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1 **PRIMARY RESEARCH**

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

4

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

6

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**29 Abstract**

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

52 future.

53

## 54 **Keywords**

55 Biodiversity, Climatic debt, Community thermal index, Historical ecology, Invasive species,

56 Precipitation, Landscape change, Thermophilisation.

57

## 58 **Introduction**

59 Recent climate change has serious consequences for species' occurrences, distributions and survival

60 (Thomas et al., 2004; Wiens, 2016), with species-level responses combining to determine changes

61 in biodiversity, both now and in the future (Steinbauer et al., 2018; Warren et al., 2001). However,

62 climate change is only one of a number of anthropogenic pressures on biodiversity. Habitat

63 destruction through land-use change is currently seen as the largest threat to species worldwide

64 (Newbold et al., 2015), associated with negative population and community-level trends across

65 taxonomic groups (Donald, Green, & Heath, 2001; Gerstner, Dormann, Stein, Manceur, & Seppelt,

66 2014; Ollerton, Erenler, Edwards, & Crockett, 2014). A third driver of biodiversity change is

67 represented by the arrival of non-native species to new regions, which has been shown to alter the

68 richness and composition of communities over time (Thomas & Palmer, 2015; Vilà et al., 2011).

69

70 The above three elements of global change do not act separately from one another, but are known to

71 interact to drive changes in populations over time. For example, past habitat destruction has been

72 linked to species failing to expand their ranges following climate change (Warren et al., 2001),

73 while climate change can compound population declines in areas subjected to high levels of habitat

74 conversion (Northrup, Rivers, Yang, & Betts, 2019). On the other hand, protection from habitat

75 destruction can facilitate climate-driven range shifts, and a more varied topography at the landscape

76 level can moderate species' negative responses to warming temperatures (Suggitt et al., 2018;

77 Thomas et al., 2012). Similarly, interactions exist between biological invasions and other global  
78 change drivers. Habitat degradation, together with climate change can lead to a higher risk of non-  
79 native species establishment and invasive spread (Didham, Tylianakis, Gemmell, Rand, & Ewers,  
80 2007; Walther et al., 2009), something that is expected to continue in the future (Early et al., 2016).

81  
82 Despite generally consistent trends, species can exhibit a range of responses to climate change  
83 (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011), which together manifest in changes at the  
84 community or landscape level. One recently-developed method of assessing the effects of large-  
85 scale species-level responses to climate change on community-level composition is through the use  
86 of simplified ‘community climatic indices’. These indices calculate the average climate association  
87 for each species within a community, with each species’ association being estimated from the  
88 average climatic conditions that occur across their distribution. Tracking changes in climatic indices  
89 over time has allowed researchers to consistently show that communities are responding to climate  
90 change, with increasing community thermal indices signalling that species with warmer temperature  
91 associations are expanding their ranges at the expense of cooler species (Bertrand et al., 2011;  
92 Devictor, Julliard, Couvet, & Jiguet, 2008; Devictor et al., 2012; Fadrique et al., 2018).

93  
94 Due to the interactions of anthropogenic pressures driving species’ change over time, interactions  
95 with land-use change and non-native species establishment should therefore be expected to affect  
96 how communities as a whole respond to climate change. Indeed, differences in forest habitat  
97 conditions can affect the level of plant community responses to climate change, either through  
98 effects on local microclimates or presenting abiotic barriers to colonisation by expanding species  
99 (De Frenne et al., 2013; Fadrique et al., 2018). At the landscape level, high levels of habitat  
100 conversion can prevent local community reorganisation following climate warming by hindering  
101 dispersal through the landscape and exacerbating negative effects on those species vulnerable to the

102 climatic changes taking place (Gaüzère, Princé, & Devictor, 2017; Oliver et al., 2017). However,  
103 like the majority of studies of ecological responses to climate change, land use has been viewed in a  
104 static manner, and it has not been investigated how the *changes* in landscapes that have occurred  
105 concurrently to climate change have impeded community shifts or helped to facilitate community  
106 responses to warming. Neither have the effects of biological invasions been considered. Non-native  
107 species originate in many cases from regions with warmer, drier or otherwise different climates to  
108 the regions that they colonise (Early & Sax, 2014; Van der Veken, Hermy, Vellend, Knapen, &  
109 Verheyen, 2008). At the same time, the spread of these species can increase landscape-level species  
110 richness without negative effects on the native flora (Thomas & Palmer, 2015). This influx of  
111 species that are potentially more suited to the climatic changes taking place could mean that  
112 community climate indices increase without local extirpation of natives unable to persist in the  
113 changing climatic conditions. As all of these drivers of biological change are occurring  
114 simultaneously, it is important also to study their concerted effects, elucidating the extent to which  
115 climate change, land-use change and the spread of non-native species act together, or in opposition  
116 to drive community change. Finally, community climate indices have almost exclusively been  
117 calculated in terms of species' thermal associations (but see Maclean, Hopkins, Bennie, Lawson, &  
118 Wilson, 2015). Moisture availability is an important determinant of species occurrences and change  
119 (Peñuelas et al., 2013), and as changing precipitation is also a key component of climate change  
120 (IPCC, 2015), it is relevant to study how communities change in relation to levels of precipitation  
121 over time.

122

123 In Sweden, climate during the 20<sup>th</sup> century has shifted to become both warmer and wetter  
124 (Kjellström et al., 2014). In this study, we calculated thermal and precipitation associations (or  
125 species climate indices) for 3066 plant species, based on observations from 18 regional biodiversity  
126 atlases (floras) across Sweden. These species-level climate associations were used to calculate

historical (early-mid 20<sup>th</sup> century) and modern (late 20<sup>th</sup> and early 21<sup>st</sup> century) community climate indices in 996 landscapes – 25 km<sup>2</sup> 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 20<sup>th</sup> 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?

