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# Neophyte species richness at the landscape scale under urban sprawl and climate warming

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## ABSTRACT

**Aim** Land use and climate are two major components of global environmental change but our understanding of their simultaneous and interactive effects upon biodiversity is still limited. Here, we investigated the relationship between the species richness of neophytes, i.e. non-native vascular plants introduced after 1500 AD, and environmental covariates to draw implications for future dynamics under land-use and climate change.

**Location** Switzerland, Central Europe.

**Methods** The distribution of vascular plants was derived from a systematic national grid of 1 $km^2$ quadrates ($n = 456$; Swiss Biodiversity Monitoring programme) including 1761 species, 122 of which were neophytes. Generalized linear models (GLMs) were used to correlate neophyte species richness with environmental covariates. The impact of land-use and climate change was thereafter evaluated by projections for the years 2020 and 2050 using scenarios of moderate and strong changes for climate warming (IPCC) and urban sprawl (NRP 54).

**Results** Mean annual temperature and the amount of urban areas explained neophyte species richness best, with a high predictive power of the corresponding model (cross-validated $D^2 = 0.816$). Climate warming had a stronger impact on the potential increase in the mean neophyte species richness (up to 191% increase by 2050) than ongoing urban sprawl (up to 10% increase) independently from variable interactions and model extrapolations to non-analogue environments.

**Main conclusions** In contrast to other vascular plants, the prediction of neophyte species richness at the landscape scale in Switzerland requires few variables only, and regions of highest species richness of the two groups do not coincide. The neophyte species richness is basically driven by climatic (temperature) conditions, and urban areas additionally modulate small-scale differences upon this coarse-scale pattern. According to the projections climate warming will contribute to the future increase in neophyte species richness much more than ongoing urbanization, but the gain in new neophyte species will be highest in urban regions.

**Keywords**

**Biological invasions, climate warming, global environmental change, non-analogue environment, non-native species richness, urban sprawl.**

## INTRODUCTION

Global environmental change and its impact on biodiversity have become a major focus in conservation biology as well as ecology in general (Vitousek *et al.*, 1997b). Beside the loss of species (Pimm *et al.*, 1995; Baillie *et al.*, 2004), spread of non-native organisms has been observed worldwide (Vitousek *et al.*, 1997a). This spread seems both to be driven by global environmental change and to be an important agent of global change itself by affecting biodiversity loss (Lodge, 1993;

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Williamson, 1999; Sala *et al.*, 2000). In a 'world without borders' (Mack *et al.*, 2000), introductions of non-native species are primarily human-induced with international trade as a general proxy (Westphal *et al.*, 2008). On the habitat level, the importance of anthropogenic land use and disturbance has been emphasized (Hobbs & Huenneke, 1992; Pyšek, 1998; Deutschewitz *et al.*, 2003), whereas at coarse resolutions the importance of climatic conditions for the naturalization and landscape spread of non-native species has been highlighted (Scott & Panetta, 1993; Walther *et al.*, 2002; Thuiller *et al.*, 2005b). Although land use and climate are both crucial components of global environmental change, they are often studied independently (Heikkinen *et al.*, 2006) and analyses considering their interactions are rare (but see Sala *et al.*, 2000; Bomhard *et al.*, 2005; Jetz *et al.*, 2007). Thus, our understanding of interactive effects of different aspects of global change on biodiversity is still limited (Didham *et al.*, 2007).

Our goal was to analyse the joint effects of climate and land-use change upon the richness of neophytes, i.e. non-native vascular plants with first occurrences after 1500 AD. To do so, we addressed the following questions: (1) What are the main environmental covariates of neophyte species richness at the landscape scale in Switzerland and how do they differ from those of other vascular plants? (2) What implications for the future dynamics of neophyte species richness can be inferred from environmental scenarios with a focus on land-use and climate change?

## METHODS

### Study area

The study area encompasses Switzerland, which covers 41,244 km$^2$ in Central Europe (45°49′–47°48′ N latitude, 5°57′–10°30′ E longitude; Fig. 1). About 70% of the country is mountainous (60% Alps, 10% Jura Mountains) and the average elevation is *c.* 1300 m a.s.l. Switzerland is characterized by strong environmental gradients, with elevations ranging from 193 to 4634 m a.s.l., mean annual temperature between −10.5 and 12.5 °C, and annual precipitation from 438 to 2950 mm (Zimmermann & Kienast, 1999).

### Plant distribution data

We used the present-day distributions of vascular plants derived from the Swiss Biodiversity Monitoring programme (BDM, Weber *et al.*, 2004). One of the BDM-indicators surveys species richness at the landscape scale. On a systematic national grid, 520 plots of size 1 km$^2$ are being surveyed by sampling along a transect of 2500 m length and 5 m width, thus providing a transect species richness for each plot (Plattner *et al.*, 2004). We used data of 477 plots recorded during the first survey period 2001–2005 and supplemented by eight plots in urban environments recorded in 2006. Plots with a lake fraction >50% and plots near the border of Switzerland had been excluded from further analyses because of biased or missing data. The remaining data of vascular plant distributions totalled 456 plots and 104,620 occurrences of 1761 species (Fig. 1). The classification of neophytes follows Moser *et al.* (2002), verified by comparison with Landolt (2001). The remaining species list included 2465 occurrences of 122 neophyte species. Neophyte richness per plot ranged between zero and 33 species with a mean species richness of 5.41 ± 0.31.

