

PREDICTION OF EXTINCTION IN PLANTS: INTERACTION OF EXTRINSIC THREATS AND LIFE HISTORY TRAITS

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Abstract. The global extinction of species proceeds through the erosion of local populations. Using a 60-year time series of annual sighting records of plant species, we studied the correlates of local extinction risk associated with a risk of species extinction in the Park Grass Experiment where plants received long-term exposure to nutrient enrichment, soil acidification, and reductions in habitat size. We used multivariate linear models to assess how extrinsic threats and life history traits influence extinction risk. We investigated effects of four extrinsic threats (nitrogen enrichment, productivity, acidification, and plot size) as well as 11 life history traits (month of earliest flowering, flowering duration, stress tolerance, ruderalness [plant species' ability to cope with habitat disturbance], plant height, diaspore mass, seed bank, life form, dispersal mode, apomixes [the ability for a species to reproduce asexually through seeds], and mating system). Extinction risk was not influenced by plant family. All of the 11 life history traits except life form and all threat variables influenced extinction risk but always via interactions which typically involved one threat variable and one life history trait. We detected comparatively few significant interactions between life history traits, and the interacting traits compensated for each other. These results suggest that simple predictions about extinction risk based on species' traits alone will often fail. In contrast, understanding the interactions between extrinsic threats and life history traits will allow us to make more accurate predictions of extinctions.

Key words: biomass; extinction risk; habitat fragmentation; life history traits; nitrogen; Park Grass Experiments; pH; plants.

INTRODUCTION

The preservation of biodiversity and its benefits depends on the continued survival or replacement of local populations (Hughes et al. 1997). High rates of local extinction (Thomas et al. 2004) are harbingers of a much wider problem, which has often been described as the sixth great mass extinction in the history of life (Lawton and May 1995). Indeed, direct or indirect anthropogenic habitat alteration, by reducing the number of suitable habitats and their connectivity, increases the risk that local extinction overwhelms colonization/recolonization events. Thus, the local attrition of a species, if repeated across its geographic range, ultimately risks its global extinction (Ceballos and Ehrlich 2002), and hence understanding local extinction is of greater than local importance. In analyzing extinction patterns, we can distinguish between extrinsic threats arising from changes in the environment and intrinsic vulnerabilities related to extinction associated with particular life history traits.

Though the distinction is conceptually useful, extrinsic threats and intrinsic vulnerabilities interact and cannot always be separated. For example, narrow-habitat specialists tend to be particularly vulnerable to local extinction through a combination of intrinsic specialization and extrinsic habitat scarcity (McKinney 1997, Henle et al. 2004). More generally, small population size, which several studies have confirmed increases extinction probability, may arise from both the biological attributes of species and from environmental change. Except where populations are small enough for demographic or genetic stochasticity to be important, vulnerability to extinction does not become apparent unless a population is exposed to some extrinsic risk. Thus, in order to disentangle the mechanisms involved in the process of local extinction, intrinsic and extrinsic factors must be analyzed simultaneously (Henle et al. 2004).

Species that are locally rare, habitat specialists, herbaceous, short-lived, or of short stature have been identified as especially vulnerable to extinction (Robinson et al. 1994, Leach and Givnish 1996, Turner et al. 1996, Fischer and Stocklin 1997, Rooney and Dress 1997, Duncan and Young 2000, Warren et al. 2001, Kotiaho et al. 2005). Nevertheless, though many studies have focused on the relationship between extinction risk and life history traits (McKinney 1997, Purvis et al.

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2000), the observed variation in vulnerability to extinction is still poorly explained by species' traits alone (Lawton and May 1995, Owens and Bennett 2000, Blackburn and Gaston 2002). The difficulty in recognizing general trends may arise because the relationships between extinction risk and life history traits are likely to depend upon the extrinsic threat. Indeed, while extrinsic threats arising from direct or indirect effects of human activity such as nitrogen deposition (Stevens et al. 2004, Suding et al. 2005), acidification (Roem et al. 2002), or reduction in habitat size (Burkey 1997, Krauss et al. 2003) have been suggested as possible causes of species loss, it is likely that species will respond differently to these threats depending on their biological attributes. For instance, one may expect species with low dispersal ability to be more sensitive to habitat fragmentation than more mobile species. Similarly, stress-tolerant species are expected to be less prone to extinction than nontolerant ones in plots with low nitrogen enrichment. However, until now very few studies have assessed the joint effect of extrinsic and intrinsic factors on species vulnerability to extinction (Owens and Bennett 2000, Blackburn and Gaston 2002, Fisher et al. 2003, Rooney et al. 2004), and none have done so in a situation where multiple extrinsic threats were experimentally controlled.

