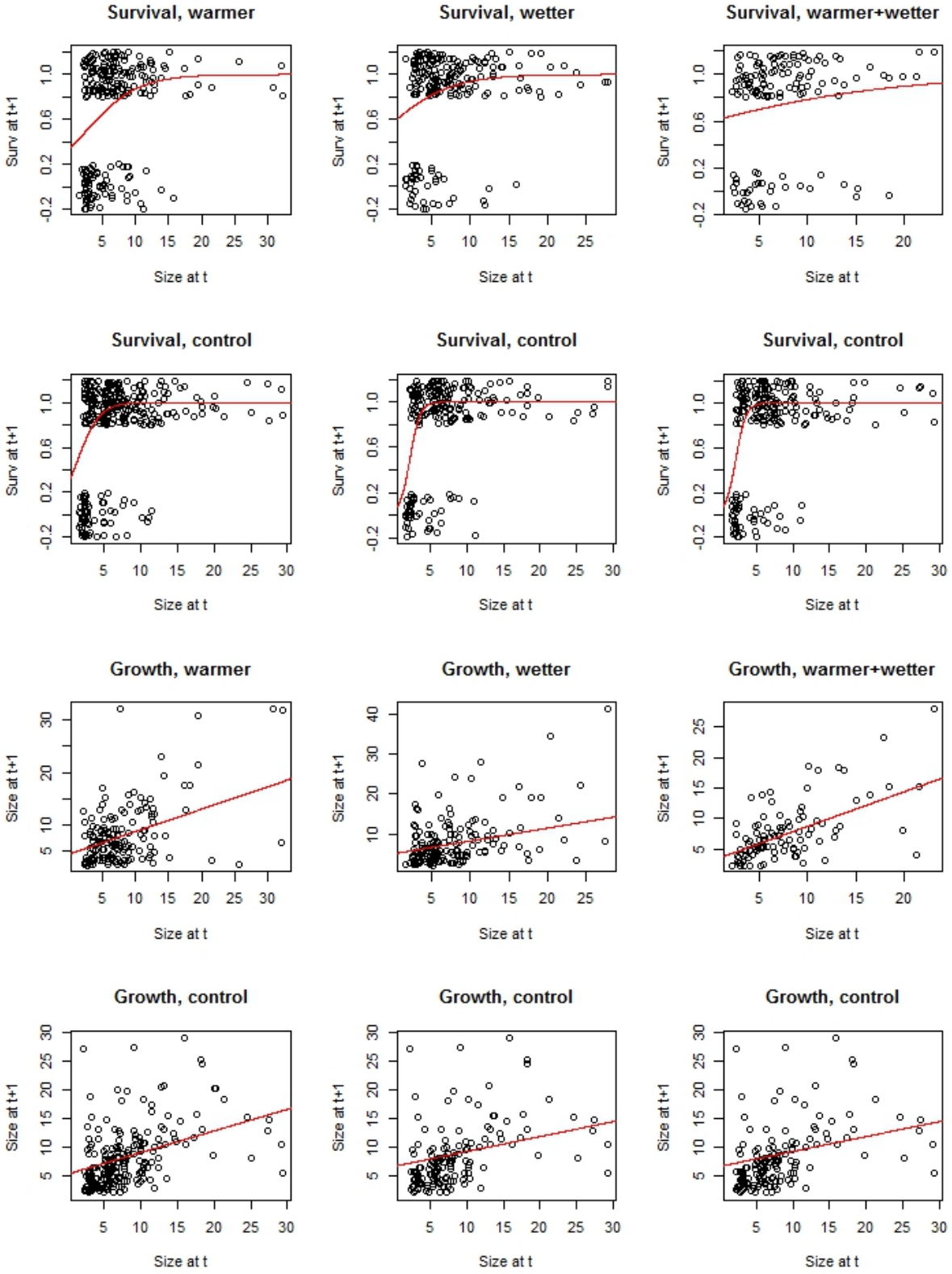
Supporting Methods Figure 1. Survival and growth models for climate transplants and their respective controls in *Viola biflora*. Black open circles represent the original data. Closed red circles represent sequential means.



