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Predicting mechanisms across scales: amplified effects of abiotic constraints on the recruitment of yew *Taxus baccata*

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Efforts to disentangle the mechanisms underlying large-scale spatial patterns need to rely on multi-scale approaches. We illustrate this key issue by analyzing the spatial consistency across scales of the effects of abiotic constraints on the regeneration of English yew *Taxus baccata* in Europe. We hypothesized that the recruitment rates in a given population would be strongly affected by water availability, which should result in a predictable pattern of regeneration success at regional and continental scales. Accordingly, we predicted: 1) at the regional scale water availability should be higher in sites occupied by yew populations than in random locations; 2) at the regional scale regeneration success should decrease when water availability is lower; and 3) at the continental scale, regeneration success should also decrease where water availability is lower, resulting in decreasing regeneration southwards. To test these predictions we first monitored seedling emergence and survival in two central Spanish populations over two years, and confirmed that yew recruitment is limited by water availability. Additionally, our analysis supported predictions 1 and 2: water availability strongly affected yew presence and regeneration success. At the continental scale (prediction 3), our results confirmed lower regeneration in southern European populations. Assessing the effect of climatic constraints across scales in key population parameters can help to improve large-scale assessments of impacts of climate change on biodiversity.

Macroecology has been intensively describing large-scale biological patterns on the basis that they could be explained by a mechanistic evaluation of processes operating at different spatial scales (Brown 1999). However, one crucial issue is still unresolved, that is, the evaluation of the effect of mechanisms in macroecological patterns across scales. Firstly, only a few macroecological studies incorporate the mechanisms responsible for biotic diversity gradients in spatially explicit models (Rahbek et al. 2007). Secondly, progress in documenting mechanisms of continental patterns across scales has been modest because of the difficulty of incorporating biotic variables at each relevant scale. Advances in this area are of particular importance because understanding and predicting effects of global change on biodiversity requires integrative studies across scales (Kühn et al. 2008). Herein, we illustrate a potential way to make progress on this issue.

Integrative studies on plant population dynamics have shown that local-scale interactions may be partly responsible for plant distributions at a broader, landscape scale (Chown et al. 2004). Theoretically these bottom-up effects could also take place from the regional to the continental scale. In practice, however, bottom-up effects are often tested in a limited spatial context (Davis et al. 1998, Lipscomb and Nilsen 1999). Less is known about the consistency of mechanisms across the whole continuum of scales.

Widely distributed plants that are highly sensitive to abiotic stress are ideal organisms to identify the multi-scale effects of abiotic factors on plant distributions (Rabinowitz et al. 1986). Climate-induced limitations might exert a strong influence on these plants at various scales, for example by locally influencing the chance of seedling recruitment (Brèda et al. 2006). As successful recruitment is a prerequisite for the maintenance of viable populations, local recruitment can ultimately shape species' range boundaries (Gaston 2003). As an example, one consequence of variation in recruitment success through a species' range is the centre-periphery gradient in population performance, which tends to be explained by range-wide variation in climatic stress (Brown et al. 1996).

Here we examine the spatial consistency across scales of the effects of abiotic constraints on the process of plant recruitment. In using English yew *Taxus baccata*, Taxaceae, as a model species, we scale-up the effect of water availability to regional and continental scales. We hypothesized that recruitment rates in a given population are affected by water availability, which in turn results in a predictable pattern of regeneration success at regional and continental scales. Therefore, we predicted that: 1) at the regional scale water availability should be higher in sites occupied by yew populations than in random locations; 2) at regional scale regeneration success should decrease when water availability is lower; and 3) at the continental scale, regeneration success should also decrease when water availability is lower, which would ultimately result in lower regeneration success in southern Europe.

Methods

Yew distribution

English yew is a dioecious, long-lived tree species with a Eurasian distribution (Thomas and Polwart 2003; Fig. 1). Most regions occupied by yew occur in Europe from 65° to 35°N latitude. Regeneration of yew is closely related to abiotic factors such as water and light availability (García et al. 2000b, Dovciak 2002, Mysterud and Ostbye 2004, Iszkulo and Boratynski 2006). Previous studies have also shown that biotic interactions, such as the dispersal of seeds by avian frugivores and browsing by ungulates, can shape local demographic structure and landscape distribution patterns (García and Obeso 2003, García and Ortiz-Pulido 2004).