The Park Grass Experiment (PGE) at Rothamsted Experimental Station, Hertfordshire, UK is perhaps unique in providing an opportunity for the plant traits associated with vulnerability to be studied in a situation where the environmental conditions that expose populations to extinction risk have been controlled and replicated over a long period of time. Before it began in 1856, the experimental area contained meadow grassland vegetation of uniform composition, with over 90 species of flowering plants. These species grow in grassland types that have widespread analogs around the world and are thus representative of a wide range of plant communities. We investigated how four extrinsic threats, productivity, acidification, nitrogen enrichment, and plot size, affected extinction risk. The PGE was initially set up to investigate how various fertilizers applied to different plots would improve the productivity of hay meadows. Since 1856, all plots, including the unfertilized ones, have experienced a significant decline in species number. Nevertheless, variation among plots in the magnitude of species loss has been observed, mainly as a result of plot productivity and acidification (Silvertown 1980). More recently, the present spatial distribution of plant species richness in the PGE has been shown to depend both on the productivity and the amount of nitrogen applied (Crawley et al. 2005), suggesting that these two variables may act either additively or synergistically on extinction risk. This prompted us to select both nitrogen enrichment and productivity as potential extrinsic threats, although productivity was not a controlled factor in the experiment. While human-induced nutrient enrichment and

acidification have already been suggested as important drivers of current biodiversity loss (Roem et al. 2002, Stevens et al. 2004, Suding et al. 2005), the effect of productivity on species richness is still unclear (see Crawley et al. 2005). Understanding such an effect is critical, as human activities are likely to affect directly or indirectly ecosystem productivity through many different processes. For instance, recent climate changes have enhanced net primary production in most latitudes (Nemani et al. 2003). Finally, we also included plot size as an extrinsic threat. Indeed, despite the relatively small scale of the PGE, genetic and ecological data suggest that plots are quite isolated from each other (Snaydon 1970, Snaydon and Davies 1972, Kunin 1998, Silvertown et al. 2005), suggesting that the experimental set up led to both habitat loss and habitat fragmentation.

Life history traits such as mating system, ruderalness (plant species' ability to cope with habitat disturbance), and phenology have also been shown to affect significantly species dynamics in the PGE (Dodd et al. 1995, Silvertown et al. 2002). Thus, existing data suggest that species extinction in the PGE is driven by habitat change and that vulnerability may depend upon certain life history traits. We here investigate explicitly how extinction risk is dependent on the interaction between life history traits and extrinsic threats by applying a new method of measuring extinction risk developed by Solow and Roberts (2003) to a 60-year time series of annual observations.

METHODS

The Park Grass Experiment

The Park Grass Experiment was begun in 1856 at Rothamsted Experimental Station (Hertfordshire, UK) with the aim of investigating the effect of different fertilizer regimes on the yield of a hay meadow grassland. The hay meadow was initially of uniform vegetation composition and soil type. It was divided into plots of between 0.05 and 0.2 ha. Fertilizer regimes differing in the amount and the form of nitrogen fertilizer have been applied to most plots, and two plots have been kept as unfertilized controls. Details of the fertilizer schemes are given by Williams (1978). Following the application of fertilizers, a rapid decline in the number of species was observed and a liming scheme was initiated at the beginning of the 20th century. In 1903, most plots were divided in half and one half of the plots was limed at regular intervals. In 1920, three plots (plots 18, 19, and 20) were each divided into three sections, and two of these subplots received lime. Most of the plots were subdivided again in 1965 and different liming treatments were applied in order to provide different degrees of acidification. Following the last division in 1965, the size of the plots ranged from 0.015 to 0.063 ha. Out of more than 80 plots, only 42 plots, which have been receiving the same fertilizer and liming treatments since 1920, were included in our study. A

plan of the 42 selected plots can be found in Dodd et al. (1995).

Measuring extinction risk

The presence/absence of species was assessed visually in every plot between 1920 and 1979. The surveys were carried out from the edge of each plot to avoid damaging the vegetation. The number of surveys per year decreased from up to nine during the mid-thirties to two surveys at the end of the period (see Fig. 2 in Dodd et al. 1995). The number of surveys per year had little effect on the total number of species detected per plot (Dodd et al. 1995). A species was considered as present on a given year in a particular plot if it was recorded there in at least one survey performed that year. Using the sighting record of each species in each plot, we applied a nonparametric test for extinction (Solow and Roberts 2003); it tests the null hypothesis H_0 that a species is extant at a given time against the alternative hypothesis H_1 that it is extinct. This method offers two advantages over alternative methods for inferring extinction from sighting records. First, this test does not make assumptions about the sampling distribution of the sighting rate (which is rarely known) under the null hypothesis that the species is still extant. Second, this test is less sensitive to deviations from the underlying statistical model (Solow and Roberts 2003), such as changes in the sighting rate during the observation period that may arise, for instance, from variations in sampling effort or species abundance. The reduced sensitivity of the method to variations in sampling effort and species abundance is particularly important regarding the aims of our study. It is likely that the distribution of the sighting rate depends on life history traits that could influence detectability, such as flowering duration or plant height. These could be confounded with sampling effort, as highly observable plants require less effort to detect.