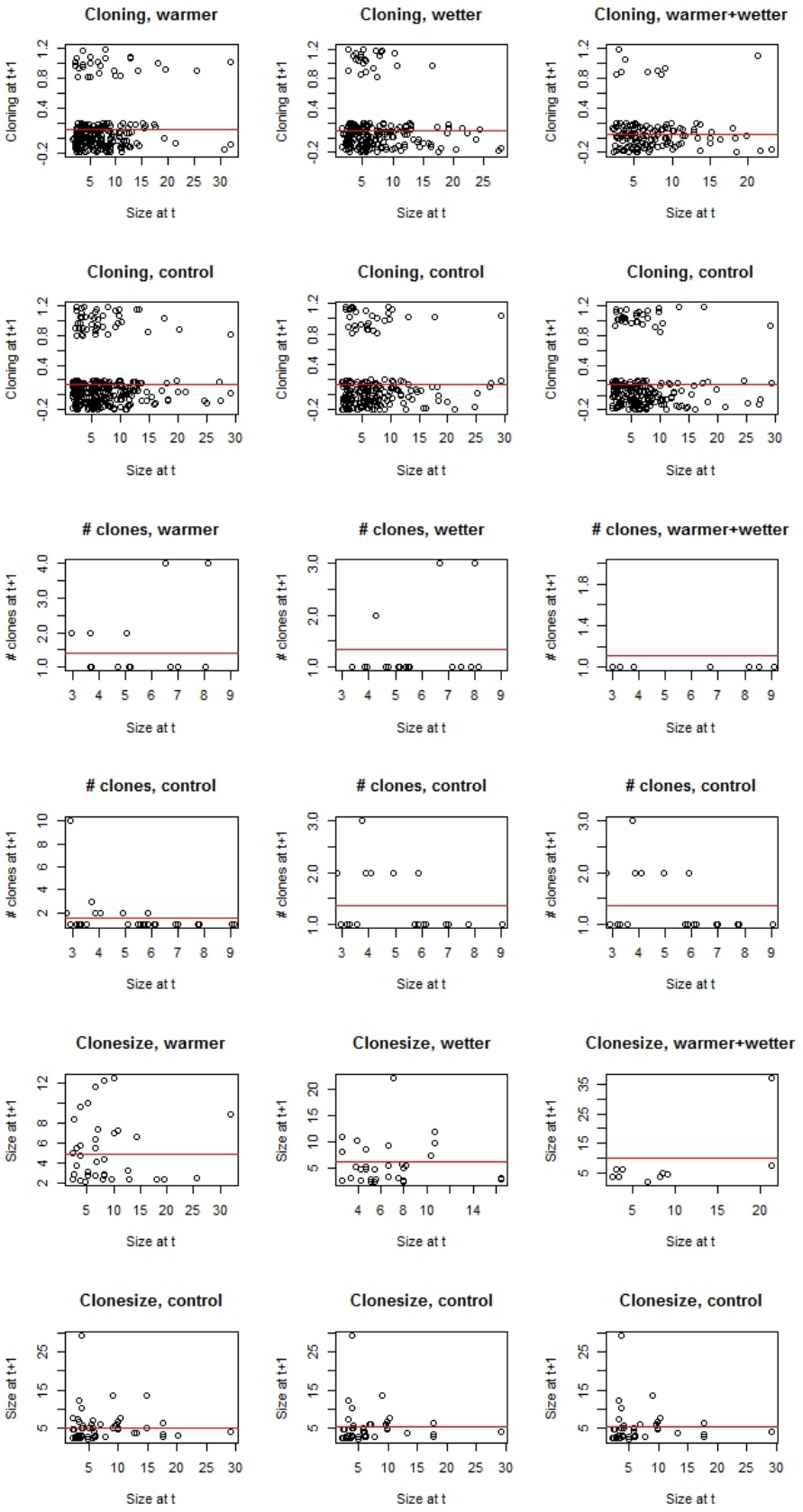
Supporting Methods Figure 2. Clonality models for climate transplants and their respective controls in *Viola biflora*. Black open circles represent the original data. Closed red circles represent sequential means.



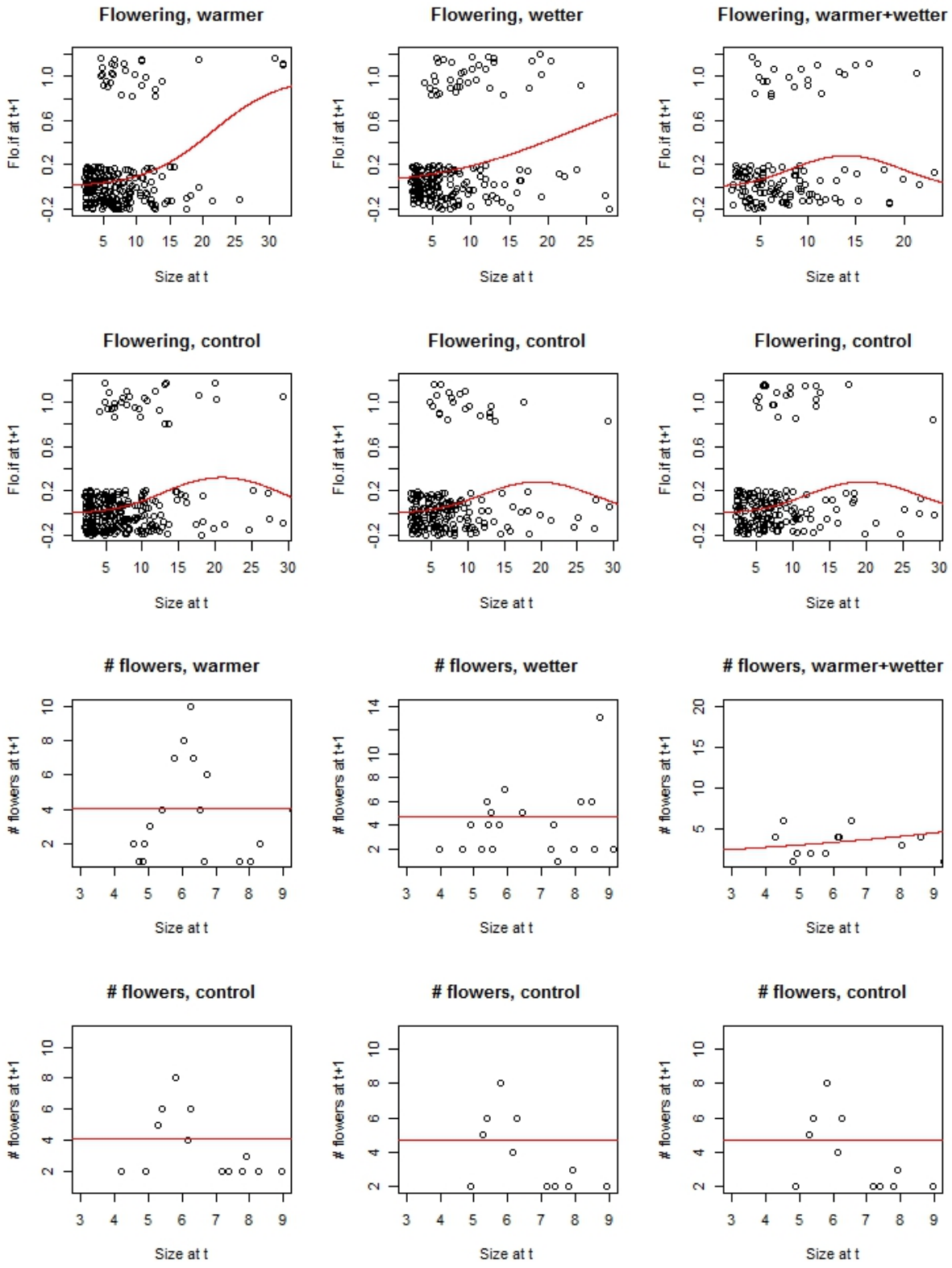
