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Can trait-based analyses of changes in species distribution be transferred to new geographic areas?

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ABSTRACT

Aim Anthropogenic environmental change is having a major impact on biodiversity. By identifying traits that correlate with changes in species range, comparative studies can shed light on the mechanisms driving this change; but such studies will be more useful for conservation if they have true predictive power, i.e. if their trait-based models can be transferred to new regions. We aim to examine the ability of trait-based models to predict changes in plant distribution across seven geographic regions that varied in terms of land cover and species composition.

Location Britain and Flanders (Belgium).

Methods We estimated distribution change for more than 1000 species for over 70 years of data (1930s to 2004), using data from published plant atlases. We identified regional trait-based models of plant distribution change. Traits included morphological characteristics, Ellenberg values and distribution-based traits. The trait models were then used to predict change in all other regions, with the level of linear correlation between predicted and observed changes in range used as a measure of transferability. We then related transferability to land cover and species similarity between regions.

Results We found that trait correlates of range change varied regionally, highlighting the regional variation in the drivers of range change in plants. These trait models also varied in the amount of variation explained, with r^2 values ranging from 0.05 to 0.17. A key cross-regional difference was the variation in the relationship between soil nutrient association (Ellenberg N) and distribution change, which was strongly positive in Flanders and southern England but significantly negative in northern Scotland. We found that transferability between regions was significantly correlated with the level of similarity in land cover.

Main conclusions We conclude that trait-based models can predict broad-scale changes in species distributions in regions that share similar land-cover composition; however, predictions between regions with differing land-cover cover tend to be poor.

Keywords

Biodiversity loss, comparative analysis, conservation, environmental change, predicting change, traits.

INTRODUCTION

The impacts of anthropogenic environmental change on biodiversity are well documented, with habitat loss, climate change

and invasive species all frequently related to changes in species distributions (Parmesan & Yohe, 2003; Blackburn *et al.*, 2004; Mace *et al.*, 2005; Butchart *et al.*, 2010). However, not all species respond in the same way to these environmental pressures

(Chen *et al.*, 2011), with species life-history traits explaining some of the variation (Purvis *et al.*, 2000; Koh *et al.*, 2004; Reynolds *et al.*, 2005; Walker *et al.*, 2009; Murray *et al.*, 2010; Angert *et al.*, 2011). An advantage of trait-based approaches is that they can allow generalizations to be extended to other species and can help determine the potential drivers of change (Fisher & Owens, 2004). Many comparative studies have linked change in range size to life-history traits (e.g. Verheyen *et al.*, 2003; Walker & Preston, 2006; Mattila *et al.*, 2008; Van Landuyt *et al.*, 2008; Ozinga *et al.*, 2009). A common goal of such studies is to help inform conservation efforts; however, there is little evidence of such studies directly affecting conservation practice – rather, they have acted as ‘calls to action’ highlighting the decline in biodiversity (Cardillo & Meijaard, 2011). One reason for this is that although such studies explain the responses of biodiversity within their own datasets, they seldom test the predictive ability of their models in new regions (Fisher & Owens, 2004; Pocock, 2011).

The transferability of trait-based comparative models has been examined using trends in population abundance of European and North American farmland birds (Pocock, 2011). That study found that the relationships from one region poorly predicted population trends in other regions, and that there was no significant improvement in model predictions when comparing environmentally similar regions (Pocock, 2011). These findings support the view that inconsistencies in the results of comparative studies limit their value to applied conservation (Cardillo & Meijaard, 2011). In this study we extend the predictive work of Pocock, (2011) by using a larger, high-quality dataset of the spatiotemporal distribution of plants from Flanders (Belgium) and six environmental regions in Britain to examine if the results from trait-based approaches can be used to predict change in new regions. We aim to test whether transferability is related to similarity in land cover and/or similarity of species composition between regions in an attempt to determine if, and when, it is possible to predict change from trait-based models.

Vascular plants are an ideal taxon for this investigation: they are the primary producers of most terrestrial ecosystems, are good indicators of the state of the environment (Godefroid, 2001; Landsberg & Crowley, 2004), and have some of the best trait and distribution data of any taxonomic group in Great Britain. Previous analyses have shown that similar drivers of range change can have similar effects across different regions. For example, the flora of Flanders has shown marked declines in species specialized for nutrient-poor habitats. This is probably because of increased nitrogen deposition, and analogous relationships were found in a trait-based study of trends in plant species prevalence in Bedfordshire, England (Van Landuyt *et al.*, 2008; Walker *et al.*, 2009). However, trait–trend relationships are not always congruent across regions; for example Fritz *et al.* (2009) showed marked geographic variation in trait-based relationships of extinction risk in mammals.

