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The climatic debt is growing in the understorey of temperate forests: Stand characteristics matter

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1 The climatic debt is growing in the understory of 2 temperate forests: **stand characteristics matter**

3 *Running title:*

- 4 • **Explaining** the climatic debt of temperate forests

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The climatic debt is growing in the understory of temperate forests: **stand characteristics matter**

Running title:

- **Explaining** the climatic debt of temperate forests

Abstract

Aim

Climate warming reshuffles biological assemblages towards less cold-adapted but more warm-adapted species, a process coined thermophilization. However, the velocity at which this process happens is generally lagging behind the velocity of climate change, generating a climatic debt which temporal dynamic remains misunderstood. Relying on high-resolution time series of vegetation data from a long-term monitoring network of permanent forest plots, we aim at quantifying the temporal dynamic – up to a yearly resolution – of the climatic debt in the understory of temperate forests before identifying the key determinants allowing to modulate it.

Location

France

Time period

1995-2017

Taxa studied

Vascular plants

21 **Methods**

22 We used the community temperature index (CTI) to produce a time series of
23 understory plant community thermophilization, which we subsequently compared to
24 a time series of mean annual temperature changes over the same period and for the
25 same sites. The direction and magnitude of the difference (i.e. the climatic debt) was
26 finally analyzed using linear mixed-effect models to assess the relative contribution
27 of abiotic and biotic determinants, including forest **stand characteristics**.

28 **Results**

29 We found a significant increase in CTI values over time (0.08–0.09°C/decade),
30 **whereas** the velocity of mean annual temperature changes was three times higher
31 over the same period (0.22–0.28°C/decade). Hence, the climatic debt increased over
32 time and was greater in forest stands with higher basal area or older trees **as well as**
33 **under warmer macroclimate**. By contrasts, a greater frequency of anthropogenic
34 disturbances decreased the climatic debt, **while natural disturbances and herbivory**
35 **had no impact**.

36 **Conclusions**

37 Although often overlooked in understanding the climatic debt of forest biodiversity,
38 changes in forest stand characteristics may modulate the climatic debt by locally
39 modifying microclimatic conditions. **Notably, the buffering effect** of the upper canopy
40 layer **implies microclimate dynamics that** may provide more time for understory
41 plant communities to locally adapt.

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3 42 *Keywords*
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6 43 Biodiversity, climate change, climatic debt, anthropogenic disturbances, long-term
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9 44 monitoring, plant community, thermophilization
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For Peer Review

46 Introduction

47 Climate change induces a global redistribution of biodiversity at various spatial
48 scales, with profound consequences on ecosystem functioning and the provision of
49 ecosystem services (Hooper *et al.*, 2012; Pecl *et al.*, 2017). Typical biodiversity
50 redistribution consists of species shifting their geographical range poleward in
51 latitude and/or upslope in elevation (Lenoir & Svenning, 2015), tracking shifting
52 isotherms through colonization and local extinction processes (Jump & Peñuelas,
53 2005; Dullinger *et al.*, 2012). **Locally, changes in species' abundance and population
54 dynamics, preceding species range shifts, are leading to important re-assemblages in
55 community composition** (Hillebrand *et al.*, 2010; Walther, 2010). For example, some
56 studies reported that local species assemblages are increasingly dominated by
57 warm-adapted species (i.e. species from lower elevations and/or latitudes) at the
58 expense of cold-adapted species (i.e. species from higher elevations and/or latitudes),
59 a process referred to as “thermophilization” of communities (Gottfried *et al.*, 2012;
60 De Frenne *et al.*, 2013; Zellweger *et al.*, 2020). However, species and communities
61 may respond asynchronously and most likely with time lags relative to the forcing
62 environmental changes, so that plant species assemblages shifting from one
63 equilibrium state to another may not reflect environmental conditions prevailing at
64 the time of the survey but may rather reflect former environmental conditions
65 (Davis, 1984, 1989; Blonder *et al.*, 2017). Such discrepancies between the observed
66 velocity of climate change and the slower velocities at which species and
67 communities are actually responding have been termed “climatic debt” (i.e. the fact