### Environmental data

We used the same environmental variable sets as for modelling total species richness of vascular plants in Wohlgemuth *et al.* (2008): (1) a topography set ($n$ = 10) including elevation, slope and aspect variables, (2) an environment set ($n$ = 61) considering climate, substrate and water bodies and (3) a land-use/cover set ($n$ = 9) derived from airborne remote sensing (Table 1). All predictor variables were originally available as 1 ha grids and were then aggregated to the 1 km resolution of the dependent variable using a 1 km$^2$ moving window and focal statistics. For further details see Wohlgemuth *et al.* (2008) and Zimmermann & Kienast (1999). Climatic variables

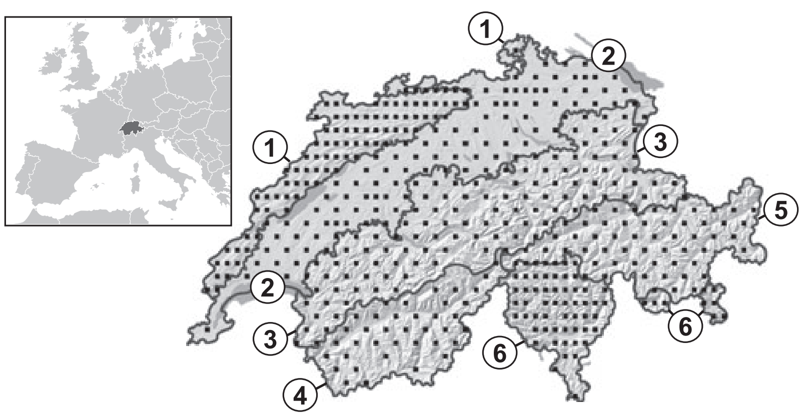


Figure 1 Locations of the sample plots ($n$ = 456) and the six biogeographic regions of Switzerland (1 = Jura, 2 = Central Pateau, 3 = Nothern Prealps, 4 = Western Central Alps, 5 = Eastern Central Alps, 6 = Southern Alps) following Gonseth *et al.* (2001).

| Variable root (1 ha) | Focal statistic (1 km$^2$) | Source (variable root) |
|---|---|---|
| Topography set | | |
| Elevation [m] | Avg, max, min, ran, SD | BFL (1994) |
| Slope: < 3° = flat; 3–30° = sloped; > 30° = steep [%] | Sum | BFL (1994) |
| Aspect: 340–50° (north); 160–230° (south) [%] | Sum | BFL (1994) |
| Environmental set | | |
| Temperature, mean annual [°C] | Avg, max, *min*, *ran*, *SD* | Zimmermann & Kienast (1999) |
| Temperature, January [°C] | *Avg*, *max*, *min*, *ran*, *SD* | Zimmermann & Kienast (1999) |
| Temperature, July [°C] | *Avg*, *max*, *min*, *ran*, *SD* | Zimmermann & Kienast (1999) |
| Temperature, variation: T7 – T1 [°C] | Avg, *max*, *min*, ran, *SD* | Zimmermann & Kienast (1999) |
| Precipitation, year [mm] | Avg, max, *min*, *ran*, *SD* | Zimmermann & Kienast (1999) |
| Precipitation, July [mm] | *Avg*, *max*, *min*, *ran*, SD | Zimmermann & Kienast (1999) |
| Potential direct solar radiation, March | Avg, max, min, ran, *SD* | Zimmermann & Kienast (1999) |
| Potential direct solar radiation, July | Avg, max, min, ran, *SD* | Zimmermann & Kienast (1999) |
| Water balance, July [mm] | Avg, max, *min*, *ran*, SD | Zimmermann & Kienast (1999) |
| Glaciers [%] | Sum | De Quervain *et al.* (1963–1967) |
| Lakes [%] | Sum | De Quervain *et al.* (1963–1967) |
| Calcareous substrates [%] | Sum | De Quervain *et al.* (1963–1967) |
| Siliceous substrates [%] | Sum | De Quervain *et al.* (1963–1967) |
| Lake shores [m] | Avg, max, *ran*, SD | BFS GEOSTAT/Bundesamt für Landestopographie |
| River length [m] | *Avg*, max, *ran*, SD | BFS GEOSTAT/Bundesamt für Landestopographie |
| Creek length [m] | Avg, max, *ran*, SD | BFS GEOSTAT/Bundesamt für Landestopographie |
| Land cover | | |
| Closed forest [%] | Sum | BFS (1992/97) |
| Open woody formations [%] | Sum | BFS (1992/97) |
| Agriculture lowlands [%] | Sum | BFS (1992/97) |
| Agriculture alps [%] | Sum | BFS (1992/97) |
| Lakes [%] | Sum | BFS (1992/97) |
| River [%] | Sum | BFS (1992/97) |
| Unproductive vegetation [%] | Sum | BFS (1992/97) |
| Bare areas (glaciers, rocks, sand, screes) [%] | Sum | BFS (1992/97) |
| Urban areas [%] | Sum | BFS (1992/97) |

**Table 1** Environmental variables used for modelling neophyte species richness. Additional predictors derived from the root variables by focal statistics (avg = focal mean, max = focal maximum, min = focal minimum, ran = focal range, SD = focal standard deviation, sum = focal sum). Variables excluded from the environmental set because of collinearity are in italic. For each variable set the remaining variables after initial model selection are underlined.

of the environment set are based on normals of the reference period 1961–1990.