142

## 143 **Materials and Methods**

### 144 *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 20<sup>th</sup> 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 20<sup>th</sup> and early 21<sup>st</sup> 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<br>(km <sup>2</sup> ) | Landscapes | Historical inventory  | Modern inventory   |
|-----------------|----------------------------|------------|---|--|
| <b>Medelpad</b> | 7058                       | 65         | 1860-1935, mostly 1901-1920 (Several sources, listed in modern flora). All species. | 1975-2010, all species (Lidberg & Lindström, 2010).        |
| <b>Uppland</b>  | 12 813                     | 594        | 1910s-1930s, 438 mapped species (Almqvist, 1929)                                    | 1990-2010, all species (Jonsell, 2010).                    |
| <b>Bohuslän</b> | 4400                       | 258        | 1920s-1945, all species (Fries, 1945).  | 1990s-2011, all species (Blomgren, Falk, & Herloff, 2011). |
| <b>Öland</b>    | 6698                       | 79         | 1910s-1930s, 286 mapped species (Sternér, 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 (°C) 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 (°C 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

217 system, and digitised maps were therefore resampled to match the modern grid. Proportions of the  
 218 four land-use categories were calculated per landscape, and landscape heterogeneity was calculated  
 219 as the Shannon diversity of these categories. Present-day land use was attained from the 2016  
 220 Swedish terrain map ([https://www.lantmateriet.se/en/maps-and-geographic-information/oppna-](https://www.lantmateriet.se/en/maps-and-geographic-information/oppna-data/)  
 221 [data/](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  
 222 S1 in the Supporting Information). Semi-natural grasslands from the publicly-available national  
 223 database (TUVA– <http://www.sjv.se/tuva>) were added as open land. Proportion area and  
 224 heterogeneity of the four land-use categories were then calculated per map sheet as with the  
 225 historical maps, with change over time calculated by subtracting the values of the historical data  
 226 from the values of the modern data. Change in landscape heterogeneity was inverted ( $-1 \times$  Shannon  
 227 diversity) to describe the prevailing trend of landscape simplification: i.e., a higher positive value  
 228 indicates that land use became more homogeneous over time.

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

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

242

243 *Data analysis*

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

249

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

260

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

267

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

271

272 Predictor variables were thus: change in climate (temperature for thermal indices and precipitation  
 273 for precipitation indices), magnitude of landscape simplification, change in fraction neophytes, and  
 274 the two-way interactions between the above variables. Landscape simplification was chosen as the  
 275 sole landscape variable due to non-independence across land-use categories and because it  
 276 represents an informative gradient of land-use change across Sweden based on the limitations of the  
 277 historical maps (Auffret, Kimberley, Plue, & Waldén, 2018; Figure S1). Change in species richness  
 278 was added as a further single fixed term to account for this potential effect. Because of the strong  
 279 spatial structure of the data, the latitude and longitude of each landscape, plus their interaction were  
 280 added as fixed effects in the models, while province was included as a random effect. Due to the  
 281 well-known correlation between latitude and longitude and climate (change), latitude and longitude  
 282 were included in the models as the residual variation after removal of their effect on climate.

283 Residuals were extracted from separate Gaussian generalised linear models (one each for latitude  
 284 and longitude) with each landscape's latitude or longitude as the dependent variable and change in  
 285 precipitation, change in temperature and their interaction as predictor variables. In all community  
 286 climate index models, fixed predictor effects were zero-mean scaled prior to analysis and those  
 287 predictors that were included in the same models were comfortably below acceptable limits for  
 288 collinearity, having variance inflation factors of less than 2 (Zuur et al., 2009) and Pearson  
 289 correlations below 0.4 (Dormann et al., 2013; Zuur et al., 2009; Table S2).

290

291 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).

310

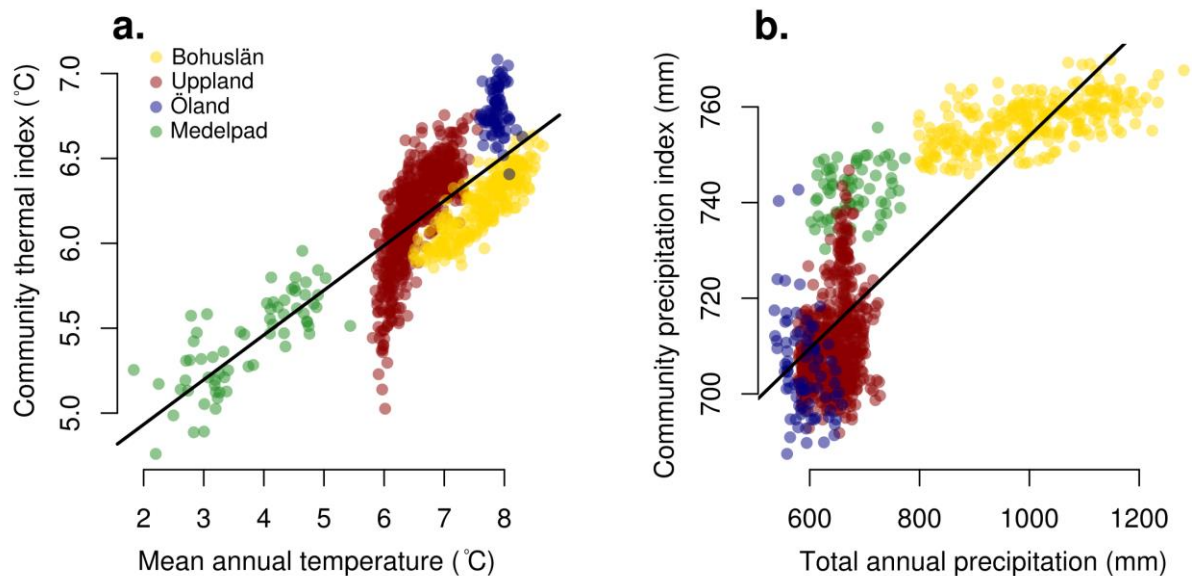
311

## 312 **Results**

### 313 *Community climate shifts*

314 Both thermal and precipitation indices were significantly related to ambient climate conditions,  
 315 confirming a (macro-)climatic influence on plant community composition at the landscape scale  
 316 (Figure 1, Table S3). The relationship between ambient climate and community climate indices was

317 clearly stronger for temperature than for precipitation, with community precipitation means in  
 318 Medelpad generally having a different relationship with measured precipitation levels than those in  
 319 the other provinces.



