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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 20th 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 20th 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

127 historical (early-mid 20th century) and modern (late 20th and early 21st century) community climate
128 indices in 996 landscapes – 25 km² in size – spread across four provinces where floras from both
129 time periods exist. In addition to measuring community shifts through changes in the mean values
130 of climate associations of species within a landscape, we also calculated how the range of
131 associations across the community changed over time, giving an indication of the relative influences
132 of the immigration of warm-associated species and the extirpation of cool-associated species. We
133 then used historical and modern land-use and climate data to evaluate how land-use change and
134 changing fractions of non-native species have contributed to the observed community shifts. In
135 doing so, we addressed the following questions:

136 [1] How have plant communities responded to changes in both temperature *and* precipitation during
137 the mid-late 20th century?

138 [2] Have communities homogenised in terms of climate associations, driven by colonisations of
139 warm/wet-associated species and simultaneous extirpations of cool/dry-associated species?

140 [3] How do shifts in community climate indices relate to the interacting effects of climate change,
141 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*

145 Observation data were obtained from plant biodiversity atlases (floras) from the historical Swedish
146 provinces of Bohuslän, Medelpad, Öland and Uppland (Table 1). These provinces cover a
147 latitudinal gradient of approximately 750 km and longitudinal gradient of 400 km, covering a range
148 of landscape types dominated by arable, pastoral and silvicultural land uses. All historical floras
149 contained observations from the 1800s but the majority of records were based on later inventories
150 by the author of each flora, until the early-mid 20th century. For Bohuslän and Medelpad, the
151 historical data were digitised for the publication of the modern floras from written inventory reports

152 and the historical flora itself, permitting full characterisation of community changes. For Öland and
 153 Uppland, only a subset of species had published distribution maps in the historical flora, but the
 154 historical floras did include a full list of species known to the province (the historical species pool).
 155 Distribution maps were scanned, georeferenced and each occurrence point was digitised in a
 156 Geographic Information System. This was carried out by Maad, Sundberg, Stolpe, & Jonsell (2009)
 157 for Uppland and by AGA for Öland for the current study using QGIS. Inventories for the modern
 158 floras generally took place over 2-3 decades in the late 20th and early 21st century. For both the
 159 historical and the modern floras, *inventories* correspond to the recording of observed species in an
 160 area resulting from a large number of visits over a long period of time, rather than structured
 161 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.



162

163 Each observation was assigned to a 5 × 5 km national grid square. These grid squares (hereafter
 164 landscapes) were historically used for mapping purposes and are now the unit of inventory for all
 165 modern-day biodiversity atlases in Sweden. They are also the smallest unit to which occurrence
 166 points from the historical floras' distribution maps can be accurately assigned. Occurrence records

167 of a coarser resolution than this grid were discarded. In order to analyse community change in
168 landscapes that were well-visited in both time periods, we retained only those landscapes for
169 analysis in which there were at least 25 observations in both the historical and the modern
170 inventories, resulting in 996 landscapes. Species names across all floras were harmonised to the
171 species level (i.e. *Genus epithet* only), according to the Swedish Taxonomic Database
172 (<https://www.dyntaxa.se/>; retrieved April 2016), with some species of e.g. *Alchemilla*, *Rubus*,
173 *Ranunculus* and a number of Asteraceae assigned to Section only.

174

175 *Calculation of species' climate associations*

176 To calculate the thermal and precipitation associations for each plant species, we used occurrence
177 data from all 18 available published and ongoing provincial flora inventories from 1965 until 2017.
178 These regions cover the major land-use and climatic gradients of Sweden, from the southernmost
179 tip to the far north and into the Scandes mountains. Data were downloaded from the Swedish
180 Species Gateway (<https://www.artportalen.se/>) or obtained directly from the responsible botanical
181 society. Species names were harmonised as above, and there were in total more than 7.3 million
182 observations of 3066 species (2241 of which present in the four focal provinces). For climate data,
183 we used the Swedish Meteorological and Hydrological Institute's 4 km gridded climate data from
184 1961-2011 (database *ptHBV*, <http://luftweb.smhi.se/>). For each observation, the means of the mean
185 annual temperature (°C) and total annual precipitation (mm) were calculated as the means
186 (temperature) and totals (precipitation) of each calendar month's values for the year of observation
187 and the four preceding years. Observations after 2012 were assigned climate data from 2011. The
188 mean values for each species were then assigned as that species' thermal and precipitation
189 association.