Supporting Methods Figure 3. Fecundity models for climate transplants and their respective controls in *Viola biflora*. Black open circles represent the original data. Closed red circles represent sequential means.



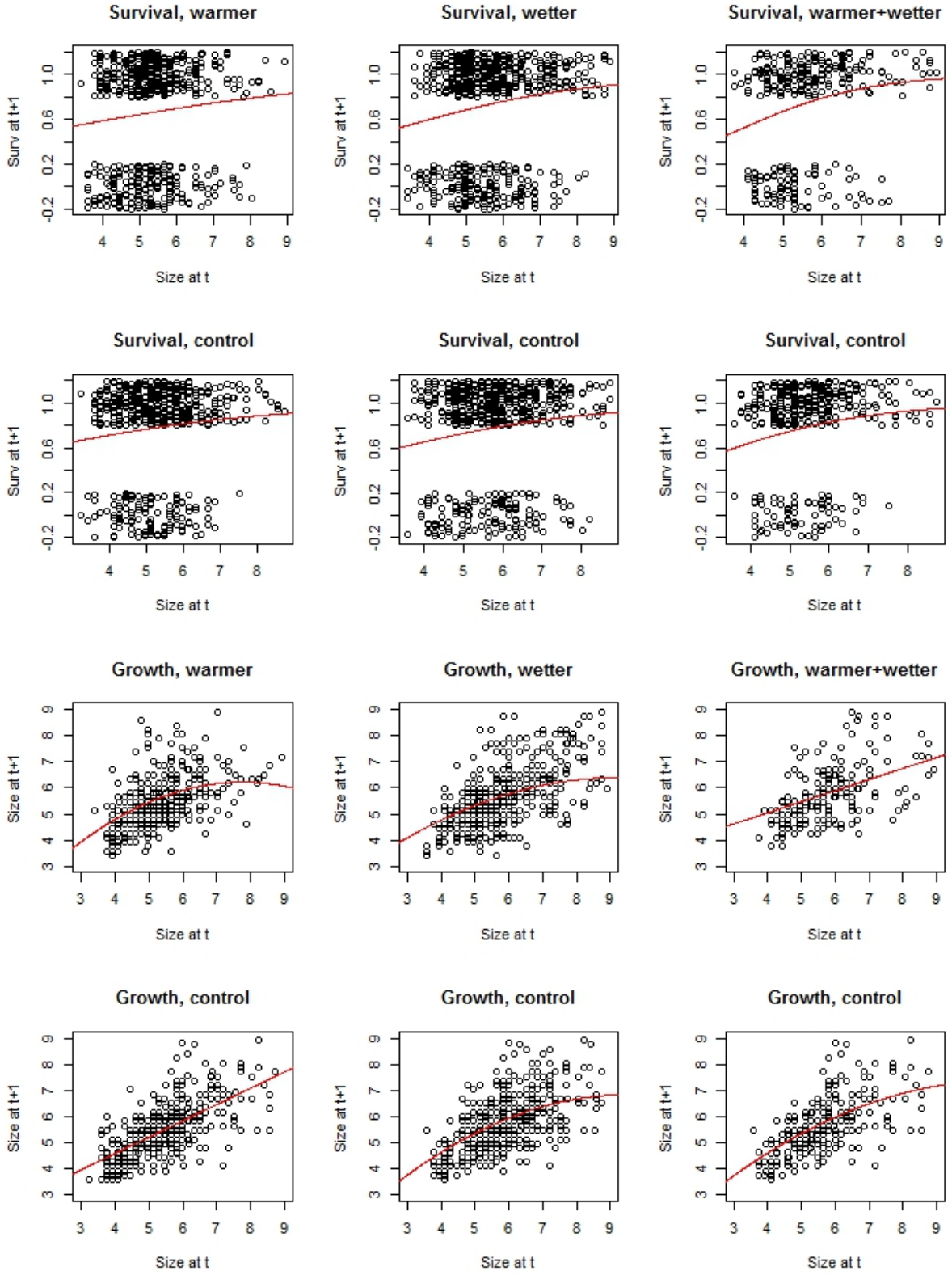
Supporting Methods Figure 4. Survival and growth models for climate transplants and their respective controls in *Viola palustris*. Black