## Climate scenarios

In order to study the effect of climate change upon neophyte species richness we downscaled the TYN SC 1.0 time series (Mitchell *et al.*, 2003) of projected future climates over the study area. We used the Hadley Centre Coupled Model (HadCM3) output provided in this data set. In addition, we used the CRU TS 1.2 data set representing spatially interpolated monthly climate series from 1901 to 2002 (Mitchell *et al.*, 2003) available at the same spatial resolution (10′) for deriving future anomalies. Data were downscaled from 10′ spatial resolution in two steps. First, we derived anomalies for each basic climate variable (monthly minimum and maximum temperature) and each month from 2001 up to 2100 compared with the mean of the reference period of 1961–1990. By this, we determined to what degree each month was expected to deviate in the future from the current climate layers represented by the climate normals. Second, the 10′ grid values were sampled with a point lattice that matched the centre of each 10′ pixel. The climate anomalies of these points were then re-projected to the Swiss National coordinate system and spatially interpolated to a 1 km spatial resolution using inverse distance weighed interpolation. In a third step, the 1 km anomalies were downscaled to a 100-m resolution using bilinear interpolation. The projected anomalies of each month were now available at the same resolution and extent as represented by the original environment set of predictor variables. Next, we added the temperature anomalies to the temperature grids.

From these projected climate series, we derived the same environment sets for future time steps by averaging 5-year intervals into future sets. To demonstrate the effects, we calculated a 2020 (=2016–2020) and 2050 (=2046–2050) set, which was aggregated to the 1 km resolution in the same way as the calibration data set explained above. We used the A1FI (as hi-scenario, projecting an extreme warming) and the B2 (as low-scenario, projecting a moderate warming) IPCC scenario, representing two different sets of assumptions regarding the future development of human activities and corresponding climate trajectories (IPCC 2007). Since these IPCC scenarios do not differ severely until 2050, we decided to only apply 50% of projected changes to the B2 scenario. Thus, our B2 scenario represents a very conservative estimate of possible climate futures, while the A1FI scenario represents a rather severe scenario of the climate future by 2050 (Fig. 2a).

## Urban sprawl scenarios

The delineation of the areas of urban development for the year 2002 was based on the VECTOR25 data by Swisstopo, Berne (scale of 1:25,000). 'Urban areas' included residential and industrial areas. Only those traffic areas were included that are located within the settlements, because roads in the open landscape do not contribute to 'urban sprawl' sensu Jaeger & Bertiller (2006), see also Jaeger *et al.* (2009). Historic topographic maps of Switzerland were digitized for 1960 and 1980 to create times series of urban development (Fig. 2b) (Jaeger *et al.*, 2008).

To predict the extent and spatial distribution of urban areas for the years 2020 and 2050, Jaeger *et al.* (2008) generated a set of nine scenarios. The scenarios were built on the map of the current situation (2002; 2372.1 km$^2$ urban area, i.e., 5.7% of the land area, Fig. 2b), on the projected increase of the human population, and on region-specific values of urban area per inhabitant (Jaeger *et al.*, 2008). The scenarios with the highest (hi-scenario) and lowest (low-scenario) total increases of urban area were used for projecting future species richness. These two scenarios differ in the increase of human population and in the spatial distribution of the new urban areas (dispersed distribution in the hi-scenario and clumped distribution in the low-scenario). The total increase in urban area was 395.6 km$^2$ (+16.7%; hi-2020), 796.8 km$^2$ (+33.6%; hi-2050), 188.7 km$^2$ (+8.0%; low-2020), 220.9 km$^2$ (+9.3%; low-2050). The amount of urban area was finally aggregated to the 1-km$^2$ resolution of the response variable.

## Present-day modelling

For the present-day model of neophyte species richness, we used the same steps of analysis as described in Wohlgemuth *et al.* (2008): First, we reduced collinearity ($R^2 \geq 0.9$) in the large environment set (Table 1) and continued using the same 30 variables as in Wohlgemuth *et al.* (2008). In a second step, generalized linear models (GLM, McCullagh & Nelder, 1989) were fitted for each variable set using R ver. 2.6.2 (R Development Core Team 2008). We assumed the species richness to be a Poisson-distributed count variable and used the log-link function. All variables entered the model with linear and quadratic terms. Starting with the best performing single variable model and based on Akaike's information criterion (AIC), the number of variables per predictor set was increased until the change in explained deviance $D^2$ dropped below 1%. Without the $D^2$ stop criterion, the final model would have included additional variables accounting for a very small increase in $D^2$ (see below). This refers to the well-known feature, that AIC tends to include a large proportion of irrelevant variables (George, 2000). Each of the best *n*-variable models was determined by comparing all *n*-variable combinations. A fourth model (i.e. the synthetic model) was built in the same way considering all best variables of the three variable sets after reducing collinearity again (average elevation was removed because of its high collinearity with the biologically more meaningful mean annual temperature). Outliers and influential plots were tested by examining standard regression diagnostics (residual vs. prediction plot, Q–Q plots and Cook's distance). By this, no outlier or highly influential plot was detected. Finally, linear and quadratic terms of the synthetic model were tested separately by backward elimination based on AIC, and non-significant parameters were excluded. We

