PRIMARY RESEARCH

Synergistic and antagonistic effects of land use and non-native species on community responses to climate change

Running title: *The warming and wetting of plant communities*

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Abstract

Climate change, land-use change and introductions of non-native species are key determinants of biodiversity change worldwide. However, the extent to which anthropogenic drivers of environmental change interact to affect biological communities is largely unknown, especially over longer time periods. Here, we show that plant community composition in 996 Swedish landscapes has consistently shifted to reflect the warmer and wetter climate that the region has experienced during the second half of the 20th century. Using community climatic indices, which reflect the average climatic associations of the species within each landscape at each time period, we found that species compositions in 74% of landscapes now have a higher representation of warm-associated species than they did previously, while 84% of landscapes now host more species associated with higher levels of precipitation. In addition to a warmer and wetter climate, there have also been large shifts in land use across the region, while the fraction of non-native species has increased in the majority of landscapes. Landscape-level temperature increases appeared to favour the colonisation of warm-associated species, while also potentially driving losses in cool-associated species. However, increases in community thermal means were apparently buffered by landscape simplification (reduction in habitat heterogeneity within landscapes) in the form of increased forest cover. On the other hand, increases in non-native species, which generally originate from warmer climates than Sweden, were a strong driver of community-level warming. In terms of precipitation, both landscape simplification and increases in non-natives appeared to favour species associated with drier climatic conditions, to some extent counteracting the climate-driven shift towards wetter communities. Anthropogenic drivers can act both synergistically and antagonistically to determine trajectories of change in biological communities over time. Therefore, it is important to consider multiple drivers of global change when trying to understand, manage and predict biodiversity in the future.

Keywords

Biodiversity, Climatic debt, Community thermal index, Historical ecology, Invasive species, Precipitation, Landscape change, Thermophilsation.

Introduction

Recent climate change has serious consequences for species' occurrences, distributions and survival (Thomas et al., 2004; Wiens, 2016), with species-level responses combining to determine changes in biodiversity, both now and in the future (Steinbauer et al., 2018; Warren et al., 2001). However, climate change is only one of a number of anthropogenic pressures on biodiversity. Habitat destruction through land-use change is currently seen as the largest threat to species worldwide (Newbold et al., 2015), associated with negative population and community-level trends across taxonomic groups (Donald, Green, & Heath, 2001; Gerstner, Dormann, Stein, Manceur, & Seppelt, 2014; Ollerton, Erenler, Edwards, & Crockett, 2014). A third driver of biodiversity change is represented by the arrival of non-native species to new regions, which has been shown to alter the richness and composition of communities over time (Thomas & Palmer, 2015; Vilà et al., 2011).

The above three elements of global change do not act separately from one another, but are known to interact to drive changes in populations over time. For example, past habitat destruction has been linked to species failing to expand their ranges following climate change (Warren et al., 2001), while climate change can compound population declines in areas subjected to high levels of habitat conversion (Northrup, Rivers, Yang, & Betts, 2019). On the other hand, protection from habitat destruction can facilitate climate-driven range shifts, and a more varied topography at the landscape level can moderate species' negative responses to warming temperatures (Suggitt et al., 2018; Thomas et al., 2012). Similarly, interactions exist between biological invasions and other global change drivers. Habitat degradation, together with climate change can lead to a higher risk of non-native species establishment and invasive spread (Didham, Tylianakis, Gemmell, Rand, & Ewers, 2007; Walther et al., 2009), something that is expected to continue in the future (Early et al., 2016).

Despite generally consistent trends, species can exhibit a range of responses to climate change (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011), which together manifest in changes at the community or landscape level. One recently-developed method of assessing the effects of large-scale species-level responses to climate change on community-level composition is through the use of simplified 'community climatic indices'. These indices calculate the average climate association for each species within a community, with each species' association being estimated from the average climatic conditions that occur across their distribution. Tracking changes in climatic indices over time has allowed researchers to consistently show that communities are responding to climate change, with increasing community thermal indices signalling that species with warmer temperature associations are expanding their ranges at the expense of cooler species (Bertrand et al., 2011; Devictor, Julliard, Couvet, & Jiguet, 2008; Devictor et al., 2012; Fadrique et al., 2018).

Due to the interactions of anthropogenic pressures driving species' change over time, interactions with land-use change and non-native species establishment should therefore be expected to affect how communities as a whole respond to climate change. Indeed, differences in forest habitat conditions can affect the level of plant community responses to climate change, either through effects on local microclimates or presenting abiotic barriers to colonisation by expanding species (De Frenne et al., 2013; Fadrique et al., 2018). At the landscape level, high levels of habitat conversion can prevent local community reorganisation following climate warming by hindering dispersal through the landscape and exacerbating negative effects on those species vulnerable to the climatic changes taking place (Gaüzère, Princé, & Devictor, 2017; Oliver et al., 2017). However, like the majority of studies of ecological responses to climate change, land use has been viewed in a static manner, and it has not been investigated how the *changes* in landscapes that have occurred concurrently to climate change have impeded community shifts or helped to facilitate community responses to warming. Neither have the effects of biological invasions been considered. Non-native species originate in many cases from regions with warmer, drier or otherwise different climates to the regions that they colonise (Early & Sax, 2014; Van der Veken, Hermy, Vellend, Knapen, & Verheyen, 2008). At the same time, the spread of these species can increase landscape-level species richness without negative effects on the native flora (Thomas & Palmer, 2015). This influx of species that are potentially more suited to the climatic changes taking place could mean that community climate indices increase without local extirpation of natives unable to persist in the changing climatic conditions. As all of these drivers of biological change are occurring simultaneously, it is important also to study their concerted effects, elucidating the extent to which climate change, land-use change and the spread of non-native species act together, or in opposition to drive community change. Finally, community climate indices have almost exclusively been calculated in terms of species' thermal associations (but see Maclean, Hopkins, Bennie, Lawson, & Wilson, 2015). Moisture availability is an important determinant of species occurrences and change (Peñuelas et al., 2013), and as changing precipitation is also a key component of climate change (IPCC, 2015), it is relevant to study how communities change in relation to levels of precipitation over time.

In Sweden, climate during the 20th century has shifted to become both warmer and wetter (Kjellström et al., 2014). In this study, we calculated thermal and precipitation associations (or species climate indices) for 3066 plant species, based on observations from 18 regional biodiversity atlases (floras) across Sweden. These species-level climate associations were used to calculate historical (early-mid 20th century) and modern (late 20th and early 21st century) community climate indices in 996 landscapes – 25 km^2 in size – spread across four provinces where floras from both time periods exist. In addition to measuring community shifts through changes in the mean values of climate associations of species within a landscape, we also calculated how the range of associations across the community changed over time, giving an indication of the relative influences of the immigration of warm-associated species and the extirpation of cool-associated species. We then used historical and modern land-use and climate data to evaluate how land-use change and changing fractions of non-native species have contributed to the observed community shifts. In doing so, we addressed the following questions:

[1] How have plant communities responded to changes in both temperature *and* precipitation during the mid-late 20th century?

[2] Have communities homogenised in terms of climate associations, driven by colonisations of warm/wet-associated species and simultaneous extirpations of cool/dry-associated species?

[3] How do shifts in community climate indices relate to the interacting effects of climate change, land-use change and the introduction and spread of non-native species?

