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Variation in habitat suitability does not always relate to variation in species' plant functional traits

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Habitat suitability models, which relate species occurrences to environmental variables, are assumed to predict suitable conditions for a given species. If these models are reliable, they should relate to change in plant growth and function. In this paper, we ask the question whether habitat suitability models are able to predict variation in plant functional traits, often assumed to be a good surrogate for a species' overall health and vigour. Using a thorough sampling design, we show a tight link between variation in plant functional traits and habitat suitability for some species, but not for others. Our contrasting results pave the way towards a better understanding of how species cope with varying habitat conditions and demonstrate that habitat suitability models can provide meaningful descriptions of the functional niche in some cases, but not in others.

Keywords: ecological niche; mixed models; information theory; intraspecific variability

1. INTRODUCTION

The concept of an ecological niche, traditionally used to describe how a species responds to the environment (Austin *et al.* 1990), has further been used in biogeography to explain why species occur where they do by relating observed presence/absence to environmental gradients, leading to the development of habitat suitability models (Guisan & Thuiller 2005). Predictions from these models are generally thought to be good indicators of habitat suitability, and thus of species' performance. The basic assumption is that, among the habitats occupied by the species, the more frequent are also the more suitable (Albert & Thuiller 2008).

To our knowledge, this assumption has been little investigated (Wright *et al.* 2006; Elmendorf & Moore 2008) and no extensive *in situ* observations have been used to assess whether this simplification of the original definition of the species niche is realistic. While it is difficult to obtain real measures of species performance along environmental gradients, it has been shown that functional traits (physiological, morphological or phenological) could be considered good surrogates (Violle *et al.* 2007). If habitat suitability models relate to change in functional traits (e.g. intraspecific variability), they give a relevant proxy for species performance. Indeed, species should have a higher performance in the core of their niche (i.e. where conditions are more suitable) than at their edges (Pulliam 2000).

In this paper, we investigate, for a set of common plant species, whether species' functional trait measured along gradients are related to predicted habitat suitability. Using 16 plant species in two study areas in the French and Swiss Alps, we demonstrate empirically that habitat suitability and trait expression closely covary for some species, whereas no relationship is detectable for other species, providing moderate support to the use of empirical habitat suitability models to deliver functionally meaningful descriptions of species' niches.

2. MATERIAL AND METHODS

We performed *in situ* trait measurements, habitat suitability modelling and confrontation of trait variation and predicted habitat suitability in two different study areas (see the electronic supplementary material, figure S1): 'Guisane' in the central French Alps (1200–2700 m) and 'Anzeindaz' in the western Swiss Alps (1100–2400 m).

(a) *Species and functional traits selection*

We selected a set of common plant species representing various alpine life forms (dwarf-woody, tall-woody, grass and herbaceous). Sixteen species were chosen in Guisane and five of these in Anzeindaz (table 1). Presence/absence data of the selected species were extracted from the database of the Conservatoire Botanique National Alpin (French site) and from the Swiss Floristic Center (CRSF) database in Geneva (see the electronic supplementary material).

We measured three functional traits strongly related to species' functional strategies (Westoby *et al.* 2002): maximum vegetative height ($H_{\max}$, distance between the top of photosynthetic tissue and the ground) which is associated with the plant competitive vigour; leaf dry matter content (LDMC: the oven-dry mass of a leaf divided by its water-saturated fresh mass, expressed in $\mathrm{mg\,g^{-1}}$) which is usually negatively correlated with the relative growth rate; and leaf nitrogen content (LNC: the total amount of nitrogen per unit of dry leaf mass, in $\mathrm{mg\,g^{-1}}$) which is closely linked to the maximum photosynthetic rate (Cornelissen *et al.* 2003).

(b) *Field traits measurements*

To measure how these plant functional traits vary within species, we sampled each species in several contrasted environmental conditions. To maximize the sampled environmental heterogeneity, we stratified the study sites by two orthogonal climatic gradients for each site (Guisane: minimum temperature of the coldest month and solar radiation in August; and Anzeindaz: mean January temperature and solar radiation in August). We then combined this environmental stratification with known occurrences (see the electronic supplementary material, figure S1) to select between 6 and 18 plots for each species in each study site. In each plot, three sub-plots were randomly selected and in each sub-plot three mature and non-grazed individuals were randomly selected and measured (figure 1).