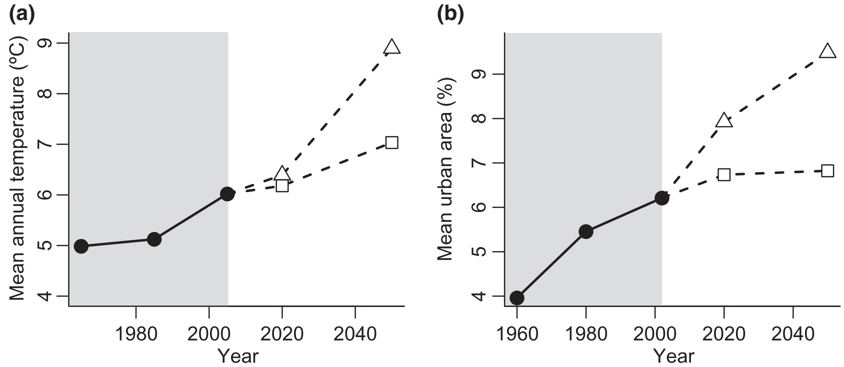


Figure 2 Past and projected future increase in (a) mean annual temperature and (b) mean urban area of the analysed 456 plots. Future projections (background in white) assume moderate or strong environmental changes. Standard errors of all mean values are below 0.1°C and 0.1% respectively.

also considered potential overdispersion and calculated for the final model the ratio of residual deviance and degrees of freedom. The robustness of the explained deviance $D^2$ of the final model was evaluated with 10-fold cross-validation. For robust results, the mean of 100 cross-validations was used. Both, the independent and joint effects of single variables of the final model were analysed by hierarchical partitioning (Chevan & Sutherland, 1991; MacNally, 1996). We used the R-function 'partition' of the R-package 'hier.part' (MacNally & Walsh, 2004) with the GLM-deviance as goodness of fit, and focused on the variable level by aggregating linear and quadratic terms.

A predicted map for the present-day neophyte species-richness in Switzerland was generated by applying the final model to the fine-grained variable grids (1 ha pixels with focal statistics of the 1 km$^2$ moving window). Because the environmental data for model calibration do not cover the full ranges of environmental gradients in Switzerland, in some areas the present-day predictions and especially the future projections of species richness had to be regarded as extrapolations to non-analogue environments. As with single species distribution models (Thuiller *et al.*, 2004b) such extrapolations may have serious restrictions and are of limited significance. Therefore, we tested the robustness of our results by excluding areas of extrapolation depending on two different definitions. *Type I*: All predictions/projections with values of a single predictor falling outside its calibration range were treated as extrapolations. *Type II*: For the second definition we considered the combinations of predictors and calculated envelopes in the bivariate calibration space based on alpha-shapes (Edelsbrunner *et al.*, 1983). All environmental conditions outside the envelope were treated as non-analogue environment. Alpha-shapes are a generalization of ordinary convex hulls and a subgraph of the Delaunay triangulation. In contrast to convex hulls their shapes can also be concave. Their level of detail in describing the shape of a point pattern is controlled by a single parameter alpha. We used $\alpha = 2.0$ on the basis of standardized predictors and visualized the corresponding hull by scatter plots. Because of the simplicity of the final model (see below) the bivariate alpha-shape was sufficient to describe the environmental space of the model calibration and no multivariate approach had to be applied. Both, the uni- and bivariate definition of extrapolation were used to find areas of safe predictions/projections in analogue environments, which are represented by the available calibration data. The definition Type II (bivariate) applies a stricter rule in comparison to Type I (univariate).

### Scenario modelling

To get a sound starting point for projections and to exclude the risk that changes in species richness are simply caused by the transition from the variables used for the initial calibration to the scenario variables used for projections, the final model was recalibrated using scenario data from the survey period (2001–2005).

Because future interactions among present-day drivers are poorly known and good model fit on present-day distribution data does not necessarily translate into good future projections (Araújo *et al.*, 2005), we compared two different assumptions, which we call here 'future interaction types': (1) there are no interactions, i.e. the species richness changes by single drivers are additive as implicated in a standard GLM-formula without any interaction term; (2) the interactions are antagonistic sensu Sala *et al.* (2000), i.e. changes in future species richness will only respond to the environmental variable which has the highest impact. This variable was found on the plot level by comparing model predictions with varying single variable scenarios. Both interaction types were calculated with and without a regular GLM-interaction term.

To sum up, the projections of future neophyte species richness were compared under different urban sprawl and climate warming scenarios, using different assumptions about variable interactions, and they were evaluated by including or excluding different types of model extrapolations to non-analogue environments.

## RESULTS

### Modelling present-day species richness of neophytes

For each variable set the best variables after model selection are listed in Table 1. The variable selection for the final model returned the mean annual temperature and the amount of urban areas as the two main environmental correlates of neophyte species richness at the landscape scale in Switzerland (Table 2). Despite the simplicity of the two-variable model, it covers a remarkable high degree of variation ($D^2 = 0.821$; cross-validated $D^2 = 0.816$). Predictions showed a mean absolute error (MAE) of 1.88 species (10-fold cross-validated

**Table 2** Coefficients of the final model of neophyte species richness for standardized variables.

| | Linear term | | | Quadratic term | | |
|---|---|---|---|---|---|---|
| | Estimate | Standard error | *P*-value | Estimate | Standard error | *P*-value |
| Intercept | 0.9288 | 0.0457 | ≤ 0.0001 | | | |
| Urban area | 1.7459 | 0.0830 | ≤ 0.0001 | −0.3474 | 0.0487 | ≤ 0.0001 |
| Mean annual Temperature | 0.3793 | 0.0327 | ≤ 0.0001 | −0.0514 | 0.0070 | ≤ 0.0001 |