Water limitation of seedling establishment

We first aimed to confirm that water actually played a critical role in population recruitment with intensive field sampling. Field work was conducted in the western Sistema Central mountain range (Cáceres province), a central Spanish region located in the southern edge of the species' range (Fig. 1). The climate is continental Mediterranean with dry summers and cold winters. The study was performed in two populations which were 62 km apart, namely Escobarejos and Cerezal. The elevation, slope, precipitation, and mean annual temperature of both populations were within the range of values for a regional pool of 43 populations. The Escobarejos population was located at 1500 m elevation and was comprised of 34 adult trees associated with seasonal streams surrounded by shrublands dominated by *Erica australis* and *Cytisus oromediterraneus.* Fleshy-fruited tree species (*Sorbus aucuparia* and *Ilex aquifolium*) were also present in low numbers. The Cerezal population was located at 900 m elevation and it comprised 53 adult trees. Yew trees grew close to streams in the understorey of a mixed montane forest with *Quercus ilex* and *Arbutus unedo* as dominant species.

We focused our attention on the emergence and the fate of seedlings as the main determinants of population recruitment (García et al. 1999, 2000a, Jordano et al. 2004). The study was performed with one-year old seedlings belonging to two different cohorts that emerged in spring 2005 and 2006. One-year old seedlings were easily recognized by their short, green, and flexible stems. First, we established the study area of both populations as the minimum convex polygon defined by all the trees present. Within this area, a complete survey of seedlings emerging each year was carried out in late May, June, and July. Secondly, for each seedling found we noted the distance (m)

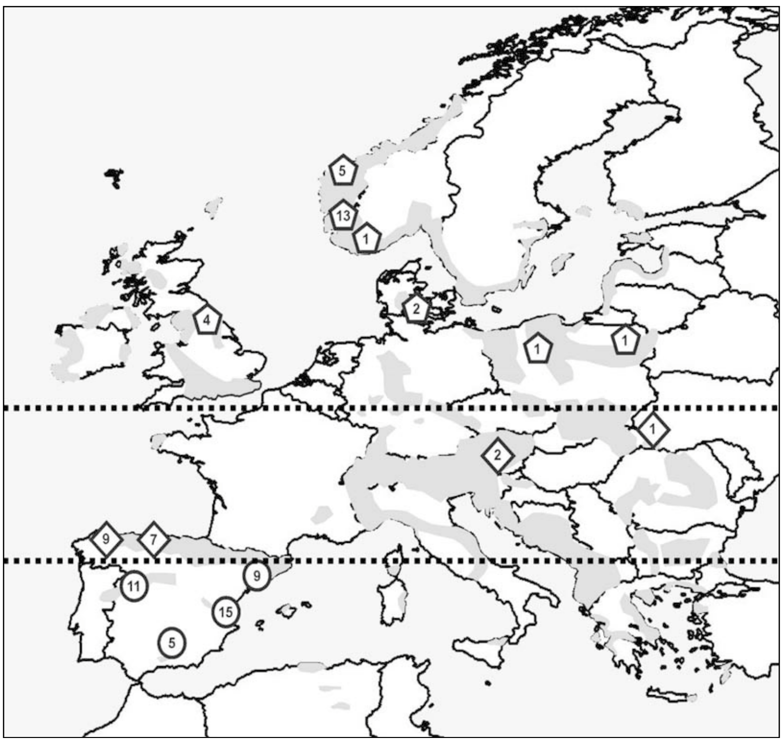

Figure 1. Distribution of yew *Taxus baccata* in Europe (shaded area) redrawn and modified from Thomas and Polwart (2003). Also shown is the location of the sites for which indices of regeneration were available. Different polygons refer to different latitudinal belts (delimitated by dotted lines at 50°N and 43°N), the figure inside de polygon indicating the number of sites sampled (see Supplementary material for a complete list).

to the nearest stream as a proxy variable for water availability. Since both populations are located along streams in the bottom of mountain valleys, soil moisture at any given point will be a function of the amount of water flow accumulation (*f*; the area of the catchment contributing water to such point) and the slope angle (*s*). A measure of moisture at such point can be calculated as: $w = \ln [f/\tan (s)]$, where w is a wetness index, f is the area of flow accumulation, and s is the slope angle (Beven and Kirkby 1979). Since the area of the drainage basin over a given point increases with decreasing distances from the stream, wetness should increase accordingly. Also, at a smaller spatial scale, soil moisture is expected to decrease at increasing distances from the stream from which water permeates into the soil. Our empirical data for distance and soil moisture show that both variables were significantly correlated in two yew stands located close to the study populations: $r = -0.444$, $p = 0.010$ in Nogaledas, and $r = -0.563$, $p = 0.004$ in Regaderas ($n = 24$ sampling points where volumetric soil moisture content was measured in June 2006 with a 15 cm Thetaprobe Sensor, Delta-T Devices, UK).