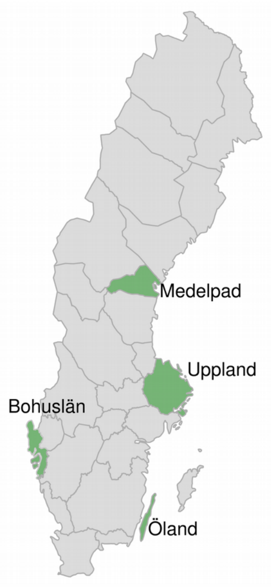
Materials and Methods

Species observation data: historical and modern-day floras

Observation data were obtained from plant biodiversity atlases (floras) from the historical Swedish provinces of Bohuslän, Medelpad, Öland and Uppland (Table 1). These provinces cover a latitudinal gradient of approximately 750 km and longitudinal gradient of 400 km, covering a range of landscape types dominated by arable, pastoral and silvicultural land uses. All historical floras contained observations from the 1800s but the majority of records were based on later inventories by the author of each flora, until the early-mid 20th century. For Bohuslän and Medelpad, the historical data were digitised for the publication of the modern floras from written inventory reports and the historical flora itself, permitting full characterisation of community changes. For Öland and Uppland, only a subset of species had published distribution maps in the historical flora, but the historical floras did include a full list of species known to the province (the historical species pool). Distribution maps were scanned, georeferenced and each occurrence point was digitised in a Geographic Information System. This was carried out by Maad, Sundberg, Stolpe, & Jonsell (2009) for Uppland and by AGA for Öland for the current study using QGIS. Inventories for the modern floras generally took place over 2-3 decades in the late 20th and early 21st century. For both the historical and the modern floras, *inventories* correspond to the recording of observed species in an area resulting from a large number of visits over a long period of time, rather than structured vegetation surveys.

Table 1. Summary information about the four study provinces and their relative locations on a map of Sweden. Historical inventory times specify the main observation period, but earlier observations are included. Number of landscapes indicates the number of 5 × 5 km Swedish grid squares in which 25 species were recorded in both the historical and modern flora data.

	Size (km^2)	**Landscapes**	**Historical inventory**	**Modern inventory**
Medelpad	7058	65	1860-1935, mostly 1901-1920 (Several sources, listed in modern flora). All species.	1975-2010, all species (Lidberg & Lindström, 2010).
Uppland	12 813	594	1910s-1930s, 438 mapped species (Almquist, 1929)	1990-2010, all species (Jonsell, 2010).
Bohuslän	4400	258	1920s-1945, all species (Fries, 1945).	1990s-2011, all species (Blomgren, Falk, & Herloff, 2011).
Öland	6698	79	1910s-1930s, 286 mapped species (Sterner, 1938).	2000-2016, all species. Unpublished.



Each observation was assigned to a 5 × 5 km national grid square. These grid squares (hereafter landscapes) were historically used for mapping purposes and are now the unit of inventory for all modern-day biodiversity atlases in Sweden. They are also the smallest unit to which occurrence points from the historical floras' distribution maps can be accurately assigned. Occurrence records of a coarser resolution than this grid were discarded. In order to analyse community change in landscapes that were well-visited in both time periods, we retained only those landscapes for analysis in which there were at least 25 observations in both the historical and the modern inventories, resulting in 996 landscapes. Species names across all floras were harmonised to the species level (i.e. *Genus epithet* only), according to the Swedish Taxonomic Database (https://www.dyntaxa.se/; retrieved April 2016), with some species of e.g. *Alchemilla*, *Rubus*, *Ranunculus* and a number of Asteraceae assigned to Section only.

Calculation of species' climate associations

To calculate the thermal and precipitation associations for each plant species, we used occurrence data from all 18 available published and ongoing provincial flora inventories from 1965 until 2017. These regions cover the major land-use and climatic gradients of Sweden, from the southernmost tip to the far north and into the Scandes mountains. Data were downloaded from the Swedish Species Gateway (https://www.artportalen.se/) or obtained directly from the responsible botanical society. Species names were harmonised as above, and there were in total more than 7.3 million observations of 3066 species (2241 of which present in the four focal provinces). For climate data, we used the Swedish Meteorological and Hydrological Institute's 4 km gridded climate data from 1961-2011 (database *ptHBV*, http://luftweb.smhi.se/). For each observation, the means of the mean annual temperature (ºC) and total annual precipitation (mm) were calculated as the means (temperature) and totals (precipitation) of each calendar month's values for the year of observation and the four preceding years. Observations after 2012 were assigned climate data from 2011. The mean values for each species were then assigned as that species' thermal and precipitation association.

Response variable: community climate indices

For each of the 996 landscapes, we calculated community climatic indices based on the species present in a landscape for the historical period and for the modern period. For Bohuslän and

Medelpad, where the historical occurrence data were more complete, this involved all recorded species across both time periods. For Öland and Uppland, indices for historical communities were based on mapped species only, while for the modern dataset we included all mapped species plus all species recorded in the modern flora that were not present in the historical species pool (i.e., neither mapped nor mentioned in the historical flora's text). We also checked whether community reorganisation is detectable through the redistribution of existing species without the addition of new species to a region. To do this, we calculated modern community climatic indices in all four provinces based only on species occurring in the historical time period. These results are only shown in the Supporting Information. Community thermal and precipitation means (ºC and mm, respectively) were calculated as the mean of the climatic indices for each species present in each landscape at each time period. The range of species' climate associations within a landscape was calculated as the interquartile range of the species' temperature and precipitation associations for all species within a landscape. Interquartile ranges were chosen to avoid the effect of individual species with unusually high or low values for climate associations skewing absolute ranges. Absolute ranges were also calculated to ensure that our conclusions are robust.

Explanatory variables: land-use change, climate change and non-native species

For land-use change, we used digitisations of the Swedish Economic Map, which was created between the 1930s and 1960s over the study area (Auffret, Kimberley, et al., 2017a, 2017b). The 1 m resolution digitisations were aggregated to 5 m, and distinguish arable fields, forest, open areas (mainly grasslands, but also wetlands and urban land uses) and surface water. For Öland, Uppland and Medelpad, map sheets corresponded to the 5 × 5 km landscapes used for the species observation data. Historical land use in Bohuslän was mapped according to a different (older) grid system, and digitised maps were therefore resampled to match the modern grid. Proportions of the four land-use categories were calculated per landscape, and landscape heterogeneity was calculated as the Shannon diversity of these categories. Present-day land use was attained from the 2016 Swedish terrain map (https://www.lantmateriet.se/en/maps-and-geographic-information/oppna-data/), which was rasterised and recoded to match the broad categories of the historical map (Table S1 in the Supporting Information). Semi-natural grasslands from the publicly-available national database (TUVA– http://www.sjv.se/tuva) were added as open land. Proportion area and heterogeneity of the four land-use categories were then calculated per map sheet as with the historical maps, with change over time calculated by subtracting the values of the historical data from the values of the modern data. Change in landscape heterogeneity was inverted (-1 × Shannon diversity) to describe the prevailing trend of landscape simplification: i.e., a higher positive value indicates that land use became more homogeneous over time.

For climate change, we used the same 1961-2011 gridded climate data as for the calculation of species climate indices. The 5 × 5 km landscape grid from the flora data was overlain with the climatic data and the mean average temperature and annual precipitation for the periods 1961-1970 and 2001-2010 were calculated as the historical and modern climatic conditions, respectively.

Fractions of non-native species were also calculated per landscape and time period. We used neophytes as our definition of non-native species, which are species where their first recorded observation in Sweden was in 1492 or later, according to the European Network on Invasive Alien Species (Nobanis database https://www.nobanis.org/; retrieved July 2017). Data were processed in the R environment (R Development Core Team, 2017) using the packages *gdalUtils* (Greenberg & Mattiuzzi, 2015), *rgdal* (Bivand, Keitt, & Rowlingson, 2017), *raster* (Hijmans, 2016), and *vegan* (Oksanen et al., 2016).

Data analysis

We first assessed whether landscape-level community climate indices could be related to landscape-level climatic conditions. To do this, we built separate linear mixed models for temperature and precipitation using the modern community and climate data, where thermal/precipitation index was the response variable, mean annual temperature/precipitation a single fixed predictor variable and province set as a random effect.

Next, we assessed the direction of shifts in community climate indices within landscapes. Due to non-normality in response variables, we used Wilcoxon signed rank tests to test the hypothesis that mean temperature and precipitation index values had increased, indicating community-level shifts in accordance with the observed climatic changes in the study region. We then tested the hypothesis that the interquartile range of index values of the species within a landscape had decreased between the historical and modern floras, indicating a combined colonisation of warm- and wet-adapted species and the extirpation of cool- and dry-adapted species. We also calculated confidence intervals (95%) for change in community climatic indices across all landscapes by building linear mixed effects models for change in each index, with no fixed effects and province as a random effect.