190

191 *Response variable: community climate indices*

192 For each of the 996 landscapes, we calculated community climatic indices based on the species
193 present in a landscape for the historical period and for the modern period. For Bohuslän and
194 Medelpad, where the historical occurrence data were more complete, this involved all recorded
195 species across both time periods. For Öland and Uppland, indices for historical communities were
196 based on mapped species only, while for the modern dataset we included all mapped species plus all
197 species recorded in the modern flora that were not present in the historical species pool (i.e., neither
198 mapped nor mentioned in the historical flora's text). We also checked whether community
199 reorganisation is detectable through the redistribution of existing species without the addition of
200 new species to a region. To do this, we calculated modern community climatic indices in all four
201 provinces based only on species occurring in the historical time period. These results are only
202 shown in the Supporting Information. Community thermal and precipitation means (°C and mm,
203 respectively) were calculated as the mean of the climatic indices for each species present in each
204 landscape at each time period. The range of species' climate associations within a landscape was
205 calculated as the interquartile range of the species' temperature and precipitation associations for all
206 species within a landscape. Interquartile ranges were chosen to avoid the effect of individual species
207 with unusually high or low values for climate associations skewing absolute ranges. Absolute
208 ranges were also calculated to ensure that our conclusions are robust.

209
210 *Explanatory variables: land-use change, climate change and non-native species*

211 For land-use change, we used digitisations of the Swedish Economic Map, which was created
212 between the 1930s and 1960s over the study area (Auffret, Kimberley, et al., 2017a, 2017b). The 1
213 m resolution digitisations were aggregated to 5 m, and distinguish arable fields, forest, open areas
214 (mainly grasslands, but also wetlands and urban land uses) and surface water. For Öland, Uppland
215 and Medelpad, map sheets corresponded to the 5 × 5 km landscapes used for the species
216 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.

229

230 For climate change, we used the same 1961-2011 gridded climate data as for the calculation of
231 species climate indices. The 5×5 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.

234

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

292 assessed by calculating confidence intervals at the 95% level for each fixed predictor variable.
293 Models were then evaluated by calculating marginal and conditional R^2 values, which inform how
294 well each model's fixed effects alone (marginal R^2) and fixed plus random effects (conditional R^2)
295 explain the variation in the dependent variable (Nakagawa & Schielzeth, 2013). Because R^2 values
296 were somewhat low in some of the above models, we also tested whether our predictor variables
297 could adequately explain community responses to climate change by comparing each model to an
298 equivalent null model that only contained the random effect (province), using a Chi-square
299 likelihood-ratio test (Plue & Cousins, 2018). We then built four new models, this time generalised
300 linear mixed models with binomial error distributions to assess the extent to which our explanatory
301 variables could explain the *occurrence* of directional shifts in community climate indices
302 (1=increased mean or decreased range, 0=other or no change). These models had the same structure
303 as those described above, and were evaluated in the same ways. All eight models were significant
304 improvements on their equivalent null model, but they differed in explanatory power. Models were
305 much better at explaining the occurrence of shifts in community thermal indices and the magnitude
306 of shifts in precipitation indices. It is the results of these models that will presented and discussed in
307 the main text. Models were created using R's *lme4* package (Bates, Maechler, Bolker, & Walker,
308 2014), figures were created with the help of the *scales* package (Wickham, 2017) and interaction
309 effects were interpreted with the help of the *visreg* package (Breheny & Burchett, 2017).