In addition, for each seedling we noted the microhabitat in which it grew: under fleshy-fruited shrubs, under non fleshy-fruited shrubs, under the canopy of adult yew and on open ground. Also we noted the microsite in which the seedling grew, as it could reflect the moisture environment experienced. Categories used were bare ground, moss, and small patches of grass. Survival of seedlings was checked at 3-month intervals from May 2005 to November 2006. As potential causes of seedling mortality we considered dessication (when seedlings completely lost stem flexibility and turned from green to pale yellow colour), defoliation (either affecting whole plants or their parts), trampling (irreversible bending of stems), and burial, which could be the result of soil displacement by animals or physical factors.

Finally, to evaluate the degree of microhabitat selectivity, we estimated the percentage cover of the different microhabitats and we compared it with the percentage of seedlings emerging in them. Cover of microhabitats was estimated by randomly selecting 200 points (5 m apart from each other) along parallel transects defined in each stand. On each point we placed an upright stick and noted the type of microhabitat encountered.

We tested for the effect of environmental variables on seedling recruitment by means of generalized linear models (GLZ) with cohort, population, microhabitat and microsite as factors, and distance as a continuous predictor. Survival was considered as a dichotomous response variable (0, 1) with a binomial distribution. We used the logit link function and the Wald statistic for significance testing. For evaluating whether the emergence of new seedlings was randomly distributed between the different microhabitats and between different distances to stream classes, the observed and expected frequencies were compared with Chi-square tests.

Test of predictions at regional scale

The study at the regional scale addressed the effect of water availability on the distribution and the regeneration success of yew populations. The region studied was ca 300 km^2 in area. At this scale we made a complete survey to locate isolated yew trees and populations. At each site we counted the number of saplings and juveniles within a distance of 20 m on both sides of the spring where adults were found. In addition we recorded the coordinates, size (diameter at breast height at 1.3 m, DBH), and sex of adult trees. From this information we derived frequency distributions of size classes and a regeneration index computed as the ratio of saplings plus juveniles to the total number of individuals including adults. This calculation rendered a standardized index ranging from 0 to 1 (recruits fraction, RF hereafter). Saplings were individuals above one year old and up to 50 cm, while juveniles were non-reproductive individuals above 50 cm and up to 3 m. Trees were considered as "adults" if they were taller than 3 m and/or they bore reproductive structures. Estimates of size as a surrogate of age have been widely used in previous studies of yew (Hulme 1996).

To evaluate the influence of water availability on yew presence we tested whether yew distribution departed significantly from random with respect to several proxy variables related to water availability. Firstly, we obtained the values of these variables for random and yew points by introducing their coordinates in a digital terrain model with Sextante on gvGIS 0.1 version (Olaya 2005). Then we recorded the values of elevation, slope, aspect, and distance to the nearest stream for 182 points with presence of yew trees and for 222 points selected at random within the altitudinal range of yew in the study region (903–1703 m). Comparison of both datasets allowed us to test prediction 1. We used parametric tests (Student t) when data of physiognomic variables had a normal distribution or when they could be normalized, and non-parametric tests (Mann-Whitney U) when data could not be normalized. In addition, using data from 16 meteorological stations and a digital terrain model we estimated the amount of annual and summer precipitation by spline interpolation. In addition, irradiance, water flow accumulation and wetness index were estimated to account for topographical effects on water availability (see above). By testing for the effects of these indices on RF by means of multiple regression analysis we evaluated prediction 2.

Test of predictions at continental scale

For this goal we took advantage of the large number of studies addressing stand structure of yew in Europe (Fig. 1). By checking published papers or unpublished reports we obtained the number of saplings, juveniles, and adults in each population. In two regions in central and eastern Spain for which a very large number of nearby populations had been studied, we randomly selected 15 stands to increase the independence of the data. For the resulting 88 European sites (Supplementary material) we obtained figures of summer and total annual precipitation for the period 1961–1990 (New et al. 1999).