open circles represent the original data. Closed red circles represent sequential means.



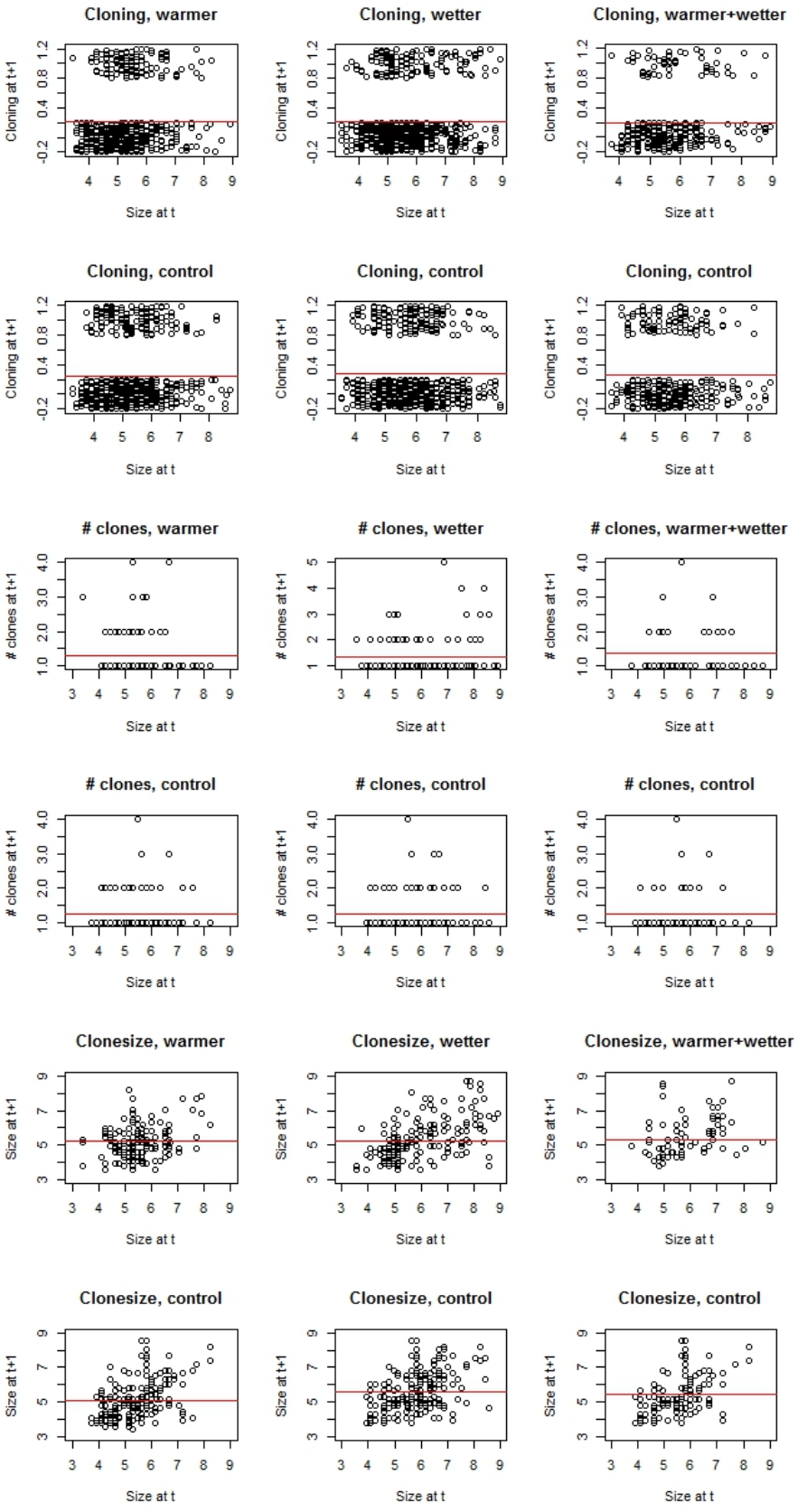
Supporting Methods Figure 5. Clonality models for climate transplants and their respective controls in *Viola palustris*. Black open circles represent the original data. Closed red circles represent sequential means.