In this study, we use trait-based models to understand the key drivers of change in plant distribution in seven different regions. These models were then used to predict change in all other regions, with the level of linear (Pearson) correlation between

predicted and observed range change used as a measure of transferability. Transferability was then related to similarity of land cover and species composition between regions, to determine if, and when, trait-based models can be used to predict change.

METHODS

Study regions

In this study, Britain was split into six environmental regions as identified by the Centre for Ecology and Hydrology Countryside Survey (Haines-Young *et al.*, 2000). The division is based mainly on the geographic distribution of the major land classes but is also split by the English–Scottish border (Fig. 1). An overview of the study areas can be found in Appendix S1 in Supporting Information.

Distribution and trait data

Presence-only gridded distribution data for vascular plant species in Britain (10 km × 10 km grid) and Flanders (4 km × 4 km grid) were taken from two plant atlases: 1930–69 and 1987–99 (Preston *et al.*, 2002) and 1939–71 and 1972–2004 (Van Landuyt *et al.*, 2006), respectively. Recently established alien species may have distributions that have not reached equilibrium range dynamics since their introduction. The rapid range expansion associated with many introduced species would be likely to bias our estimates of range change and trait–trend relationships, so we therefore only included native and archaeophyte species in the analyses. Data on plant life-history traits were taken from PLANTATT (Hill *et al.*, 2004). Eleven traits were included in the analyses, all of which have been associated with changes in plant distribution; they are listed and briefly described in Table 1 (Ellenberg, 1974; Liem *et al.*, 1985; Preston, 2000; Godefroid, 2001; Haines-Young *et al.*, 2003; Braithwaite *et al.*, 2006; Walker & Preston, 2006; Van Landuyt *et al.*, 2008). Ellenberg scores represent the niche position of species along ecological gradients and are derived from subjective expert opinion alongside objective calculations (Ellenberg, 1974; Hill *et al.*, 1999; Schaffers & Sýkora, 2000). There was increased survey effort for water plants in Britain in the second time period due to targeted surveys of Scottish lochs (Preston & Croft, 1997; Preston *et al.*, 2002). Therefore we excluded species with an Ellenberg moisture value greater than 9 (aquatic plants) from the analysis as they may have had artificially high estimates of distribution change.

Range change

We measured distribution change across two distinct time periods as defined by the survey periods of the atlases (Britain 1930–69 and 1987–99; Flanders 1939–71 and 1972–2004). Distribution change was measured with the widely used relative change index (CI). The CI method aims to reduce problems associated with temporal variation in recorder effort, which were likely to be present in the data (Telfer *et al.*, 2002; Pocock