For testing our prediction 3 we used data only from central and southern yew populations ($n = 61$; see below). We excluded the northernmost populations because we had no prior reason to expect any trend concerning the effect of water availability at the northern margin. We calculated the Pearson r correlation between RF and summer rainfall and annual rainfall for 19 central and 42 southern populations ($n = 61$). We accounted for the effect of the spatial autocorrelation on the degrees of freedom following Dutilleul (1993). We also used multiple regressions to control for the possible effect of population size on RF.

A supplementary analysis was conducted to test for the existence of a latitudinal trend in RF at the scale of the whole European range. The 50°N latitude was established as the border line separating central and northern populations, whereas the 43°N line was established as the border between central Temperate and southern Mediterranean zones (Fig. 1). We used linear and non-linear regression techniques with latitude (N degrees) as an independent variable and RF as response variable. Throughout the text means are shown ± 1 standard error (SE) unless otherwise stated. For data analysis we used the packages Statistica (release 6.0, StatSoft 2003), Idrisi Kilimanjaro (Clark Labs 2003) and SAM (Rangel et al. 2006).

Results

Water limitation of seedling establishment

A total of 490 newly emerged seedlings were monitored in the two study years. This figure included 307 in the 2005 cohort (122 in Escobarejos and 185 in Cerezal) and 183 in the 2006 cohort (80 in Escobarejos and 103 in Cerezal). Almost all seedlings emerged at very short distances from the closest stream (our proxy variable for water availability), that is, within the first distance class (0–10 m). This emergence pattern was consistent for all populations and years, as shown by strong deviation of the frequencies of emergence in four different distance classes from random expectations ($\chi^2 > 27.47$, $DF = 3$, $p < 0.001$ in all possible combinations). In addition, emergence was significantly concentrated with respect to microhabitat, in such a way that, along stream banks, >80% of seedlings were found beneath yew trees or under fleshy-fruited shrubs.

Seedling survival was extremely low in all populations and years. Only 15.9% of the seedlings monitored survived after the first summer. More seedlings survived in 2006 (28% in Escobarejos and 18% in Cerezal) than in 2005 (14 and 10%, respectively). These figures contrast with survival for the second summer, with all second-year seedlings surviving. There were significant effects of distance to stream, population, and microsite on the probability of seedling establishment after the first summer (Table 1). Concerning microsite, survival was clearly enhanced within patches of mosses (69%) as compared with bare ground (13%) or grasses (40%). When microhabitat was included in the model its effect was not significant. However, the fact that both shrub categories pooled clearly enhanced survival (Table 2), suggests an additional effect of microhabitat that was independent of the distance to the stream.

The most important factor causing seedling death was water availability in summer, which accounted for 52 and 67% of mortality in 2005 and 2006, respectively. Second in importance were trampling by large herbivores in Escobarejos (29–40%) and accidental burial in Cerezal (15–21%).

Table 1. Results from generalized linear models analysis testing for the effects of year (2005, 2006), population (Cerezal, Escobarejos), and microsite (moss, grass, bare soil) on the establishment of yew seedlings after the first summer in two marginal populations of central Spain.

Predictor	Wald	DF	p
Distance to stream	12.374	1	<0.001
Year	0.200	1	0.654
Population	11.362	1	<0.001
Microsite	5.650	1	0.017
Year × Population	11.484	1	<0.001
Year × Microsite	1.283	1	0.257
Population × Microsite	0.501	1	0.479
Year × Population × Microsite	0.000	1	0.999

Predictions at regional scale

Distance to the nearest stream was by far the most significant variable explaining yew presence (mean value for random points was 151.4 ± 135.0 m as compared to 4.5 ± 2.1 m for yew points). Statistical comparisons of mean values for yew points and random points indicated very significant selectivity for streams ($U = 15.94$, $p < 0.001$, $n = 188, 200$), whereas no effect was evident for altitude ($t = 0.31$, $DF = 386$, $p = 0.760$). Also the species was more likely to occur in northeast orientations ($U = 6.04$, $p < 0.001$, $n = 188, 200$) and steeper slopes ($t = 5.82$, $DF = 386$, $p < 0.001$) than available. Overall, these results clearly support our prediction 1.