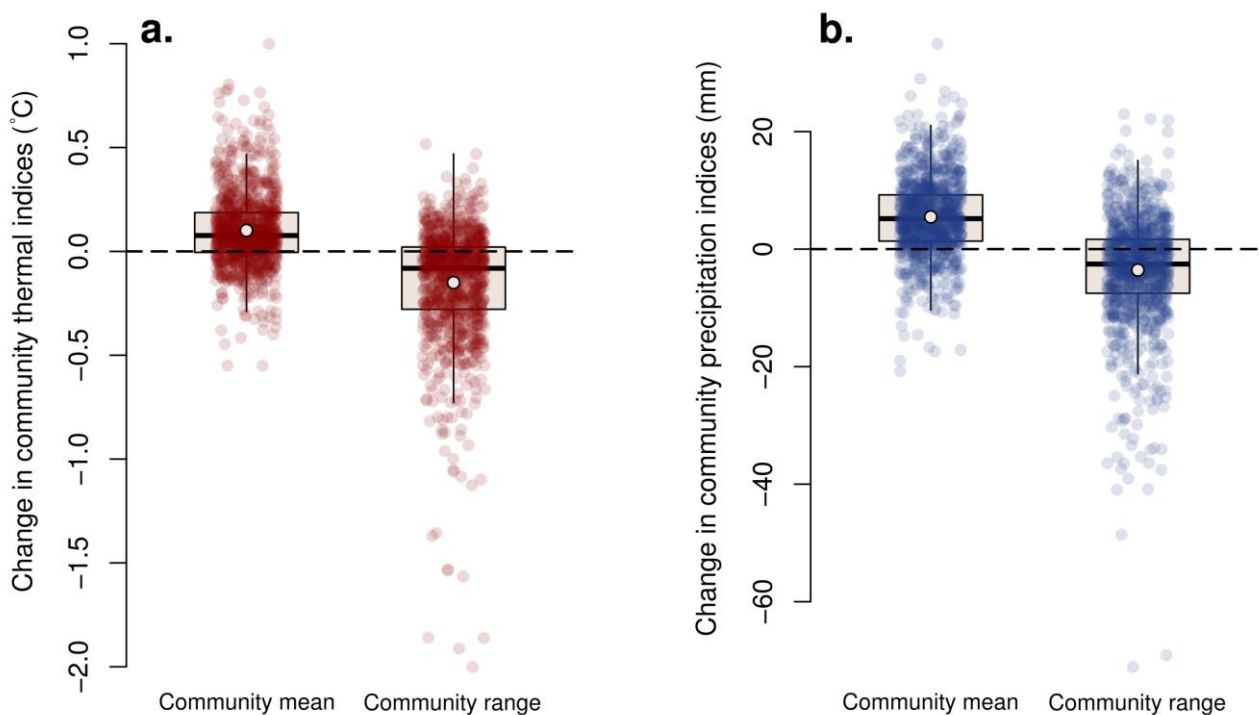
320

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

327

328 During the course of the 20<sup>th</sup> century, communities have exhibited significant (Wilcoxon  $P < 0.001$ )  
 329 shifts towards increased frequencies of species with warmer and wetter climatic associations, with  
 330 almost three-quarters (74%) of our 996 landscapes increasing in community thermal index (Figure  
 331 2). Community warming (mean shift  $+0.1$  °C, 95% CI:  $+0.066$  to  $+0.177$  °C) was consistent with the  
 332 prevailing direction of climate change, where 100% of landscapes warmed between 1961-1970 and  
 333 2001-2010, with an mean  $\pm$ sd of  $1.4 \pm 0.13$  °C. Patterns were similar for community precipitation  
 334 indices. Almost all landscapes (98%) experienced an increase in precipitation during the study  
 335 period of  $67.69 \pm 48.49$  mm, which was reflected in the significant increases in community  
 336 precipitation (mean shift  $+5.5$  mm, 95% CI:  $+1.31$ mm 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  $-0.15^{\circ}\text{C}$  (95% CI:  $0.013 - 0.47^{\circ}\text{C}$  reduction) while the reduction was  $-3.5\text{ mm}$  ( $0.987 - 15.0\text{ mm}$  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  $\pm$  sd of  $28.5 \pm 8\%$  of species in early- to mid-20<sup>th</sup> century landscapes to  $33.7 \pm 7.3\%$  today. Along with the expansion of neophytes, the total number of species has risen in 81% of landscapes, with a net increase of  $63.9 \pm 71.1$  (mean $\pm$ sd) species per landscape, from  $186 \pm 148.3$  to  $250 \pm 161.3$  (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 20<sup>th</sup> 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

379 effects on one another (Figure 3g). This means that landscapes that became increasingly simplified  
380 were more likely to exhibit decreasing variation of species in terms of temperature associations over  
381 time. These results are robust to overall changes in species richness, which did not have a consistent  
382 effect on community warming and were negatively associated with thermal homogenisation (Table  
383 S5). This implies that the landscapes with the highest levels of community warming and thermal  
384 homogenisation lost relatively high proportions of their original cold-adapted species.