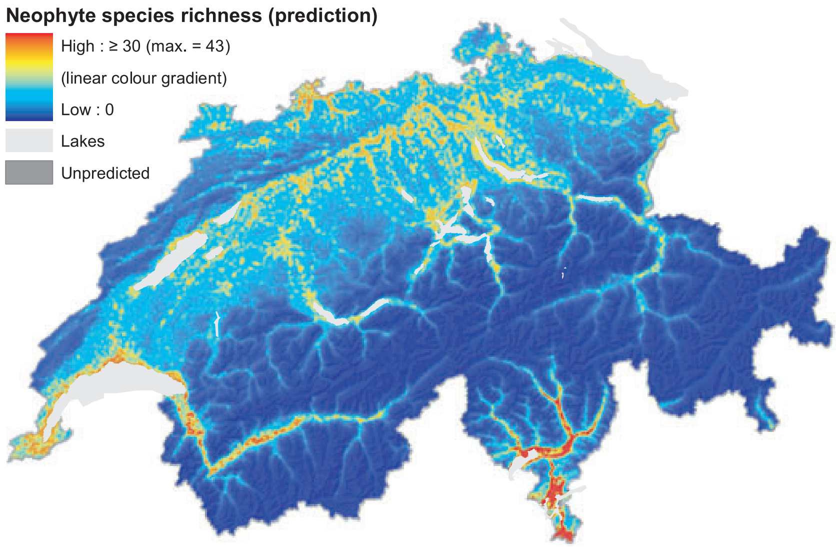


Figure 3 Predicted map of present-day neophyte species richness in Switzerland.

1.92 species). Without the $D^2$ stop criterion during variable selection, the final model would have included six additional variables accounting for an increase in $D^2$ of only 0.019. The ratio of the residual deviance and the degrees of freedom was 1.34, i.e. a slight overdipsersion, but no critical violation of the model assumptions (Burnham & Anderson, 2002). Using 'quasipoisson' for the error distribution showed no changes for the estimated coefficients. Hierarchical partitioning revealed the mean annual temperature to have a stronger independent effect ($D^2$-fraction = 58.2%) than urban land use ($D^2$-fraction = 23.9%) together with a joint effect of 18.6%. When adding the interaction term among the two variables the cross-validated $D^2$ increased only marginally from 0.816 to 0.823. Because this increase is <1% and following the criteria of the previous variable selection, the interaction term was not considered for predictive mapping.

Figure 3 shows the predicted present-day map for the landscape species richness of neophytes in Switzerland based on the final model. The map illustrates a coarse pattern with a clear gradient from species-poor highlands (Alps, Jura Mountains) to higher richness in neophyte species in the lowlands (Central Plateau, Ticino). Within the lowlands the predicted neophyte species richness is especially high in urban areas and in the warmest parts of Switzerland. However, some of these areas are also detected as extrapolations as are highest mountain tops (Fig. 4; extrapolation Type I = 3.3%, Type II = 5.0% of the land area).

## Model recalibration using present-day scenario data

When using the scenario data of the survey period for mean annual temperature (2001–2005) and urban areas (2002) to recalibrate the model of neophyte species richness, the cross-validated deviance slightly increased from 0.816 to 0.820 and the predictions were highly correlated ($r$ = 0.988) and similar (mean absolute difference 0.49 ± 0.04 species; mean predicted species richness after recalibration 5.41 ± 0.30 species). During

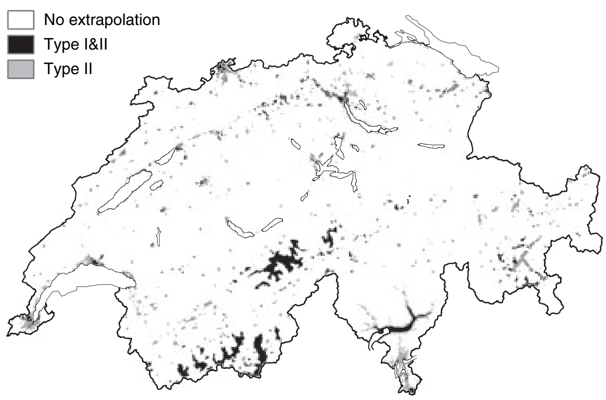


Figure 4 Non-analogue areas of present-day predictions of neophyte species richness using two different definitions of model extrapolation.

the survey period both IPCC-scenarios show very similar values ($r$ = 0.995; maximum absolute difference < 0.1 °C) and the B2-scenario was used for recalibration. The correlation between the originally used amount of urban areas and values of the 2002 urban sprawl layer used for the scenarios was 0.963.

## Projection of future neophyte species richness

The different definitions of extrapolation are visualized in Fig. 5 by comparing the present-day environmental space used for recalibration with the two scenarios of strong changes by 2050. Under extrapolation Type I only a few 1 km$^2$ plots represent unsafe projections because of mean annual temperatures exceeding the observed present-day maximum ($n$ = 14 of 456). In contrast, with the more constrained definition Type II a high number of plots ($n$ = 108) would move outside the recalibration space by 2050.