The size structure of populations showed a general regeneration failure as indicated by the low frequency of non-adult age classes, which were present in only 16.3% of the stands. Frequency distribution of RF was extremely right-skewed even when the index was decomposed by separately using saplings (recent regeneration) and juveniles (past regeneration; Fig. 2). A multiple regression analysis including all physiognomic and climatic variables and population size as predictors showed significant effects of summer precipitation ($p = 0.040$) and population size ($p = 0.00008$; Table 3). When we considered only 11 populations with five or more adults, the multiple model was not significant (results not shown). Nevertheless, summer precipitation successfully predicted RF in a simple linear

Table 2. Percentage of seedlings surviving after the first summer in different microhabitats in 2005 and 2006 in the marginal populations of Escobarejos and Cerezal, central Spain. The number of seedling found in each category is shown in parentheses.

	Escobarejos		Cerezal	
	2005	2006	2005	2006
Fleshy-fruited shrubs	23.5 (17)	75 (12)	26.4 (110)	22.8 (57)
Non fleshy-fruited shrubs	42.8 (21)	88.2 (17)	0 (1)	–
Yew	0 (68)	17 (47)	11.9 (42)	2.3 (44)
Open	12.5 (16)	25 (4)	28.1 (32)	50 (2)

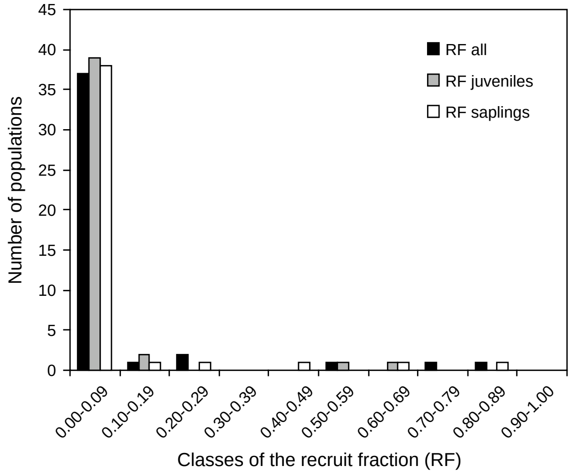

Figure 2. Frequency distribution of the index of regeneration (RF all), computed as the ratio of saplings plus juveniles to the total number of individuals including adults in a given population (n = 43 sites within the study region of northern Extremadura, central Spain). Also shown are a RF estimated for saplings (recent regeneration) and a RF estimated for juveniles (older regeneration).

regression ($t = 2.398$, DF = 9, $p = 0.039$), in agreement with our prediction 2.

Predictions at continental scale

Fifty-one (60%) out of 88 populations had values of RF below 0.5 and virtually no regeneration (RF < 0.1) was found in 27 (32%) populations (Supplementary material). RF was significantly affected by water availability when considering either summer precipitation ($r = 0.532$, $p = 0.019$) or annual precipitation ($r = 0.567$, $p = 0.032$; $n = 61$ central and southern populations). The values of RF increased linearly with water availability (Fig. 3), supporting our prediction 3. This was confirmed when, besides precipitation, population size was included as a predictor of RF in a multiple regression analysis. This analysis also showed a significant effect of summer precipitation and a non-significant effect of population size (Table 4).

To evaluate the strength of whole-range trends in RF we performed the above analyses including also data for 27 populations in northern Europe ($n = 88$; Supplementary material). There were significant differences in RF between latitudinal zones after removing the influence of population size in an ANCOVA ($F = 10.213$, DF = 2, 83, $p < 0.001$). On average central European populations showed significantly higher RF values than populations located at the northern ($p < 0.001$) and southern margins ($p < 0.001$; Fisher LSD post hoc tests). Therefore, the relationship between RF and latitude was much better described by quadratic rather than linear models ($R^2 = 14.62$, $p < 0.001$ in a linear model and $R^2 = 32.49$, $p < 0.001$ in a quadratic model; Fig. 4).

Discussion

Water-driven recruitment limitation: direct and indirect effects

Our results illustrate that yew emergence and recruitment were consistently enhanced in places with higher soil moisture availability. Thus, both demographic processes were controlled by a simple abiotic effect, as they depended only on a close spatial association with water sources, as found with other relict tree species in the Mediterranean (Brèda et al. 2006, Pulido et al. 2008). However, meeting water requirements was also dependent on biotic interactions, which determined the likelihood propagules reached well-watered places. Thus, seedling emergence was concentrated under the canopy of fleshy-fruit producing trees. This spatial pattern cannot be explained only by shared microhabitat requirements of seedlings and adult trees, but also by directional dispersal by frugivorous birds using fleshy-fruited trees as perches while foraging (García et al. 2000b, García and Obeso 2003).