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3 68 that biotic responses are lagging behind climate change) (Menéndez *et al.*, 2006;
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5 69 Bertrand *et al.*, 2011, 2016; Devictor *et al.*, 2012; Zellweger *et al.*, 2020).
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9 70 To assess the magnitude of the climatic debt or lag between the velocity of
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11 71 mean annual temperature (MAT) changes and the velocity of thermophilization of
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13 72 communities, one needs first to quantify the degree of thermophilization of local
14
15 73 species assemblages. The most straightforward approach is to compute the
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17 74 community temperature index (CTI) (Devictor *et al.*, 2008; Zellweger *et al.*, 2020).
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19 75 The CTI is the average value of either individual species' thermal optima or species-
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21 76 indicator values for temperature across all species co-occurring in a focal
22
23 77 community. How CTI changes over time (i.e. the proportion of cold- and warm-
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25 78 adapted species appearing or disappearing from the focal community) likely reflects
26
27 79 how communities are responding to climate changes (Devictor *et al.*, 2008; Bertrand
28
29 80 *et al.*, 2011). This index thus provides an intuitive proxy to estimate the velocity of
30
31 81 thermophilization of communities, and can be subsequently compared to the velocity
32
33 82 of observed temperature changes (e.g. both expressed in units of degrees Celsius per
34
35 83 decade; Devictor *et al.*, 2008). Changes in CTI (or analogous index) over time have
36
37 84 already been used to document thermophilization and delayed biotic responses of a
38
39 85 wide range of taxonomic groups (e.g. plants, butterflies, fishes and birds; Devictor *et*
40
41 86 *al.*, 2012; Bertrand *et al.*, 2011; Cheung *et al.*, 2013; Gaüzère *et al.*, 2017). However,
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43 87 most of these studies relied on a relatively restricted number of observations over
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45 88 time, usually a baseline survey and one or two resurveys at best, to compute
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47 89 changes in CTI values over time (Savage & Vellend, 2015; Ash *et al.*, 2017; Fadrique
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3 90 *et al.*, 2018). Some previous studies even relied on non-permanent or quasi-
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5 91 permanent plots to assess changes in CTI values over time (Bertrand *et al.*, 2011; De
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8 92 Frenne *et al.*, 2013; Becker-Scarpitta *et al.*, 2019; Zellweger *et al.*, 2020).
9
10 93 Unfortunately, such studies relying on non-permanent plots tend to infer temporal
11
12 94 changes blurred by space-for-time substitutions, which are known to overestimate
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14
15 95 the magnitude of thermophilization of communities in response to contemporary
16
17 96 climate warming (Elmendorf *et al.*, 2015). Even when studies rely on strictly
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19
20 97 permanent plots, it requires more than one or two resurveys to build a detailed time
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22 98 series of community composition changes from long-term monitoring programs.
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25 99 Strictly permanent monitoring programs relying on frequent resurveys (e.g. from
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27 100 one-year to five-year intervals) during a sufficiently long time period (e.g. at least
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30 101 two decades) are needed to capture a temporal dynamic in the velocity of community
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32 102 thermophilization and confirm linearity over time. Although such long-term time
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34 103 series of biodiversity monitoring already exist (Dornelas *et al.*, 2018), we still lack a
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37 104 good knowledge and understanding of the temporal dynamic of the climatic debt.
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40 105 Whether the climatic debt of plant communities is steadily growing over time
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42 106 and what are the main underlying determinants of this dynamic remain open
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45 107 questions in global change ecology (Essl *et al.*, 2015; Bertrand *et al.*, 2016; Zellweger
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47 108 *et al.*, 2020). For instance, a previous study focusing on temperate forests has
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50 109 suggested an increasing climatic debt in the response of understory plant
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52 110 communities from the lowlands (Bertrand *et al.*, 2011). A follow-up study has
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54 111 revealed that this growing climatic debt involved a complex combination of abiotic
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3 112 and biotic factors with the greatest effect size captured by environmental conditions
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5 113 during the baseline surveys (i.e. a greater climatic debt for plant communities
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8 114 occurring within initially warmer conditions) (Bertrand *et al.*, 2016). Noteworthy,
9
10 115 the same authors also found that **anthropogenic** disturbances contributed very little
11
12 116 and unexpectedly to the climatic debt. Yet, previous and more recent findings
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14
15 117 suggest the opposite with local disturbances amplifying forest community responses
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17 118 to climate change (De Frenne *et al.*, 2013; Stevens *et al.*, 2015; Perring *et al.*, 2018;
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19 Brice *et al.*, 2019). A more recent study has even demonstrated that the climatic lag
20 119
21 120 in forest plant communities is primarily controlled by forest microclimate dynamics
22
23 121 suggesting **forest stand characteristics** to be a strong determinant of the climatic
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25 122 debt (Zellweger *et al.*, 2020). These discrepancies call for more in-depth
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27 123 investigations on the temporal dynamic of the climatic debt in forest understory
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29 124 plant communities and the relative contribution of **anthropogenic and natural**
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31 125 disturbances.