385

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

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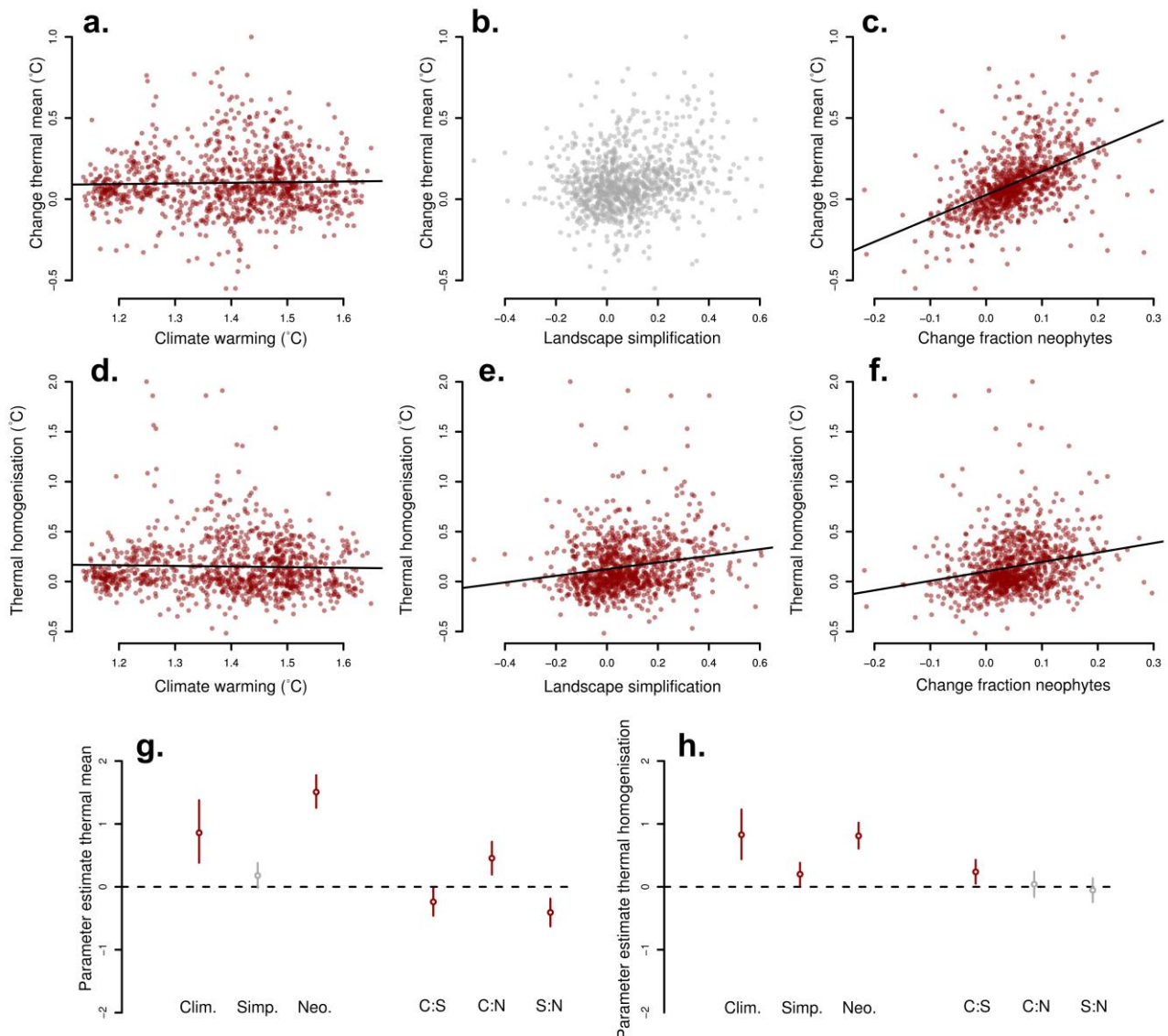
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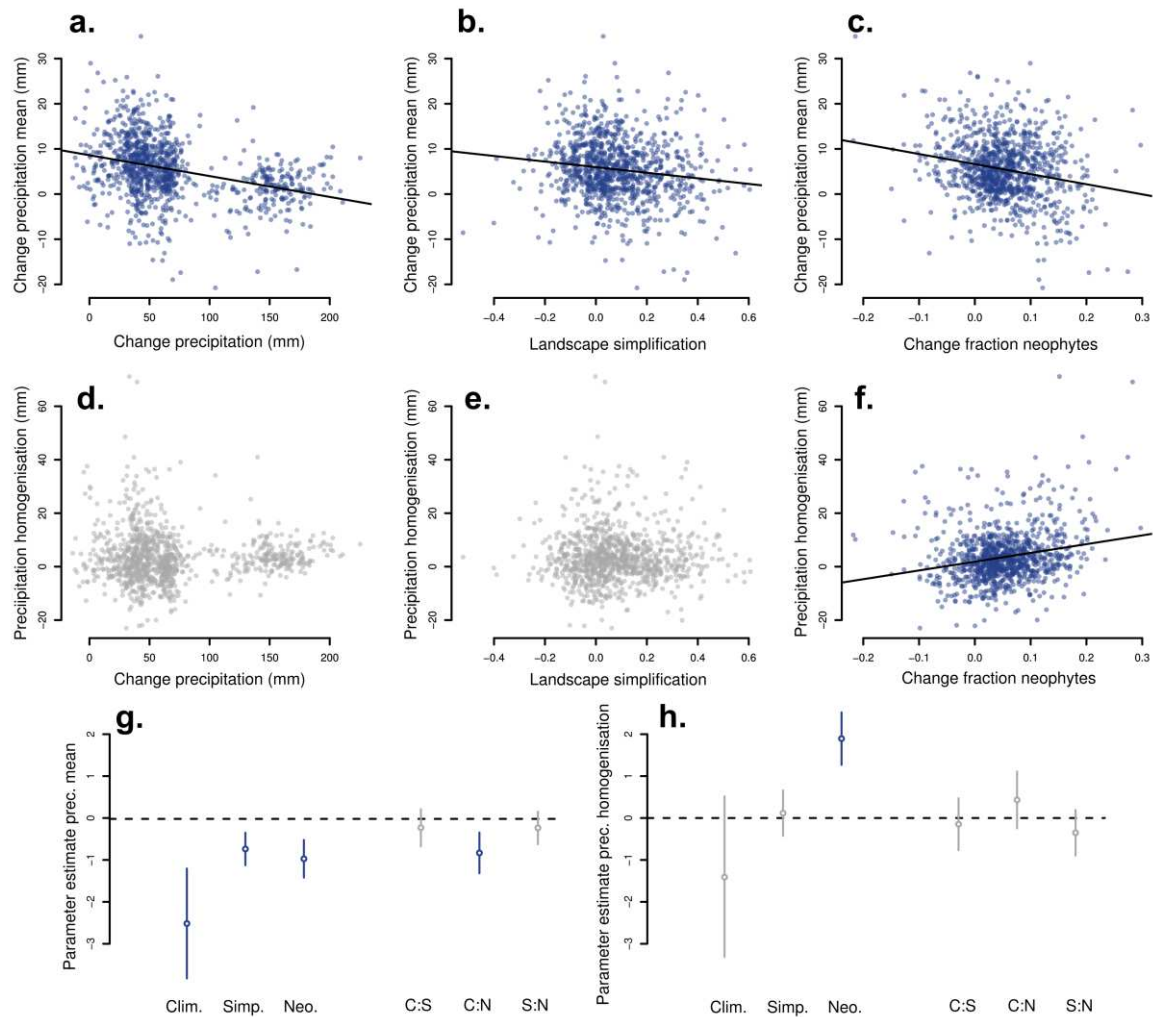
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**Figure 3.** Effect of increasing temperatures, landscape simplification and changes in fractions of neophytes (introduced species first observed in Sweden post-1492) and their interactions on shifts in community thermal indices in 996 landscapes 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.