Two additional plant-mediated effects may influence the spatial arrangement of yew recruits. Firstly, it was apparent that the transition from seedling to sapling was more likely to occur under shrubs. This survival pattern could be the result of a nurse effect involving microclimate amelioration, a mechanism that has been previously documented in Mediterranean populations of several gymnosperms (García et al. 2000a, Castro et al. 2004). Second, a positive effect of mosses on seedling survival was also found. Presence of mosses has been previously reported as a good predictor of survival, presumably due to a high water retention capacity (Mejías et al. 2002, Dovciak et al. 2007).

Table 3. Results from multiple regression analysis at a regional scale ($n = 43$ yew sites located in northern Extremadura, central Spain) using physiognomic and climatic variables, and population size as predictors of the regeneration success (recruits fraction, RF, estimated as the ratio of saplings plus juveniles to the total number of individuals). Results for the whole model are: $R^2 = 45.54$, $F = 4.868$, DF = 8, 29, $p = 0.0007$).

	β	SE β	B	SE B	t	p
Intercept			1.689	1.229	1.373	0.189
Elevation	0.362	0.169	0.000	0.000	2.145	0.040
Irradiance	−0.343	0.137	−0.003	0.001	−2.297	0.018
Flow accumulation	0.118	0.195	0.000	0.000	0.607	0.548
Wetness index	−0.020	0.192	−0.003	0.024	−0.109	0.913
Summer rainfall	0.432	0.201	0.015	0.007	2.147	0.040
Annual rainfall	−0.211	0.199	−0.001	0.001	−1.056	0.299
Distance to stream	0.027	0.131	0.000	0.001	0.207	0.836
Population size	0.594	0.129	0.011	0.002	4.589	8×10^{-5}

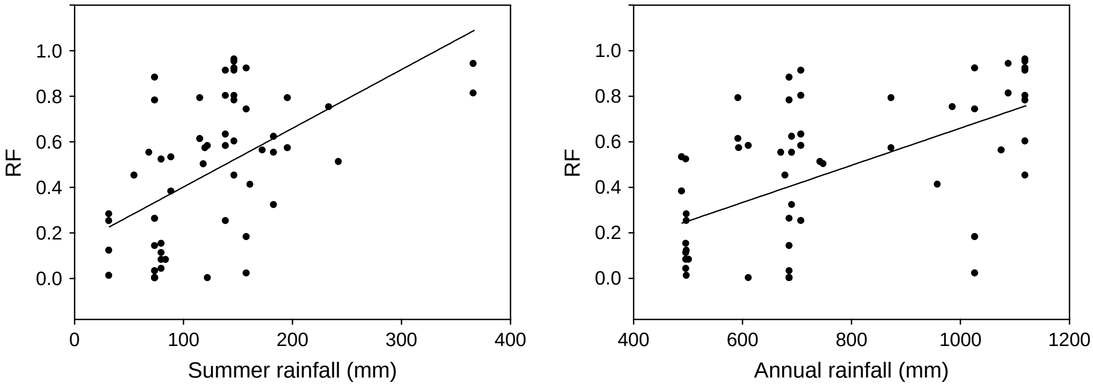

Figure 3. Relationships between the amount of summer and annual rainfall and the regeneration success of yew (as estimated by the recruit fraction, RF, computed as the ratio of saplings plus juveniles to the total number of individuals including adults). Data refer to 61 central and southern European populations of yew located between 36° and 50°N latitude. Partial correlations between RF and rainfall, after accounting for population size, are $r = 0.408$, $p = 0.004$ for annual rainfall, and $r = 0.560$, $p < 0.001$ for summer rainfall.

Abiotic constraints acting at a regional scale

At a regional scale adult yew trees grew in close spatial association with streams, where they experienced lower water demands, thus supporting prediction 1. This distributional pattern also could be influenced by anthropogenic disturbances, such as burning and grazing, whose impact could be lower in the less accessible mountain streams where yew stands are usually found. Nevertheless, drought stress was by far the most important cause of seedling death in all years and populations. On the other hand, yew stands concentrated not only in the close vicinity of streams, but also in north-facing slopes where summer drought could be alleviated due to reduced incidence of solar irradiance.