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37 126 In addition to baseline environmental conditions and stand characteristics
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39 127 modulated by **anthropogenic and natural disturbances**, ungulates directly impact
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41 128 vegetation dynamics (Post & Pedersen, 2008; Olofsson *et al.*, 2009; Boulanger *et al.*,
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43 129 2018). **On the one hand**, Olofsson *et al.* (2009) have shown that herbivores inhibit
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45 130 the climate-driven shrub expansion towards high latitudes, **indicating that**
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47 131 **herbivores could contribute to the climatic debt. On the other hand**, Post & Pedersen
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49 132 (2008) have shown that plant community composition (e.g. dwarf birch, willow,
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51 133 graminoids, forbs and mosses) on warmed plots (open-top chambers) did not differ
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3 134 from that on ambient plots where herbivores grazed, **suggesting no effect of**
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5 135 **herbivory on the climatic debt**. Altogether, these findings **show contrasting impacts**
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8 136 **of herbivory on** the climatic debt.
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11 137 Here, we rely on a long-term (1995-2017) national (France) monitoring
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13 138 network of permanent forest plots organized in a paired design of enclosure (fenced
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15 139 area excluding ungulates) *vs.* control plots – the RENECOFOR monitoring program
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18 140 – with multiple resurveys (every year to every five years) to generate a high-
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20 141 resolution and unprecedented time series of CTI values for understory plant
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22 142 communities inside and outside the fenced area. Using this information-rich time
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24 143 series, we aimed to: (i) compare the rates of CTI changes to the velocity of MAT
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26 144 changes during the period 1995-2017; (ii) test whether the climatic debt of
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28 145 understory plant communities increased steadily over time; and (iii) assess the
29
30 146 relative contribution of several abiotic and biotic factors known to be influential
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32 147 from the scientific literature, including baseline environmental conditions, stand
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34 148 characteristics that are influenced by **anthropogenic and natural disturbances**, and
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36 149 biotic disturbances from large herbivores.
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44 150 **Materials and Methods**

47 151 *A long-term national monitoring network of forest ecosystems*

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51 152 To assess changes in understory plant communities, we used vegetation data
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53 153 collected every five years, and even every year for some sites, throughout a long-
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55 154 term French monitoring network of forest ecosystems (RENECOFOR,
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3 155 <http://www1.onf.fr/renecofor>). The RENECOFOR network belongs to the European
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5 156 ICP Forests Level II monitoring program (ICP Forests, <http://www.icp-forests.org>)
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7
8 157 and aims at monitoring the health and functioning of forest ecosystems. This
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10 158 monitoring network was established in 1992 by the French National Forest Service
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12 159 (ONF, Office National des Forêts). It includes 102 permanent plots distributed in
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15 160 state and communal forests throughout the whole metropolitan French territory
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17 161 (www1.onf.fr/renecofor/sommaire/sites) (Ulrich, 1995 ; Nicolas *et al.*, 2014). All plots
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19 162 are located in mature and even-aged pure stands, and cover an area of 2 ha with a
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22 163 central fenced zone of 0.5 ha to exclude large herbivores (**Fig. 1**) (for more details,
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25 164 see Boulanger *et al.*, 2018).