The influence of climate change, land-use change and the fraction of non-native species on shifts in community climate indices over time were then tested using mixed models. Four linear mixed models with Gaussian error distributions and log-likelihood estimate calculations were built to assess [1] change in community thermal mean, [2] reduction in community thermal interquartile range, [3] change in community precipitation mean, and [4] reduction in community precipitation interquartile range. Each model had the following structure:

Change in community climate index ~ (change in climate × landscape simplification) + (change in *climate × change in fraction neophytes) + (change in fraction neophytes × landscape simplification) + change in species richness + (latitude × longitude) + (1 | Province)*

Predictor variables were thus: change in climate (temperature for thermal indices and precipitation for precipitation indices), magnitude of landscape simplification, change in fraction neophytes, and the two-way interactions between the above variables. Landscape simplification was chosen as the sole landscape variable due to non-independence across land-use categories and because it represents an informative gradient of land-use change across Sweden based on the limitations of the historical maps (Auffret, Kimberley, Plue, & Waldén, 2018; Figure S1). Change in species richness was added as a further single fixed term to account for this potential effect. Because of the strong spatial structure of the data, the latitude and longitude of each landscape, plus their interaction were added as fixed effects in the models, while province was included as a random effect. Due to the well-known correlation between latitude and longitude and climate (change), latitude and longitude were included in the models as the residual variation after removal of their effect on climate. Residuals were extracted from separate Gaussian generalised linear models (one each for latitude and longitude) with each landscape's latitude or longitude as the dependent variable and change in precipitation, change in temperature and their interaction as predictor variables. In all community climate index models, fixed predictor effects were zero-mean scaled prior to analysis and those predictors that were included in the same models were comfortably below acceptable limits for collinearity, having variance inflation factors of less than 2 (Zuur et al., 2009) and Pearson correlations below 0.4 (Dormann et al., 2013; Zuur et al., 2009; Table S2).

The direction and strength of effects of predictor variables on community climate indices were assessed by calculating confidence intervals at the 95% level for each fixed predictor variable. Models were then evaluated by calculating marginal and conditional R^2 values, which inform how well each model's fixed effects alone (marginal R^2) and fixed plus random effects (conditional R^2) explain the variation in the dependent variable (Nakagawa & Schielzeth, 2013). Because R^2 values were somewhat low in some of the above models, we also tested whether our predictor variables could adequately explain community responses to climate change by comparing each model to an equivalent null model that only contained the random effect (province), using a Chi-square likelihood-ratio test (Plue & Cousins, 2018). We then built four new models, this time generalised linear mixed models with binomial error distributions to assess the extent to which our explanatory variables could explain the *occurrence* of directional shifts in community climate indices (1=increased mean or decreased range, 0=other or no change). These models had the same structure as those described above, and were evaluated in the same ways. All eight models were significant improvements on their equivalent null model, but they differed in explanatory power. Models were much better at explaining the occurrence of shifts in community thermal indices and the magnitude of shifts in precipitation indices. It is the results of these models that will presented and discussed in the main text. Models were created using R's *lme4* package (Bates, Maechler, Bolker, & Walker, 2014), figures were created with the help of the *scales* package (Wickham, 2017) and interaction effects were interpreted with the help of the *visreg* package (Breheny & Burchett, 2017).

Results

Community climate shifts

Both thermal and precipitation indices were significantly related to ambient climate conditions, confirming a (macro-)climatic influence on plant community composition at the landscape scale (Figure 1, Table S3). The relationship between ambient climate and community climate indices was clearly stronger for temperature than for precipitation, with community precipitation means in Medelpad generally having a different relationship with measured precipitation levels than those in the other provinces.

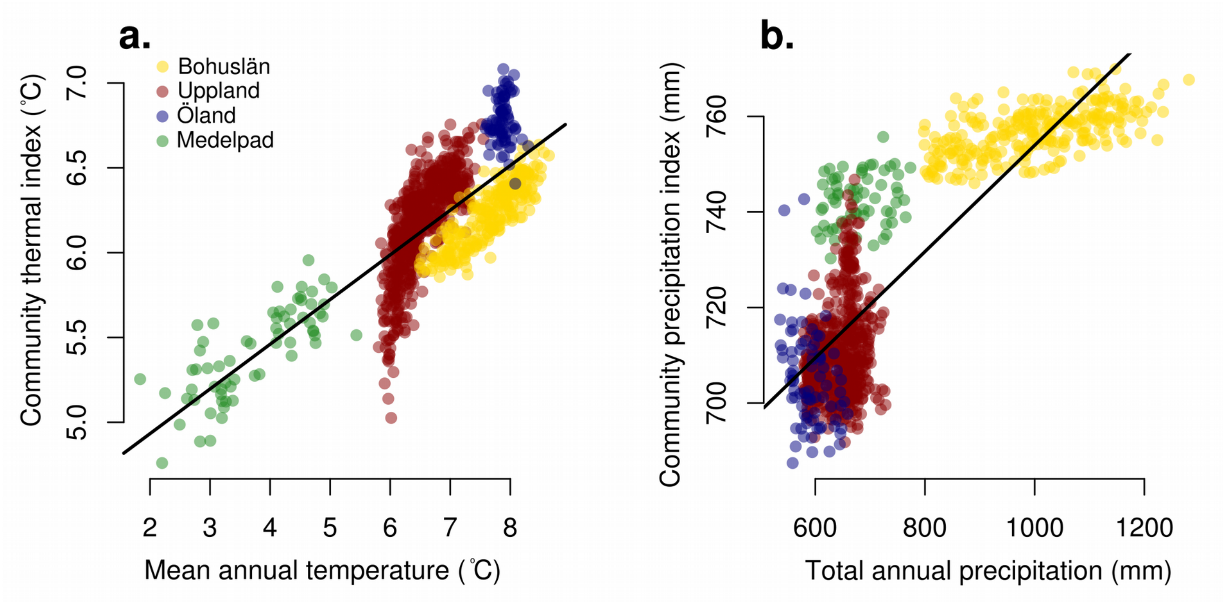


Figure 1. Relationship between indices of community thermal (a) and precipitation (b) calculated from the species occurring in 996 landscapes (coloured points), with the annual mean temperature (a) and precipitation (b) from the same landscapes, using modern flora and climate data. Scatter plots show data from four provinces of Sweden, lines are best-fit lines of the raw data. Models of precipitation indices are similar both when landscapes from Bohuslän (yellow points) are included and excluded, showing that such a linear relationship is accurate (Table S3).

During the course of the 20th century, communities have exhibited significant (Wilcoxon P=<0.001) shifts towards increased frequencies of species with warmer and wetter climatic associations, with almost three-quarters (74%) of our 996 landscapes increasing in community thermal index (Figure 2). Community warming (mean shift +0.1 ºC, 95% CI: +0.066 to +0.177 ºC) was consistent with the prevailing direction of climate change, where 100% of landscapes warmed between 1961-1970 and 2001-2010, with an mean±sd of 1.4 ± 0.13 ºC. Patterns were similar for community precipitation indices. Almost all landscapes (98%) experienced an increase in precipitation during the study period of 67.69 ± 48.49 mm, which was reflected in the significant increases in community precipitation (mean shift +5.5 mm, 95% CI: +1.31mm to +9.22 mm). In addition to increased community means, there was also significant (Wilcoxon P=<0.0001) homogenisation in community composition, as indicated by reduced interquartile ranges in species-level thermal and precipitation associations within landscapes. Interquartile ranges in species' temperature associations within a landscape decreased with a mean of -0.15 ºC (95% CI: 0.013 – 0.47 ºC reduction) while the reduction was -3.5 mm (0.987 – 15.0 mm reduction) for precipitation indices (Figure 2, Table S4).