For each species i and each plot j , the approximate P value in testing H_0 against H_1 was calculated as follows:

$$P_{ij} = \frac{T_{nij} - T_{(n-1)ij}}{T - T_{(n-1)ij}} \quad (1)$$

with T_{nij} the most recent sighting of species i in plot j , $T_{(n-1)ij}$ the second most recent sighting of species i in plot j and T the end of the observation period. Other things being equal, P_{ij} will thus take smaller values for plots and species where extinction is more likely. Given Eq. 1, low P_{ij} values characterize species that have not been recorded for a long time in a given plot (T_n much smaller than T) and that had been spotted on a very regular basis before the last sighting (low value of $T_n - T_{n-1}$). In contrast, high P_{ij} values are expected in two different situations: first, when the species' sighting is frequent (T_n close to T and low value of $T_n - T_{n-1}$), and second, when the species' sighting is rare (large value of $T_n - T_{n-1}$). This is expected for species that have metapopulation dynamics with extinction/recoloniza-

tion of plots during the time period studied. Thus, we do not study local extinction in the context of turnover and metapopulation dynamics (that may or may not threaten species persistence). Rather, we focus on local extinction associated with a risk of species extinction (i.e., decreasing number of occupied plots) at the scale of the PGE. Eq. 1 was applied to all species that were sighted at least twice on the same plot during the observation period. Values of P_{ij} were calculated separately for the intervals 1920–1965 and 1965–1979 because most plots were further sub-divided in 1965. Fertilizer treatments remained constant for each of the 42 plots from 1920 to 1979.

Extrinsic threats

We investigated how two continuous variables, productivity (measured as plot biomass) and plot size, and two categorical variables, soil acidification and nitrogen enrichment, affect extinction risk. We calculated the mean biomass of hay harvested from each plot using annual records of dry matter yield between 1920–1964 and 1965–1979. The size of each plot ranged from 0.015 to 0.096 ha for the period 1920–1964 and from 0.015 to 0.063 ha for the period 1965–1979. Data on soil pH have been collected periodically since the beginning of the PGE. We were able to use measurements made within five years of the end of each time period (1959 and 1975). We classified each plot as having a pH ≤ 4.5 (acid) or >4.5 (non-acid). This threshold value is known to be critical for the mineralization processes that occur in the soil. Moreover, species diversity has been shown to drop drastically in plots of the PGE falling below pH = 4.5 (Silvertown 1980). Soil pH has decreased since 1856. The soil pH variable thus reflects the amplitude of acidification since the beginning of the experiment. We also investigated how nitrogen enrichment affected extinction risk by ranking plots into five classes: plots receiving (0) no nitrogen, (1) organic nitrogen, (2) inorganic nitrogen at a level of less than 48kg/ha, (3) inorganic nitrogen at a level of 96kg/ha, (4) inorganic nitrogen at a level of 144 kg/ha.

Life history traits

We analyzed 11 life history traits (Appendix A). Seven traits were treated as continuous variables: month of earliest flowering (Early Fl), duration of the flowering period (Duration Fl), stress tolerance (S), ruderalness (R), plant height, diaspore mass, and seed bank longevity. We analyzed four life history traits as categorical variables: life form, dispersal mode (Dispersal), apomixes, and mating system (Mating). Life history traits were taken mainly from Grime et al. (1988), the Ecological Flora Database (Fitter and Peat 1994), and Hodgson et al. (1995). Missing values of diaspore mass were completed using data reported in Eriksson and Jakobsson (1998). Seed bank data were taken from Thompson et al. (1997) and converted into a seed bank longevity index as defined in Thompson et al.

(1998). Stress tolerance and ruderalness were converted into numerical scores ranging from 0 to 12 as in Dodd et al. (1995). We classified species into three categories of life form representing a gradient in life span: (1) annual species, (2) perennial species without clonal reproduction, and (3) perennial species with clonal reproduction. We also classified species into three categories likely to reflect an increase in dispersal ability: (1) species with unassisted dispersal, i.e., with diaspores having no morphological features enhancing dispersal, (2) species having animal-specialized diaspores that are dispersed by adhesion or active transport, (3) species having wind-specialized diaspores, carrying for instance a pappus, wings, or hairs. The reproductive strategy of each species was characterized by the presence or absence of apomixis, i.e., the ability for a species to reproduce asexually through seeds (Nogler 1984) and the mating system. As described in the Ecological Flora Database (Fitter and Peat 1994), species were classified into three categories of mating system that reflect the frequency of selfing vs. outcrossing events: (1) predominantly selfing species, (2) species having a mixed-mating system, and (3) predominantly outcrossing species. For 12 species, the classification was made using estimates of outcrossing rates recorded in the PGE (Silvertown et al. 2002). A total of 93 species was recorded in the PGE between 1920 and 1979. Any species with fewer than two sighting records or missing data for life history traits was excluded from the analysis, resulting in analyses of 63 and 48 species for the first and second observation period, respectively (Appendix A).

Statistical analysis

We investigated how P_{ij} depended on extrinsic threats, life history traits, and their interaction by fitting mixed general linear models to our data set containing each plot/species occurrence (1400 cases for 1920–1964 and 931 cases for 1965–1979). Threat variables, life history traits, time period, and their appropriate interactions were treated as fixed effects, whereas plot and species and their interaction were treated as random. To test for effects of phylogenetic relationship among species upon correlations, the random component for species was modeled as the sum of a term for the family to which each species belonged and a term for species nested within family. Classical methods such as phylogenetically independent contrast could not be applied, as a given species was present in many different habitats. In order to satisfy the assumptions of linear analyses, P_{ij} values were subjected to the arcsine square-root transformation and continuous variables were transformed as necessary. Moreover, all continuous variables were centered by subtracting their means in order to improve the accuracy of parameter estimation.