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28 165 Since 1995, vegetation surveys have been conducted every five years (baseline
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30 166 survey in 1995 and resurveys in 2000, 2005, 2010 and 2015). From the total pool of
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33 167 102 permanent plots, we discarded 58 plots which suffered from major data gaps
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35 168 throughout the studied time period (e.g. the resurvey of 2010 was systematically
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38 169 missing for 53 plots due to a shortage in funding). This yielded a total of 44 plots for
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40 170 which a full time series, at a 5-yr interval, was available between 1995 and 2015,
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42 171 hereafter referred to as the five-year dataset (**Fig. 1**). Among these 44 plots, 8 plots
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45 172 were monitored annually without discontinuity between 1995 and 2017, hereafter
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47 173 referred to as the yearly dataset (**Fig. 1**). The whole workflow of analyses was
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50 174 carried out separately for both the five-year and yearly datasets, as these two
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52 175 datasets are very complementary (*Supporting Information App. Fig. 1*). Although
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54
55 176 the five-year dataset covers a large spatial extent representative of all temperate
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3 177 forests in France, its temporal resolution is rather coarse. *Per contra*, the yearly
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5 178 dataset covers a restricted spatial extent but provides a very detailed time series at
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8 179 high temporal resolution. More information on the spatial location and dominant
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10 180 tree species for each of 44 study plots are provided in *Supporting Information App.*
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12
13 181 *Table 1.*
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16 182 During each monitoring campaign, the vegetation was surveyed by expert
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18 183 botanists according to standardized protocols under a quality assurance and quality
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20 184 control procedure. The quality assurance and quality control procedure involved
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22 185 intercalibration exercises organized the year before each monitoring campaign with
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24 186 all expert botanists surveying the same plots in the same forest (Camaret &
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26 187 Brêthes, 2004; Archaux *et al.*, 2009). During each monitoring campaign, all plots
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28 188 were surveyed both at spring and in summer/autumn, to cover the entire growing
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30 189 season. All vascular plants were recorded in eight 2 m × 50 m subplots: four inside
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32 190 and four outside the fenced area of 0.5 ha (**Fig. 1**). The cover-abundance of all taxa
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34 191 occurring in four vegetation layers (tree: > 7 m; high shrub: 2–7 m; low shrub: 0.3–2
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36 192 m; herb: < 0.3 m) was recorded. Species names were standardized following the
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38 193 nomenclature of *Flora Europaea* (Tutin *et al.*, 2001). A total of 877 taxa were
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40 194 recorded in all vegetation layers, including 751 occurring in the herb layer
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42 195 (hereafter understory plants). Here, we restricted our analyses to understory plants,
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44 196 including tree seedlings, because they represent a relevant component of forest
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46 197 biodiversity which is not directly (but indirectly via the upper canopy layers)
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48 198 impacted by forest management practices, and are expected to be the most
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3 199 responsive to climate warming. Only taxa identified at the species or subspecies
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5 200 levels were kept for analyses. Identifications at the genus level were considered as
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7 201 incomplete and excluded from our analyses (i.e. 80 taxa excluded; see the list of
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9 202 species provided in *Supporting Information App. Table 2*). Our dataset encompassed
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11 203 a total of 782 vegetation records, including 347 records from the yearly dataset (492
12
13 204 species) and 435 records from the five-year dataset (593 species). Seasonal surveys
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15 205 (spring and summer/autumn) were aggregated by year with the maximum cover-
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17 206 abundance coefficient retained whenever a species was recorded at both dates. This
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19 207 yielded to a total of 186 and 220 vegetation records for the yearly and five-year
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21 208 dataset, respectively.