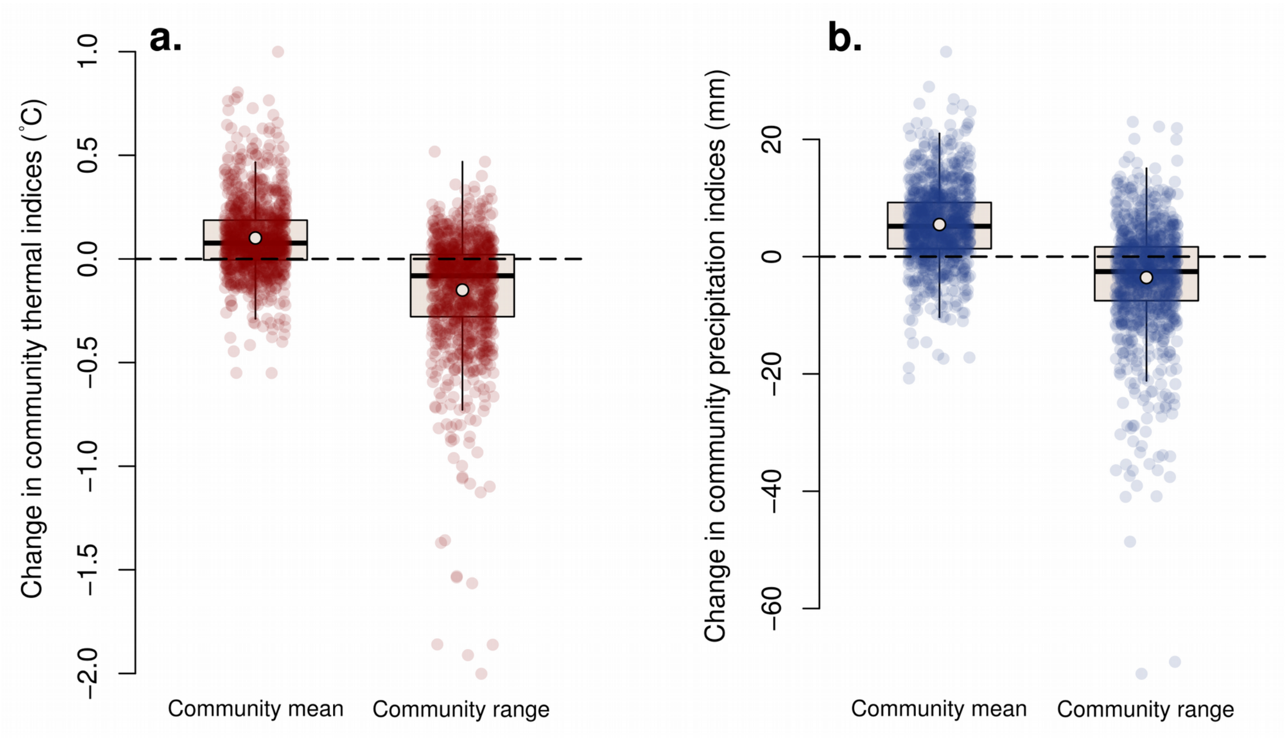


Figure 2. Twentieth-century shifts in community climate means and interquartile ranges for temperature (a) and precipitation (b) in 996 landscapes (coloured points). Boxes show median and interquartile range, with whiskers indicate range excluding outliers. White points indicate the mean shift in each case.

Effect of climate change, land-use change and non-native species

At the same time as temperature and precipitation increased, a widespread landscape simplification (loss in land-use heterogeneity) occurred across the study region, with more than two thirds of all landscapes experiencing such a shift. These changes were particularly prevalent in landscapes which had historically higher grassland and forest cover, both of which experienced forest expansion, leading to simplified landscapes. Historically arable-dominated landscapes were more likely to exhibit increases in landscape heterogeneity following abandonment of arable land (Auffret et al., 2018; Figure S1). Alongside changes in land use, non-native neophytes have increased their representation in the landscape. The fraction of neophytes within a landscape increased in 82% of landscapes, although the average increase was modest, from a mean ± sd of 28.5 ± 8% of species in early- to mid-20th century landscapes to 33.7 ± 7.3% today. Along with the expansion of neophytes, the total number of species has risen in 81% of landscapes, with a net increase of 63.9 ± 71.1 (mean±sd) species per landscape, from 186 ± 148.3 to 250 ± 161.3 (34% increase). However, these values should not be interpreted as absolute changes in species richness, as for two of the four provinces this estimate of species richness change excludes trends in occurrence for the majority of plant species, which were noted for the province in the historical data but their distributions not mapped.

The three studied drivers of global change – climate change, land-use change and non-native species – had significant and interacting effects on the turnover of species during the 20th century towards more thermo- and pluviophilic communities (Figures 3-4; Table S5). Plant communities became warmer (increased in mean thermal index) in landscapes with higher degrees of warming and where the representation of non-native species grew (increased fraction of neophytes; Figure 3a-c). Increases in community thermal means due to climate warming were more likely where there were larger increases in neophytes, and in landscapes that had been subjected to less simplification. In other words, there was a stronger effect of warming in less simplified landscapes. The effect of increased fraction neophytes on community warming reduced with increasing levels of landscape simplification (Figure 3g). A warming climate, landscape simplification and increases in non-native species also contributed to the thermal homogenisation (reduction in interquartile range) of plant communities (Figure 3d-f), with climate warming and landscape simplification having reinforcing effects on one another (Figure 3g). This means that landscapes that became increasingly simplified were more likely to exhibit decreasing variation of species in terms of temperature associations over time. These results are robust to overall changes in species richness, which did not have a consistent effect on community warming and were negatively associated with thermal homogenisation (Table S5). This implies that the landscapes with the highest levels of community warming and thermal homogenisation lost relatively high proportions of their original cold-adapted species.

In contrast with community responses to warming, increases in wet-adapted plant species in the landscape were counteracted by the main drivers of global change. Levels of increasing precipitation, landscape simplification and increased fractions of neophytes were all negatively associated with increases in community precipitation means, although increasing proportions of neophytes dampened the negative effect of precipitation change (Figure 4a-c, g). Therefore, community reorganisation in response to a wetter climate seems to occur *in spite* of the prevailing changes in the main drivers of global change, indicating an antagonistic effect of the global change drivers operating at landscape scales. On the other hand, homogenisation of precipitation associations within a landscape appeared synergistic with respect to increased fractions of neophytes (Figure 4d-f, h, Table S5).