For each time period, the following general model was fitted: arcsine square-root $P_{ij} = \mu + \alpha_{1,i}x_{1,i} +$ similar terms for other life history effects and two-way interactions $+ \beta_{1,j}y_{1,j} +$ similar terms for other habitat

effects and two-way interactions $+ \text{terms for two way interactions between habitat variables and life history traits} + \phi_f + \eta_{i(f)} + v_j + \varepsilon_{ij}$.

Here, μ is the overall mean, $x_{1,i}$ is the value of the first life history variable for species i and $\alpha_{1,i}$ the corresponding coefficient, $y_{1,j}$ is the value of the first environmental variable for plot j and $\beta_{1,j}$ the corresponding coefficient. ϕ_f , $\eta_{i(f)}$, v_j , and ε_{ij} are the normally distributed random error terms for family, species within family, plot, and species–plot combinations, respectively. Although the data set contained a large number of species–plot combinations, it was not possible to fit models that contained very large numbers of interactions between explanatory variables because of the occurrence of severe aliasing. In order to counteract this problem, a stepwise modeling procedure (described in Appendix B) was used, leading to a single optimal model. Mixed linear models were fitted using residual maximum likelihood (REML) in GenStat version 7 (NAG Ltd, Oxford, UK) and R (Ihaka and Gentleman 1996). Correlations among explanatory variables were used to guide the interpretation of the model results.

RESULTS

The optimal model explained 44% of the variance in the response, arcsine square-root P_{ij} , 33% from the fixed effects included (threat variables, life history traits, and their interactions), and 11% from the random effects. A model that simply included the threat variables, but no life-history variables, explained only 5% of the variance in the response. Similarly, a model that included life history traits but no threat variables explained only 21% of the variance. A model that included both habitat and life history variables but no interactions between them explained 25% of the variance, far less than was explained by the optimal model that included interactions.

With the sole exception of life form, all explanatory variables appeared in the model and were significant in an interaction term (Table 1; see Appendix C for detailed results of the multivariate analysis). Taxonomic family was not a significant term in this model, so species were treated as independent units. The random effect of plot was also not significant, indicating that the threat variables accounted for all the significant variation in P_{ij} between plots. The optimal model included 51 fixed terms, out of which 13 appeared as main effects, 17 (out of the 44 possible) as two-way interactions involving threat variables and life history traits, five (out of 55 possible) as two-way interactions involving a pair of life history traits, nine as interactions between a trait and period, five as three-way interactions involving time period, a threat variable, and a life history trait, and two as three-way interactions involving time period and a pair of life history traits (Table 1, Appendix C). None of the main effects were interpreted, as all were involved in significant interactions. Relationships between P_{ij} and life history traits mostly depended upon extrinsic threats

TABLE 1. Results for fixed effects in the optimal general linear model, omitting terms that were dropped during fitting.

Term	df	<i>F</i>	<i>P</i>
Two-way interactions			
Trait × threat interactions			
Mating system × nitrogen	8, 2189	3.258	0.0011
Apomixis × biomass	1, 2189	8.792	0.0031
Apomixis × pH	1, 2189	9.567	0.0020
Seed bank × nitrogen	4, 2189	8.738	<0.0001
Seed bank × plot size	1, 2189	7.602	0.0059
Plant height × nitrogen	4, 2189	6.451	<0.0001
Plant height × biomass	1, 2189	49.156	<0.0001
Flowering duration × plot size	1, 2189	7.909	0.0050
Month of earliest flowering × nitrogen	4, 2189	6.943	<0.0001
Month of earliest flowering × biomass	1, 2189	14.024	0.0002
Month of earliest flowering × plot size	1, 2189	12.321	0.0005
Dispersal × pH	2, 2189	4.531	0.0109
Trait × trait interactions			
Plant height × month of earliest flowering	1, 48	10.301	0.0024
Stress tolerance × ruderalness	1, 48	5.072	0.0289
Flowering duration × dispersal	2, 48	9.993	0.0002
Period (temporal) interactions			
Mating system × period	2, 2189	14.168	<0.0001
Diaspore mass × period	1, 2189	0.762	0.3827
Plant height × period	1, 2189	15.327	0.0001
Month of earliest flowering × period	1, 2189	16.390	0.0001
Three-way interactions			
Trait × threat × period interactions			
Diaspore mass × biomass × period	1, 2189	4.559	0.0329
Diaspore mass × pH × period	1, 2189	4.100	0.0430
Stress tolerance × biomass × period	1, 2189	15.600	0.0001
Flowering duration × pH × period	1, 2189	8.356	0.0039
Dispersal × nitrogen × period	8, 2189	2.169	0.0271
Trait × trait × period interactions			
Seed bank × month of earliest flowering × period	1, 2189	33.578	<0.0001
Diaspore mass × month of earliest flowering × period	1, 2189	12.534	0.0004

Notes: Only significant terms that are not involved in a higher order interaction are shown (see Appendix C for the whole results). The table gives degrees of freedom (df) for the numerator and the denominator of the *F* statistic for testing each term in the presence of the other terms and the corresponding *P* value.

because interactions between traits and threats formed the largest class of effect included in the optimal model (Table 1). We detected no interactions between two or more threat variables influencing extinction risk. Out of 51 fixed terms, the model included only five significant two-way interactions between a pair of life history traits and two three-way interactions involving a pair of life history traits and time period.