422

423

**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.

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## 438 **Discussion**

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

449

450 As well as the effect of increased temperatures driving community warming and homogenisation,  
451 land-use change and increases in non-native species were also shown to influence the climate-  
452 driven turnover of species (Figure 3; Table S5). There was no clear direct effect of landscape  
453 simplification on community warming, but the driving effect of increasing temperature was lower in  
454 more simplified landscapes. In Sweden, the trend towards more simplified landscapes is primarily  
455 associated with an increase in wooded area at the expense of arable and open land (Auffret et al.,  
456 2018; Figure S1). Temperatures within forests are generally found to be cooler than open areas (De  
457 Frenne et al., 2019; Frey et al., 2016; Greiser, Meineri, Luoto, Ehrlén, & Hylander, 2018). This  
458 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

484 alter the potential for species to disperse to new areas (Auffret, Rico, et al., 2017) .

485

486 Non-native species were also shown to drive turnover towards warmer and more climatically  
487 homogeneous communities. Warmer index values with increasing fractions of non-natives are to be  
488 expected because species introduced to Sweden's relatively northern latitudes are, on average, likely  
489 to originate from warmer climates. However, the modest increases in the fraction of non-natives  
490 during the 20<sup>th</sup> century (from 28.5% to 33.7% per landscape, on average) implies that much of this  
491 trend was due to the internal spread of species that are still expanding within provinces (Crooks,  
492 2005). Increases in neophytes also interacted with both of the other drivers of global change to  
493 explain community climatic shifts. A positive, reinforcing statistical interaction between  
494 temperature change and increases in neophytes further supports the assertion that this species group  
495 is linked to warmer temperatures, as well as previous work linking climate change to the increased  
496 risk of biological invasions (Stachowicz, Terwin, Whitlatch, & Osman, 2002; Walther et al., 2009).  
497 The negative interaction between landscape simplification and increasing neophytes suggests that  
498 more heterogeneous landscapes contain more suitable habitats for colonisation specifically by  
499 incoming neophytes (Hejda et al., 2009). Another possibility is that as more heterogeneous  
500 landscapes in our case were related to agricultural land uses, the interaction between landscape and  
501 non-native species could also reflect the fact that non-native species are generally introduced and  
502 spread by humans. Increasing neophytes and related increases in species richness in our study  
503 follows a general trend of increasing species richness at spatial scales that lie between the local and  
504 the global (Thomas & Palmer, 2015; Vellend et al., 2017). Non-native species have driven  
505 community changes in the past, and, in Sweden and other cool parts of the world, clearly have the  
506 potential to respond positively to ongoing climate change.

507

508 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 20<sup>th</sup> 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 °C 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



534 of °C temperature and mm precipitation, and to compare rates of change in community climate  
 535 indices across studies. As is the case in our study, climate indices for plant species are often based  
 536 on occurrences that do not cover the species' full geographic range (Bertrand et al., 2011; Lenoir et  
 537 al., 2013; Maclean et al., 2015; but see De Frenne et al., 2013). Secondly, climate data is usually  
 538 available at a different (larger) spatial scale compared to community data whose response is being  
 539 tested, which can affect comparisons over time, although in our case these scales were relatively  
 540 well matched. Finally, our community indices could only be based on presence-absence rather than  
 541 weighted by abundances, as well as being based on incomplete communities for two of the four  
 542 study provinces. This will naturally have influenced our estimates of community change over time,  
 543 but such limitations are common when working with historical data, which are still an important  
 544 tool for understanding ecological responses to environmental change (Vellend, Brown, Kharouba,  
 545 McCune, & Myers-Smith, 2013). Despite such issues, community climate indices are an  
 546 increasingly popular way of broadly studying ecological responses to climate change, and  
 547 ecologically meaningful trends of direction, apparent time lags and the influence of land use are  
 548 shared across space, time and taxa (De Frenne et al., 2013; Flanagan, Jensen, Morley, & Pinsky,  
 549 2019; Gaüzère et al., 2017; Oliver et al., 2017).

550

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

558

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 562 digitizing these observations and making them available for research. AGA is supported by the  
 563 Swedish Research Council Formas (2015-1065).

564

## 565 Data availability

566 Analysed predictor and response variables for each landscape have been deposited at the Figshare  
 567 data repository, together with the climatic indices for 3066 Swedish plant species.

568 <http://dx.doi.org/XXXXX>.

569

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572     **Synergistic and antagonistic effects of land use and biological invasions on determining**  
573                     **community responses to climate change**

574                     Alistair G. Auffret & Chris D. Thomas

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576                     **SUPPORTING INFORMATION**

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**Table S1.** Reclassification of present-day terrain map to match the historical dataset. Water in the historical dataset was added as a contemporary layer from the terrain map and therefore exactly matches the modern map. Valuable grasslands from the semi-natural grassland database (<http://www.sjv.se/tuva>) were added on top of the modern map as open land.

| Historical Map | Present-day map [Swedish Terrain Map 2016:<br><a href="https://www.lantmateriet.se/sv/Kartor-och-geografisk-information/Kartor/oppna-data/hamta-oppna-geodata">https://www.lantmateriet.se/sv/Kartor-och-geografisk-information/Kartor/oppna-data/hamta-oppna-geodata</a> ] |
|----------------|---|
| Arable         | Arable land   |
|                | Fruit farm  |
| Open           | Other open land   |
|                | Group of buildings with courtyard   |
|                | High-rise buildings   |
|                | Low-rise buildings  |
|                | Industrial area   |
| Forest         | Leisure homes   |
|                | Other open land with isolated trees   |
|                | Forest, coniferous and mixed  |
|                | Deciduous forest  |
| Water          | Water body  |
|                | Water body with unclear shoreline   |