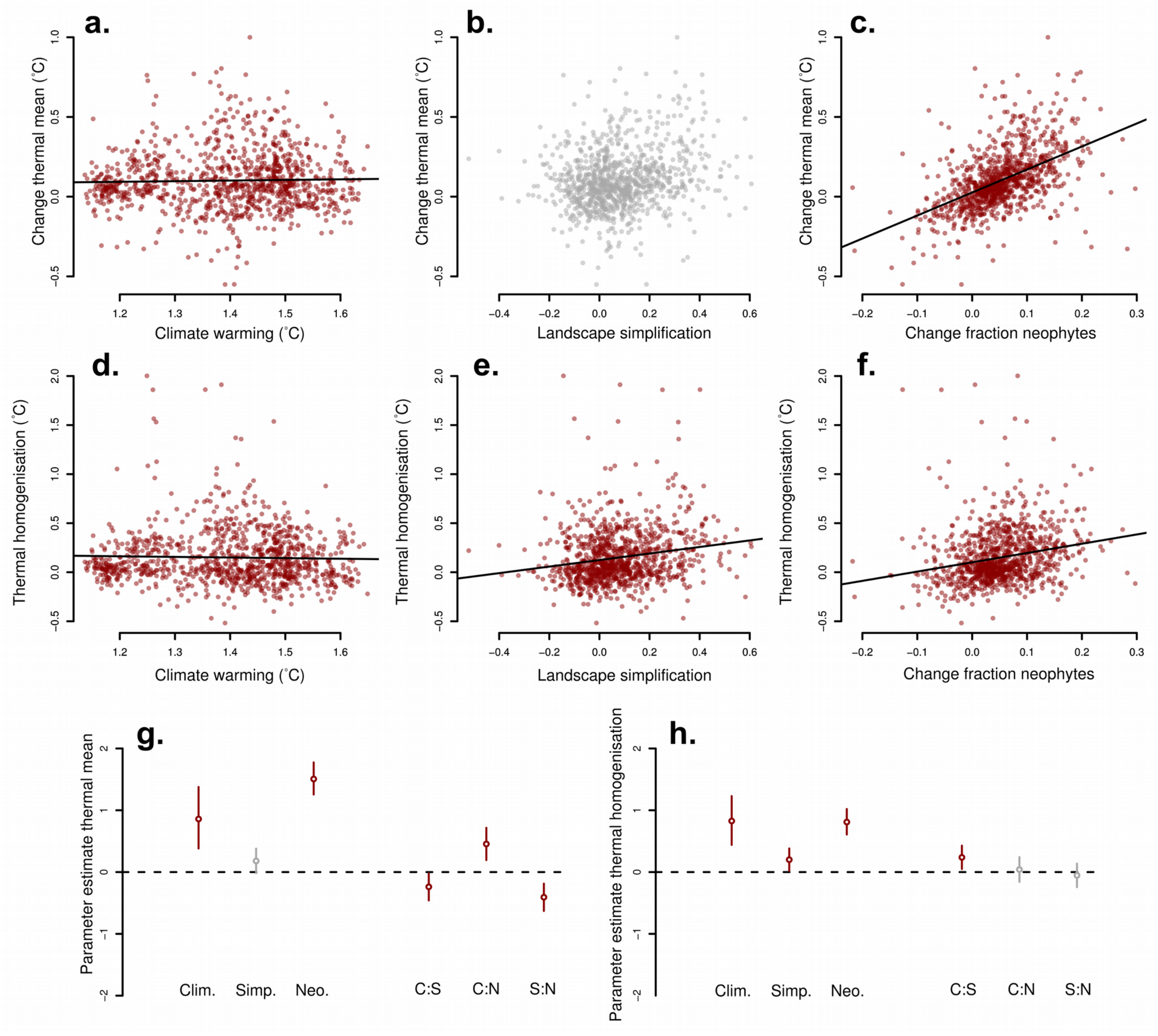


Figure 3. Effect of increasing temperatures, landscape simplification and changes in fractions of neophytes (introduced species first observed in Sweden post-1492) and their interactions on shifts in community thermal indices in 996 landscapes for both changes in mean (a-c & g; model R^2 marginal = 0.41 and conditional = 0.54) and homogenisation (d-f & h; model R^2 marginal = 0.28 and conditional = 0.84). Scatter plots show raw data with best-fit lines while point-and-bar plots show parameter estimates and 95% confidence intervals in mixed models. Note that climate warming has a positive effect on both thermal mean and thermal homogenisation. Estimates of drivers of the *occurrence* of shifts are shown, with grey panels/bars indicating non-significant model terms (confidence intervals cross zero), while red panels/bars are significant. Model coefficients for all variables (including species richness, latitude and longitude) plus further metrics of model performance are shown for these models and those explaining the *magnitude* of shifts in Tables S5 & S6.

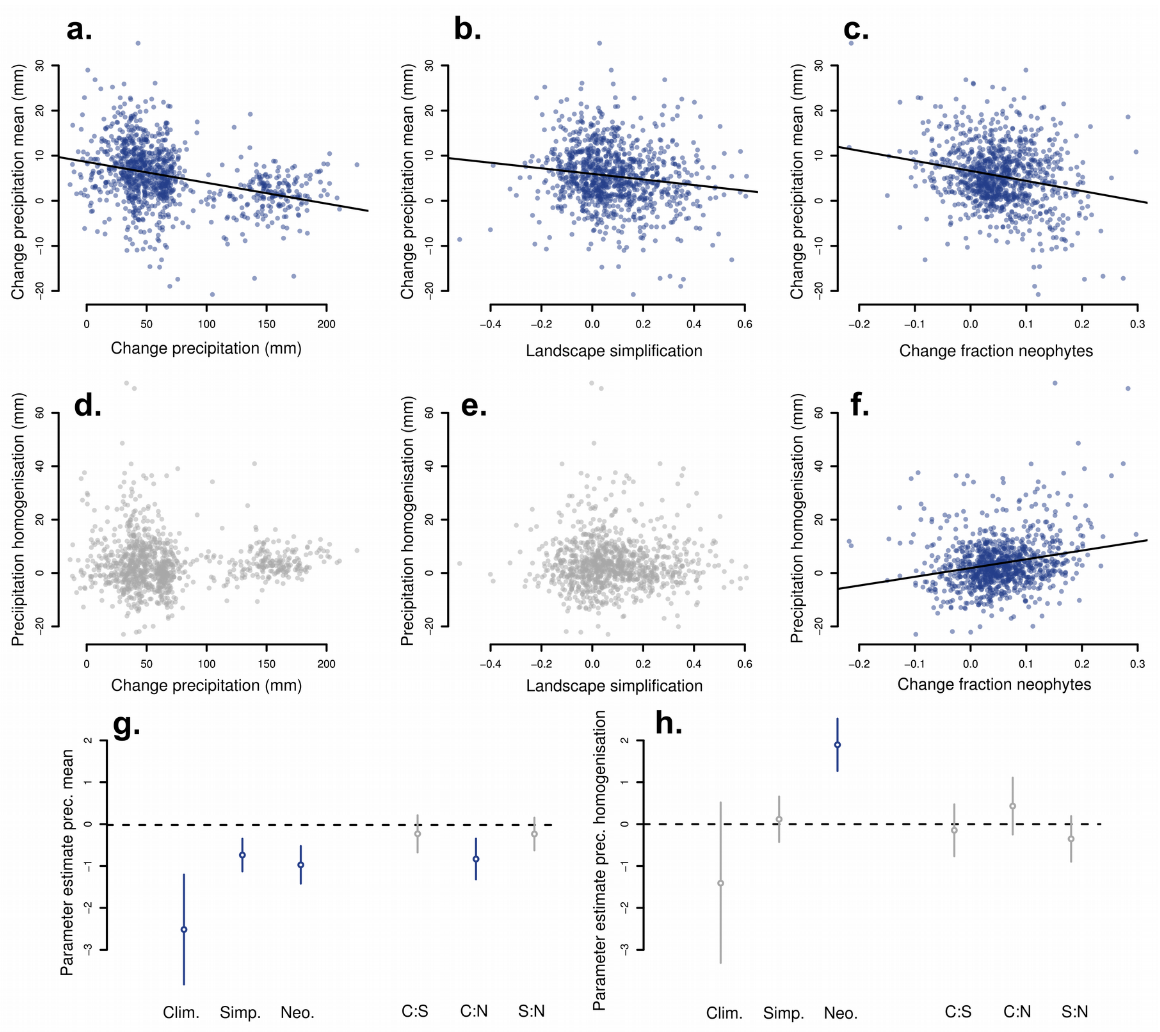


Figure 4. Effect of increasing precipitation, landscape simplification and changes in fractions of neophytes (introduced species first observed in Sweden post-1492) and their interactions on shifts in community precipitation indices in 996 landscapes for both changes in mean (a-c & g; model R^2 marginal = 0.43 and conditional = 0.87) and homogenisation (d-f & h; model R^2 marginal = 0.14 and conditional = 0.93). Scatter plots show raw data with best-fit lines while point-and-bar plots show parameter estimates and 95% confidence intervals in mixed models. Estimates of drivers of the *magnitude* of shifts are shown, with grey panels/bars indicating non-significant model terms (confidence intervals cross zero), while blue panels/bars are significant. Model coefficients for all variables (including species richness, latitude and longitude) plus metrics of model performance are shown for these models and those explaining the *occurrence* of shifts in Tables S5 & S6.