Besides yew distribution, the regeneration success was influenced by summer precipitation, thus supporting prediction 2. We can thus conclude that the main abiotic constraint acting at the population level also shaped the spatial structure and regeneration success of yew at a regional level. Though our characterization of the moisture environment at a regional scale relied on simple proxies and not on direct measures, we were able to detect a consistent relationship between water supply and yew distribution and regeneration.

Scaling up the continental scale

A trend towards decreased regeneration at the southern edge was observed as predicted, since the prevailing climate at the southern edge is characterized by a pronounced summer drought. This is critical for tree recruitment, in concurrence with results obtained at the population and regional levels. In addition, the recent and predicted trend towards decreased precipitation in the Mediterranean (IPCC 2001) can be hypothesized to affect range dynamics by 1) lowering population viability in the southern belt (the rear edge) and 2) by increasing it at the leading edge (sensu Hampe and Petit 2005). Our results show that the former process is in fact taking place and it may well increase the risk of extinction of the southern populations in the coming decades.

The trend towards water-driven increased regeneration northwards did not hold when including populations at the highest latitudes. In fact, regeneration values in this zone were significantly lower than those recorded for central and southern populations. These results illustrate the existence of a centre-periphery trend towards decreased population viability in both northern and southern marginal areas (Lawton 1993, Brown et al. 1996). In the case of yew, factors like light availability (Iszkulo and Boratynski 2006) and frost and/or herbivore damage (Dovciak 2002,

Table 4. Results from multiple regression analyses at a continental scale with summer and annual rainfall and population size (number of adult trees) as predictors, and the index of regeneration (recruits fraction, RF, estimated as the ratio of saplings plus juveniles to the sum of all individuals) as dependent variable.

	β	SE β	B	SE B	t	p
Intercept			0.121	0.163	0.741	0.462
Population size	0.119	0.138	0.000	0.000	0.895	0.394
Annual rainfall	0.037	0.188	0.000	0.000	0.200	0.841
Summer rainfall	0.637	0.203	0.002	0.001	3.123	0.003

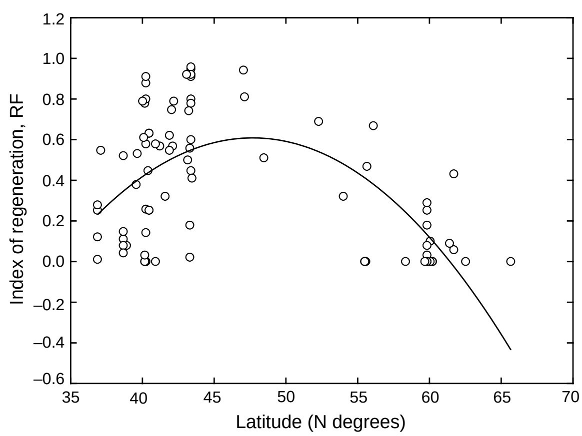

Figure 4. Relationship between latitude (N degrees) and the index of regeneration (RF, computed as the ratio of saplings plus juveniles to the total number of individuals including adults) for 85 European populations of yew. The best fit was that of a quadratic model: $RF = -10.55 + 0.48 \times L - 0.01 \times L^2$ ($R^2 = 35.30$).

Mysterud and Ostbye 2004, Iszkulo and Boratynski 2005) may be more important than water. Therefore, our results suggest a disparity in the factors regulating yew persistence across its range (Stewart Jr and Nilsen 1995, Santamaría et al. 2003).

Concluding remarks

We have shown that water availability regulates the persistence of yew populations. This in turn allowed us to predict the pattern of regeneration success at a continental scale and to gain insight into the ability of populations to face climate change. A plethora of recent studies using climatic envelope models (CEMs; Pearson and Dawson 2003), have assessed the risk of extinctions of thousands of species during the 21st century due to climate change (Thuiller et al. 2005). However, it is increasingly recognized that climate alone cannot adequately predict species distributional responses (Araújo and Luoto 2007, Svenning and Skov 2007). Thus, we propose that our future challenges should be: 1) to incorporate historical and biotic drivers into models predicting distribution shifts (Diniz-Filho and Bini 2008), and 2) to clarify how environmental factors control processes involved in species persistence through multiple scales (Whittaker et al. 2001). The approach developed in this paper sheds light on one of the potential ways to achieve this second goal.

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