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Life history evolution under climate change and its influence on the population dynamics of a long-lived plant

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Summary

1. One of the key components of an organism's life history is the delay of reproduction until it reaches or returns to an optimal size. While we know climate can influence vital rates that shape life-history strategies, it is also critical to understand the effects of climate change on rapid life history evolution, which might modify the influence of climate change on population dynamics.

2. We asked how realistic changes in temperature and precipitation influence vital rates, costs of reproduction, and ultimately, evolutionarily stable (ES) flowering size in a long-lived perennial plant, *Orchis purpurea*. We also explored how evolution of flowering size could influence population persistence under changing climate.

3. Our approach combined model selection methods to characterize climate dependence in vital rates, stochastic integral projection models to integrate vital rates into an estimate of fitness, and adaptive dynamics to identify ES flowering sizes.

4. Vital rates responded uniquely to seasonal temperature and precipitation, with the largest response in the size-dependent probability of flowering. The predicted ES flowering size closely matched that observed, and responded strongly to adjusting the frequencies of extreme climate years. For example, increasing the frequency of extreme drought conditions was predicted to favour smaller reproductive sizes (and hence a shorter reproductive delay), despite observation that smaller plants were less likely to flower in dry years. This apparent discrepancy stems from a smaller payoff to delaying reproduction due to lower costs of reproduction in dry years.

5. The model of stochastic population dynamics predicted long-term persistence of the focal populations, even under the most extreme climate scenarios, while incorporating rapid life history evolution into predictions reduced the sensitivity of population growth to changing climate.

6. *Synthesis*. Our results illustrate that long-lived organisms can exhibit complex demographic responses to changing climate regimes. Additionally, they highlight that long-term evolutionary responses may be in opposing directions from short-term plastic responses to climate and emphasize the need for demographic models to integrate ecological and evolutionary influences of climate across the life cycle.

Key-words: adaptive dynamics, evolutionarily stable strategy, flowering size, integral projection model, orchid, perennial plant, plant–climate interactions, reproductive delay, stochastic population growth

Introduction

Understanding life histories and the selection pressures that shape them within and across species is a fundamental goal of evolutionary ecology. One key component of the life history is the duration of the reproductive delay, that is, how long an organism waits to reproduce (Roff 1992; Metcalf, Rose & Rees 2003). Reproductive delays are shaped by the balance between demographic costs and benefits, as expressed through the vital rates of growth, reproduction and survival.

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In organisms with indeterminate growth, the delay is typically quantified in terms of the size at reproduction (Ernande, Dieckmann & Heino 2004; Metcalf *et al.* 2008; Miller *et al.* 2012). Demographic models provide a way to integrate the costs and benefits into measures of fitness, and thus to understand selection on reproductive delays and on life-history strategies in general (Rees & Rose 2002; Metcalf, Rose & Rees 2003; Metcalf & Pavard 2007; Metcalf *et al.* 2008; Rees & Ellner 2009; Williams 2009; Shefferson, Warren & Pulliam 2014).

The vital rates underlying demographic models are responsive to climate, with some more so than others (Pfister 1998; Morris *et al.* 2008; Ozgul *et al.* 2010; Smallegange, Deere & Coulson 2014). If climate is changing directionally, then vital rates influenced by climate are also subject to change, whether those responses are due to phenotypic plasticity or to adaptive evolution (Reed, Schindler & Waples 2011). If vital rates are changing, then it follows that the costs and benefits of alternative life-history strategies are also changing. For example, if environments that elevate the risk of mortality become more common, the payoff of delayed reproduction is reduced, selecting for smaller reproductive sizes (Reznick, Bryga & Endler 1990; Hutchings 2005; Rose, Louda & Rees 2005; Franks & Weis 2008). We are beginning to understand the influence of climate variation on the demography and population dynamics of perennial plants (Doak & Morris 2010; Dalgleish *et al.* 2011; Nicolè *et al.* 2011; Sletvold *et al.* 2013). We know much less about how these changes translate to selection on life-history strategies, although first principles suggest that they should.

Evolutionary responses to shifting climates have the potential to affect population dynamics. Therefore, predicting population dynamics under climate change may require that we account for life history evolution (Visser 2008; Ellner, Geber & Hairston 2011; Ohlberger *et al.* 2011). For example, selective harvesting of large fish selects for sexual maturity at smaller size and younger age, and these shifts in life history can lead to reductions in population growth (Ernande, Dieckmann & Heino 2004; Hutchings 2005), although this is not always the case (Kuparinen & Hutchings 2012). In plants, both phenotypically plastic and evolutionary responses to climate have been detected in multiple taxa and can occur rapidly (Franks, Weber & Aitken 2014). Whether evolutionary responses are sufficient and/or occur quickly enough to offset negative effects of shifting climates [‘evolutionary rescue’ (Gonzalez *et al.* 2013)] has yet to be resolved. More generally, studies that quantify both the influence of evolutionary processes and the ecological dynamics are still uncommon (Schoener 2011).

Predicting evolutionarily stable life-history strategies for populations in stochastic environments with climatic variability is challenging (Metcalf *et al.* 2008; Rees & Ellner 2009). It requires data to parameterize a set of vital rate functions that characterize the costs and benefits of the life history in a demographic framework, collected over a sufficient number of years to characterize the distribution of environmental variability. Explicitly quantifying the influence of climate on these vital rate functions adds a layer of complexity that is not commonly included in demographic models (Doak & Morris 2010; Dalgleish *et al.* 2011; Nicolè *et al.* 2011; Sletvold *et al.* 2013). However, understanding how populations of long-lived individuals that cannot move will respond to climate change due to both evolutionary and ecological processes is a critical step to better understand and predict population viability in the face of environmental change.

Our work focused on the orchid *Orchis purpurea*, a long-lived, iteroparous perennial plant, which like many perennials delays reproduction until it reaches a critical size. Previous studies showed that *O. purpurea* experiences a significant cost of reproduction, measured as a negative effect of flowering on individual growth (Jacquemyn, Brys & Jongejans 2010). The observed costs and benefits of reproduction explain the observed reproductive delay very well (Miller *et al.* 2012). Here, we build on these results to investigate the influence of climate on demographic vital rates – including the cost of reproduction – and hence evolutionarily stable (ES) flowering strategies. We further ask how evolutionary responses to climate change may influence population dynamics.