The projections of neophyte species richness are summarized in Table 3. The results showed significant differences when urban sprawl or climate warming scenarios were applied

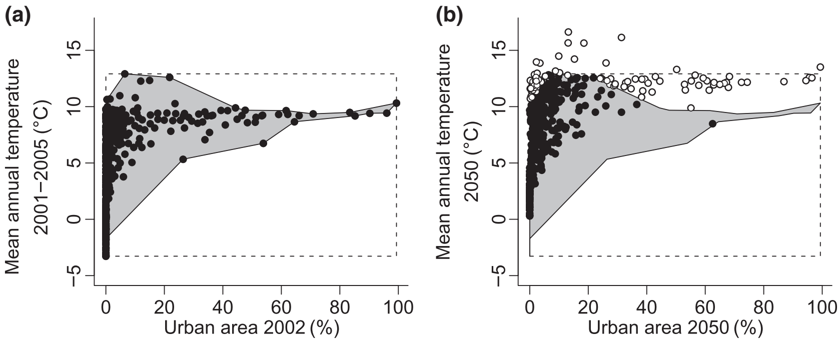


Figure 5 Environmental space of recalibration and the plot locations ($n$ = 456) during (a) the survey period and (b) under strong environmental changes by 2050. The dashed line represents the area of safe predictions/projections according extrapolation Type I. The corresponding area of Type II is shown in grey and unsafe projections are indicated by open circles.

Table 3 Projected future changes in mean neophyte species richness per plot by the years 2020 and 2050 under the condition of moderate (low) or strong (hi) environmental changes. Model specifications include (yes) or exclude (no) extrapolations of Type II, the GLM-interaction term, and use antagonistic or additive future variable interactions.

| Scenarios | Urban sprawl | | | Climate warming | | | Urban sprawl and climate warming | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Model specification | | | | | | | | | | |
| Extrapolations (Type II) | Yes | Yes | No | Yes | Yes | No | Yes | Yes | Yes | No |
| Interaction term (GLM) | No | Yes | Yes | No | Yes | Yes | No | No | Yes | Yes |
| Future interaction type | – | – | – | – | – | – | Antagon. | Additive | Additive | Additive |
| Number of plots | 456 | 456 | 348 | 456 | 456 | 348 | 456 | 456 | 456 | 348 |
| Mean species richness | | | | | | | | | | |
| Scenarios | | | | | | | | | | |
| 2001–2005 | 5.41 | 5.41 | 3.06 | 5.41 | 5.41 | 3.06 | 5.41 | 5.41 | 5.41 | 3.06 |
| 2020, low | 5.46 | 5.47 | 3.10 | 5.96 | 5.89 | 3.43 | 5.97 | 6.02 | 5.95 | 3.47 |
| 2050, low | 5.47 | 5.48 | 3.10 | 7.86 | 7.62 | 4.72 | 7.86 | 7.95 | 7.66 | 4.79 |
| 2020, hi | 5.62 | 5.62 | 3.21 | 6.67 | 6.53 | 3.91 | 6.68 | 6.93 | 6.73 | 4.11 |
| 2050, hi | 5.80 | 5.81 | 3.36 | 13.31 | 13.25 | 8.90 | 13.31 | 14.26 | 13.33 | 9.72 |
| % Increase (vs. 2001–2005) | | | | | | | | | | |
| Scenarios | | | | | | | | | | |
| 2020, low | 1.0 | 1.2 | 1.2 | 10.2 | 8.9 | 12.0 | 10.5 | 11.3 | 10.0 | 13.4 |
| 2050, low | 1.1 | 1.3 | 1.5 | 45.5 | 40.9 | 54.4 | 45.5 | 47.1 | 41.7 | 56.5 |
| 2020, hi | 3.9 | 3.9 | 5.1 | 23.5 | 20.7 | 27.9 | 23.6 | 28.3 | 24.6 | 34.2 |
| 2050, hi | 7.2 | 7.5 | 9.8 | 146.2 | 145.0 | 191.1 | 146.2 | 163.7 | 146.6 | 217.7 |

separately. Independent from model specifications, climate warming had a much higher impact on shifts in neophyte biodiversity (up to 191% increase in mean species richness by 2050) than had urban sprawl (up to 10%) and returned only marginally lower richness values than the combined scenario models. Different model specifications of the interaction term as well as the future interaction type did not clearly change these strong differences. In contrast, the exclusion of extrapolated plots (Type II) had a strong quantitative influence on the mean species richness. Yet again, it did not affect the clear differences between the impacts of urban sprawl and climate warming.

Figure 6 shows the potential gain in neophyte species for each plot along the elevation gradient for the year 2050 under the assumption of strong changes of both urban sprawl and mean annual temperature. The gains in neophyte species are much stronger in the lowlands than in mid elevations or high mountain regions. The potential gain in neophyte species in settlements and urban landscapes are up to twice as high as in rural landscapes. However, many lowland areas represent non-analogue conditions showing a strong effect of the two definitions of extrapolation (Fig. 7; extrapolation Type I = 4.7%, Type II = 24.7% of the land area).

## DISCUSSION

Modelling neophyte species richness at the landscape scale in Switzerland resulted in a comparably simple model containing only two predictors with a remarkably high predictive power. At the same time, the model considered both climate and land use as two main agents of global environmental change.