Discussion

Our results show that communities have consistently responded to the prevailing direction of climate change in Sweden (Kjellström et al., 2014), with changes in community climatic indices over time suggesting that the vegetation is increasingly composed of species that are associated with warmer and wetter conditions. We also found that the flora has become more homogeneous with respect to species' climatic associations over time. The combination of increasing means and decreasing ranges indicates that community turnover during the 20th century has been characterised both by the expansion of warm- and wet-adapted species, and also by the climate-driven extirpations of cooler- and dry-adapted species. Importantly, we found that changes in land use and increases in non-native species exert both synergistic and antagonistic effects on community responses to climate change at landscape scales.

As well as the effect of increased temperatures driving community warming and homogenisation, land-use change and increases in non-native species were also shown to influence the climate-driven turnover of species (Figure 3; Table S5). There was no clear direct effect of landscape simplification on community warming, but the driving effect of increasing temperature was lower in more simplified landscapes. In Sweden, the trend towards more simplified landscapes is primarily associated with an increase in wooded area at the expense of arable and open land (Auffret et al., 2018; Figure S1). Temperatures within forests are generally found to be cooler than open areas (De Frenne et al., 2019; Frey et al., 2016; Greiser, Meineri, Luoto, Ehrlén, & Hylander, 2018). This could mean that increased forest cover in simplified landscapes has buffered increasing temperatures to some extent, resulting in a lower likelihood of increased community thermal means (De Frenne et al., 2013). On the other hand, higher levels of landscape simplification were linked to a loss of variation in species' temperature associations within a landscape (Figure 3; Table S5). Another implication of landscape simplification could be that because different land-cover types have different microclimates (Greiser et al., 2018; Morecroft, Taylor, & Oliver, 1998), those landscapes experiencing higher levels of landscape simplification are also losing microclimatic variability at the landscape level. This means that as well as potentially buffering the effects of a warming climate in terms of limiting shifts in community thermal means, increased landscape simplification may have driven thermal homogenisation through having a lower variation in microclimates and fewer refugia in which cool-adapted species could persist (Lenoir et al., 2013; Maclean et al., 2015; Suggitt et al., 2018). Cooler-distributed species would then be more likely to disappear from landscapes undergoing higher levels of landscape simplification, contributing to the observed increase in community thermal mean and thermal homogenisation. Indeed, the effect of warming on thermal homogenisation was higher more simplified landscapes, as indicated by the positive interaction between temperature change and landscape simplification in the model.

Previous studies that examined the effects of landscape composition on changes in community thermal indices consider the current 'simplicity' of the landscape as opposed to change over time (Bertrand et al., 2011; Gaüzère et al., 2017; Oliver et al., 2017). These studies find that community change is impeded in already more simplified landscapes, i.e. those with more agricultural land uses that could be expected to inhibit dispersal and as a result prevent community reorganisation. Our results also found that landscape simplification may be inhibiting shifts in community thermal means, but in different ways. It is clear that landscape change can affect how communities respond to climate change both at the local scale through variation in available habitat and microclimate (Lenoir et al., 2013; Suggitt et al., 2018), but also through how changes in landscape structure can alter the potential for species to disperse to new areas (Auffret, Rico, et al., 2017) .

Non-native species were also shown to drive turnover towards warmer and more climatically homogeneous communities. Warmer index values with increasing fractions of non-natives are to be expected because species introduced to Sweden's relatively northern latitudes are, on average, likely to originate from warmer climates. However, the modest increases in the fraction of non-natives during the 20th century (from 28.5% to 33.7% per landscape, on average) implies that much of this trend was due to the internal spread of species that are still expanding within provinces (Crooks, 2005). Increases in neophytes also interacted with both of the other drivers of global change to explain community climatic shifts. A positive, reinforcing statistical interaction between temperature change and increases in neophytes further supports the assertion that this species group is linked to warmer temperatures, as well as previous work linking climate change to the increased risk of biological invasions (Stachowicz, Terwin, Whitlatch, & Osman, 2002; Walther et al., 2009). The negative interaction between landscape simplification and increasing neophytes suggests that more heterogeneous landscapes contain more suitable habitats for colonisation specifically by incoming neophytes (Hejda et al., 2009). Another possibility is that as more heterogeneous landscapes in our case were related to agricultural land uses, the interaction between landscape and non-native species could also reflect the fact that non-native species are generally introduced and spread by humans. Increasing neophytes and related increases in species richness in our study follows a general trend of increasing species richness at spatial scales that lie between the local and the global (Thomas & Palmer, 2015; Vellend et al., 2017). Non-native species have driven community changes in the past, and, in Sweden and other cool parts of the world, clearly have the potential to respond positively to ongoing climate change.

Despite moisture availability being a known driver of vegetation change worldwide (Peñuelas et al., 2013), changes in community precipitation or moisture indices over time been studied to a much lesser extent than thermal indices. However, results from this study and a study from the UK

(Maclean et al., 2015) show that plant communities respond directionally both to increases and reductions in precipitation. Shifts in community precipitation indices were strongly region-driven, with a large effect of province in the model, as well as the surprising negative effect of measured precipitation increases on the observed increases in precipitation indices from the plant communities (Figure 4, Table S5). This is likely to be due to the much wetter province of Bohuslän also having the largest increases in precipitation that were not matched in changes in the flora. This region was probably already characterised by species with 'wet' distributions in the historical period, and so the magnitude of shifts in precipitation indices was much lower than in the other provinces. The introduction and spread of neophytes also had antagonistic effects on changes in precipitation indices. Again, non-native species are likely to originate from warmer and drier regions than Sweden, but the prevailing trend towards a wetter climate did not act as a hinder to their colonisation and spread during the 20th century. Given that changes in precipitation have varied widely across space (IPCC, 2015) and that there is considerable uncertainty in future predictions (Knutti & Sedláček, 2013), these antagonistic interactions suggest that understanding how communities will respond to future in precipitation changes represents a major challenge.

Our analysis showed clear directional community responses to climate change, though these responses appear slow when compared to the rate of increased temperature and precipitation in the study region. Rates of community warming at around 0.1 ºC also appear to be up to an order of magnitude slower than previously measured rates (Bertrand et al., 2011; De Frenne et al., 2013; Fadrique et al., 2018). Previous studies have been based on plot-scale plant communities, and it is understandable that changes will occur more slowly at landscape scales. However, it is difficult both to directly compare change in community climate indices with change in measured climate in terms of ºC temperature and mm precipitation, and to compare rates of change in community climate indices across studies. As is the case in our study, climate indices for plant species are often based on occurrences that do not cover the species' full geographic range (Bertrand et al., 2011; Lenoir et al., 2013; Maclean et al., 2015; but see De Frenne et al., 2013). Secondly, climate data is usually available at a different (larger) spatial scale compared to community data whose response is being tested, which can affect comparisons over time, although in our case these scales were relatively well matched. Finally, our community indices could only be based on presence-absence rather than weighted by abundances, as well as being based on incomplete communities for two of the four study provinces. This will naturally have influenced our estimates of community change over time, but such limitations are common when working with historical data, which are still an important tool for understanding ecological responses to environmental change (Vellend, Brown, Kharouba, McCune, & Myers-Smith, 2013). Despite such issues, community climate indices are an increasingly popular way of broadly studying ecological responses to climate change, and ecologically meaningful trends of direction, apparent time lags and the influence of land use are shared across space, time and taxa (De Frenne et al., 2013; Flanagan, Jensen, Morley, & Pinsky, 2019; Gaüzère et al., 2017; Oliver et al., 2017).

Our results indicate that the evaluation of biological responses to global change should explicitly consider the synergistic and antagonistic effects of different anthropogenic drivers of change. Understanding these interactions and their outcomes can be useful not only for evaluating the key processes involved, but also for designing effective conservation schemes to both facilitate colonisation by incoming species, and to consider management options that may either temporarily (given time lags) or permanently permit individual species and communities to persist where it would not otherwise be expected.

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Data availability

Analysed predictor and response variables for each landscape have been deposited at the Figshare data repository, together with the climatic indices for 3066 Swedish plant species. http://dx.doi.org/XXXXX.