We integrated long-term demographic and climatic data with a combination of modelling approaches, including model selection methods to characterize climate dependence in vital rates, stochastic integral projection models to integrate multiple vital rates into an estimate of fitness, and, finally, adaptive dynamics to identify evolutionarily stable flowering strategies. Specifically, we addressed three questions: (i) How does variation in temperature and precipitation influence vital rates and vital rate trade-offs (costs of reproduction) in *Orchis purpurea*? (ii) How would realistic changes in temperature and precipitation affect the ES strategy for flowering size in *O. purpurea*? (iii) Would rapid life history evolution modify the response of population dynamics to climate change?

Materials and methods

STUDY SYSTEM

Orchis purpurea (Lady Orchid) is a long-lived iteroparous orchid (Rose 1948) that grows mainly in forests and calcareous grasslands. The core of its range is the Mediterranean region, where it is fairly common (Rose 1948). At the northern edge of its range in the UK, Belgium (where our focal populations are located) and the Netherlands (Kretzschmar, Eccarius & Dietrich 2007), the species is rare and endangered, with very few populations remaining (Jacquemyn *et al.* 2007). Changes in forest management (conversion of coppicing to high wood) and associated alterations in light conditions are the most important threats to its persistence. Data on *O. purpurea* demography were collected at two sites in eastern Belgium (Voeren) that were more than 1 km apart and where >25% of the incoming radiation reached the vegetation. In this region, the climate is temperate, with a mean annual temperature of 10.8 °C, and mean annual precipitation of 811 mm (1991–2012).

As in most *Orchis* species, the main perennating organ in *O. purpurea* is a tuber (strictly a rootstem tuber). Each year the tuber is wholly replaced by a new tuber, which gives rise to the above-ground plant in the following growing season. Although the old and new

tubers remain connected, the old tuber usually becomes completely exhausted and contributes little or nothing to the next year's growth. Leaves appear above-ground in early February and are fully developed in May, when the flowering stalk has also developed. Dormancy (i.e. the failure of above-ground parts to appear in a growing season and the reappearance of full-sized photosynthetic plants in subsequent seasons) is rarely observed: on average, ~1% of marked plants were dormant in each year (range: 0.4–2.4%) (Jacquemyn, Brys & Jongejans 2010; Miller *et al.* 2012).

Flowering in *O. purpurea* carries the demographic costs of reduced vegetative growth (Jacquemyn, Brys & Jongejans 2010; Miller *et al.* 2012). Flowers are nectarless, pollinated by generalist pollinators and fruit set is generally low, varying between 5 and 20% of flowers (Jacquemyn, Brys & Honnay 2009; Jacquemyn & Brys 2010). Seed capsules ripen by the end of June, followed by dehiscence and seed dispersal in August. From mid-August onwards, no green parts are observed above-ground.

DEMOGRAPHIC DATA

Between 2003 and 2013, both study sites were visited at least three times per year. During this period, a total of 697 individuals were monitored. In early March, when the vegetation was short and seedlings were easily observed, sites were visited to locate previously mapped individuals and to map new recruits. Each individual was tagged with a plastic tag. Sites were visited for a second time in early May, when all plants were fully grown and flowering. At that time, the size of each plant was recorded and new plants were tagged and added to the data set. For each individual, we counted the number of leaves and measured the length (L) and width (W) of each leaf to the nearest mm. Total leaf area of each plant was calculated by summing the leaf area, calculated for each individual leaf as $A = \frac{\pi LW}{4}$, of all leaves. If plants were flowering, we also counted the number of flowers. At the beginning of July, all sites were visited for a third time to count the number of fruits produced by each flowering stalk. At each site, seed sowing experiments were conducted to determine the seed germination percentage (Rasmussen & Whigham 1993). To do so, at each site 20 seed packages containing about 150 seeds were buried into the soil and retrieved 2 years later. For each package, the number of germinated seeds was counted and averaged across seed packages. Because it was impossible to repeat the germination experiments over time, seed germination did not vary across years in the model.

INTEGRAL PROJECTION MODEL

Here, we briefly describe the basic IPM for *O. purpurea* (see also Miller *et al.* 2012); later, we describe modifications that made the model stochastic and climate-dependent. The orchid IPM consists of a continuously size-structured population of above-ground plants [$N(x)$] plus three discrete below-ground stages: protocorms (P), tubers (T) and dormant plants (D).

An IPM 'kernel' is composed of demographic functions that characterize all possible transitions from size in one year (x) to size in the next (y). These transitions depend on the probability of growth from size x to size y [$\gamma(y, x)$], probability of survival [$\phi(x)$], probability of flowering [$\beta(x)$], number of flowers produced [$\omega(x)$] and probability of dormancy [$\mu(x)$], all based on size (x), the natural logarithm of total leaf area, $\log_e(\text{cm}^2)$. For more details on the structure of the IPM and the transitions between continuous and discrete stages, see Appendix S1 in the Supporting Information.

ESTIMATING SIZE- AND CLIMATE-DEPENDENT VITAL RATES

We used the long-term demographic data to examine the effects of climate on the size-dependent vital rate functions. Daily climatic data were collected between 1 January 1990 and 31 July 2013 at the nearest weather station (Ransberg, 20 km from sites), where maximum, minimum and average daily temperature (°C) and daily rainfall (mm day^{-1}) were recorded. To connect climate variability to orchid demography, we divided the calendar year into four seasons, reflecting different phenological events in the life cycle of *O. purpurea*: spring (February 1–May 15) covers the period from early growth to flowering; summer (May 16–August 15) covers the period from flowering and fruit set to senescence of above-ground parts; autumn (August 16–October 31) covers the period in which no green parts occur above-ground; and winter (November 1–January 31) covers the period of emergence. For each period (starting with summer 1990 and ending with spring 2013), we calculated the mean average temperature, mean daily precipitation and proportion of days with any precipitation (proportion wet days). We used two measures of precipitation because precipitation in this region is expected to change in one or both of two ways: the frequency of precipitation events (indicated by the proportion wet days) and the total amount of rainfall in a given season (indicated by mean daily precipitation) (van Vliet *et al.* 2012). We also calculated the same climate metrics for a growing year that matched the timing of the monitoring period and transition year: May 16, year t – May 15, year t+1 (transition year reported in the paper is t+1). Thus, we could compare the relative influence of seasonal effects of climate to annual effects for each vital rate function.