### Main correlates of present-day neophyte species richness

The importance of climate conditions for the naturalization and spread of non-native species has been demonstrated in a number of studies using data of coarse resolutions or large

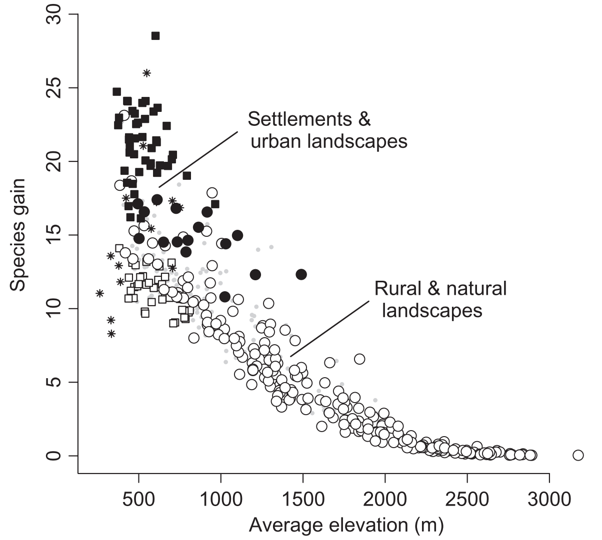


Figure 6 Potential gains in neophyte species on the plot level ($n$ = 456) by 2050 under high urban sprawl and climate warming. Open symbols belong to rural and natural landscapes (urban area by 2050 < 1%), filled symbols in black are settlements and urban landscapes (urban area > 10%). Extrapolations of Type II are shown with rectangles, Type I by stars, others with circles in grey.

extent (Scott & Panetta, 1993; Thuiller *et al.*, 2004a, 2005b). On the landscape or habitat level, land use – especially urbanization and increased anthropogenic disturbance in particular – has been emphasized (Hobbs & Huenneke, 1992; Pyšek, 1998; Deutschewitz *et al.*, 2003; Chytry *et al.*, 2009) and the use of remote sensing based land-use information has been recommended (Zimmermann *et al.*, 2007). However, only a few studies found both climate and land use to be the main drivers of non-native species richness in a similar analytical framework as in our study. We attribute our findings to the steep climatic gradients in our study area and the high extent/grain ratio in our data including a grain size that allowed the detection of nearby differences in land use where climate was similar. This is in accordance with observations, that the effect of land-use/cover on biodiversity (Luoto *et al.*, 2007) and especially of interactions between land-use/cover and climate (de Chazal & Rounsevell, 2009) stongly depends on the study scale. It is also in accordance with findings that cities act as important sources and origins for the naturalization and landscape spread of non-native vascular plant species (Pyšek, 1998; Lonsdale, 1999; von der Lippe & Kowarik, 2008). In addition, annual temperature (or elevation) and urban areas have also been found as drivers of neophyte species richness in studies at differing spatial scales, although scale-specific factors like habitat type at smaller scales (Chytry *et al.*, 2008) or geological diversity at larger scales (Kühn *et al.*, 2003) prevailed.

Yet, we are aware that both mean annual temperature and amount of urban areas may be only surrogates for several highly correlated drivers that affect neophyte species richness more directly. For the mean annual temperature, e.g. the number of frost days (Walther *et al.*, 2007) or the length of vegetation period may directly influence the occurrences of neophytes. Examples of important direct factors for urban areas include species introduction and long distance dispersal by trade (Westphal *et al.*, 2008), dispersal along roads (von der Lippe & Kowarik, 2007) or railway networks (Huber, 1992), gardening using ornamental plants (Dehnen-Schmutz *et al.*, 2007), propagule pressure (Lockwood *et al.*, 2005), or favoured naturalization and landscape spread because of anthropogenic disturbances (Hobbs & Huenneke, 1992).

## Present-day neophyte versus total species richness

In comparison with the more complex model of total species richness (Wohlgemuth *et al.*, 2008), the two-variable model of neophyte species richness is not only much more parsimonious, yet it is also of higher calibration strength – and predictive power (as shown by cross-validated $D^2$ and MAE). Because

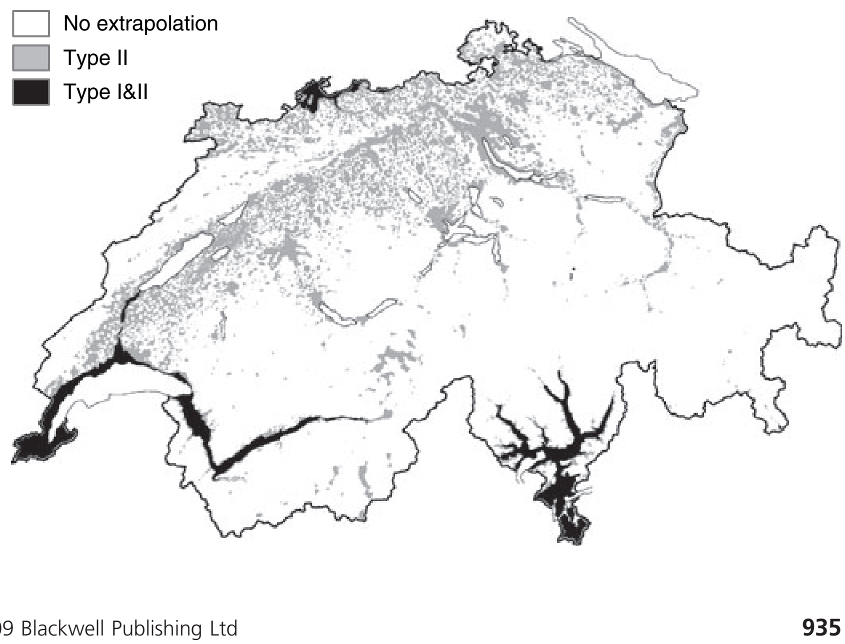


Figure 7 Non-analogue areas of projected neophyte species richness under high urban sprawl and climate warming using two different definitions of model extrapolation.