References

Auffret, A. G., Kimberley, A., Plue, J., Skånes, H., Jakobsson, S., Waldén, E., … Tränk, L. (2017a). Data from: HistMapR: Rapid digitization of historical land-use maps in R. *Figshare Data Repository*, url: dx.doi.org/10.17045/sthlmuni.4649854. https://doi.org/10.17045/sthlmuni.4649854

Auffret, A. G., Kimberley, A., Plue, J., Skånes, H., Jakobsson, S., Waldén, E., … Tränk, L. (2017b). HistMapR: Rapid digitization of historical land-use maps in R. *Methods in Ecology and Evolution*, *8*(11), 1453–1457. https://doi.org/10.1111/2041-210X.12788

Auffret, A. G., Kimberley, A., Plue, J., & Waldén, E. (2018). Super-regional land-use change and effects on the grassland specialist flora. *Nature Communications*, *9*(1), 3464. https://doi.org/10.1038/s41467-018-05991-y

Auffret, A. G., Rico, Y., Bullock, J. M., Hooftman, D. A. P., Pakeman, R. J., Soons, M. B., … Cousins, S. A. O. (2017). Plant functional connectivity – integrating landscape structure and effective dispersal. *Journal of Ecology*, *105*(6), 1648–1656. https://doi.org/10.1111/1365-2745.12742

Bates, D., Maechler, M., Bolker, B. M., & Walker, S. (2014). lme4: Linear mixed-effects models using Eigen and S4. *R Package Version 1.1-7*, *http://CRAN.R-project.org/package=lme4*.

Bertrand, R., Lenoir, J., Piedallu, C., Riofrío-Dillon, G., de Ruffray, P., Vidal, C., … Gégout, J.-C.

(2011). Changes in plant community composition lag behind climate warming in lowland forests. *Nature*, *479*(7374), 517–520. https://doi.org/10.1038/nature10548

Bivand, R., Keitt, T., & Rowlingson, B. (2017). rgdal: Bindings for the “Geospatial” Data Abstraction Library. *R Package Version 1.2-16*, url: https://CRAN.R-project.org/package=rgdal.

Blomgren, E., Falk, E., & Herloff, B. (2011). *Bohusläns Flora*. Lund, Sweden: Förrningen Bohusläns Flora.

Breheny, P., & Burchett, W. (2017). Visualization of Regression Models Using visreg. *The R Journal*, *9*, 57–71.

Chen, I.-C., Hill, J. K., Ohlemüller, R., Roy, D. B., & Thomas, C. D. (2011). Rapid Range Shifts of Species Associated with High Levels of Climate Warming. *Science*, *333*(6045), 1024–1026. https://doi.org/10.1126/science.1206432

Crooks, J. A. (2005). Lag times and exotic species: The ecology and management of biological invasions in slow-motion. *Ecoscience*, *12*(3), 316–329. https://doi.org/10.2980/i1195-6860-12-3-316.1

De Frenne, P., Rodríguez-Sánchez, F., Coomes, D. A., Baeten, L., Verstraeten, G., Vellend, M., … Verheyen, K. (2013). Microclimate moderates plant responses to macroclimate warming. *Proceedings of the National Academy of Sciences*, *110*(46), 18561–18565. https://doi.org/10.1073/pnas.1311190110

De Frenne, P., Zellweger, F., Rodríguez-Sánchez, F., Scheffers, B. R., Hylander, K., Luoto, M., … Lenoir, J. (2019). Global buffering of temperatures under forest canopies. *Nature Ecology & Evolution*, *3*(5), 744. https://doi.org/10.1038/s41559-019-0842-1

Devictor, V., Julliard, R., Couvet, D., & Jiguet, F. (2008). Birds are tracking climate warming, but not fast enough. *Proceedings of the Royal Society of London B: Biological Sciences*, *275*(1652), 2743–2748. https://doi.org/10.1098/rspb.2008.0878

Devictor, V., van Swaay, C., Brereton, T., Brotons, L., Chamberlain, D., Heliölä, J., … Jiguet, F. (2012). Differences in the climatic debts of birds and butterflies at a continental scale. *Nature Climate Change*, *2*(2), 121–124. https://doi.org/10.1038/nclimate1347

Didham, R. K., Tylianakis, J. M., Gemmell, N. J., Rand, T. A., & Ewers, R. M. (2007). Interactive effects of habitat modification and species invasion on native species decline. *Trends in Ecology & Evolution*, *22*(9), 489–496. https://doi.org/10.1016/j.tree.2007.07.001

Donald, P. F., Green, R. E., & Heath, M. F. (2001). Agricultural intensification and the collapse of Europe’s farmland bird populations. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *268*(1462), 25–29. https://doi.org/10.1098/rspb.2000.1325

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., … Lautenbach, S. (2013). Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, *36*(1), 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x

Early, R., Bradley, B. A., Dukes, J. S., Lawler, J. J., Olden, J. D., Blumenthal, D. M., … Tatem, A. J. (2016). Global threats from invasive alien species in the twenty-first century and national response capacities. *Nature Communications*, *7*, 12485. https://doi.org/10.1038/ncomms12485

Early, R., & Sax, D. F. (2014). Climatic niche shifts between species’ native and naturalized ranges raise concern for ecological forecasts during invasions and climate change. *Global Ecology and Biogeography*, *23*(12), 1356–1365. https://doi.org/10.1111/geb.12208

Fadrique, B., Báez, S., Duque, Á., Malizia, A., Blundo, C., Carilla, J., … Feeley, K. J. (2018). Widespread but heterogeneous responses of Andean forests to climate change. *Nature*, *564*(7735), 207. https://doi.org/10.1038/s41586-018-0715-9

Flanagan, P. H., Jensen, O. P., Morley, J. W., & Pinsky, M. L. (2019). Response of marine communities to local temperature changes. *Ecography*, *42*(1), 214–224. https://doi.org/10.1111/ecog.03961

Frey, S. J. K., Hadley, A. S., Johnson, S. L., Schulze, M., Jones, J. A., & Betts, M. G. (2016). Spatial models reveal the microclimatic buffering capacity of old-growth forests. *Science Advances*, *2*(4), e1501392. https://doi.org/10.1126/sciadv.1501392

Gaüzère, P., Princé, K., & Devictor, V. (2017). Where do they go? The effects of topography and habitat diversity on reducing climatic debt in birds. *Global Change Biology*, *23*(6), 2218–2229. https://doi.org/10.1111/gcb.13500

Gerstner, K., Dormann, C. F., Stein, A., Manceur, A. M., & Seppelt, R. (2014). Effects of land use on plant diversity – A global meta-analysis. *Journal of Applied Ecology*, *51*(6), 1690–1700.

https://doi.org/10.1111/1365-2664.12329

Greenberg, J. A., & Mattiuzzi, M. (2015). gdalUtils: Wrappers for the Geospatial Data Abstraction Library (GDAL) Utilities. *R Package Version 2.0.1.7*, url: http://CRAN.R-project.org/package=gdalUtils.

Greiser, C., Meineri, E., Luoto, M., Ehrlén, J., & Hylander, K. (2018). Monthly microclimate models in a managed boreal forest landscape. *Agricultural and Forest Meteorology*, *250–251*, 147–158. https://doi.org/10.1016/j.agrformet.2017.12.252

Hejda, M., Pyšek, P., Pergl, J., Sádlo, J., Chytrý, M., & Jarošík, V. (2009). Invasion success of alien plants: do habitat affinities in the native distribution range matter? *Global Ecology and Biogeography*, *18*(3), 372–382. https://doi.org/10.1111/j.1466-8238.2009.00445.x

Hijmans, R. J. (2016). raster: Geographic Data Analysis and Modeling. *R Package Version 2.5-8*, url: http://CRAN.R-project.org/package=raster.

IPCC. (2015). *Climate change 2014: synthesis report* (R. K. Pachauri & L. Mayer, Eds.). Geneva, Switzerland: Intergovernmental Panel on Climate Change.

Jonsell, L. (2010). *Upplands Flora*. Uppsala, Sweden: SBF Förlaget.