22 209 *Time series of temperature data*

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28 210 To compare the velocity of mean annual temperature (MAT) changes with the
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30 211 velocity of temperature changes inferred from understory plant communities, we
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32 212 first extracted time series of MAT changes. We obtained macroclimate temperature
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34 213 time series from the global dataset TerraClimate (Abatzoglou *et al.*, 2018), which
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36 214 provides monthly climate data for every year from 1958 up to 2018 at a spatial
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38 215 resolution of 2.5 arc-minute ($\sim 3.3 \text{ km} \times 4.64 \text{ km}$ at 45° of latitude). We also extracted
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40 216 climatic time series from the CHELSA database (Karger *et al.*, 2017) but found very
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42 217 similar trends between TerraClimate and CHELSA (*Supporting Information App.*
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44 218 *Fig. 2*). Thus, we decided to use only TerraClimate in our subsequent analyses as it
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46 219 better covers the end of our study period (i.e. 2017). **As TerraClimate provides only**
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48 220 **maximum and minimum monthly temperatures, we first calculated the monthly**
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221 mean for each of the 44 studied plots (by averaging maximum and minimum
 222 temperature values for each month), and then computed mean annual temperature
 223 (hereafter MAT) for each year between 1958 and 2017. Between 1958 and 2017,
 224 MAT increased across all 44 studied plots, leading to a shift from negative to only
 225 positive anomalies towards the end of the reference period (1958–2017) (*Supporting*
 226 *Information App. Fig. 3*). From the very beginning (1992) of the RENECOFOR
 227 monitoring program until 2017, anomalies were mostly positive (values ranging
 228 from -0.56 to 1.54 over the period 1992-2017), except for three years (1993, 1996 and
 229 2010), for which anomalies were negative.

230 To infer temperature conditions from local species assemblages, we used the
 231 community temperature index (CTI) (Devictor *et al.*, 2008, 2012) (see Equation 1).
 232 The CTI was computed based on occurrence data by averaging the indicator values
 233 (IVs) for temperature across all species i (Sp_i) occurring in a given relevé j
 234 (containing S species, with $S \geq 2$). Here, we used presence/absence data instead of
 235 weighting IVs by each species' abundance/dominance in the relevés. We did that to
 236 give the same weight to common and rare species. As each RENECOFOR plot
 237 includes 8 subplots, we calculated the CTI values at the subplot level and kept this
 238 information at the subplot level without aggregating it at the plot level.

$$(1) \quad CTI_j = \frac{\sum_{i=1}^S IV \text{ Temperature } Sp_i}{S}$$

240 Species' IVs for temperature were extracted from both the CATMINAT (Julve, 1998)
 241 and EcoPlant (Gégout *et al.*, 2005) databases, and we used them in combination to
 242 take advantage of their respective strengths (*Supporting Information App. Fig. 4*).

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3 243 On the one hand, the CATMINAT database is based on expert knowledge similarly
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5 244 to Ellenberg's IVs (Ellenberg et al., 1992), with temperature preferences of plant
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8 245 species coded along an ordinal scale from cold (1) to warm (9) conditions. It contains
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10 246 almost all of species recorded in our dataset (858 out of the 877 species recorded in
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12 247 all vegetation layers), but CTI values are unitless and direct comparisons with
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15 248 macroclimatic temperatures are not possible. On the other hand, EcoPlant IVs for
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17 249 temperature are directly expressed in degrees Celsius (Gégout et al., 2005) allowing
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20 250 the direct computation of CTI values in degrees Celsius, but much less species from
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22 251 our dataset are recorded (396 out of 877 species). Based on these two databases, we
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25 252 calibrated a transfer function to produce CTI values directly expressed in degrees
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27 253 Celsius and transform the unitless CTI values from the CATMINAT database into a
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29 254 CTI value expressed in degrees Celsius (*Supporting Information App. Fig. 4 & 5*
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32 255 and see Lenoir *et al.*, 2013 for a similar approach).

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35 256 Based on the time series of MAT values and the time series of CTI values,
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37 257 both expressed in degrees Celsius, we computed the lag as the difference between
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40 258 the two (MAT – CTI), thus getting a new time series of the difference: the climatic
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43 259 debt (Bertrand *et al.*, 2016).

44 45 46 260 *The main determinants of the climatic debt*

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49 261 Although we were primarily interested in assessing the temporal dynamic of the
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51 262 difference between MAT and CTI values, thereby testing the effect of time itself on
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54 263 the direction and magnitude of this difference – as we assumed the climatic debt to

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3 264 increase over time – we also assessed the relative contributions of several abiotic
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5 265 and biotic determinants known to potentially modulate the climatic debt. For
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8 266 instance, it has already been demonstrated that MAT during or prior to the baseline
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10 267 survey was a strong and positive determinant of the climatic debt in understory
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12 268 plant communities, suggesting greater lags in initially warmer areas (Bertrand *et*
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15 269 *al.*, 2016). Hence, to account for that potential confounding effect, we computed
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17 270 baseline temperature conditions from TerraClimate as the average of MAT values
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20 271 during the 1961-1990 reference period (i.e. 30-yr average typically used to capture
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22 272 long-term climatic conditions) and added it as a covariate to explain the climatic
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25 273 debt.