310

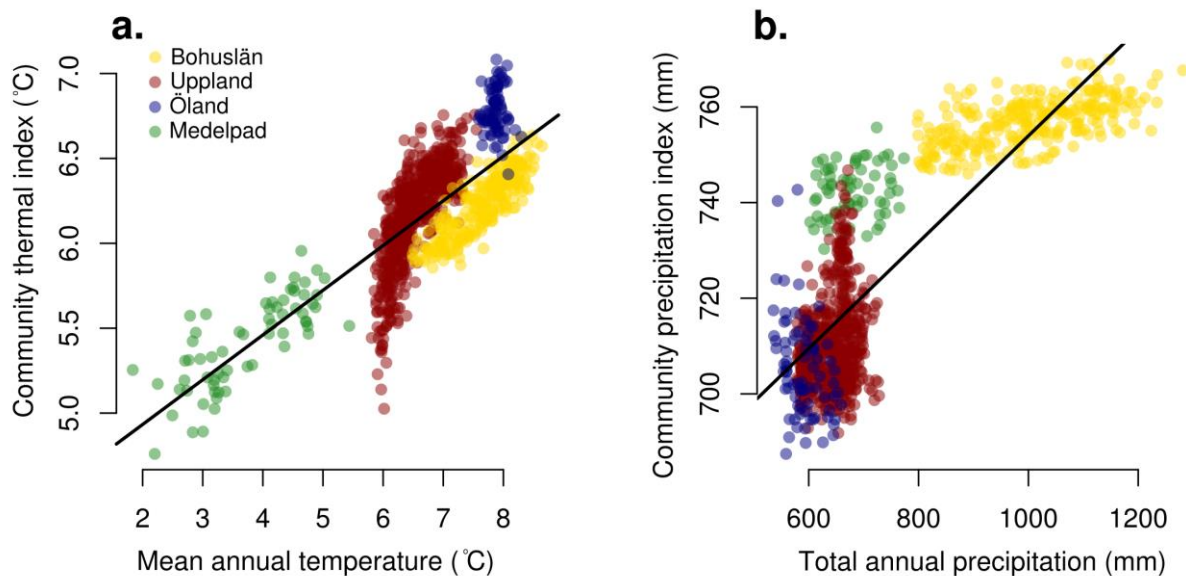
311

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.