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**Table S2.** Pearson correlation coefficients and Variance Inflation Factors (VIF) of variables used to explain shifts in community climate indices for plant communities in 996 landscapes across four regions of Sweden. Correlations were tested for *changes* in landscape simplification, neophytes, temperature, precipitation and species richness, while latitude and longitude are the residual effects of latitude and longitude after accounting for variation in temperature and precipitation change.

|                             | Landscape<br>simplification | Neophytes | Temperature | Precipitation | Species<br>richness | Latitude | Longitude |
|-----------------------------|-----------------------------|-----------|-------------|---------------|---------------------|----------|-----------|
| Landscape<br>simplification |                             | 0.058     | 0.07        | 0.09          | 0.14                | 0.18     | -0.078    |
| Neophytes                   | 0.058                       |           | -0.13       | 0.005         | 0.26                | -0.34    | 0.047     |
| Temperature                 | 0.07                        | -0.13     |             | 0.60          | -0.21               | <0.001   | <-0.001   |
| Precipitation               | 0.09                        | 0.005     | 0.60        |               | 0.12                | <-0.001  | <0.001    |
| Species<br>richness         | 0.14                        | 0.26      | -0.21       | 0.12          |                     | 0.041    | -0.39     |
| Latitude                    | 0.18                        | -0.34     | <0.001      | <-0.001       | 0.041               |          | 0.064     |
| Longitude                   | -0.078                      | 0.047     | <-0.001     | <0.001        | -0.39               | 0.064    |           |
| VIF                         | 1.12                        | 1.35      | 1.73        | 1.65          | 1.42                | 1.25     | 1.26      |

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**Table S3.** Generalized Linear Mixed Models with parameter estimates, z-values and confidence intervals (CI) explaining the relationship between community thermal and precipitation indices (modern data) with average mean annual temperatures and total annual precipitation for the 2001-2010 period in 996 landscapes across four regions of Sweden. Region identity was included as a random variable.

|   | <b>Estimate</b> | <b>Stand. Error</b> | <b>CI 2.5</b> | <b>CI 97.5</b> | <b>z</b> |
|---|-----------------|---------------------|---------------|----------------|----------|
| <i>Community thermal index</i>                                |                 |                     |               |                |          |
| (Intercept)   | 6.26            | 0.14                | 5.92          | 6.61           | 46.11    |
| Temperature   | 0.43            | 0.01                | 0.4           | 0.46           | 32.12    |
| <i>Community precipitation index</i>                          |                 |                     |               |                |          |
| (Intercept)   | 728.96          | 8.71                | 706.82        | 751.1          | 83.7     |
| Precipitation   | 5.42            | 0.68                | 4.08          | 6.76           | 7.97     |
| <i>Community precipitation index<br/>(excluding Bohuslän)</i> |                 |                     |               |                |          |
| (Intercept)   | 719.57          | 8.57                | 695.64        | 743.53         | 83.97    |
| Precipitation   | 1.96            | 0.39                | 1.19          | 2.72           | 5.03     |

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**Table S4.** Results of paired Wilcoxon tests assessing increases in community thermal and precipitation means and decreases in community thermal and precipitation interquartile and full ranges of plant communities in 996 landscapes across four regions of Sweden.

|                                    | V-statistic | P       |
|------------------------------------|-------------|---------|
| <i>Redistribution</i>              |             |         |
| Mean temperature                   | 358307      | <0.0001 |
| Interquartile range temperature    | 97068       | <0.0001 |
| Range temperature                  | 133381      | <0.0001 |
| Mean precipitation                 | 374111      | <0.0001 |
| Inter-quartile range precipitation | 131669      | <0.0001 |
| Range precipitation                | 154599      | <0.0001 |
| <i>Addition</i>                    |             |         |
| Mean temperature                   | 397724      | <0.0001 |
| Interquartile range temperature    | 101692      | <0.0001 |
| Range temperature                  | 176384.5    | <0.0001 |
| Mean precipitation                 | 442006      | <0.0001 |
| Inter-quartile range precipitation | 145390      | <0.0001 |
| Range precipitation                | 247118      | 1       |

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**Table S5.** Models with parameter estimates and confidence intervals (CI) explaining the occurrence (Generalized Linear Mixed Models; give z- and p-values) and magnitude (Linear Mixed Models; give t- and no p-values) of increases in thermal and precipitation mean and decreases in thermal and precipitation range of plant communities in 996 landscapes across four regions of Sweden. Landscape refers to change in landscape heterogeneity, Neophytes to change in fraction neophytes in a community, Richness to changes in species richness, while Temperature and Precipitation refer to changes in climate from 1961-70 and 2001-2010. Region identity was included as a random variable. Bold models are those displayed in Figures 3&4 in the main text.