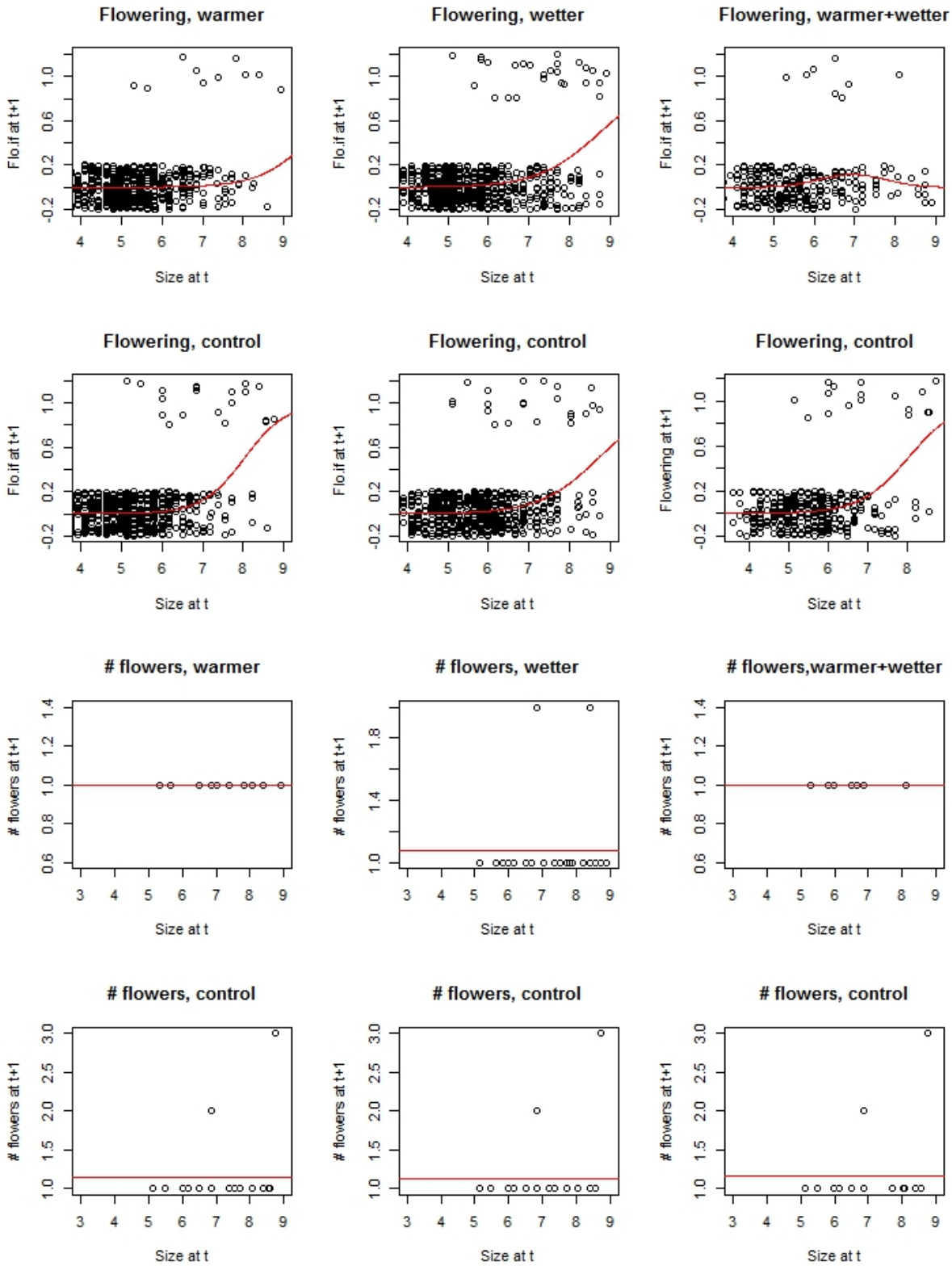
Supporting Methods Figure 6. Fecundity models for climate transplants and their respective controls in *Viola palustris*. Black open circles represent the original data. Closed red circles represent sequential means.