both models are based on the same initial data of species distributions, the same environmental covariates, and the same approach of model selection, it demonstrates that the species richness of neophytes was much easier to predict than total species richness. This is in accordance with Deutschewitz *et al.* (2003) who found higher explained variance in species richness of neophytes than for archaeophytes and native vascular plants on a regional scale in Germany. On the other hand it has been argued that neophytes have not yet achieved biogeographical equilibrium distribution with climate in Europe. The argument arises because of low compositional similarity and a strong decay in similarity with distance when comparing urban floras (La Sorte *et al.*, 2008). In contrast to those continental scale findings at the species composition level, our results at the species richness level and landscape scale suggest that neophytes are characterized by a quite regular, simple and well defined richness pattern. This is not necessarily a contradiction as a comparison of biological invasions with earthquakes may illustrate (Williamson, 1999): While single earthquakes (occurrences of single neophyte species) are difficult to predict, areas of high earthquake density (high neophyte species richness) may be well known (see also Peterson, 2003).

In addition, unlike total species richness, which shows in the study area a mid-elevation peak (Wohlgemuth *et al.*, 2008), species richness of neophytes generally decreased with higher altitudes. For Switzerland this general pattern was also found by Becker *et al.* (2005). Therefore, neophytes obviously differ in richness patterns compared with the other vascular plants in Switzerland, and the regions of highest species richness of both groups do not coincide at the given spatial scale.

### Projection of future neophyte species richness

In our study, climate warming revealed a much stronger impact on the potential increase in neophyte species richness than did ongoing urbanization. However, the increase driven by climate change was considerably higher in urban environments than in rural or natural landscapes (Fig. 6). Therefore, not land-use change in terms of ongoing urbanization, but the already existing land-use pattern with urban areas seems to be important for the future increase in neophyte species richness. The relevance of interactions between climate change and filters that limit or favour the future spread of non-native species has been pointed out by several authors (Heikkinen *et al.*, 2006; Didham *et al.*, 2007; Theoharides & Dukes, 2007). Accordingly, our findings provide evidence that urban areas act as such an important filter for the future spread of non-native species under climate change.

The exclusion of bivariate extrapolations showed a strong effect on the number of safely projected plots (Fig. 5b), and the large areas of non-analogue future environments clearly highlight the limitations of the projections (Fig. 7). While it had little influence on our qualitative results, such unsafe projections were only detected by applying the bivariate definition of extrapolation. Therefore, we recommend more constrained bi- or multivariate definitions of non-analogue environments for predictive mapping as well as for model projections.

There still is an ongoing controversy about different modelling approaches (Pearson & Dawson, 2003; Wilson *et al.*, 2007; Thuiller *et al.*, 2008), although there is now general agreement about their potential (Elith *et al.*, 2006; Guisan *et al.*, 2007). Methods based on present-day environmental data for model parameterization and calibration, like climate envelope or climatic niche models (Guisan & Zimmermann, 2000; Thuiller *et al.*, 2005a), have been criticized for not considering the dynamics and complexity of invasion like residence time (Wilson *et al.*, 2007) and time lags of invasions (Kowarik, 1995), dispersal including propagule pressure (Lockwood *et al.*, 2005), biotic interactions (Araújo & Luoto, 2007), or genetic variation and adaptive evolution (Dlugosch & Parker, 2007). On the other hand, it has been argued that it is impossible to encapsulate the whole complexity and stochasticity of the processes involved (e.g. Hulme, 2003). Such arguments are also valid in our study. Yet, we argue that the validity or at least robustness of our results is supported by the following arguments: (1) our model captures an exceptionally high amount of variability in neophyte species richness. Hence, there is no need to increase the complexity of the model; (2) modelling present-day patterns of species richness seems to be much easier and thus more robust than single-species distributions; (3) our projections were tested by excluding non-analogue areas; (4) the general differences between the impacts of climate warming and ongoing urban sprawl remained stable with different model specifications and types of future variable interactions. Still, it is important to state that we do not assume that neophytes will directly track environmental change. Thus, we view our projections rather as potentials than as forecasts of what the neophyte species richness will be by 2020 or 2050.

### Conclusions

In contrast to other vascular plants, the prediction of neophyte species richness at the landscape scale in Switzerland is quite simple, and the regions of highest species richness of the two groups do not coincide. The present-day pattern of neophyte species richness is basically driven by climatic (temperature) conditions, and urban areas additionally modulate small-scale differences upon this coarse-scale pattern. According to our projections, climate warming will affect the future increase in neophyte species richness in Switzerland much more than ongoing urbanization, but the gain in new neophyte species will be highest in the urbanized regions.

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## BIOSKETCHES

All authors are interested in landscape and environmental changes at different spatial and temporal scales; their measurement, assessment, and modelling (J.A.G.J., N.E.Z); and their impact on biodiversity (M.P.N., N.E.Z.). M.P.N. conceived the ideas of this study, carried out the analyses and led the writing. J.A.G.J. provided the urban sprawl scenarios, N.E.Z. the climate scenarios, and both co-authors contributed to the writing.

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