Mating system significantly affected extinction risk, but its effect varied with nitrogen enrichment. Outcrossing was of increasing advantage (lowering extinction risk) compared to mixed mating and selfing with increasing N application (Fig. 1). Apomixis was associated with a reduced extinction risk at high biomass and on nonacid plots. Short plants were favored at low biomass and taller ones at high biomass (Fig. 2). Greater plant height consistently lowered extinction risk at all N levels, except the highest, where the effect reversed. Stress tolerance decreased extinction on low biomass plots but increased extinction at high biomass. Interactions between species' flowering phenology and various threat

factors also affected extinction risk. Longer flowering duration was associated with decreasing extinction risk, the effect being stronger in acid plots (Fig. 3) and as plot size increased. The patterns for month of earliest flowering were complicated. Extinction risk was lower for species with a late start to flowering at low biomass, but the effect reversed to favor an early start at high biomass. Early flowering lowered extinction risk at low N, but raised it at high N. An early start to flowering was favored on small plots, but the effect was reversed on large plots. The effect of diaspore mass on extinction risk depended on both pH and plot biomass, with extinction risk decreasing with increasing diaspore mass in nonacid plots and in low and medium biomass plots but increasing in acid and high biomass plots. Species with greater seed bank longevity were less likely to go extinct, except on plots receiving the highest level of N application. Seed bank longevity decreased extinction risk more in larger plots (Fig. 4). We found that the effect of dispersal on extinction risk depended on nitrogen enrichment and pH. Wind-dispersed species were at

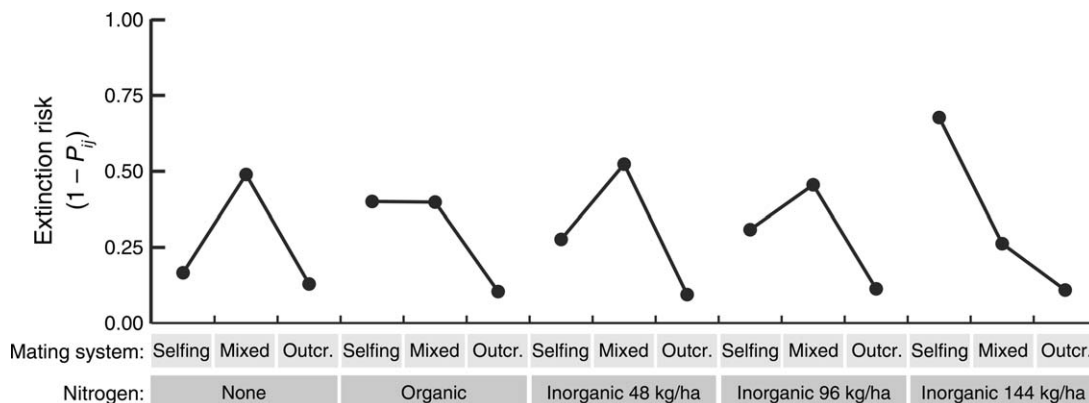


FIG. 1. Effect of the interaction between mating system and nitrogen enrichment on extinction risk. Values of $1 - P_{ij}$ were plotted after back-transforming the response variable arcsine square-root P_{ij} predicted by the optimal multivariate model. High extinction risk is thus associated with high $1 - P_{ij}$ values. Predicted values were calculated with GenStat version 7 (NAG Ltd, Oxford, UK) for each combination of mating system and nitrogen categories, all continuous explanatory variables being averaged and using equal weights for all remaining categorical variables. Note that because we set all other explanatory variables to their mean values, the graph illustrates the direction and strength of the relationship between extinction risk, extrinsic threat, and life history traits, rather than the real values of $1 - P_{ij}$ observed in our data set (observed values of $1 - P_{ij}$ ranged from 0 to 0.977). The lines linking the points have been added solely to improve the clarity of the graph.