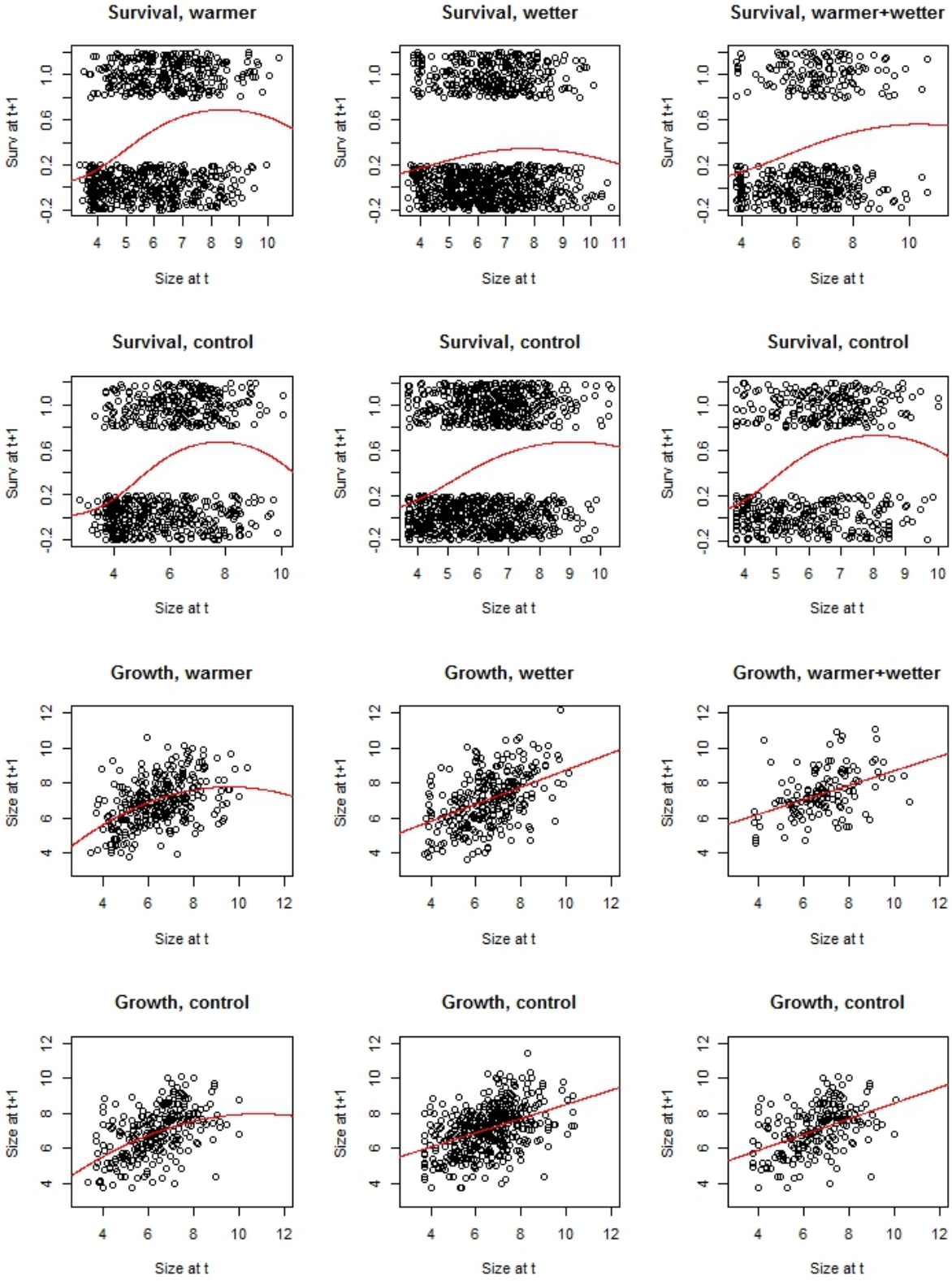
Supporting Methods Figure 7. Survival and growth models for climate transplants and their respective controls in *Veronica alpina*. Black open circles represent the original data. Closed red circles represent sequential means.