In estimating the effects of climate on vital rates, our general approach was to identify climate variables that were correlated with interannual variation in demography, considering climate variables in both the current and the previous year. We then used a model selection approach to choose one or, at most, two climate variables that best explained demographic performance (for details, see Appendix S2 in Supporting Information). Our approach closely follows that of Dalgleish *et al.* (2011). Data from both sites were pooled together as previous analyses found no effect of site on vital rates (Miller *et al.* 2012).

All models were fit in R 3.0.1 (R Core Development Team 2013); we used the lm and glm functions for the fixed-effects models, and lmer and glmer in package LME4 (Bates *et al.* 2013) for the mixed models (see Appendix S2).

STOCHASTIC POPULATION GROWTH

We used numerical simulations to calculate the stochastic population growth rate (λ_s) for the recent (1991–2013) climate regime and for a range of possible future climate scenarios. First, for the observed recent climate, calendar year was assigned randomly to each year of the simulation with equal probability, and the climate values observed in the associated transition year (May t-1 – May t) were applied to the vital rate functions. In addition, random year-to-year variation was included for each vital rate function by drawing from the fitted random effects. By drawing years instead of climate values, this approach retains correlations among climate variables and vital rates without having to model correlations explicitly. Population dynamics were simulated for 50 000 years (Rees & Ellner 2009; Hunter *et al.* 2010). We estimated λ_s as the geometric mean of the annual growth rates (Rees & Ellner 2009).

Secondly, to model the influence of shifting climates, we followed similar methodology but instead of drawing climate years with equal

probability, we sampled years with 'extreme' climate (unusually hot, cold, wet or dry) disproportionately to their actual occurrence, as these may become more or less likely under climate change (Karl & Trenberth 2003; van Vliet *et al.* 2012). As above, by altering the frequency of climate-year types and not individual climate variables, our approach has the advantage of retaining correlations among climate variables across years. For each climate variable that was included in the vital rate models, we identified 'extreme' years as those in which the climate variable was greater or less than 1 standard deviation of the mean (Fig. S1 in Supporting Information). For example, in the dry summer scenario (years with summer precipitation ≥1 SD below the mean), climate variables from 1991, 1995 and 1996 were drawn with increasing probability among the 23 possible years. The number of 'extreme years' varied from 2 to 4 across climate scenarios. We opted against a more extreme criterion (e.g. 2 SD of the mean) because it limited the number of years from which we could sample such that high- or low-frequency climate scenarios were dominated by single years. Our approach is therefore conservative in that 'extreme' years were not drastically different than average. We varied the frequency of extreme year types from 0.25 to 0.75 in intervals of 0.125. We chose these frequencies as cut-offs, because the variances of many climate variables began to drop considerably outside this interval (Fig. S2 in Supporting Information). We aimed to model trends in mean climate keeping variance roughly constant, as variance itself can affect λ_s (Tuljapurkar 1982).

EVOLUTIONARILY STABLE STRATEGIES FOR FLOWERING SIZE UNDER VARYING CLIMATES

We identified evolutionarily stable (ES) strategies for the size at flowering across a range of climate scenarios, given observed trade-offs between growth and reproduction, using adaptive dynamics, a powerful approach for understanding trait evolution in stochastic environments (Childs *et al.* 2004; Metcalf *et al.* 2008; Rees & Ellner 2009). Adaptive dynamics provides a framework for quantifying ES strategies based on the criterion of 'invasibility'. This approach considers whether a rare mutant flowering strategy can invade an environment dominated by a different, resident strategy. The rare mutant will generally be at a disadvantage due to density-dependent competitive effects of the dominant, resident strategy and should be unable to invade unless its strategy provides a fitness advantage. The success or failure of the mutant invasion is quantified by its stochastic growth rate in the face of competition with the resident; successful invasion requires that $\lambda_s > 1$ for the rare mutant. An ES strategy is 'unbeatable': it can invade all other strategies as a rare mutant but cannot be invaded as a dominant resident.

The strategy of interest for our analysis is the median flowering size, that is the size at which the probability of flowering equals 0.5. For a simple size-dependent binomial flowering function, median flowering size is given by $-c_0/c_1$ and is thus determined by both the intercept (c_0) and the slope with respect to size (c_1) (Table 1; note that our flowering function has additional coefficients for climate effects). Evolutionary optimization of the slope c_1 results in a step function such that the probability of flowering jumps abruptly from 0 to 1 at a threshold size, which is widely considered to be unrealistic (Childs *et al.* 2003; Rees & Ellner 2009). Therefore, following previous studies (Hesse, Rees & Müller-Schärer 2008; Metcalf *et al.* 2008; Miller *et al.* 2012), we define the flowering strategy as the intercept (c_0), which we allow to vary, while holding the slope (c_1) at its fitted value. Mutants and residents therefore differ only in c_0. Lesser or greater values of c_0 correspond to a smaller or larger median size at the onset of flowering, respectively.

A central premise of the adaptive dynamics approach is that flowering strategies can affect each other's fitness through density-dependent competition. Implementing this approach therefore required that we quantify the strength of density dependence for *O. purpurea*. Given the often wide spacing between established plants, we assume that competition for suitable regeneration sites is stronger than resource competition among established plants and focus on regeneration as the transition sensitive to density. We quantified the strength of this type of density dependence using the observed relationship between seed production and recruitment.