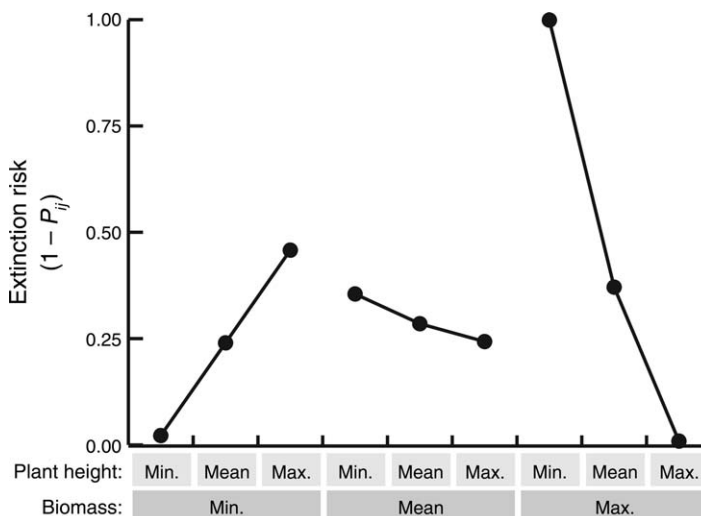
higher risk of extinction overall and more particularly in low nitrogen plots and acid plots. Extinction risk depended on only five two-way interactions between a pair of life history traits (Table 1), and these traits acted always in a compensatory manner. For instance, increasing seed bank longevity decreased extinction risk for species with an early start to flowering, but the effect was reversed for species having a late start.

FIG. 2. Effect of the interaction between plant height and plot biomass on extinction risk. Predicted values were calculated using the second smallest (min.), the mean, and the second largest (max.) values of plot biomass and plant height observed in our data set. The minimum plant height observed in the Park Grass Experiment (PGE) at Rothamsted Experimental Station, UK (7.5 cm for *Bellis perennis*) led to a negative predicted value of arcsine square-root P_{ij} for the maximum value of plot biomass, but such species/plot combinations did not occur in the PGE, as *Bellis perennis* was not recorded in plots with the highest biomass. Similarly the maximum plant height (200 cm for *Rosa* sp.) led to a predicted value of arcsine square-root P_{ij} that was too large to correspond to a value of P_{ij} between 0 and 1 for the maximum value of plot biomass; but again this combination of great height and high biomass did not occur in the PGE. Note that the lines linking the points have been added solely to improve the clarity of the graph: because we back-transformed the response variable, the relationship between the predicted value of $1 - P_{ij}$ and continuous explanatory variables is not linear, but the lines do indicate the direction of the relationship, in the sense that where a straight line in the graph shows an increasing or decreasing relationship, the relationship in the model increases or decreases in a nonlinear manner. See the legend of Fig. 1 for additional details.

DISCUSSION

Determinants of extinction risk in the Park Grass Experiment

Interspecific variation in extinction risk was best explained by a model including interaction terms that involved all four extrinsic threats and 10 out of the initial 11 life history traits. The optimal model explained



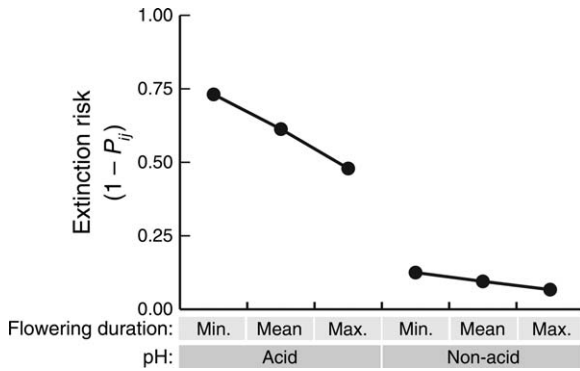


FIG. 3. Effect of the interaction between flowering duration and pH on extinction risk during the first period. The same trend was observed during the second period, slopes being slightly steeper. For each category of pH, predicted values were calculated using the minimum (min.), mean, and maximum (max.) values of flowering duration observed in our data set. See the legends of Figs. 1 and 2 for additional details.

44% of the variance in extinction risk, suggesting that other factors not taken into account in this study may also act as important drivers to extinction in the PGE. The Park Grass communities reached equilibrium at the community level before our time series began (Silvertown 1980), so the trends in extinction risk cannot be attributed to successional or transient dynamics. In contrast, species dynamics in the PGE are expected to strongly depend on stochastic factors such as environmental stochasticity arising from variations in climate or pathogen pressures, given the small population sizes. For instance, *Holcus lanatus* and *Anthoxanthum odoratum* have been shown to be sensitive to the occurrence of drought in the PGE, whereas variation in the abundance of *Tragopogon pratensis* is affected by rust disease (Silvertown et al. 2006).

Nitrogen deposition (Stevens et al. 2004, Suding et al. 2005), increase in biomass (Silvertown 1980), acidification (Roem et al. 2002), and reduction in habitat size (Burkey 1997, Krauss et al. 2003) have all been suspected as major causes of biodiversity loss. Our study clearly demonstrates that species are not equally sensitive to these extrinsic threats. Effects of all 10 significant life history traits varied, depending upon levels of one or more of the four extrinsic threats. Moreover, life history traits interacted with different extrinsic threats.