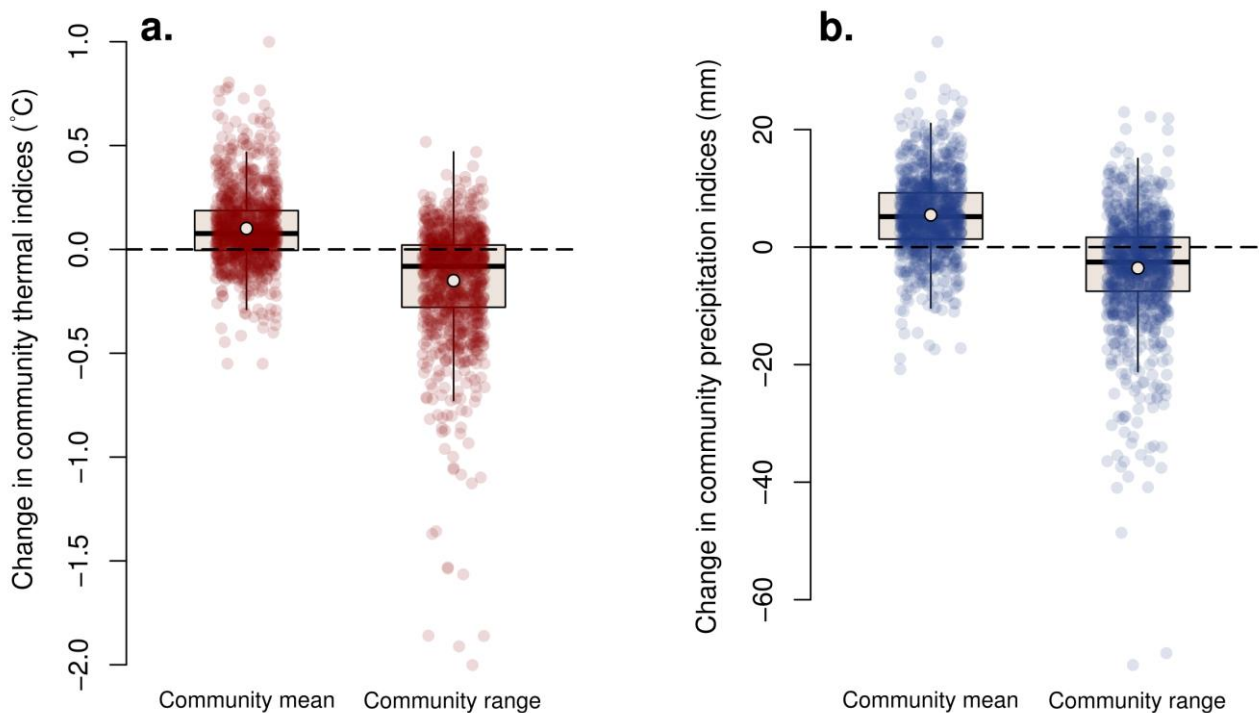
320

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 20th 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 ± 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 ± 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

337 community means, there was also significant (Wilcoxon $P < 0.0001$) homogenisation in community
 338 composition, as indicated by reduced interquartile ranges in species-level thermal and precipitation
 339 associations within landscapes. Interquartile ranges in species' temperature associations within a
 340 landscape decreased with a mean of $-0.15\text{ }^{\circ}\text{C}$ (95% CI: $0.013 - 0.47\text{ }^{\circ}\text{C}$ reduction) while the
 341 reduction was -3.5 mm ($0.987 - 15.0\text{ mm}$ reduction) for precipitation indices (Figure 2, Table S4).
 342



343

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

348

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

350 At the same time as temperature and precipitation increased, a widespread landscape simplification
 351 (loss in land-use heterogeneity) occurred across the study region, with more than two thirds of all
 352 landscapes experiencing such a shift. These changes were particularly prevalent in landscapes
 353 which had historically higher grassland and forest cover, both of which experienced forest

354 expansion, leading to simplified landscapes. Historically arable-dominated landscapes were more
355 likely to exhibit increases in landscape heterogeneity following abandonment of arable land
356 (Auffret et al., 2018; Figure S1). Alongside changes in land use, non-native neophytes have
357 increased their representation in the landscape. The fraction of neophytes within a landscape
358 increased in 82% of landscapes, although the average increase was modest, from a mean \pm sd of
359 $28.5 \pm 8\%$ of species in early- to mid-20th century landscapes to $33.7 \pm 7.3\%$ today. Along with the
360 expansion of neophytes, the total number of species has risen in 81% of landscapes, with a net
361 increase of 63.9 ± 71.1 (mean \pm sd) species per landscape, from 186 ± 148.3 to 250 ± 161.3 (34%
362 increase). However, these values should not be interpreted as absolute changes in species richness,
363 as for two of the four provinces this estimate of species richness change excludes trends in
364 occurrence for the majority of plant species, which were noted for the province in the historical data
365 but their distributions not mapped.