In the absence of regeneration site limitation, there should be a positive relationship between seed production and subsequent seedling recruitment. By contrast, if most suitable sites are saturated, seedling recruitment should be roughly constant, regardless of how many propagules are produced. In *O. purpurea*, recruits must pass through the protocorm and tuber stages before they can be detected as seedlings. Thus, there is a three-year lag between the production of a seed and its detection as a seedling. In the absence of density dependence, there should be a positive relationship between seed production in year t-3 and seedling recruitment in year t. We tested this relationship using our long-term census data. For each of the two sites in each year, we multiplied the total fruits produced across all flowering plants by the mean number of seeds per fruit to generate an estimate of the total seeds produced. Our demographic census provided direct estimates of the number of seedlings at each site in each year. We pooled pairs of $\text{seeds}_{t\text{-}3}/\text{seedlings}_t$ across the two sites for a total of 11 observations (six at site 1 and five at site 2) and used Pearson's r to test for a relationship. We found that seed production and seedling recruitment were uncorrelated ($r = 0.29$, $t_9 = 0.92$, $P = 0.37$), suggesting that availability of suitable sites limits recruitment in a density-dependent manner. We do not know exactly where in the life cycle between seeds and seedlings density dependence operates. We therefore combined these transitions into a single density-dependent process, where the number of seedlings in year t was defined as a saturating function of the number of seeds produced in t-3 (Fig. S3 in Supporting Information). We used maximum likelihood to fit a saturating, Michaelis–Menton-type function to the data (Fig. S3) that was then used in the adaptive dynamics to impose density dependence.

Having specified the density-dependent environment, we estimated the ES flowering strategy, following the methods of Metcalf *et al.* (2008), for the recent climate regime and for a range of possible future climate scenarios. First, we sampled climate years from the assigned distribution, following methods described above. We then ran simulations in which we tested the invasibility of a range of resident flowering strategies (c_0) by the same range of invader strategies. For each combination of resident and invader strategies, we quantified the stochastic growth rate of the invader introduced at low density in an environment saturated by the resident strategy and subject to the assigned climate regime. We assume that, because it is rare, the invader does not contribute to density dependence; rather, density dependence is set exclusively by the resident strategy. Thus, the invader's per-seed probability of recruitment declined with the total density of seeds produced by the resident but not by the invader itself. We estimated the stochastic growth rate of the invader over 50 000 iterations, using the same sequence of climate and random year effects experienced by the resident, such that all but the flowering strategy was equal between resident and invader. If the invader's stochastic growth rate was positive, then it was able to invade the resident strategy. For a given climate regime, the results can be summarized in a pairwise invasibility plot (PIP) showing whether or not the rare mutant strategy can invade the resident strategy. We identified the 'unbeatable'

Table 1. Best-fit vital rate functions and coefficients used in integral projection model

Vital rate	Climate variables in best-fit function	Best-fit function	Parameter estimates	*D*
Growth (n = 3198; n = 1254 (Reproductive); n = 1867 (Vegetative)	Winter temperature (1-year lag) Summer precipitation (1-year lag) Summer precipitation (1-year lag) × flowering	$y_R = a_0 + a_1x + a_2{*}sum.ppt.lag1 + a_3{*}wint.T.lag1 + a_4{*}\text{fruits} + \varepsilon_1$ $y_V = b_0 + b_1x + b_2{*}sum.ppt.lag1 + b_3{*}wint.T.lag1 + \varepsilon_2$	$a_0 \sim \mathcal{N}(-0.221, 0.0178)$, $a_1 = 0.963$, $a_2 = 0.0769$, $a_3 = 0.0535$, $a_4 = -0.110$, $\varepsilon_1 \sim \mathcal{N}(0, 0.314)$ $b_0 \sim \mathcal{N}(0.435, 0.0390)$, $b_1 = 0.830$, $b_2 = 0.131$, $b_3 = 0.061$, $\varepsilon_2 \sim \mathcal{N}(0, 0.530)$	0.061
Probability of flowering (n = 3693)	Spring precipitation (1-year lag) Spring precipitation (1-year lag) × size Winter precipitation (no lag)	$\beta(x) = logit(c_0 + c_2{*}spr.ppt.lag1 + c_3{*}wint.ppt.nolag + (c_1{+}c_4{*}spr.ppt.lag1)x)$	$c_0 \sim \mathcal{N}(-8.150, 0.811)$, $c_1 = 0.452$, $c_2 = -8.033$, $c_3 = 1.541$, $c_4 = 1.875$	0.098
Number of flowers (n = 1446)	Year average temperature (no lag)	$\omega(x) = d_0 + d_1x + d_2{*}yr.T.nolag$	$d_0 \sim \mathcal{N}(-20.03, 2.224)$, $d_1 = 16.193$, $d_2 = -2.62$	0.046
Fruit set (fruits:flower) (n = 1445)	No climate effect	$\upsilon = logit(f_0)$	$f_0 \sim \mathcal{N}(-2.251, 0.433)$	NA
Recruit size (n = 396)	Spring precipitation (1-year lag)	$\eta_S = g_0 + g_1{*}spr.ppt.lag1 + \varepsilon_3$	$g_0 \sim \mathcal{N}(1.361, 0.225)$, $g_1 = 0.631$, $\varepsilon_3 = \mathcal{N}(0, 0.834)$	0.065
Survival (n = 3350)	No climate effect	$\phi(x) = logit(h_0 + h_1x)$	$h_0 = 1.224$, $h_1 = 0.532$	NA
Dormancy (n = 3350)	No climate effect	$\mu(x) = logit(j_0 + j_1x)$	$j_0 = \mathcal{N}(-5.804, 0.413)$, $j_1 = 0.271$	NA

For all functions, plant size [log(leaf area (cm^2)] in year t is indicated by x, and by y in year t+1. D is a measure of proportional reduction in deviance as a measure of the contribution of the climate variable(s) to explaining variation in each vital rate (Appendix S2). $\mathcal{N}$ (μ, σ) is a normal distribution with mean μ and standard deviation σ (among year variation). Logit is the logistic function, where $logit(k) = e^k/(1+e^k)$. See Table S2 for remaining IPM parameters.

flowering intercept (c_0*) strategy across all climate scenarios. For the recent climate scenario, we compared the predicted ES strategy to our empirical estimate for the intercept of the flowering function. To compare the ES strategy across climate scenarios, we compared median flowering sizes, as spring and winter precipitation also influenced the probability of flowering (c_2, c_3, c_4 in Table 1). That is, at each climate frequency, we calculated the median flowering size based on the expected adaptive responses (c_0*) plus the influence of spring and winter precipitation on flowering size, which can be interpreted as plastic responses to current climate.