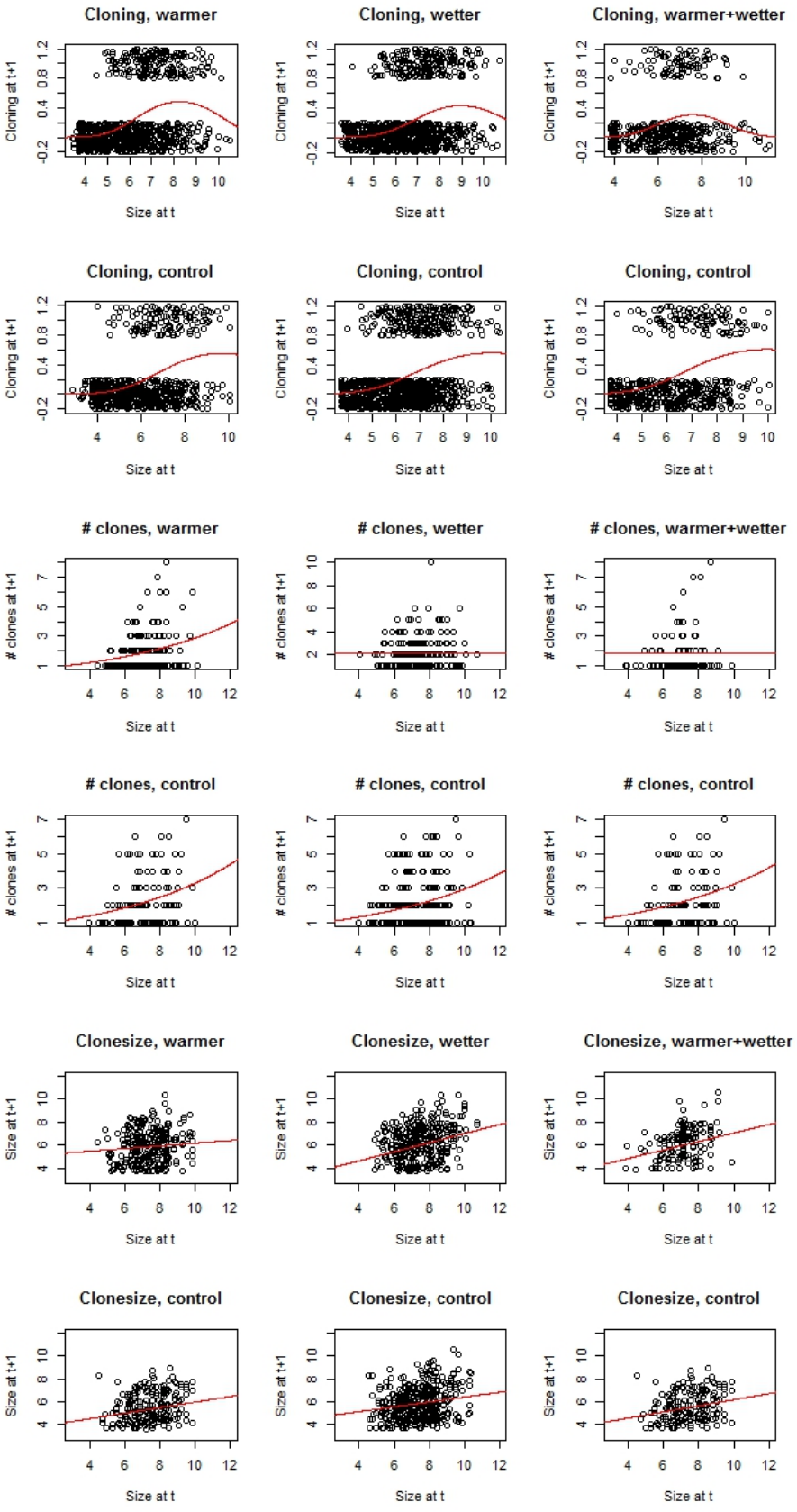
Supporting Methods Figure 8. Clonality models for climate transplants and their respective controls in *Veronica alpina*. Black open circles represent the original data. Closed red circles represent sequential means.