366

367 The three studied drivers of global change – climate change, land-use change and non-native
368 species – had significant and interacting effects on the turnover of species during the 20th century
369 towards more thermo- and pluviophilic communities (Figures 3-4; Table S5). Plant communities
370 became warmer (increased in mean thermal index) in landscapes with higher degrees of warming
371 and where the representation of non-native species grew (increased fraction of neophytes; Figure
372 3a-c). Increases in community thermal means due to climate warming were more likely where there
373 were larger increases in neophytes, and in landscapes that had been subjected to less simplification.
374 In other words, there was a stronger effect of warming in less simplified landscapes. The effect of
375 increased fraction neophytes on community warming reduced with increasing levels of landscape
376 simplification (Figure 3g). A warming climate, landscape simplification and increases in non-native
377 species also contributed to the thermal homogenisation (reduction in interquartile range) of plant
378 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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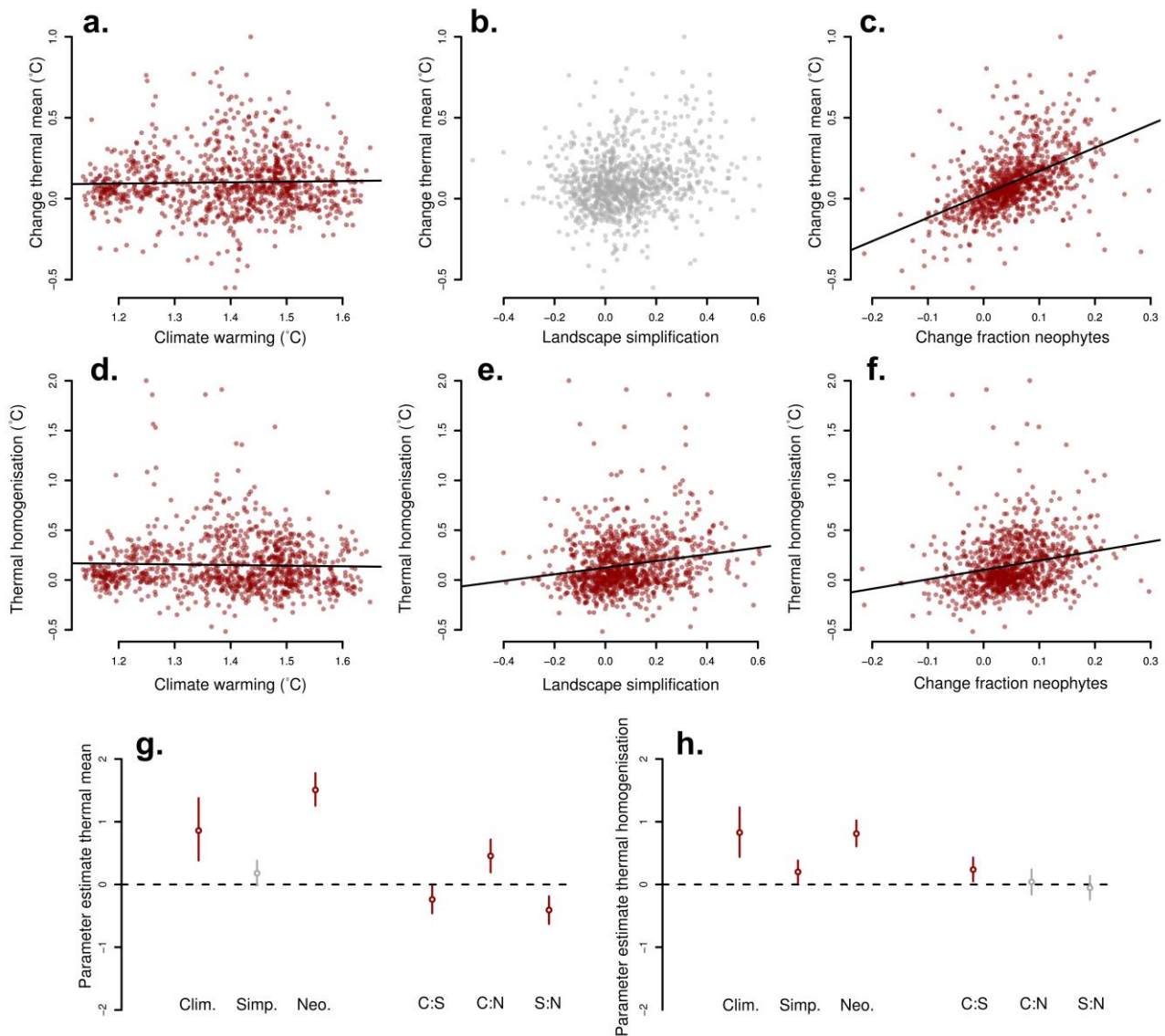