The effect of nitrogen enrichment on extinction risk depended on various life history traits. While selfing species were always more prone to extinction than outcrossing species, selfing species were more likely to go extinct as nitrogen enrichment increased. Though genetic models suggest that selfing species may be more prone to extinction than outcrossing species, supporting data from natural populations are still scarce (Takebayashi and Morrell 2001). The difference in extinction risk between selfing and outcrossing species could reflect the immediate effects of inbreeding depression or perhaps restricted evolvability in selfing populations, increasing susceptibility to changing environments (Silvertown et al. 2002). Local adaptation in the PGE has already been reported in *Anthoxanthum odoratum* L. (Poaceae), an outcrossing grass in which populations were found to have evolved increased resistance to mildew on high nitrogen plots (Snaydon and Davies 1972). Disease incidence was usually higher in plots receiving nitrogen, posing an increased risk to populations that were unable to evolve resistance (Snaydon and Davies 1972). The effect of nitrogen enrichment on extinction risk also depended on dispersal. We found that wind-dispersed species were less likely to persist at the scale of the PGE than animal-dispersed species and species with unspecialized diaspores, particularly in low nitrogen plots and acid plots. Wind dispersed seeds are

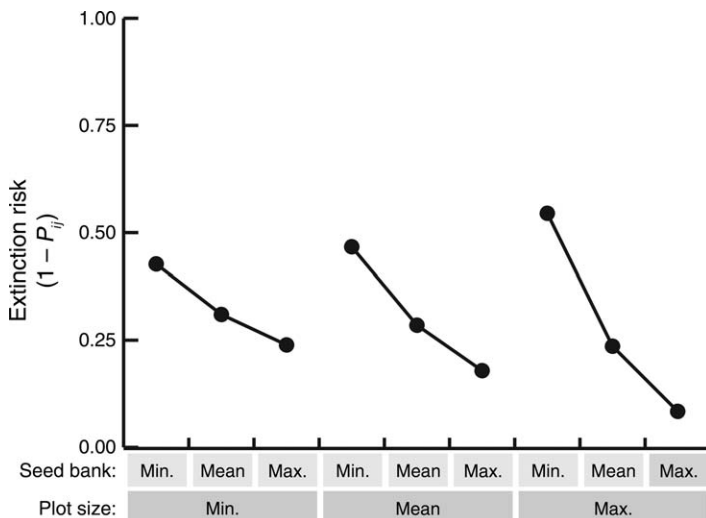


FIG. 4. Effect of the interaction between seed bank and plot size on extinction risk. Predicted values were calculated using the minimum (min.), mean, and maximum (max.) values of seed bank longevity and plot size observed in our data set. See the legends of Figs. 1 and 2 for additional details.

likely to disperse farther than seeds that are animal dispersed (Clark et al. 1999). Thus our findings remain puzzling.

Plot biomass affected extinction risk differently depending on species' life history traits. While short plant species were overall at higher risk of extinction compared to tall species in the PGE, as shown by other plant studies (Leach and Givnish 1996, Duncan and Young 2000), this was not the case in low biomass plots, where the reverse trend was observed. A negative correlation between plot biomass and its coefficient of variation over time has been reported in the PGE (Dodd et al. 1994). One thus expects short species to gain an advantage by allocating less energy to supportive tissue in low biomass plots where competition for light is expected to be reduced. Similar results were observed in Wisconsin remnant prairies (Leach and Givnish 1996, Duncan and Young 2000), where local extirpation of short species increased along a productivity gradient from dry to wet prairies, as expected under increasing interspecific competition. The effect of plot biomass on extinction risk also depended on the level of stress tolerance. Overall, the fate of stress tolerators and ruderals was consistent with Grime's (1979) definitions of these strategies. Stress tolerance and ruderality had opposing effects on extinction risk, as one would expect for alternative strategies. Stress tolerance lowered extinction risk at low plot biomass (where soil nutrients would be in short supply), but it increased extinction risk at high biomass where interspecific competition would be strongest. Plot biomass also affected extinction risk differently depending on the presence/absence of apomixis. Apomixis increased persistence with increasing plot biomass and in nonacid plots. Despite its frequent occurrence among plants (Richards 2003), the evolutionary implications of apomixis and the ecological conditions that may favor it are still obscure, making these results difficult to interpret.

Acidification also had contrasting effects on extinction risk depending on species' attributes. Extinction risk decreased with increasing flowering duration, this trend being strongest in acid plots. Plant communities in acid plots have been found to show higher temporal variation in hay biomass in the PGE (Dodd et al. 1994). In such habitats, one expects species that are able to set seeds during a longer period of time during the year to be more able to recruit, and thus to be less prone to extinction. A similar positive effect of flowering duration was also found in another grassland community in the UK, where species with longer flowering duration were shown to be overrepresented compared to the expectations of a null model (Tofts and Silvertown 2000). Acidification also affected extinction risk differently depending on diaspore mass. Heavier diaspores enhanced species persistence in nonacid plots and in low biomass plots but reduced persistence in acid plots and high biomass plots. Similarly, small-seeded species experienced the greatest declines following fire suppres-

sion in Wisconsin remnant prairies (Leach and Givnish 1996).

Finally, the effect of plot size on extinction risk also affected species differently depending on their life history traits, such as seed bank. For instance, while overall extinction risk decreased with increasing longevity in the seed bank as found in grassland plants in Switzerland (Stöcklin and Fischer 1999), this effect was strongest in large plots, possibly because seed distributions in the soil are so patchy that there is a chance that seed banks may be less abundant in smaller plots.