Finally, we asked how rapid life history evolution could modify population dynamics under climate change. To do this, we reran simulations to estimate the stochastic population growth rate (λ_s) across climate scenarios (see 'Stochastic Population Growth'), this time substituting the flowering intercept estimated from the data with the predicted ES strategy c_0*. We assume here that orchids can perfectly and instantaneously match the predicted ES strategy as climate shifts. In nature, low trait heritabilities, insufficient genetic variation and lagged responses due to longevity and life cycle complexity would all dampen the evolutionary responses of flowering strategies. We therefore interpret our approach as an upper bound on the influence of rapid life history evolution on population dynamics.

Results

VITAL RATE FUNCTIONS AND CLIMATE

Most vital rates varied significantly across years in ways that corresponded to climatic variables, but the magnitudes of their responses differed (Table 1, Fig. 1; see also Table S1 in Supporting Information for model selection results). In general, vital rates related to reproduction and recruitment were more strongly climate-dependent than growth (Fig. 1). Only in the cases of survival and dormancy were there no significant inter-annual variation and hence no detectable influence of climate.

The probability of flowering was dependent on two climate drivers: a wet spring in the previous year and a dry winter in the current year significantly increased the size-dependent probability of flowering in the current year (Table 1, Fig. 1c, d; see also Table S1). Spring precipitation increased both the median flowering size (significant effect on intercept) and the size dependence of the relationship (significant size × spring precipitation interaction). Thus, in the year following a dry spring, plants were less likely to flower than in the year following a wet spring, and this was especially so for larger plants (Fig. 1d). These climate effects collectively led to large differences in median flowering size (at which plants have a 50% probability of flowering) between the most extreme years. For example, the predicted median flowering size was more than two times as large following the driest spring compared to the wettest spring (302.4 cm² vs. 129.3 cm²).

Warm years negatively affected the number of flowers produced per plant equally across sizes (significant effect on intercept) (Fig. 1e). Finally, the size of new recruits was significantly dependent on spring precipitation in the previous year (Fig. 1f). Following wet springs, recruits were, on average, more than 2.5 times larger than in years following dry springs (mean sizes: 17.1 and 6.5 cm², respectively; Fig. 1f).

Plant growth responded most strongly to two climate drivers, winter temperature and summer precipitation, and these effects were lagged by one year. Warmer winters and wetter summers led to, on average, greater increases in size in subsequent years (Fig. 1a,b, and Table 1). Flowering plants followed a slower growth trajectory than non-flowering plants due to a cost of reproduction (Fig. 1 a,b). Climate modified the cost of reproduction, as indicated by the significant flowering × summer precipitation interaction: the growth of vegetative plants was more strongly reduced by dry summers than that of flowering plants, leading to a smaller difference between vegetative and flowering plants and hence a lower cost of flowering (Fig. 1b inset). By contrast, wet summers disproportionately benefitted vegetative plants, amplifying the cost.

ES STRATEGY FOR FLOWERING SIZE IN STOCHASTIC AND CLIMATE VARYING ENVIRONMENTS

The ES flowering strategy in a variable environment, with observed climate years (1991–2013) drawn with equal probability, is shown in Fig. 2. In this pairwise invasibility plot, the shaded areas indicate that the resident flowering strategy resists invasion by the mutant, while the white areas indicate that the mutant strategy can invade the resident. The diagonal, the line from the lower left to the top right where the grey area meets the white area, indicates equivalence of the resident and mutant strategies. The intersection of diagonal with areas of mutant invasion (white) gives the ES strategy, the 'unbeatable' phenotype than can invade all others but not be invaded. In Fig. 2, we have transformed the ES intercept into