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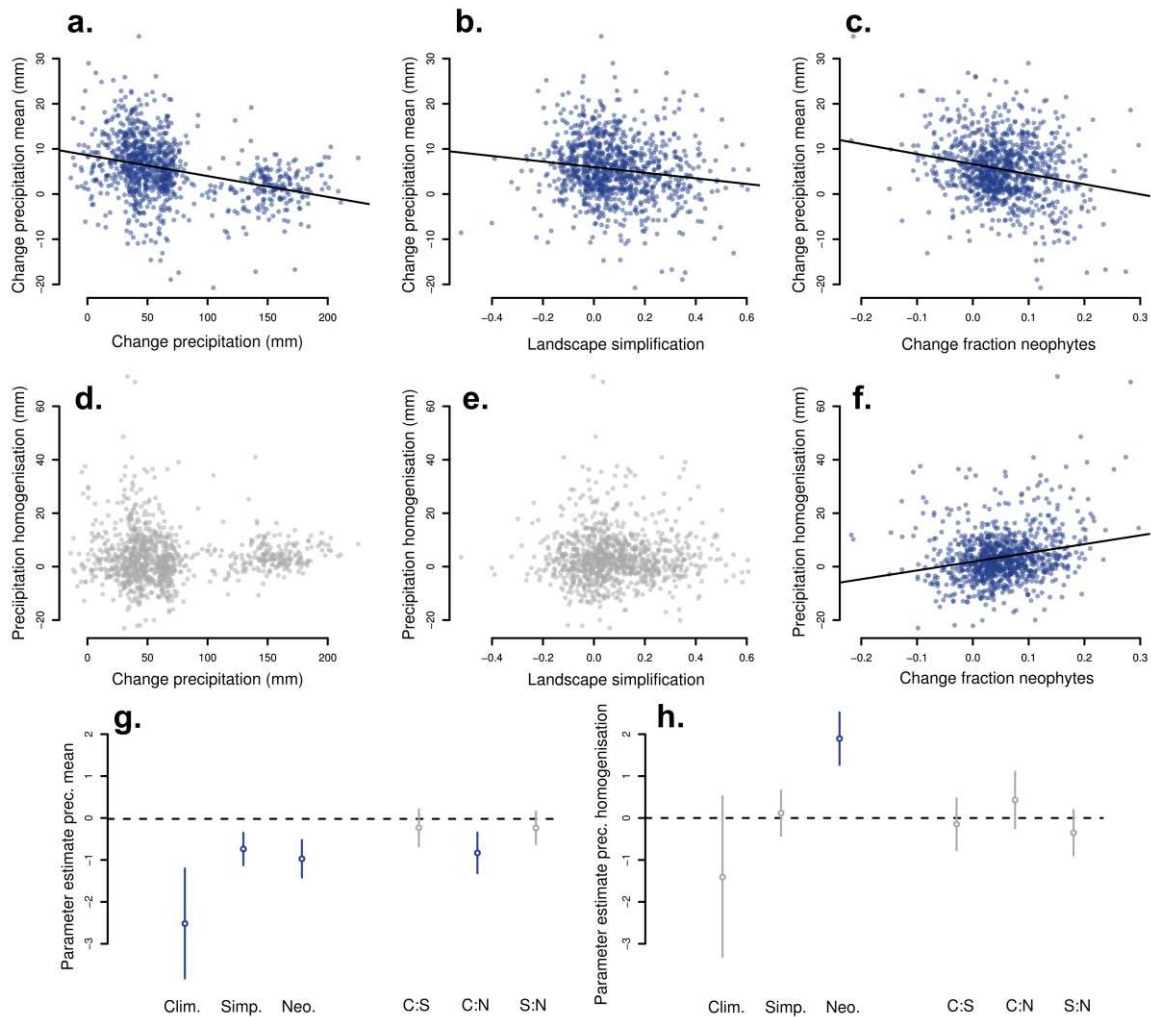
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408 **Figure 3.** Effect of increasing temperatures, landscape simplification and changes in fractions of
 409 neophytes (introduced species first observed in Sweden post-1492) and their interactions on shifts
 410 in community thermal indices in 996 landscapes for both changes in mean (a-c & g; model R^2
 411 marginal = 0.41 and conditional = 0.54) and homogenisation (d-f & h; model R^2 marginal = 0.28
 412 and conditional = 0.84). Scatter plots show raw data with best-fit lines while point-and-bar plots
 413 show parameter estimates and 95% confidence intervals in mixed models. Note that climate
 414 warming has a positive effect on both thermal mean and thermal homogenisation. Estimates of
 415 drivers of the *occurrence* of shifts are shown, with grey panels/bars indicating non-significant
 416 model terms (confidence intervals cross zero), while red panels/bars are significant. Model
 417 coefficients for all variables (including species richness, latitude and longitude) plus further metrics