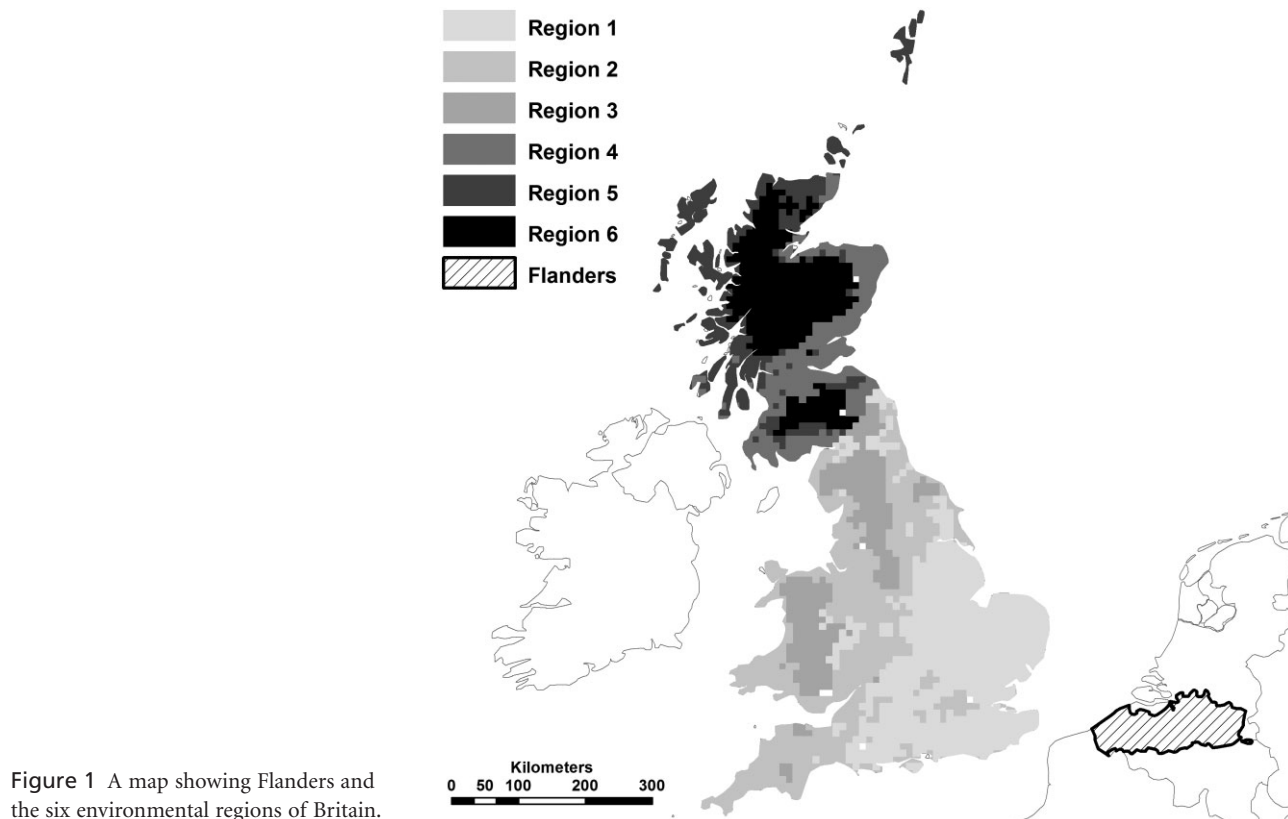


Figure 1 A map showing Flanders and the six environmental regions of Britain.

Table 1 A list and brief description of the species traits included in the analyses.

Trait	Description
Plant height (cm)	Plant height
Mean January temperature (°C)	Mean January temperature of all UK 10-km squares occupied, 1961–90
Mean annual precipitation (mm)	Mean annual precipitation of all UK 10-km squares occupied, 1961–90
Ellenberg <i>L</i>	Ellenberg value for light association (1 = deep shade, 9 = full light)
Ellenberg <i>S</i>	Ellenberg values for salt tolerance (0 = absent from saline soils, 9 = extremely saline conditions)
Ellenberg <i>N</i>	Ellenberg values for nitrogen association (soil fertility) (1 = extremely infertile, 9 = extremely rich in nitrogen)
Ellenberg <i>R</i>	Ellenberg values for pH (1 = extreme acid soils, 9 = high-pH soils)
Ellenberg <i>F</i>	Ellenberg values for moisture association (1 = dry, 9 = wet-site indicator)
Habitat breadth	A count of the number of habitat categories the species occupies (based on the 23 categories in PLANTATT)
Biome	Major biome of the species European range. Northern (1–5 in PLANTATT), widespread (6 in PLANTATT), temperate (7 in PLANTATT), southern (8–9 in PLANTATT)
Life cycle type	Species categorized as either annual, biennial or perennial

For PLANTATT, see Hill *et al.* (2004).

et al., 2006; Van Calster *et al.*, 2008; Van Landuyt *et al.*, 2008; Mace *et al.*, 2010). The CI (Z in the equation below) was calculated as the deviation between the observed and the predicted range size proportions, both on a logit scale:

$$Z_k = \text{logit}(P_{2k}) - [a + b, \text{logit}(P_{1k})]$$

where P_{1k} and P_{2k} are the range size proportions for the k th species for the first and second time period, a and b are the intercept and the slope of the regression.

Fitting of the regression line was weighted by the reciprocal of the variance in the logit proportions to account for heteroscedasticity (Telfer *et al.*, 2002). The intercept and slope of the regression include the effects of change in range size and variation in recorder effort across all species. Small-ranged species have a greater capacity for expansion than decline, which can cause curvature in the relationship between grid cell counts in the earlier and later time periods. To account for this, species that occupied fewer than five grid cells in the first time period were excluded from the analysis (for full details see Telfer *et al.*, 2002). The CI was

calculated separately for each region in the analysis (for regional plots of the CI regressions, see Appendix S2).