In addition to the importance of interactions between threats and species' attributes in influencing extinction risk, our study highlights two other main results. First, interactions between extrinsic threats were entirely absent, indicating that each threat operated independently. The two variables, pH and biomass, were already found to have additive (rather than synergistic) effects upon species richness in the Park Grass Experiment (Silvertown 1980). We now find that the four variables, pH, biomass, N, and plot size, all operate additively. Second, among the few interacting life history traits found to significantly influence extinction risk, all traits compensated for each other. Few other studies have examined the interaction between species' traits in the estimation of extinction risk. Traits had synergistic effects on extinction risk of beetle species in a habitat fragmentation experiment (Davies et al. 2004). Beetle species that were locally rare habitat specialists were far more prone to extinction than expected if traits had additive effects. These results, different from our own, emphasize the need to take into account interactions between species' traits in order to better understand the ecological mechanisms that drive species to extinction.

Methodological issues

Any extinction study relying on presence/absence data must consider the uncertainty that is usually inherent in determining whether a species is extinct or not. Moreover, in comparative studies that investigate correlates of extinction with life history traits, this so-called pseudo-turnover effect may induce spurious correlations if the probability of sighting depends on life history traits.

The assessment of extinction risk was based on visual inspection of presence/absence of species from the border of plots which could be of a size up to 25×38 m, leading to the possibility that a species that was actually present might be missed in some years. Such sampling error is very unlikely to have biased our results for four reasons. First, only highly detectable species, such as flowering species and those obvious in the vegetative state were recorded (Dodd et al. 1995). Second, the assessment of extinction risk is based on the two most recent sightings, whereas the presence/absence of every species has been recorded annually at least twice a year. The probability of missing a species for a long period when it is actually present was thus

very small. Third, no species that disappeared from a plot during the first period (P values < 0.05) was ever found in the second period. This indicates that all recorded extinctions were genuine. Fourth, if one assumes that short species and species with a short flowering season are less easily detected, such species are expected to have upward biased P_{ij} values because of the artificially increasing interval between two consecutive sightings. Under the hypothesis that extinction risk is independent of plant height and flowering duration, we might thus expect a spurious positive relationship between extinction risk and these two traits. Such significant methodological bias can be ruled out for flowering duration, as extinction risk was negatively correlated with this trait in the PGE. Extinction risk was also negatively correlated with plant height, except at the highest N level and in low biomass plots.

The number of visual surveys per year decreased from up to nine during the mid-1930s to two at the end of the 1930s with the abandonment of observations from January to early May (Dodd et al. 1995: Fig. 2), increasing the risk of overlooking a species over time. Such variation in the sampling effort is very unlikely to produce spurious relationships in our data set. First, we observed the same trends among the two time periods, whereas the sampling effort remained constant during the second period. Second, as visual surveys performed early in the year were progressively omitted, one may have expected a spurious negative relationship between extinction risk and the month of earliest flowering during the first period. Such a trend was not observed.

Implications for conservation issues

Understanding the mechanisms that underlie extinction is a very challenging task because it is difficult to record current extinctions in the wild (Purvis et al. 2000), and there is usually a time lag between the occurrence of an extrinsic threat and the complete disappearance of a species. In this respect, microcosm experiments (Burkey 1997, Belovsky et al. 1999) and semi-natural experiments such as the PGE are of much relevance to disentangle the mechanisms that may drive species to extinction in the wild. As acknowledged earlier, our study focuses on the correlates of local extinction associated with a species decline at the particular spatial scale of the PGE. As this scale is clearly much smaller than those at which conservation issues arise in the “real world,” there is an urgent need to develop such approaches for natural systems. For instance, in our study, plot size appeared in very few significant interactions compared to the other extrinsic threats. This is likely to be a scale effect, as plot sizes were probably not variable enough to induce significant spatial variation in extinction risk. In contrast, the impacts of nitrogen deposition, increasing biomass, and acidification are likely to be amplified in natural conditions, as species dynamics in the PGE are expected to strongly depend on stochastic factors given the small population sizes.

The very few studies carried out in natural ecosystems support our finding that species are prone to different extrinsic threats depending on their life history traits. Extinction risk in 95 families of birds increased with generation time when species were faced with human persecution, whereas generation time had no significant effect on extinction risk when species experienced habitat loss (Owens and Bennett 2000). In contrast, extinction risk incurred through habitat loss was associated with greater habitat specialization. Similarly, the loss of animal-pollinated and animal-dispersed species in understory communities in northern Wisconsin was larger in protected areas with no hunting than in unprotected sites or protected sites with hunting, as a result of increasing deer pressure (Rooney et al. 2004).

From a conservation perspective, our study strengthens the emerging idea that predictions about extinction risk cannot be made on the basis of species' traits alone. By showing that variations in extinction risk are better explained when the interaction between extrinsic threats and intrinsic vulnerabilities is understood, our analysis offers some hope that population extinctions may be more accurately predicted and thus prevented.

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APPENDIX A

Investigated species and their life history traits (*Ecological Archives* XXXXXX).

APPENDIX B

Stepwise modeling procedure (*Ecological Archives* XXXXXX).

APPENDIX C

Results of the multivariate analysis showing the effects of life history traits and extrinsic threats on extinction risk (*Ecological Archives* XXXXXX).