418 of model performance are shown for these models and those explaining the *magnitude* of shifts in
 419 Tables S5 & S6.
 420
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423

424 **Figure 4.** Effect of increasing precipitation, landscape simplification and changes in fractions of
 425 neophytes (introduced species first observed in Sweden post-1492) and their interactions on shifts
 426 in community precipitation indices in 996 landscapes for both changes in mean (a-c & g; model R^2
 427 marginal = 0.43 and conditional = 0.87) and homogenisation (d-f & h; model R^2 marginal = 0.14
 428 and conditional = 0.93). Scatter plots show raw data with best-fit lines while point-and-bar plots
 429 show parameter estimates and 95% confidence intervals in mixed models. Estimates of drivers of
 430 the *magnitude* of shifts are shown, with grey panels/bars indicating non-significant model terms
 431 (confidence intervals cross zero), while blue panels/bars are significant. Model coefficients for all
 432 variables (including species richness, latitude and longitude) plus metrics of model performance are
 433 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 20th 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

459 temperatures to some extent, resulting in a lower likelihood of increased community thermal means
460 (De Frenne et al., 2013). On the other hand, higher levels of landscape simplification were linked to
461 a loss of variation in species' temperature associations within a landscape (Figure 3; Table S5).
462 Another implication of landscape simplification could be that because different land-cover types
463 have different microclimates (Greiser et al., 2018; Morecroft, Taylor, & Oliver, 1998), those
464 landscapes experiencing higher levels of landscape simplification are also losing microclimatic
465 variability at the landscape level. This means that as well as potentially buffering the effects of a
466 warming climate in terms of limiting shifts in community thermal means, increased landscape
467 simplification may have driven thermal homogenisation through having a lower variation in
468 microclimates and fewer refugia in which cool-adapted species could persist (Lenoir et al., 2013;
469 Maclean et al., 2015; Suggitt et al., 2018). Cooler-distributed species would then be more likely to
470 disappear from landscapes undergoing higher levels of landscape simplification, contributing to the
471 observed increase in community thermal mean and thermal homogenisation. Indeed, the effect of
472 warming on thermal homogenisation was higher more simplified landscapes, as indicated by the
473 positive interaction between temperature change and landscape simplification in the model.

474

475 Previous studies that examined the effects of landscape composition on changes in community
476 thermal indices consider the current 'simplicity' of the landscape as opposed to change over time
477 (Bertrand et al., 2011; Gaüzère et al., 2017; Oliver et al., 2017). These studies find that community
478 change is impeded in already more simplified landscapes, i.e. those with more agricultural land uses
479 that could be expected to inhibit dispersal and as a result prevent community reorganisation. Our
480 results also found that landscape simplification may be inhibiting shifts in community thermal
481 means, but in different ways. It is clear that landscape change can affect how communities respond
482 to climate change both at the local scale through variation in available habitat and microclimate
483 (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 20th 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.,

509 2013), changes in community precipitation or moisture indices over time been studied to a much
510 lesser extent than thermal indices. However, results from this study and a study from the UK
511 (Maclean et al., 2015) show that plant communities respond directionally both to increases and
512 reductions in precipitation. Shifts in community precipitation indices were strongly region-driven,
513 with a large effect of province in the model, as well as the surprising negative effect of measured
514 precipitation increases on the observed increases in precipitation indices from the plant
515 communities (Figure 4, Table S5). This is likely to be due to the much wetter province of Bohuslän
516 also having the largest increases in precipitation that were not matched in changes in the flora. This
517 region was probably already characterised by species with ‘wet’ distributions in the historical
518 period, and so the magnitude of shifts in precipitation indices was much lower than in the other
519 provinces. The introduction and spread of neophytes also had antagonistic effects on changes in
520 precipitation indices. Again, non-native species are likely to originate from warmer and drier
521 regions than Sweden, but the prevailing trend towards a wetter climate did not act as a hinder to
522 their colonisation and spread during the 20th century. Given that changes in precipitation have
523 varied widely across space (IPCC, 2015) and that there is considerable uncertainty in future
524 predictions (Knutti & Sedláček, 2013), these antagonistic interactions suggest that understanding
525 how communities will respond to future in precipitation changes represents a major challenge.