Regional trait-based models

For each region, we ran models that consisted of all possible combinations of the traits listed in Table 1 as predictor variables. We then used the Akaike information criterion (AIC) to determine the 'best' model for each region. Trends from the best models were examined to detect variation in the main drivers of distribution change across regions. In all analyses we tested for curved relationships by including the quadratic term for each continuous explanatory variable; significant quadratic terms were retained in the full model. We checked for collinearity between the trait variables using Pearson's correlation coefficient (r). Treating species as independent data points in statistical analyses increases the risk of Type I errors (incorrectly rejecting the null hypothesis) as closely related species might share similar traits due to common ancestry (Harvey, 1996). To account for this non-independence we used phylogenetic generalized linear models (PGLMs) and estimated Pagel's λ in all trait-based models (Pagel, 1999; Freckleton *et al.*, 2002). Pagel's λ is a measure of phylogenetic signal within a variable. It is bounded between 0 and 1, with a λ value of 0 indicative of phylogenetic independence, while a λ of 1 is complete phylogenetic dependence. A benefit of estimating Pagel's λ as part of model fitting is that problems associated with under-correcting ($\lambda = 0$) and over-correcting ($\lambda = 1$) for phylogenetic autocorrelation are reduced. We used the online tool PHYLOMATIC (Webb & Donoghue, 2005) to generate the phylogenetic framework of all species included in our analyses. The PHYLOMATIC phylogeny is based on a tree developed by the Angiosperm Phylogeny Group (APG III, 2009), and in this study all branch lengths were set to one. All analyses were carried out

using R version 2.14.2 (R Development Core Team, 2012), with the `pgls` function from the `caper` package used for the PGLMs (Orme, 2012).

Transferability

Using the best trait-based model from each region we carried out cross-region predictive analyses. For each region, CI was predicted for all species using the trait–trend relationships identified in the best models from the other regions. This resulted in six sets of species CI predictions for each region. Transferability was then estimated for all pair-wise regional comparisons as the Pearson's product moment correlation coefficient between observed CI and predicted CI. For all pair-wise regional comparisons transferability was correlated with the level of similarity in species composition and percentage similarity in land cover to help identify if, and when, trait-based models can be transferred to new regions. Due to the non-independence of the pair-wise regional comparisons, the significance was estimated using Mantel tests with 1000 iterations (Manly, 2007). For each pair-wise regional comparison we had two model predictions, one for each direction (i.e. the Flanders model predicts region 1 and the region 1 model predicts Flanders). Transferability was estimated as the mean of the pair of predictions, for use in the Mantel tests. Land-cover similarity was estimated from the proportional cover of each broad land-use class for each region using data derived from satellite imagery: Britain (Morton *et al.*, 2011) and Flanders (Wils *et al.*, 2004) (Fig. 2). We used an index of percentage similarity (Renkonen, 1938; Jost *et al.*, 2011) to calculate land-cover similarity, while the conditional Sørensen's similarity index (Lennon *et al.*, 2001) was used to calculate similarity of species composition. These similarity metrics were chosen as they are both widely used and are suitable given the type of data in this study (land-use percentage cover and species lists) (Magurran, 2004; Jost *et al.*, 2011).

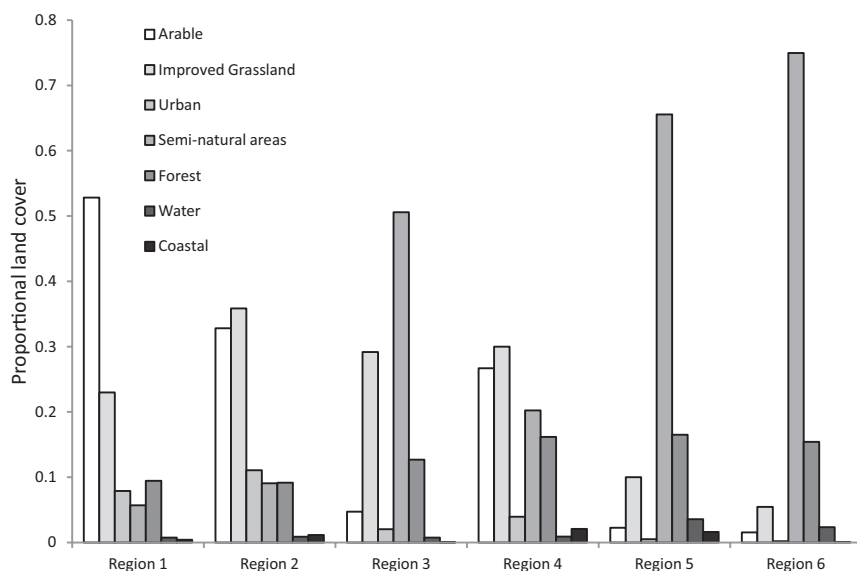


Figure 2 The land-cover composition of each region. The height of the bars represents the proportion of each land-cover class.