|                              | Estimate | Stand. Error | CI 2.5 | CI 97.5 | t or z | p     |
|------------------------------|----------|--------------|--------|---------|--------|-------|
| <i>Thermal mean</i>          |          |              |        |         |        |       |
| <i>Addition - occurrence</i> |          |              |        |         |        |       |
| (Intercept)                  | 1.9      | 0.53         | 0.33   | 3.59    | 3.58   | <0.01 |
| Landscape                    | 0.18     | 0.1          | -0.02  | 0.38    | 1.78   | 0.08  |
| Neophytes                    | 1.51     | 0.13         | 1.26   | 1.78    | 11.38  | <0.01 |
| Temperature                  | 0.86     | 0.26         | 0.38   | 1.38    | 3.29   | <0.01 |
| Richness                     | -0.18    | 0.11         | -0.39  | 0.04    | -1.63  | 0.1   |
| Latitude                     | 0.7      | 0.32         | 0.23   | 1.43    | 2.21   | 0.03  |
| Longitude                    | 0.34     | 0.15         | 0.06   | 0.63    | 2.34   | 0.02  |
| Landscape:Neophytes          | -0.41    | 0.11         | -0.63  | -0.19   | -3.61  | <0.01 |
| Landscape:Temperature        | -0.24    | 0.11         | -0.46  | -0.02   | -2.14  | 0.03  |
| Neophytes:Temperature        | 0.46     | 0.13         | 0.19   | 0.72    | 3.42   | <0.01 |
| Latitude:Longitude           | -0.01    | 0.22         | -0.45  | 0.43    | -0.06  | 0.95  |
| <i>Thermal mean</i>          |          |              |        |         |        |       |
| <i>Addition - magnitude</i>  |          |              |        |         |        |       |
| (Intercept)                  | 0.1      | <0.01        | 0.08   | 0.12    | 21.9   |       |
| Landscape                    | 0.02     | <0.01        | 0.01   | 0.03    | 4.08   |       |
| Neophytes                    | 0.11     | 0.01         | 0.1    | 0.12    | 20.65  |       |
| Temperature                  | 0.02     | <0.01        | 0.01   | 0.03    | 4.25   |       |
| Richness                     | 0.01     | 0.01         | -0.01  | 0.02    | 0.9    |       |
| Latitude                     | 0.05     | 0.01         | 0.04   | 0.06    | 8.57   |       |
| Longitude                    | 0.01     | 0.01         | <-0.01 | 0.02    | 1.45   |       |
| Landscape:Neophytes          | -0.01    | <0.01        | -0.02  | <-0.01  | -2.21  |       |
| Landscape:Temperature        | 0.01     | 0.01         | <-0.01 | 0.02    | 1.3    |       |
| Neophytes:Temperature        | 0.02     | 0.01         | 0.01   | 0.03    | 3.05   |       |
| Latitude:Longitude           | <0.01    | 0.01         | -0.02  | 0.01    | -0.38  |       |
| <i>Thermal range</i>         |          |              |        |         |        |       |
| <i>Addition - occurrence</i> |          |              |        |         |        |       |
| (Intercept)                  | 2.12     | 1.7          | -2.32  | 6.57    | 1.24   | 0.21  |
| Landscape                    | 0.2      | 0.09         | 0.02   | 0.38    | 2.18   | 0.03  |
| Neophytes                    | 0.81     | 0.11         | 0.61   | 1.02    | 7.69   | <0.01 |
| Temperature                  | 0.83     | 0.2          | 0.44   | 1.23    | 4.07   | <0.01 |
| Richness                     | -0.67    | 0.11         | -0.88  | -0.47   | -6.31  | <0.01 |
| Latitude                     | 2.23     | 0.32         | 1.61   | 2.86    | 6.96   | <0.01 |
| Longitude                    | -0.13    | 0.15         | -0.43  | 0.17    | -0.83  | 0.41  |
| Landscape:Neophytes          | -0.05    | 0.1          | -0.24  | 0.14    | -0.55  | 0.58  |
| Landscape:Temperature        | 0.24     | 0.1          | 0.05   | 0.43    | 2.46   | 0.01  |
| Neophytes:Temperature        | 0.04     | 0.1          | -0.16  | 0.24    | 0.4    | 0.69  |
| Latitude:Longitude           | 0.63     | 0.26         | 0.13   | 1.16    | 2.41   | 0.02  |

|                              | Estimate | Stand. Error | CI 2.5 | CI 97.5 | t or z | p     |
|------------------------------|----------|--------------|--------|---------|--------|-------|
| <i>Thermal range</i>         |          |              |        |         |        |       |
| <i>Addition - magnitude</i>  |          |              |        |         |        |       |
| (Intercept)                  | 0.23     | 0.13         | -0.1   | 0.56    | 1.8    |       |
| Landscape                    | 0.03     | 0.01         | 0.01   | 0.04    | 3.28   |       |
| Neophytes                    | 0.09     | 0.01         | 0.07   | 0.1     | 10.26  |       |
| Temperature                  | 0.04     | 0.02         | <0.01  | 0.08    | 2.26   |       |
| Richness                     | -0.01    | 0.01         | -0.03  | 0.01    | -0.87  |       |
| Latitude                     | 0.21     | 0.03         | 0.16   | 0.27    | 8.37   |       |
| Longitude                    | -0.03    | 0.01         | -0.05  | <-0.01  | -2.27  |       |
| Landscape:Neophytes          | -0.02    | 0.01         | -0.04  | -0.01   | -3.1   |       |
| Landscape:Temperature        | 0.01     | 0.01         | -0.01  | 0.03    | 1.11   |       |
| Neophytes:Temperature        | 0.01     | 0.01         | -0.01  | 0.03    | 0.84   |       |
| Latitude:Longitude           | 0.05     | 0.02         | 0.02   | 0.09    | 3.04   |       |
| <i>Precipitation mean</i>    |          |              |        |         |        |       |
| <i>Addition - occurrence</i> |          |              |        |         |        |       |
| (Intercept)                  | 1.94     | 0.11         | 1.28   | 2.15    | 17.96  | <0.01 |
| Landscape                    | -0.34    | 0.1          | -0.54  | -0.14   | -3.35  | <0.01 |
| Neophytes                    | -0.33    | 0.12         | -0.57  | -0.1    | -2.76  | 0.01  |
| Temperature                  | -0.44    | 0.09         | -0.73  | -0.21   | -4.66  | <0.01 |
| Richness                     | -0.51    | 0.11         | -0.74  | -0.29   | -4.54  | <0.01 |
| Latitude                     | 0.24     | 0.11         | -0.02  | 0.46    | 2.22   | 0.03  |
| Longitude                    | 0.05     | 0.12         | -0.2   | 0.52    | 0.44   | 0.66  |
| Landscape:Neophytes          | 0.15     | 0.09         | -0.04  | 0.33    | 1.55   | 0.12  |
| Landscape:Temperature        | -0.21    | 0.11         | -0.42  | -0.01   | -2.02  | 0.04  |
| Neophytes:Temperature        | -0.12    | 0.12         | -0.36  | 0.11    | -0.98  | 0.33  |
| Latitude:Longitude           | 0.36     | 0.16         | -0.16  | 0.67    | 2.21   | 0.03  |
| <i>Precipitation mean</i>    |          |              |        |         |        |       |
| <i>Addition - magnitude</i>  |          |              |        |         |        |       |
| (Intercept)                  | 5.44     | 1.69         | 2.13   | 8.74    | 3.23   |       |
| Landscape                    | -0.74    | 0.2          | -1.13  | -0.35   | -3.72  |       |
| Neophytes                    | -0.97    | 0.23         | -1.42  | -0.52   | -4.24  |       |
| Temperature                  | -2.52    | 0.67         | -3.83  | -1.21   | -3.76  |       |
| Richness                     | -0.49    | 0.24         | -0.96  | -0.02   | -2.06  |       |
| Latitude                     | -0.52    | 0.49         | -1.48  | 0.44    | -1.07  |       |
| Longitude                    | 0.88     | 0.52         | -0.13  | 1.9     | 1.7    |       |
| Landscape:Neophytes          | -0.24    | 0.2          | -0.62  | 0.15    | -1.19  |       |
| Landscape:Temperature        | -0.23    | 0.23         | -0.68  | 0.21    | -1.02  |       |
| Neophytes:Temperature        | -0.83    | 0.25         | -1.32  | -0.35   | -3.36  |       |
| Latitude:Longitude           | 0.2      | 0.47         | -0.72  | 1.11    | 0.42   |       |
| <i>Precipitation range</i>   |          |              |        |         |        |       |
| <i>Addition - occurrence</i> |          |              |        |         |        |       |
| (Intercept)                  | 1.6      | 0.54         | 0.27   | 3.03    | 2.93   | <0.01 |
| Landscape                    | -0.04    | 0.08         | -0.2   | 0.11    | -0.54  | 0.59  |
| Neophytes                    | 0.57     | 0.1          | 0.38   | 0.76    | 5.91   | <0.01 |
| Temperature                  | -0.01    | 0.26         | -0.54  | 0.48    | -0.05  | 0.96  |
| Richness                     | -0.55    | 0.11         | -0.76  | -0.34   | -5.13  | <0.01 |
| Latitude                     | 0.6      | 0.19         | 0.24   | 0.99    | 3.23   | <0.01 |
| Longitude                    | -0.21    | 0.21         | -0.63  | 0.22    | -1     | 0.32  |
| Landscape:Neophytes          | -0.26    | 0.08         | -0.43  | -0.1    | -3.14  | <0.01 |
| Landscape:Temperature        | -0.22    | 0.1          | -0.42  | -0.02   | -2.15  | 0.03  |
| Neophytes:Temperature        | 0.07     | 0.11         | -0.14  | 0.29    | 0.6    | 0.55  |
| Latitude:Longitude           | 0.23     | 0.25         | -0.26  | 0.74    | 0.89   | 0.37  |