Kjellström, E., Abrahamsson, R., Boberg, P., Jernbäcker, E., Karlberg, M., Morel, J., & Sjöström, Å. (2014). Uppdatering av det klimatvetenskapliga kunskapsläget. *SMHI Klimatologi*, *9*, 1–66.

Knutti, R., & Sedláček, J. (2013). Robustness and uncertainties in the new CMIP5 climate model projections. *Nature Climate Change*, *3*(4), 369–373. https://doi.org/10.1038/nclimate1716

Lenoir, J., Graae, B. J., Aarrestad, P. A., Alsos, I. G., Armbruster, W. S., Austrheim, G., … Svenning, J.-C. (2013). Local temperatures inferred from plant communities suggest strong spatial buffering of climate warming across Northern Europe. *Global Change Biology*, *19*(5), 1470–1481. https://doi.org/10.1111/gcb.12129

Lidberg, R., & Lindström, H. (2010). *Medelpads Flora (The vascular plants of Medelpad)*. Uppsala, Sweden: SBF Förlaget.

Maad, J., Sundberg, S., Stolpe, P., & Jonsell, L. (2009). Floraförändringar i Uppland under 1900-talet — en analys från Projekt Upplands flora [Floristic changes during the 20th century in Uppland, east central Sweden; with English summary]. *Svensk Botanisk Tidskrift*, *103*, 67–104.

Maclean, I. M. D., Hopkins, J. J., Bennie, J., Lawson, C. R., & Wilson, R. J. (2015). Microclimates buffer the responses of plant communities to climate change. *Global Ecology and Biogeography*, *24*(11), 1340–1350. https://doi.org/10.1111/geb.12359

Morecroft, M. D., Taylor, M. E., & Oliver, H. R. (1998). Air and soil microclimates of deciduous woodland compared to an open site. *Agricultural and Forest Meteorology*, *90*(1), 141–156. https://doi.org/10.1016/S0168-1923(97)00070-1

Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, *4*(2), 133–142. https://doi.org/10.1111/j.2041-210x.2012.00261.x

Newbold, T., Hudson, L. N., Hill, S. L. L., Contu, S., Lysenko, I., Senior, R. A., … Purvis, A. (2015). Global effects of land use on local terrestrial biodiversity. *Nature*, *520*(7545), 45–50. https://doi.org/10.1038/nature14324

Northrup, J. M., Rivers, J. W., Yang, Z., & Betts, M. G. (2019). Synergistic effects of climate and land-use change influence broad-scale avian population declines. *Global Change Biology*, *25*(5), 1561–1575. https://doi.org/10.1111/gcb.14571

Oksanen, J., Guillaume Blanchet, F., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., … Wagner, H. H. (2016). vegan: Community Ecology Package. *R Package Version 2.3-5*, url: http://CRAN.R-project.org/package=vegan.

Oliver, T. H., Gillings, S., Pearce-Higgins, J. W., Brereton, T., Crick, H. Q. P., Duffield, S. J., … Roy, D. B. (2017). Large extents of intensive land use limit community reorganization during climate warming. *Global Change Biology*, *23*(6), 2272–2283. https://doi.org/10.1111/gcb.13587

Ollerton, J., Erenler, H., Edwards, M., & Crockett, R. (2014). Extinctions of aculeate pollinators in Britain and the role of large-scale agricultural changes. *Science*, *346*(6215), 1360–1362. https://doi.org/10.1126/science.1257259

Peñuelas, J., Sardans, J., Estiarte, M., Ogaya, R., Carnicer, J., Coll, M., … Jump, A. S. (2013). Evidence of current impact of climate change on life: a walk from genes to the biosphere. *Global Change Biology*, *19*(8), 2303–2338. https://doi.org/10.1111/gcb.12143

Plue, J., & Cousins, S. A. O. (2018). Seed dispersal in both space and time is necessary for plant diversity maintenance in fragmented landscapes. *Oikos*, *127*(6), 780–791. https://doi.org/10.1111/oik.04813

R Development Core Team. (2017). *R: A Language and Environment for Statistical Computing*. Retrieved from http://www.R-project.org/

Stachowicz, J. J., Terwin, J. R., Whitlatch, R. B., & Osman, R. W. (2002). Linking climate change and biological invasions: Ocean warming facilitates nonindigenous species invasions. *Proceedings of the National Academy of Sciences*, *99*(24), 15497–15500. https://doi.org/10.1073/pnas.242437499

Steinbauer, M. J., Grytnes, J.-A., Jurasinski, G., Kulonen, A., Lenoir, J., Pauli, H., … Wipf, S. (2018). Accelerated increase in plant species richness on mountain summits is linked to warming. *Nature*, *556*(7700), 231. https://doi.org/10.1038/s41586-018-0005-6

Sterner, R. (1938). *Flora der insel Öland*. Uppsala, Sweden: Almqvist & Wiksells.

Suggitt, A. J., Wilson, R. J., Isaac, N. J. B., Beale, C. M., Auffret, A. G., August, T., … Maclean, I. M. D. (2018). Extinction risk from climate change is reduced by microclimatic buffering. *Nature Climate Change*, *8*, 713–717.

Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J., Collingham, Y. C., … Williams, S. E. (2004). Extinction risk from climate change. *Nature*, *427*(6970), 145–148. https://doi.org/10.1038/nature02121

Thomas, C. D., Gillingham, P. K., Bradbury, R. B., Roy, D. B., Anderson, B. J., Baxter, J. M., … Hill, J. K. (2012). Protected areas facilitate species' range expansions. *Proceedings of the National Academy of Sciences*, *109*(35), 14063–14068. https://doi.org/10.1073/pnas.1210251109

Thomas, C. D., & Palmer, G. (2015). Non-native plants add to the British flora without negative consequences for native diversity. *Proceedings of the National Academy of Sciences*, 201423995. https://doi.org/10.1073/pnas.1423995112

Van der Veken, S., Hermy, M., Vellend, M., Knapen, A., & Verheyen, K. (2008). Garden plants get a head start on climate change. *Frontiers in Ecology and the Environment*, *6*(4), 212–216. https://doi.org/10.1890/070063

Vellend, M., Baeten, L., Becker-Scarpitta, A., Boucher-Lalonde, V., McCune, J. L., Messier, J., …

Sax, D. F. (2017). Plant Biodiversity Change Across Scales During the Anthropocene. *Annual Review of Plant Biology*, *68*(1), 563–586. https://doi.org/10.1146/annurev-arplant-042916-040949

Vellend, M., Brown, C. D., Kharouba, H. M., McCune, J. L., & Myers-Smith, I. H. (2013). Historical ecology: using unconventional data sources to test for effects of global environmental change. *American Journal of Botany*, *100*(7), 1294–1305. https://doi.org/10.3732/ajb.1200503

Vilà, M., Espinar, J. L., Hejda, M., Hulme, P. E., Jarošík, V., Maron, J. L., … Pyšek, P. (2011). Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters*, *14*(7), 702–708. https://doi.org/10.1111/j.1461-0248.2011.01628.x

Walther, G.-R., Roques, A., Hulme, P. E., Sykes, M. T., Pyšek, P., Kühn, I., … Settele, J. (2009). Alien species in a warmer world: risks and opportunities. *Trends in Ecology & Evolution*, *24*(12), 686–693. https://doi.org/10.1016/j.tree.2009.06.008

Warren, M. S., Hill, J. K., Thomas, J. A., Asher, J., Fox, R., Huntley, B., … Thomas, C. D. (2001). Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature*, *414*(6859), 65–69. https://doi.org/10.1038/35102054

Wickham, H. (2017). scales: Scale Functions for Visualization. *R Package Version 0.5.0*, https://CRAN.R-project.org/package=scales.

Wiens, J. J. (2016). Climate-Related Local Extinctions Are Already Widespread among Plant and Animal Species. *PLOS Biology*, *14*(12), e2001104. https://doi.org/10.1371/journal.pbio.2001104

Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2009). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, *1*(1), 3–14. https://doi.org/10.1111/j.2041-210X.2009.00001.x