(c) *Calibration of habitat suitability models*

To calibrate habitat suitability models, we used comparable sets of non-correlated topo-climatic variables for both sites (figure 1). In Guisane we used: slope, topographic position, growing degree-days (5.56°), moisture index during the growing season, temperature of the coldest month, and annual solar radiation from the meteorological model Aurelhy (Benichou & Le Breton 1987) at 50 × 50 m. In Anzeindaz we used: slope, topographic position, mean annual temperature, mean annual solar radiations, and mean annual moisture index at 25 × 25 m (Zimmermann & Kienast 1999).

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Table 1. R^2 and signs of the relationship between variation in habitat suitability and variation in species' functional traits (only R^2 higher than 5% are noted).

	Guisane/Anzeindaz		
species	LDMC	LNC	$H_{\max}$
Carex sempervirens	69.6 [−]/—	34.1 [+]/—	—/18 [+]
Dactylis glomerata	—/—	33.7 [−]/ 48.8 [−]	—/—
Dryas octopetala	—/—	42.8 [+]/—	—/45.3 [+]
Festuca paniculata	—	—	—
Geum montanum	21.5 [+]	—	23.3 [+]
Juniperus sp.	13 [+]	—	20.9 [+]
Larix deciduas	—	45 [−]	33.8 [+]
Leucanthemum vulgare	—	64 [+]	58.5 [+]
Pinus sp.	37.4 [−]	—	31.0 [+]
Polygonum viviparum	—	62.1 [+]	—
Rhododendron ferrugineum	—	—	—
Sesleria caerulea	—/—	41.7 [+]/—	—/33.7 [−]
Salix herbacea	5.1 [+]	100 [+]	18.8 [−]
Silene nutans	—	8.5 [−]	9.7 [+]
Trifolium alpinum	—	49.5 [−]	—
Vaccinium myrtillus	—/60.2 [+]	—/25.4 [−]	63.1 [+] /51.3 [−]

We fitted models using the information-theory approach based on all possible sub-models ($2^{\text{number of candidate variables}}$) for a set of explanatory variables (see the electronic supplementary material). Inference from more than one single 'optimal' model allows the resulting habitat suitability to be the average from all possible candidate models weighted by their weights of evidence (see the electronic supplementary material).

Using this framework, we modelled species' habitat suitability with generalized additive models (see electronic supplementary material). We then extracted the predicted habitat suitability for each sampling plot where we measured the functional traits (figure 1). For each calibrated model, we calculated its predictive accuracy using the area under the curve (AUC) of a receiver operating characteristic plot (see the electronic supplementary material).

(d) *Relationship between traits and habitat suitability*

We used linear mixed models to relate measured functional trait to predicted habitat suitability (figure 1). Functional traits were defined as the response variables, habitat suitability as a fixed explanatory variable and plot and sub-plot as nested random factors (model m_1). The proportion of the plot variability explained by habitat suitability was calculated as a measure of variation explained, following Xu (2003) by

$$R^2 = 100^{*}\left(1 - \frac{(\sigma_{m_1})^2}{(\sigma_{m_0})^2}\right),$$

where σ_{m_0} and σ_{m_1} are the estimated error standard deviations at plot level estimated under the models with random effects only and under the model m_1, respectively.

3. RESULTS

The evaluation of the habitat suitability models revealed 'fair' predictions for six species, 'good' for height and 'excellent' for two of the 16 species modelled in Guisane, and 'good' for four and 'excellent' for one of the five species in Anzeindaz (see the electronic supplementary material, table S1).

The three measured traits presented strong intraspecific variability. For example, $H_{\max}$ was particularly variable, with species' coefficients of variation (CVs) between 0.19 and 0.49, while LDMC (CV in 0.08–0.25) and LNC (CV in 0.09–0.29) tended to be less variable (see the electronic supplementary material, table S2).