526

527 Our analysis showed clear directional community responses to climate change, though these
528 responses appear slow when compared to the rate of increased temperature and precipitation in the
529 study region. Rates of community warming at around 0.1 °C also appear to be up to an order of
530 magnitude slower than previously measured rates (Bertrand et al., 2011; De Frenne et al., 2013;
531 Fadrique et al., 2018). Previous studies have been based on plot-scale plant communities, and it is
532 understandable that changes will occur more slowly at landscape scales. However, it is difficult both
533 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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561 plant observations over the past 150+ years. Many thanks also to the regional botanical societies for
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/XXXXXX>.

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570 **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-](https://doi.org/10.1111/1365-2745.12742)

[2745.12742](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., Gemmill, 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.

- Macleán, 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](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>

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: https://www.lantmateriet.se/sv/Kartor-och-geografisk-information/Kartor/oppna-data/hamta-oppna-geodata]
Arable	Arable land
	Fruit farm
Open	Other open land
	Group of buildings with courtyard
	High-rise buildings
	Low-rise buildings
	Industrial area
	Leisure homes
Forest	Other open land with isolated trees
	Forest, coniferous and mixed
Water	Deciduous forest
	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 simplification	Neophytes	Temperature	Precipitation	Species richness	Latitude	Longitude
Landscape 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 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.

	Estimate	Stand. Error	CI 2.5	CI 97.5	z
<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 (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	

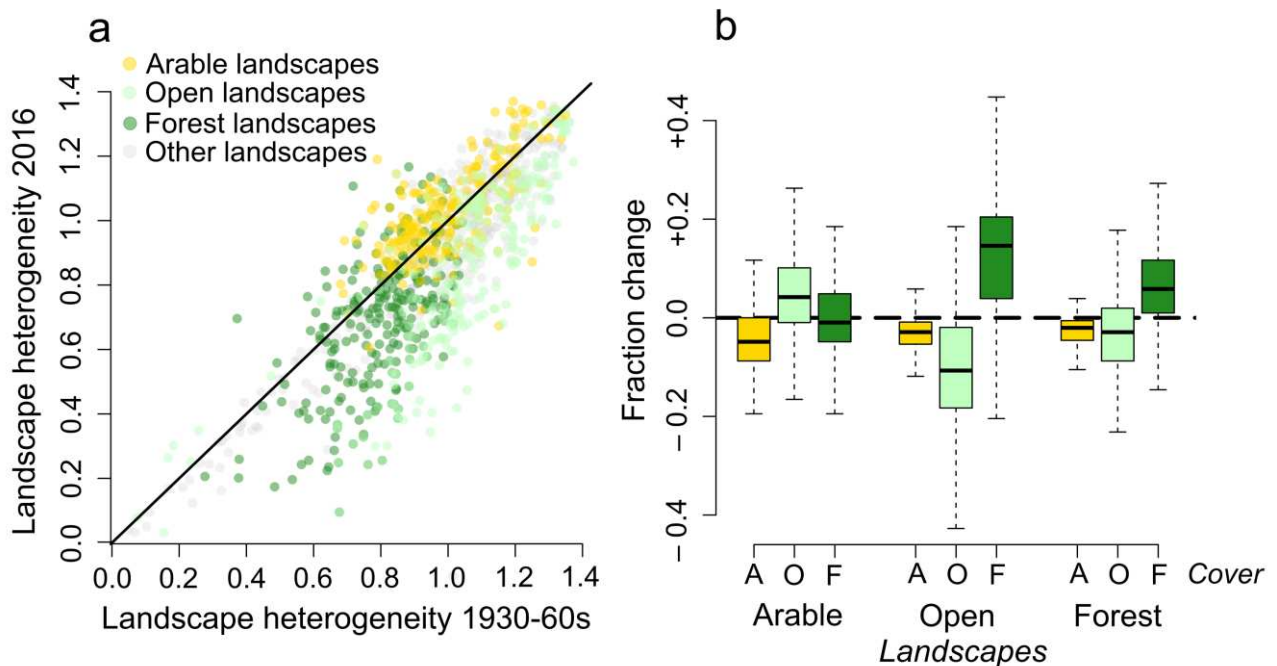
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Table S6. Performance of models explaining the occurrence (Generalized Linear Mixed Models) and magnitude (Linear Mixed Models) of increases in thermal and precipitation mean and decreases in thermal and precipitation range of plant communities in 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 R² and Conditional R² 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

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.



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