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28 274 In addition to baseline temperature conditions, we gathered information on
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30 275 anthropogenic and natural disturbances, and stand characteristics, all available
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32 276 from the RENECOFOR monitoring program. Because local disturbances may have
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35 277 significant effects on understory plant communities and are known to accelerate
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37 278 their thermophilization rates and reduce the climatic debt (Bengtsson *et al.*, 2000;
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40 279 Stevens *et al.*, 2015; Brice *et al.*, 2019), we built several variables capturing these
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42 280 local disturbances (*Supporting Information App. Fig. 6 & 7*). First, we distinguished
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45 281 between natural (e.g. windstorm) and anthropogenic disturbances (i.e. local
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47 282 disturbances associated to forest management practices such as thinning, cleaning
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50 283 and tree extraction). For each of these two types of disturbances, we computed the
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52 284 cumulative sum of disturbance events occurring within a given forest plot prior to
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55 285 each survey year. Here, we assumed that repeated disturbance events are likely to
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3 286 accelerate the thermophilization rate and thus reduce the climatic debt of
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5 287 understory plant communities. Then, irrespective of the type of disturbance, we also
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8 288 computed the anteriority, i.e. the number of years, between the last disturbance
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10 289 event and the year of the survey, assuming that a very short anteriority (less than a
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12 290 year) will impact less the difference between MAT and CTI values. Indeed, plant
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15 291 community composition is unlikely to change during the vegetation season that is
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17 292 just following a stand thinning event. However, significant changes in plant
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20 293 community composition may lag and happen during the next couple of years with
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22 294 light demanding and warm-adapted species germinating from the soil seed bank and
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25 295 increasing CTI values, thus paying off part of the climatic debt. We also retrieved
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27 296 information about stand characteristics at the plot level, including: stand basal area
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30 297 during the monitoring year; stand age in 1995; and the type of dominant tree species
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32 298 (i.e. deciduous *vs.* coniferous). We hypothesized that plots with higher stand basal
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34 299 area and located in older forest stands are likely to be more buffered against the
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37 300 adverse effect of macroclimate warming (Zellweger *et al.*, 2019), thus further
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39 301 inflating the climatic debt of understory plant communities (De Frenne *et al.*, 2013).
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41 302 The enclosure effect (i.e. fenced area excluding ungulates and large herbivores
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44 303 *vs.* control plots outside the fenced area) was added as a covariate in all our analyses
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46 304 on the temporal trends in CTI values and the climatic debt. According to the
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49 305 scientific literature, climate change impacts on vegetation dynamics tend to be
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51 306 inhibited by large herbivores (Post & Pedersen, 2008; Kaarlejärvi *et al.*, 2013), hence
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54 307 we hypothesized a greater climatic debt outside than inside the fenced area.
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308 *Statistical analyses*

309 We used linear mixed-effects models (LMMs) to assess the velocity of MAT changes
310 and thermophilization of understory plant communities. For CTI values, we used
311 the continuous variable “year” of the monitoring as the main fixed effect while
312 accounting for potentially diverging temporal dynamics between the outside and
313 inside of the fenced area, by adding the interaction effect: year \times enclosure. The
314 RENEFOR plot ID (44 or 8 levels depending on the dataset used) and the
315 vegetation subplot ID (8 levels), nested within the plot ID, were used as a random
316 term to account for the hierarchical structure of the sampling design and the
317 repeated surveys over time. For MAT values, we only used the “year” of the
318 monitoring as a fixed effect and the RENEFOR plot ID as a random term.
319 Indeed, for MAT, the subplot level was not used in the random component of LMMs
320 since all 8 subplots within a given plot have similar MAT values. To allow between-
321 site variation in the temporal dynamics of MAT and CTI values, we set the random
322 term (e.g. plot ID) of our LMMs so that it modifies the slope coefficient (i.e. random
323 slope term) of the variable “year” for each level of the random term variable. The
324 coefficient estimate of the “year” variable in our LMMs was used as a proxy for
325 estimating the velocities of temperature changes, both for MAT and CTI values.
326 Assumptions of normality and homoscedasticity of the residuals of our models were
327 visually checked and no departure from normality and homoscedasticity were
328 detected. Significance of the predictors in LMMs were assessed using Wald χ^2 tests,
329 after fitting models with the restricted maximum likelihood estimation.