Overall, the link between predicted habitat suitability and functional traits was species- and trait-specific (table 1). In general, the link between habitat suitability and $H_{\max}$ was positive (e.g. *Leucanthemum vulgare*, figure 2). For some species, there were no relationships between predicted habitat suitability and any trait (e.g. *Festuca paniculata*, *Rhododendron ferrugineum*). Interestingly, *Vaccinium myrtillus* had a positive relationship between habitat suitability and $H_{\max}$ in the French site but a negative one in the Swiss site. The sign of the relationship between habitat suitability and LNC or LDMC was species-specific (table 1). For instance, variation of LNC of *Dactylis glomerata* was negatively correlated to variation in habitat suitability in both Swiss and French sites, while it was strongly positively correlated for *Polygonum viviparum* (figure 2). The same pattern emerges for LDMC with a strong negative correlation between habitat suitability and LDMC for *Carex sempervirens* in the French site (figure 2) and a strong positive one for *V. myrtillus* in the Swiss site (table 1).

The strength of the covariation between predicted habitat suitability and trait expression was not related to the accuracy (AUC) of the habitat suitability model ($p > 0.05$).

4. DISCUSSION

Our contrasting species-specific results corroborate previous studies investigating the relationships between habitat suitability and seed recruitment (Wright *et al.* 2006), or habitat suitability and fecundity (Elmendorf & Moore 2008). Despite an inherent individual variability within plots, models of habitat suitability predict the variation in species' functional traits reliably for some species. In general, $H_{\max}$, an estimate of competitive ability (higher plants get more light), is positively related to habitat suitability, indicating that the more suitable a site, the greater the above-ground growth performance of individuals within a species. The relationship is more contrasted for the other two traits. Intraspecific variation in LDMC is not very well predicted by change in habitat suitability. The strong negative relationship we observe for *C. sempervirens* highlights the well-known trade-off between conservation and exploitation strategies in plant growth (Díaz *et al.* 1998). In a highly suitable habitat, plants tend to invest resources instead of conserving them, thus allocating dry matter to new tissues instead of storing it. Similar to $H_{\max}$, intraspecific variation in LNC, an estimate of photosynthetic activity, is positively related to predicted habitat suitability. Plants exhibit a higher photosynthetic activity in more optimal conditions. Surprisingly, this positive relationship does not hold for some species, notably *D. glomerata*.

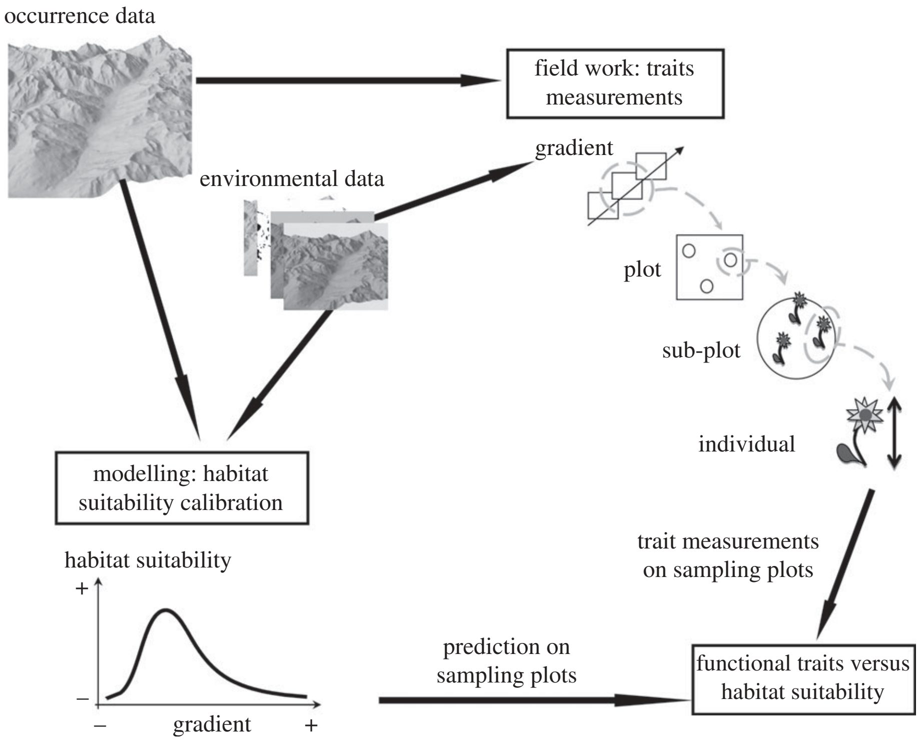

Figure 1. Flow chart of the analysis.