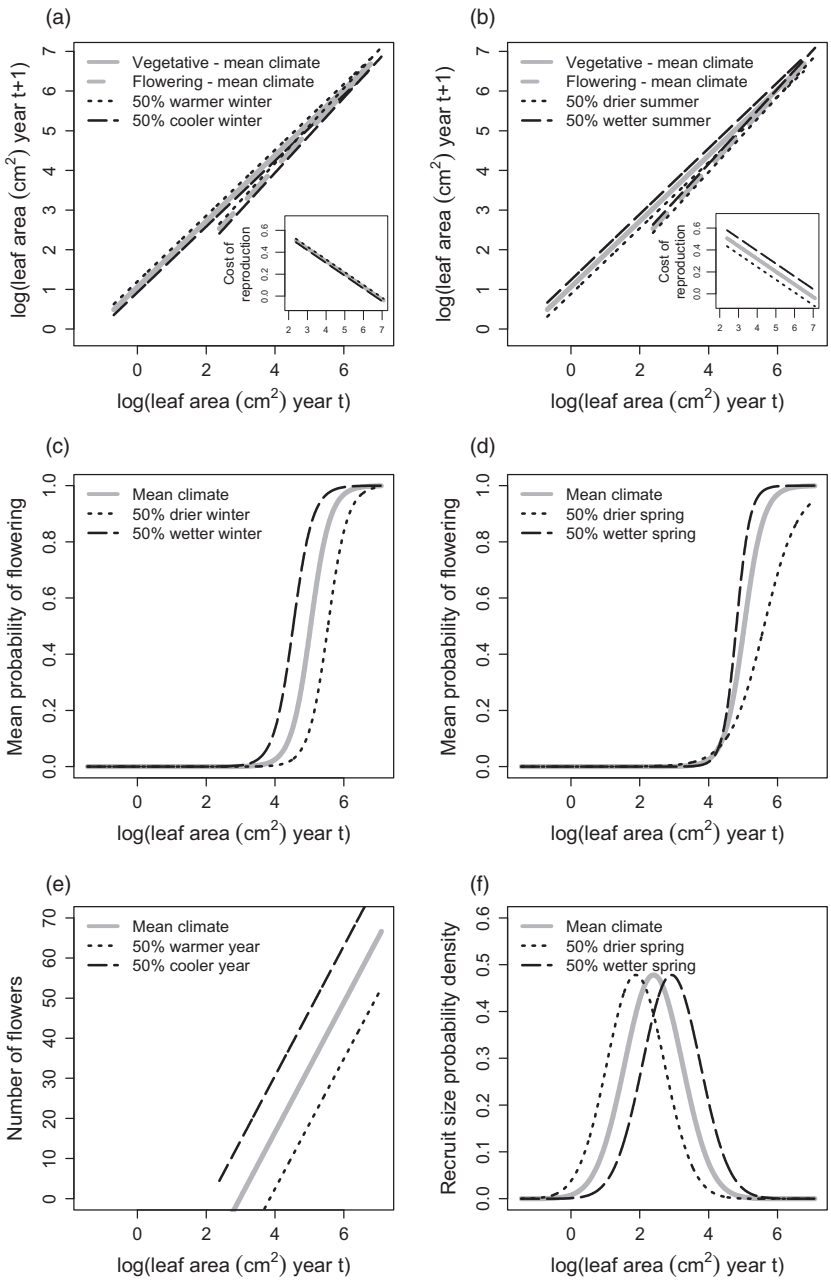

Fig. 1. Influence of climate on fitted relationships between size [log(leaf area (cm^2)] and vital rates. (a, b) Influence of winter temperature (a) and summer precipitation (b) on growth of vegetative and flowering plants. Insets in Panels a and b show climate-dependent costs of reproduction, quantified for every size (year *t*) as size (year *t*+1) achieved by vegetative plant – size (year *t*+1) achieved by flowering plant [units are log(leaf area (cm^2)]. (c, d) Influence of spring (c) and winter precipitation (d) on the relationship between size and the probability of flowering. (e) Influence of average yearly temperature on the relationship between plant size and number of flowers. (f) Influence of spring precipitation on recruit size distribution. In all panels, grey lines show best-fit model predictions (see Table 1) for mean climate values (1991–2013). Dashed and dotted black lines show predictions for 50% perturbations to climate values. For growth (a and b) and probability of flowering (c and d), where two climate variables influenced the vital rate, one climate variable is held at the mean to demonstrate the influence of the other. Observed data points for all vital rates can be viewed in Miller *et al.* (2012).

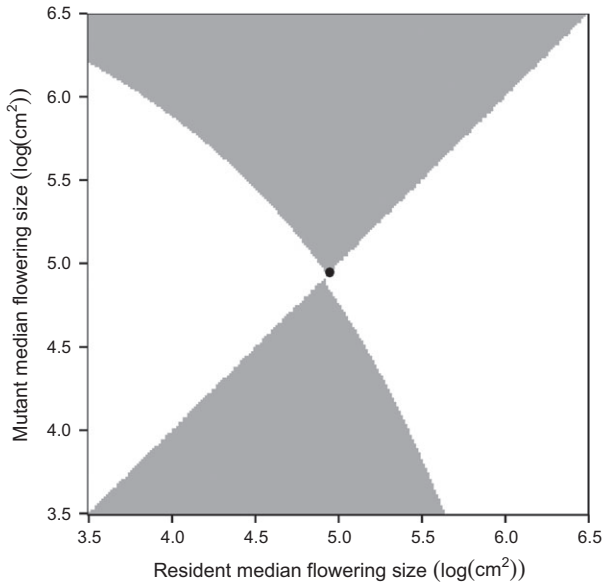

Fig. 2. Pairwise invasibility plot for median flowering size for observed climate years (1991–2013). White and shaded areas show combinations for resident and mutant strategies for which invaders can (white) versus cannot (shaded) invade the resident. The observed median flowering size during the study is indicated by the filled point.

the median flowering size for easier visualization (the PIP for c_0 is presented in Fig. S4 in Supporting Information). The ES intercept for the probability of flowering (c_0*) was −7.975, in good agreement with the observed intercept (c_0 = −8.150, Table 1), although the confidence intervals on the observed intercept are large (Fig. S4). This suggests that the adaptive dynamics model effectively captures the trade-offs associated with alternative flowering strategies.

In general, we found that increasing the frequency of wet and warm climates selected for larger median flowering sizes, thus imposing an increasing delay on flowering (Fig. 3). In contrast, increasing the frequency of drier seasons or colder winter or years led to decreases in median flowering size, and thus a higher probability of smaller plants flowering (Fig. 3). Surprisingly, results for ES flowering size under climate scenarios for spring and winter precipitation were opposite to the plastic responses observed during the study. That is, the demographic data showed that orchids exhibited a greater median flowering size following dry springs or winters (Fig. 1c,d), yet increasing the frequency of these conditions selected for a smaller flowering size (Fig. 3).

STOCHASTIC POPULATION DYNAMICS UNDER CLIMATE CHANGE

Stochastic simulations revealed how shifting the frequency of extreme climates affected stochastic population growth (Fig. 4). In general, the responses of λ_s were surprisingly consistent across different types of climate change, despite different responses at the level of individual vital rates (Fig. 1). Increasing seasonal precipitation by increasing the frequency of unusually wet springs, summers or winters led to increasing λ_s, and the converse was also true, that is decreasing seasonal precipitation led to decreasing λ_s (Fig. 4, left column). However, the influences of dry or wet climate on λ_s were not equal across seasons (wetter summers led to greater positive effects on λ_s than wetter winters), nor were the effects symmetric. For example, increasing the frequency of wet winters had a smaller positive effect on λ_s than the negative effect of increasing the frequency of dry winters. These asymmetries arise from the asymmetric distributions of the observed climate variables; some variables had extremes further from the mean in one direction than the other (Fig. S1). Similarly for temperature, increasing the frequency of warm winters or of warm years led to a projection of increasing λ_s (Fig. 4, left column). As warm years tended to have warm winters, the positive effect of warm winters on growth of vegetative and flowering plants also contributed to increasing λ_s in warm years. Even for the most extreme climate scenarios, the stochastic population growth rate was always >1.