|                             | Estimate | Stand. Error | CI 2.5 | CI 97.5 | t or z | p |
|-----------------------------|----------|--------------|--------|---------|--------|---|
| <i>Precipitation range</i>  |          |              |        |         |        |   |
| <i>Addition - magnitude</i> |          |              |        |         |        |   |
| (Intercept)                 | 8.13     | 3            | 0.51   | 15.87   | 2.71   |   |
| Landscape                   | 0.12     | 0.28         | -0.43  | 0.66    | 0.42   |   |
| Neophytes                   | 1.89     | 0.32         | 1.27   | 2.52    | 5.93   |   |
| Temperature                 | -1.41    | 0.97         | -3.31  | 0.52    | -1.45  |   |
| Richness                    | -1.18    | 0.33         | -1.83  | -0.52   | -3.53  |   |
| Latitude                    | 1.6      | 0.72         | 0.19   | 3.05    | 2.23   |   |
| Longitude                   | -0.23    | 0.75         | -1.71  | 1.24    | -0.3   |   |
| Landscape:Neophytes         | -0.35    | 0.28         | -0.9   | 0.19    | -1.27  |   |
| Landscape:Temperature       | -0.15    | 0.32         | -0.77  | 0.47    | -0.47  |   |
| Neophytes:Temperature       | 0.43     | 0.35         | -0.25  | 1.11    | 1.25   |   |
| Latitude:Longitude          | 1.45     | 0.65         | 0.15   | 2.74    | 2.21   |   |

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**Table S6.** Performance of models explaining the occurrence (Generalized Linear Mixed Models) and magnitude (Linear Mixed Models) of increases in thermal and precipitation mean and decreases in thermal and precipitation range of plant communities in 996 landscapes across four regions of Sweden. Chi-square and p-values indicate significant improvements of the model compared to a null model containing only random effects. Marginal  $R^2$  and Conditional  $R^2$  indicate the explanatory power of the fixed and fixed plus random effects of the model, respectively.

|                            | Chi-square | p       | Marginal $R^2$ | Conditional $R^2$ |
|----------------------------|------------|---------|----------------|-------------------|
| <i>Thermal mean</i>        |            |         |                |                   |
| Occurrence                 | 259.04     | <0.0001 | 0.41           | 0.54              |
| Magnitude                  | 450.37     | <0.0001 | 0.0038         | 0.0038            |
| <i>Thermal range</i>       |            |         |                |                   |
| Occurrence                 | 173.18     | <0.0001 | 0.28           | 0.84              |
| Magnitude                  | 224.27     | <0.0001 | 0.013          | 0.032             |
| <i>Precipitation mean</i>  |            |         |                |                   |
| Occurrence                 | 75.99      | <0.0001 | 0.24           | 0.24              |
| Magnitude                  | 93.51      | <0.0001 | 0.43           | 0.87              |
| <i>Precipitation range</i> |            |         |                |                   |
| Occurrence                 | 72.74      | <0.0001 | 0.12           | 0.33              |
| Magnitude                  | 51.72      | <0.0001 | 0.14           | 0.93              |

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596 **Figure S1.** Landscape change in 996 landscapes in four regions of Sweden between 1930-60s and  
 597 2016. Arable, open and forest landscapes are defined as the 25% 5×5 km landscapes with the  
 598 highest cover of those categories in the historical maps. [a] Comparison of historical and present-  
 599 day landscape heterogeneity, with 68% of all landscapes decreasing in heterogeneity over time.  
 600 Eighty-seven percent of open landscapes and 78% of forest landscapes became more simplified  
 601 over the time period, whereas 61% of arable landscapes actually increased in heterogeneity over  
 602 time. [b] Land-use trajectories (median, interquartile range and range excluding outliers) of the  
 603 different landscape categories showed that arable land was lost in arable landscapes at the expense  
 604 of forest and particularly open land. In historically open and forested landscapes, open and arable  
 605 land declined with a strong increase in forested area.