Although we do find a strong relationship between the variation in species' functional traits and variation in habitat suitability for some species, this is not a general pattern in our study with no relationship for half of the species. This suggests that species are affected by the environment in idiosyncratic ways (Hultine & Marshall 2000). This corroborates the results of Gerdol (2005) who showed that two species from the same life form (deciduous dwarf shrubs, *V. myrtillus* and *Vaccinium uliginosum*) can have very different growth performance and nutrient concentrations along environmental gradients. There are several non-exclusive possible explanations to this.

(i) The habitat suitability models may not account for species-specific abiotic factors. We have selected supposedly important topo-climatic variables but some are probably missing. The addition of pH and organic matter did not improve the relationships between habitat suitability and traits (results not shown), but we have not tested for the potential effects of geology, shifts in the microclimatic niches of species, land use, and geomorphic disturbances (data not available).

(ii) The habitat suitability models may not explicitly account for biotic interactions and population dynamics, which might strongly influence functional trait expression. Elmendorf & Moore (2008) showed a higher predictive performance of community-based models to predict seed recruitment than individual habitat suitability models.

(iii) There may be an inherent within-plot variability owing to uncontrolled factors (e.g. micro-habitat, phenotypic variability) which might

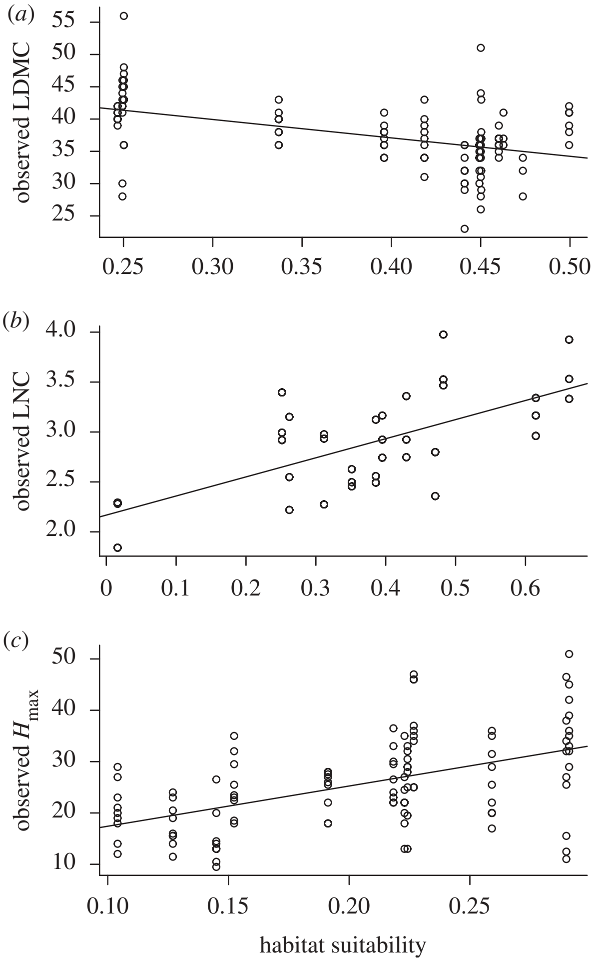

Figure 2. Variation in species' functional traits against variation in species' habitat suitability. (*a*) Maximum height of *C. sempervirens*, (*b*) leaf nitrogen content of *P. viviparum* and (*c*) leaf dry matter content of *L. vulgare*.

hide strong relationships between variation in habitat suitability and variation in species' functional traits.

(iv) Intraspecific variability in functional traits may not be influenced by the environment. This is unlikely to be the case, given the strong link already highlighted between interspecific variation in traits and the environment (Westoby *et al.* 2002)

Although extremely time consuming and data demanding, the type of analysis we presented here is necessary to demonstrate whether habitat suitability models can only discriminate species presence or absence, or can additionally inform on species performance. As the formal validation of habitat suitability models remains difficult (Guisan & Thuiller 2005), confronting their predictions to measured functional traits, as we propose here, allows a complementary evaluation of their reliability and usefulness.

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