We found that in general, rapid adaptation (plants perfectly matching the ES strategy for a given climate scenario) made the stochastic population growth rate less sensitive to climate change compared to simulations with no evolution-

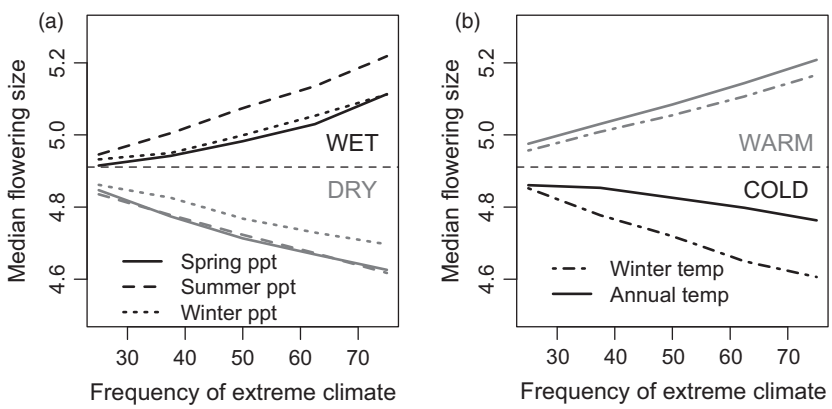

Fig. 3. Influence of climate on evolutionarily stable (ES) strategy for flowering size, expressed as the median flowering size [log (leaf area (cm^2)] for climate scenarios where the frequencies of (a) spring, summer or winter precipitation (ppt), or (b) winter or annual temperature (temp) were adjusted. Horizontal dashed line indicates ES strategy when all climate years have an equal probability of being drawn.

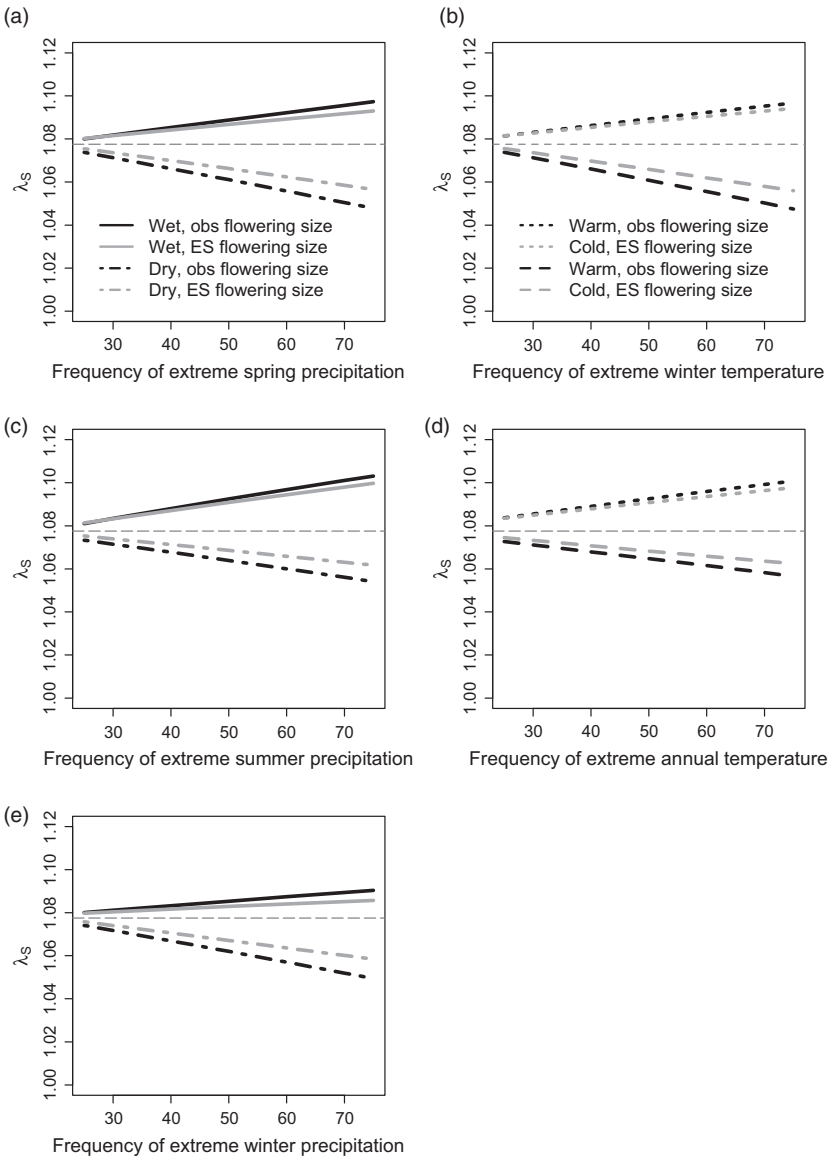

Fig. 4. Influence of simulated climate scenarios and rapid evolution on λ_s for a population at the currently observed flowering size (black lines) or one that perfectly tracks the evolutionarily stable (ES) flowering size over changing climate frequencies (grey lines) for (a) spring, (c) summer, and (e) winter precipitation; (b) winter and (d) annual temperature. For each of the climate variables that significantly influenced a vital rate function, two climate scenarios were created that increased the frequency of years when the climate variable was greater or less than one standard deviation of the mean. Horizontal dashed lines show λ_s for the observed mean climate values (1991–2013).

ary response (Fig. 4, contrast black lines (no evolutionary response) to grey lines (plants perfectly match ES flowering strategy). In particular, tracking the ES flowering strategy buffered population dynamics against the negative effects of increasingly cold or dry climates.

Discussion

To fully examine the influence of climate variation on population and evolutionary dynamics requires the following: (i) understanding the influence of climate variables on vital rates, (ii) determining how changing climate has the potential to select for changes in phenotype and (iii) predicting the potential for evolution to change the growth rate of a population. For the long-lived perennial orchid, *O. purpurea*, we found that most, but not all, vital rates were influenced by seasonal temperature or precipitation, but each vital rate was influenced by a different climate variable. Our results suggest that changes in temperature or precipitation regimes have the potential to shape the length of the delay in reproduction, as measured by the effect of climate variables on the evolutionarily stable (ES) flowering size (where a larger flowering size corresponds to a longer reproductive delay). Here, we discuss the implications of our results for the *O. purpurea* populations we studied, and more generally, how our study is relevant for understanding the interaction between ecological and evolutionary processes in the context of changing climates.

We found that each vital rate responded differently to seasonal temperature and precipitation. In general, we found that vital rates that have large contributions to population growth (growth and survival; see sensitivity analyses in Jacquemyn, Brys & Jongejans 2010) are more likely to be buffered from environmental variation, as expected (Pfister 1998). The vital rate-by-vital rate complexity of climate influences is not unique to *O. purpurea* and has been observed across a range of species and environments (Doak & Morris 2010; Dalgleish *et al.* 2011; Nicolè *et al.* 2011; Sletvold *et al.* 2013). Although some systems, such as deserts, may have more pre-

dictable, single climate drivers like precipitation (Salguero-Gómez *et al.* 2012), it is reasonable to expect that for many plant species, complex responses to diverse climate drivers should be common.