RESULTS

Comparison of regions

The proportional cover of each broad land-use type is shown in Fig. 2. In terms of land cover, Flanders is most similar to regions 1 and 2 in southern Britain (Table 2, Fig. 3); these regions are characterized by intensive agriculture and a moderate to high proportion of artificial surfaces. In contrast, regions 5 and 6 are predominantly forest and semi-natural areas with only a small amount of agricultural and artificial land. In terms of species composition, regions 1, 2 and 4 are most similar to Flanders, and there is a general trend of geographically closer regions tending to have similar species compositions (Table 2).

Trait-based relationships

The number of significant traits in the best regional models varied, from four in regions 1, 3 and 4 to seven in region 2. The direction and strength of trait relationships varied considerably across regions (Table 3). A key cross-region difference was the

variation in the relationship between Ellenberg *N* (soil nutrients) and CI: strongly positive in Flanders and region 1, but significantly negative in region 6 (Fig. 3). Life cycle type was a significant predictor of change in region 5, where annual plants showed lower CI scores compared with biennial and perennial plants. Habitat breadth was significantly positively related to CI in all regional models. The variation in CI explained by the regional models varied between 17 and 5%, with the most variance explained in the Flanders model (Table 4). In all regions, except Flanders, λ values were significantly different from 0 (λ values in Table 4).

Transferability

We found that transferability of the regional trait-based models varied across regions and ranged from negative (Pearson's $r = -0.124$) to positive ($r = 0.367$) values (Fig. 4). The most positive predictions of change were between regions 1, 2 and Flanders. The most negative prediction was found between observed CI in Flanders and predicted CI from the region 5 model. In this

Table 2 Similarity scores for all pair-wise region comparisons. The conditional Sørensen's index of the similarity of species composition between regions is above the diagonal, while Renkonen's percentage similarity index of land cover between regions is below the diagonal. The shading of the box relates to the level of similarity, the darker the shade the greater the similarity.

	Flanders	Region 1	Region 2	Region 3	Region 4	Region 5	Region 6	
Flanders	–	0.90	0.88	0.79	0.79	0.76	0.76	Species compositional similarity
Region 1	0.74	–	0.94	0.92	0.96	0.91	0.89	
Region 2	0.78	0.80	–	0.94	0.97	0.93	0.90	
Region 3	0.45	0.46	0.55	–	0.91	0.90	0.92	
Region 4	0.69	0.70	0.81	0.70	–	0.92	0.89	
Region 5	0.27	0.29	0.33	0.77	0.52	–	0.93	
Region 6	0.22	0.23	0.26	0.71	0.45	0.91	–	
	Land cover similarity							

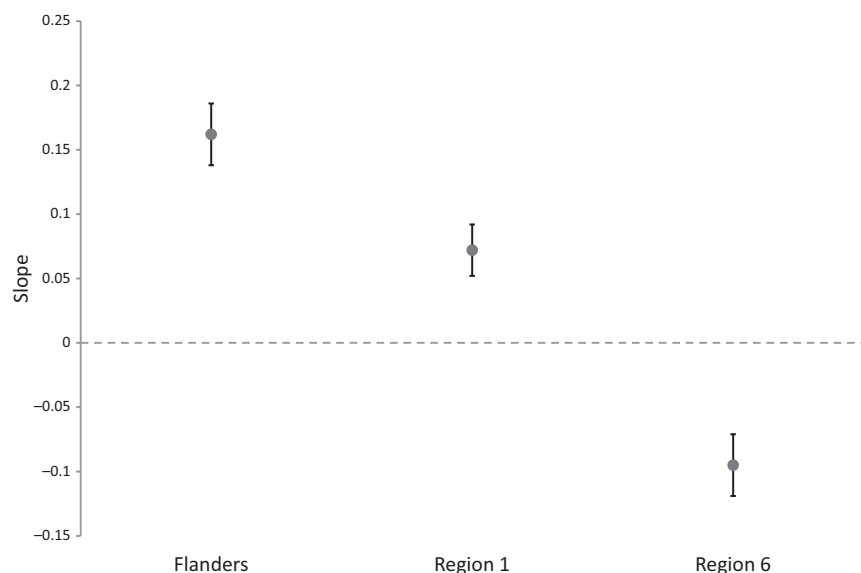


Figure 3 The slope of the relationship between Ellenberg *N* and plant range change (CI) for each region where it was retained in the best model. The error bars are the standard error of the slope.

Table 3 Parameter estimates taken from the best trait-based phylogenetic generalized linear models of plant distribution change for each region.