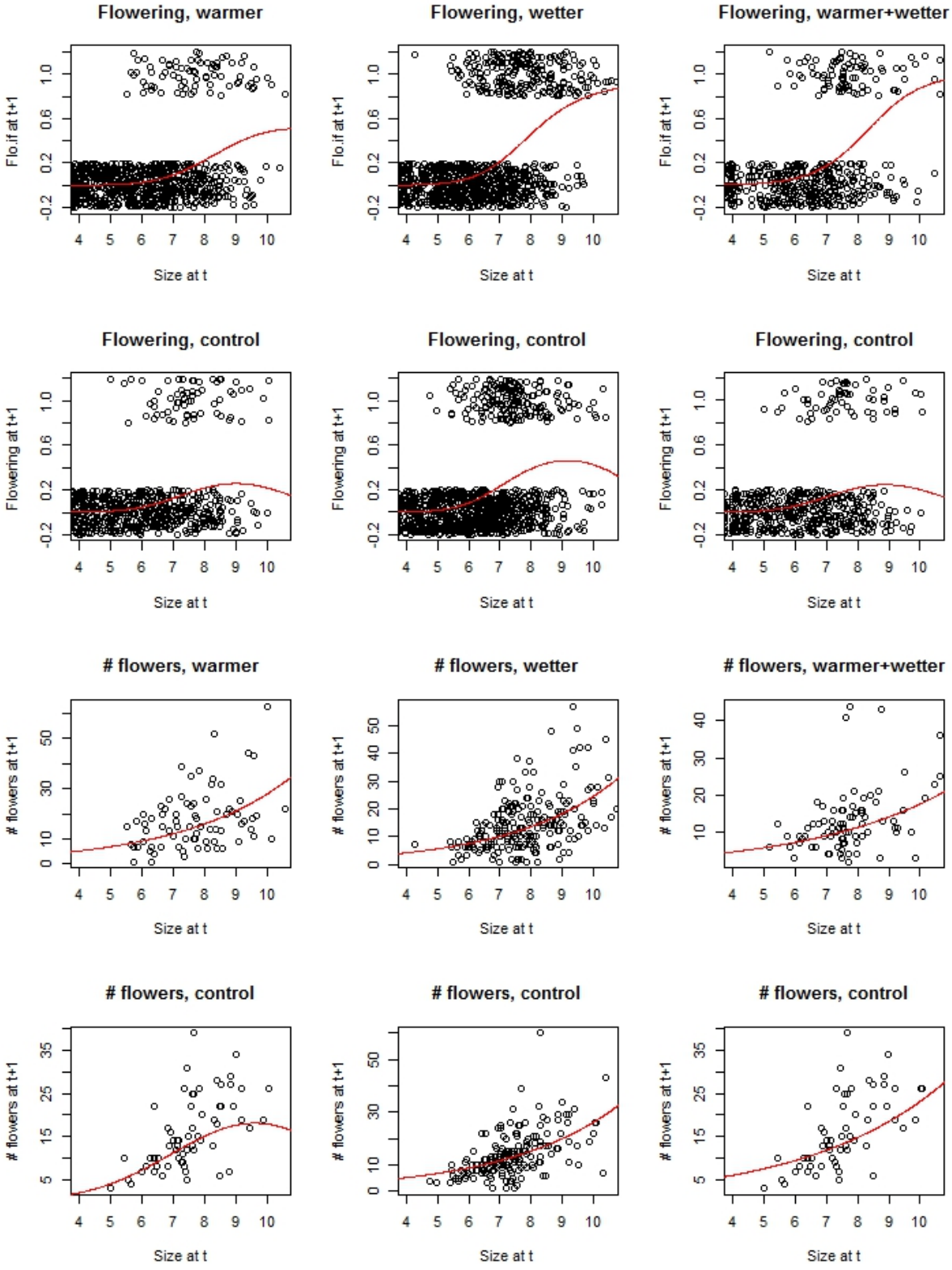
Supporting Methods Figure 9. Fecundity models for climate transplants and their respective controls in *Veronica alpina*. Black open circles represent the original data. Closed red circles represent sequential means.



Supporting Methods Figure 10. Survival and growth models for climate transplants and their respective controls in *Veronica officinalis*. Black open circles represent the original data. Closed red circles represent sequential means.



Supporting Methods Figure 11. Clonality models for climate transplants and their respective controls in *Veronica officinalis*. Black open circles represent the original data. Closed red circles represent sequential means.



Supporting Methods Figure 12. Fecundity models for climate transplants and their respective controls in *Veronica officinalis*. Black open circles represent the original data. Closed red circles represent sequential means.

Table S3. **Population growth rates (λ) for all study species in all treatments and controls.** Shown are (in this order) the 0.025, 0.5, and 0.975 quantiles for the 10 000 bootstrapped λ's in each respective control and transplant.

		Viola biflora	*Viola alpina*	*Veronica palustris*	*Veronica officinalis*
Population growth rate					
warmer	control	0.88 / 0.96 /1.04	1.05 / 1.13 / 1.22	1.05 / 1.11 / 1.17	0.97 / 1.14 / 1.31
	transplant	0.84 / 0.91 / 0.98	0.87 / 0.9 / 0.99	0.89 / 0.96 / 1.03	1.06 / 1.19 / 1.31
wetter	control	0.88 / 0.96 / 1.04	1.04 / 1.12 / 1.21	1.06 / 1.14 / 1.21	1.09 / 1.21 / 1.33
	transplant	1.02 / 1.09 / 1.17	0.94 / 1.02 / 1.11	0.95 / 1.02 / 1.09	0.68 / 0.8 / 0.93
warmer+wetter	control	0.88 / 0.96 / 1.04	1.04 / 1.12 / 1.21	1.06 / 1.15 / 1.24	1.1 / 1.3 / 1.5
	transplant	0.85 / 0.93 / 1	0.87 / 0.89 / 1.03	0.91 / 1.01 / 1.1	0.74 / 0.91 /1.09