Life-history theory makes the basic prediction that if early reproduction elevates mortality risk at small sizes, reproduction should be delayed to a future year when individuals reach a larger size (Roff 1992). Underlying that basic prediction are complexities about the balance between costs of reproduction and the anticipated benefit (or payoff) of reproducing at a smaller size, and about the predictability or variability in the environment. We found that following warm winters or wet summers, flowering plants pay a higher cost of reproduction, leading to the prediction that as the frequency of warm winters or wet summers increases, we should expect plants to flower at larger sizes. This prediction held true; the predicted median ES size of flowering increased when the frequency of either warm winters (Fig. 3b) or wet summers increased (Fig. 3a).

The predicted effects of climate change on ES flowering size exhibited an interesting contrast with the observed responses to climate variation during the study period. Specifically, we observed that dry winters and dry springs suppressed flowering in all but the largest plants (Fig. 1c,d), leading to an elevated median flowering size under these conditions. However, our adaptive dynamics analysis indicated that increasing the frequency of extremely dry winters or dry springs selected for a *smaller* flowering size (Fig. 3a). This apparent contradiction can be understood by recognizing that an optimal flowering strategy balances the benefit of waiting to reproduce at a large size, when the flowering cost is weaker (Fig. 1a,b) and fecundity greater (Fig. 1e), against the risk of dying before reaching it. Because dry winters and springs suppress flowering, an increase in the frequency of these climate conditions reduces the 'payoff' of delayed reproduction. Given an uncertain future that likely includes years that are bad for reproduction, orchids were thus selected to flower at a smaller size (i.e. a small-flowering mutant can invade a large-flowering resident), despite paying a greater reproductive cost when small. By contrast, as wet climates increase in frequency, the balance of costs and benefits tips in the other direction: there is selection for flowering at a larger size (a longer delay) because future flowering is more assured, rendering the risks of early flowering not worthwhile. We are aware of no previous studies to report such non-intuitive adaptive responses of life-history strategies to climate change. These responses could not have been detected without the integration of long-term demographic and climate data within a population dynamics framework.

The optimal (ES) intercept for the probability of flowering function corresponds to a median flowering size of 152.9 cm^2 for the climate means over the years of the study (2003–2013), which is slightly larger than that of 146.9 cm^2 previously predicted for the same populations in a deterministic scenario (Miller *et al.* 2012). Plants in these populations are thus predicted to exhibit a longer reproductive delay in a stochastic environment than in a constant environment. This result is in line with the expectation that delayed reproduction is beneficial in variable environments (Tuljapurkar 1990; Koons, Metcalf & Tuljapurkar 2008), although the differences we observed in the predicted optima are small. The predicted ES intercept also closely corresponded to the observed intercept from the same time period (Figs 2, and S4), which suggests that our model captures the optimal flowering size based on the costs of reproduction quantified in the vital rate functions for both mean and variable environments.

One of the strengths of an adaptive dynamics approach is that it allows researchers to explore how changes in complex (e.g. density-dependent, stochastic) environments can influence selection on a particular trait. The limitations to this approach are that without more detailed experiments or genetic analyses, it is impossible to separate the role of phenotypic plasticity from adaptive evolution, and thus, our results suggest the maximum bounds for change in flowering size given currently observed vital rates. Further, in populations that include individuals that recruited during multiple climate regimes due to their longevity, responses to selection may be weaker than for shorter-lived species. Finally, the details of density dependence may be important to consider in the specification of adaptive dynamics, as they may influence ES strategies (e.g. Shefferson, Warren & Pulliam 2014). We modelled density dependence in a very coarse way, based on the relationship between seed production and recruitment. We therefore assume that all density dependence in these populations occurs at the regeneration step of the life cycle. We lack the data for a more thorough analysis, but recognize that we may be underestimating the strength of density dependence. Nonetheless, correspondence between the observed and ES flowering strategies (Fig. 2) suggests that the adaptive dynamics model describes these populations well.

Despite its threatened status due to habitat loss and deterioration, the populations of *O. purpurea* we studied were predicted to persist, regardless of the changing climate scenarios. Perhaps this is not surprising, given that these populations occur at the northern range edge, and may therefore be limited by low temperatures, which current climate change predictions indicate will be moderated (van Vliet *et al.* 2012). However, the influence of rapid life history evolution on population growth or persistence under climate change was more complex. If populations could evolve to perfectly match the ES flowering size as climate changes, population growth would increase compared to maintaining observed flowering size only when the frequency of dry or cold years increases. That adaptive evolution might not lead to increased population growth is not a new idea (Haldane 1932; Ferriere & Legendre 2013). In fact, as favourable conditions became more common, we found a slight negative effect of life-history adaptation on population growth. That is, increasingly delayed reproduction was advantageous in wet and warm climates (for reasons discussed above), yet this strategy slightly retards the potential for population-level growth. We hypothesize that this result reflects the fact that life history evolution occurred in a density-dependent environment, in which case a strategy that max-

imizes individual fitness is not necessarily the strategy that maximizes the potential for population growth.

In conclusion, our study demonstrates the importance of examining not only the effects of climate change on evolution of life-history traits, but also the influence of evolution on population growth. Further studies that link evolutionary and ecological demographic processes are needed to fully determine the effects of changing climate on the dynamics of populations.

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Data accessibility

Best-fit functions and parameter estimates for all vital rates used in IPM are presented in Tables 1 and S2.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Detailed methods of integral projection model.

Appendix S2. Detailed methods of model selection approach to estimate size- and climate-dependent vital rates.

Table S1. Model selection results for influence of climate variables on vital rate functions.

Table S2. IPM parameters for non-size-dependent vital rates.

Figure S1. Histograms of climate variables (1991–2013) that explained a significant proportion of variation in vital rate functions.

Figure S2. Coefficients of variation for each climate variable in each climate scenario.

Figure S3. Relationship between seedling recruitment in year t+3 and seed production in year t.

Figure S4. Pairwise invasibility plot showing evolutionarily stable strategy for intercept of flowering function (c_0), and observed c_0.