	Coefficient	SE	<i>t</i>	<i>P</i>
(a) Flanders				
Intercept	−3.20	0.839	−3.8	< 0.001
Mean precipitation (mm)	0.003	0.002	2.1	0.040
Mean precipitation (mm) ²	-1.31×10^{-6}	7.09×10^{-7}	−1.9	0.065
Ellenberg <i>R</i>	0.436	0.149	2.9	0.004
Ellenberg <i>R</i> ²	−0.034	0.013	−2.5	0.012
Ellenberg <i>N</i>	0.162	0.024	6.8	< 0.001
Log height	−0.405	0.145	−2.8	0.005
Log height ²	0.050	0.015	3.3	0.001
Habitat breadth	0.147	0.046	3.2	0.001
(b) Region 1				
Intercept	−0.517	0.483	−1.1	0.285
Biome – southern	0.104	0.083	1.2	0.215
Biome – temperate	−0.076	0.076	−1.0	0.318
Biome – widespread	0.560	0.230	2.4	0.015
Habitat breadth	0.138	0.041	3.3	< 0.001
Log height	−0.205	0.142	−1.5	0.149
Log height ²	0.038	0.016	2.4	0.016
Ellenberg <i>N</i>	0.072	0.020	3.5	< 0.001
(c) Region 2				
Intercept	−1.369	0.732	−1.9	0.062
Biome – southern	0.148	0.100	1.5	0.137
Biome – temperate	−0.022	0.085	−0.3	0.793
Biome – widespread	0.510	0.231	2.2	0.028
Habitat breadth	0.244	0.043	5.7	0.000
Ellenberg <i>L</i>	−0.281	0.163	−1.7	0.085
Ellenberg <i>L</i> ²	0.021	0.013	1.7	0.096
Log height	0.085	0.034	2.5	0.013
Mean precipitation (mm)	0.000	0.000	2.4	0.018
Ellenberg <i>R</i>	0.075	0.024	3.1	0.002
Mean January temperature (°C)	0.129	0.061	2.1	0.036
(d) Region 3				
Intercept	−1.755	0.388	−4.5	< 0.001
Ellenberg <i>F</i>	0.090	0.022	4.1	< 0.001
Habitat breadth	0.151	0.046	3.3	0.001
Log height	0.065	0.036	1.8	0.074
Mean January temperature (°C)	0.214	0.057	3.8	< 0.001
(e) Region 4				
Intercept	−2.750	0.806	−3.4	0.001
Biome – southern	0.024	0.105	0.2	0.818
Biome – temperate	0.118	0.089	1.3	0.186
Biome – widespread	0.523	0.230	2.3	0.023
Ellenberg <i>F</i>	0.111	0.023	4.9	< 0.001
Habitat breadth	0.126	0.046	2.7	0.007
Mean precipitation (mm)	0.003	0.001	2.6	0.010
Mean precipitation ² (mm)	-1.493×10^{-6}	0.000	−2.8	0.006
(f) Region 5				
Intercept	0.356	0.406	0.9	0.381
Ellenberg <i>F</i>	0.099	0.023	4.4	< 0.001
Habitat breadth	0.122	0.045	2.7	0.007
Log height	−0.092	0.037	−2.5	0.014
Life cycle – biennial	0.543	0.199	2.7	0.007
Life cycle – perennial	0.438	0.101	4.3	< 0.001
Mean precipitation (mm)	−0.001	1.517×10^{-4}	−3.9	< 0.001
Ellenberg <i>R</i>	−0.057	0.025	−2.3	0.022
(g) Region 6				
Intercept	−0.624	0.355	−1.8	0.079
Ellenberg <i>F</i>	0.129	0.023	5.6	< 0.001
Habitat breadth	0.086	0.049	1.8	0.081
Ellenberg <i>L</i>	−0.071	0.033	−2.2	0.030
Log height	0.197	0.040	4.9	< 0.001
Ellenberg <i>N</i>	−0.095	0.024	−3.9	< 0.001

case, species with a positive CI in region 5 were likely to have a negative CI in Flanders, and vice versa.

The amount of variance explained in the predictive models varied between 1.687×10^{-6} and 0.14 (Fig. 4). Land-cover similarity (Renkonen's percentage similarity index of land cover) was significantly and positively correlated with transferability (correlation coefficient = 0.80 Mantel $p = 0.012$; Fig. 5), whereas a weaker non-significant relationship was found between similarity of species composition (conditional Sørensen's species similarity index) and transferability (correlation coefficient = 0.42, Mantel $p = 0.055$).

DISCUSSION

In this study, we examined the ability of trait-based models to predict changes in distribution in new geographic regions. We found that transferability varied across the pair-wise regional comparisons, and was correlated with the level of similarity in land cover. These results contrast with those of a previous study on bird abundance, which found that transferability was not improved when comparing regions that share similar landscape

characteristics (Pocock, 2011). This difference may be due to the greater variation in the intensity and direction of the trait–trend relationships in our study. The models in Pocock (2011) were broadly consistent across regions (declining population size tended to share such traits as medium body size, small brain size, undertaking long distance migration and specializing in farmland habitat), whereas we found that the sign of one significant relationship – that between Ellenberg N and CI – changed from positive in southern regions to negative in northern regions (Fig. 3). It should also be noted that the plant models in this study are based on approximately 25 times more species than the bird abundance models (Pocock, 2011). In addition to having

Table 4 Model coefficients from the phylogenetic generalized linear trait-based models of plant distribution change for each region.

Region	d.f.	F	SE	r^2	λ (95% CI)	Model P
Flanders	676	19.3	0.251	0.176	0.077 (0, 0.233)	< 0.001
Region 1	900	10.2	0.338	0.076	0.563 (0.308, 0.741)	< 0.001
Region 2	908	7.4	0.283	0.065	0.293 (0.126, 0.502)	< 0.001
Region 3	730	10.8	0.304	0.051	0.323 (0.112, 0.585)	< 0.001
Region 4	655	6.9	0.273	0.059	0.176 (0.042, 0.459)	< 0.001
Region 5	630	8.8	0.273	0.079	0.247 (0.081, 0.510)	< 0.001
Region 6	587	13.3	0.264	0.084	0.065 (0.016, 0.210)	< 0.001

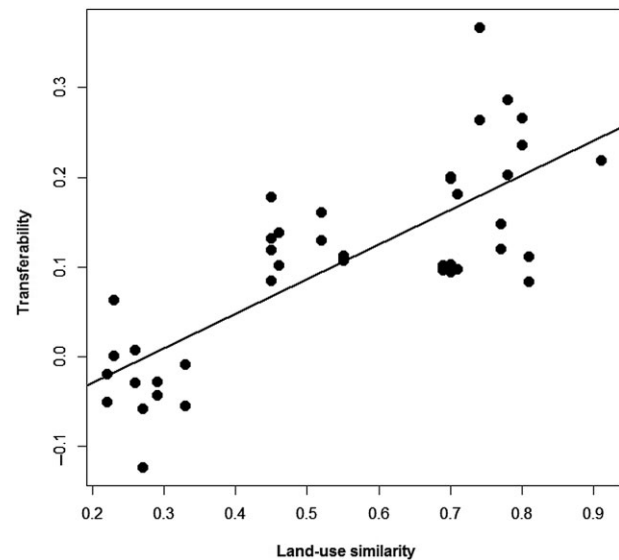


Figure 5 The significant positive relationship between transferability (pair-wise Pearson's product-moment correlations) and land-cover similarity for all pair-wise regional comparisons (slope = 0.387, SE = 0.047, $t = 8.108$, Mantel $p = 0.017$).

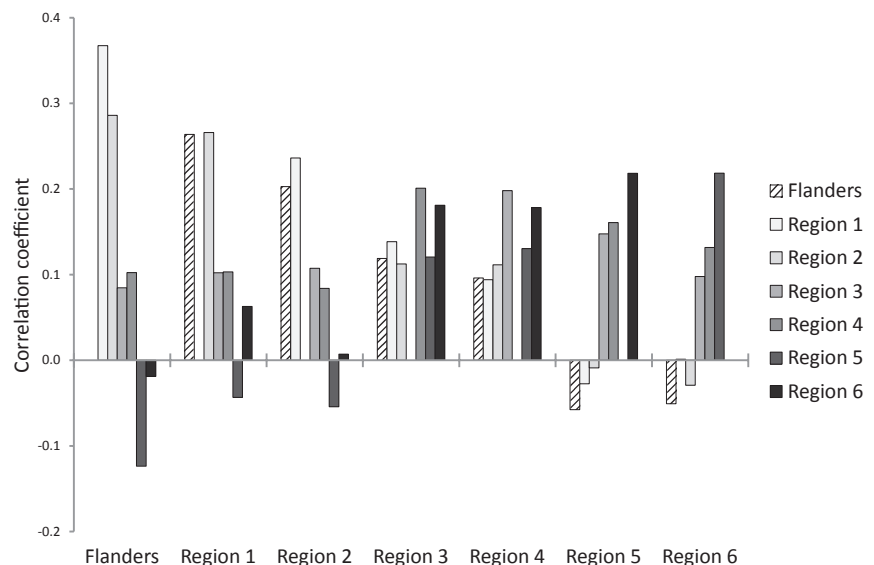


Figure 4 The Pearson's product-moment correlation coefficients between observed and predicted plant range change (CI) for each pair-wise regional comparison.

fewer species, farmland birds are likely to be a more uniform group than the plants of Flanders and Britain, meaning that there will be less opportunity for variation to occur in the trait–trend relationships between regions and this may explain the reduced variation in transferability.

Range change dynamics in Flanders were best predicted by the models from regions 1 and 2 in Britain. These regions of southern Britain were most similar to Flanders in terms of current land cover but also past changes in land use. Over the time period of this study the landscapes of Flanders and southern Britain (regions 1 and 2) have undergone extensive agricultural intensification (Haines-Young *et al.*, 2000; Stoate *et al.*, 2001; Robinson & Sutherland, 2002; Van Landuyt *et al.*, 2008), which was detected in the trait-based models: Ellenberg *N* was significantly positively related to CI. Agricultural intensification and the widespread use of fertilizers result in high levels of nitrogen deposition and in turn the decline of less competitive species that are dependent upon nutrient-poor habitats (Preston, 2000; Braithwaite *et al.*, 2006; Walker & Preston, 2006; Van Landuyt *et al.*, 2008; Walker *et al.*, 2009; McClean *et al.*, 2011). This result confirms that the same environmental drivers have similar effects on biodiversity across multiple regions, which can be detected separately by the regional trait-based models. The models for region 5 predicted the reverse CI trends in the flora of Flanders, i.e. a species with a positive CI value in Flanders was likely to have a negative CI value in region 5. This highlights our finding that transferability is low between regions with dissimilar landscapes. The trait signal in region 5 was different from that of Flanders and southern Britain; life cycle type was a key significant parameter with annual plants undergoing strong declines. This again reflects the history of land-use change: the trends are probably due to the decline in arable weeds as a result of a reduction in small-scale arable cultivation, as mixed farming gave way to purely pastoral agriculture in northern Scotland and the Scottish islands (Pearman & Preston, 2000; Evans *et al.*, 2002; Pearman *et al.*, 2008). This is emphasized by the top three declining annual plants (excluding *Euphrasia* spp. which may have artificially low CI scores due to taxonomic uncertainty) in region 5 which are all arable weeds (*Chrysanthemum segetum* CI = −4.79, *Anthemis cotula* CI = −3.96, *Stachys arvensis* CI = −2.51). We found little evidence to suggest that regions with high transferability shared a greater number of common traits in their respective models than those with poor predictive ability. However, traits that were present in both models for regions with high transferability had similar slopes, therefore driving an increase in transferability. In contrast, the trait–trend relationships tended to be different for common traits in models with low transferability (for example, the variation in the Ellenberg *N* trait–trend relationships between regions 1 and 6 and Flanders; Fig. 3).

We found low r^2 values associated with our regional trait-based models and also with the transferability of our models (also seen in Pocock, 2011). We may not expect high r^2 values because local, fine-scale drivers, including species interactions, may influence changes in plant distribution but will not be detected in the regional trait-based models. Also, despite using a

CI method to account for recorder effort bias, there may have been a small amount of residual error in estimation of range change that could have contributed to noise in the data. An alternative approach to increase the variation explained by our models would be to increase trait coverage. We examined the potential for including additional trait predictors in our models, finding that inclusion of some commonly measured leaf parameters (leaf size, specific leaf area and leaf dry matter content) from TRY (<http://www.try-db.org>) and LEDA (Kleyer *et al.*, 2008) would result in a substantial loss of species in our analysis. The negative consequences of losing species are exacerbated, as the lost species are unlikely to be a random subset, with rarer species less likely to be measured. In an attempt to improve r^2 in the transferability of our models, we re-ran our models on a subset of the data; only species that were shared between the regions were included. In general the patterns of transferability remained the same, as emphasized by the Pearson's correlation coefficients between the pair-wise transferability estimates, $r = 0.95$. In our study, we used the Pearson correlation coefficient to assess transferability. Other indices have been proposed to test for agreement between observed and predicted data, such as the root mean squared error of predictions (Roxburgh & Mokany, 2010). Testing alternative ways to assess transferability is an interesting area for further studies.

In conclusion, we found trait-based models to be sensitive to geographic variation in the main drivers of change, showing that they can detect the impact of agricultural intensification in southern England and Flanders, but also the loss of annual plants due to a shift in the agricultural practices in northern Scotland. The regional trait-based models suffered from low r^2 values, but despite this we were still able to detect that the transferability of these models was positively related to land-cover similarity. This study highlights the potential value that well specified trait-based models may have in making further progress in this area of predictive modelling for the benefit of conservation.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1 An overview of each region included in the analysis.

Appendix S2 The relationship between the early and late logit-transformed proportional counts for each region.

BIOSKETCH

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