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3 330 To analyze the temporal dynamic of the difference between MAT and CTI
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6 331 values over time (i.e. the climatic debt), we used LMMs with the value of the
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8 332 difference (MAT – CTI) as the response variable and the continuous variable “year”
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10 333 of monitoring as the main fixed effect variable. In addition to “year”, we added
11
12 334 several abiotic and biotic covariates as fixed effect variables to assess their relative
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15 335 contribution in modulating the climatic debt. These covariates were: baseline
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17 336 temperature conditions; sum of natural disturbances; sum of anthropogenic
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20 337 disturbances; disturbance anteriority; stand basal area; stand age; **type of dominant**
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22 338 **tree species in forest stand (deciduous vs. coniferous)**; and the enclosure effect. From
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24
25 339 the full model including all covariates together with time as fixed effect terms, we
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27 340 ran all possible combinations of models and ranked all candidate models using the
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29
30 341 corrected Akaike information criteria (AICc). Based on the best candidate model
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32 342 with the lowest AICc value, we then computed the difference in AICc values (ΔAICc)
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35 343 for all models relative to the best candidate model. Finally, from the set of selected
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37 344 candidate models with ΔAICc values < 2 , we used a model averaging approach to
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39 345 calculate the conditional mean value of each coefficient and its associated 95%
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42 346 confidence interval (Burnham & Anderson, 2002). All continuous predictor variables
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44 347 were standardized (z -score) before analyses to improve their interpretability on a
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47 348 comparable scale (Schielezeth, 2010). None of the fixed-effect variables included in
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49 349 our models showed multicollinearity issues ($\text{VIF} < 3$; Zuur *et al.*, 2007). Note that
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51 350 correlation values among all our explanatory variables did not exceed a Spearman’s
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54 351 r coefficient of 0.6 (*Supporting Information App. Fig. 8*). Again, we used the
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56 352 RENECOFOR plot ID (44 or 8 levels depending on the dataset used) and the
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3 353 vegetation subplot ID (8 levels), nested within the plot ID, as a random slope term
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5 354 modifying the effect of “year” of monitoring. The explained variance of LMMs was
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8 355 determined by calculating the marginal (R^2_m , associated with fixed effects only) and
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10 356 conditional (R^2_c , associated with both fixed and random effects) R^2 values
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13 357 (Nakagawa & Schielzeth, 2013) using the `r.squared.GLMM` function from the MuMIn
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15 358 package.

18 359 All statistical analyses were performed with the R software version 3.6.0 (R
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20 360 Core Team, 2019). Models were performed with the nlme package v.3.1-140 (Pinheiro
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22 361 *et al.*, 2019), and the model selection procedure was assessed with the MuMIn package
23
24 362 v.1.43.6 (Bartoń, 2019), using the dredge function. Other packages were used for
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26 363 data handling extraction and graphical visualization: dplyr v.0.8.3 (Wickham *et al.*,
27
28 364 2019); raster v.2.9-23 (Hijmans, 2019); ggplot2 v.3.2.0 (Wickham, 2016); cowplot
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30 365 v.1.0.0 (Wilke, 2019); and sf v.0.7-7 (Pebesma, 2018).

36 366 Results

37 367 *Temporal trends in macroclimate and community temperatures*

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40 368 Using the 5-yr interval dataset, mean annual temperature (MAT) during 1995–2015
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42 369 increased by 0.23 ± 0.02 °C/decade (95 % Confidence Intervals (CI): 0.18-0.28, $t =$
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44 370 9.05, $P < 0.001$; **Fig. 2a**). In the yearly dataset, MAT increased by 0.31 ± 0.05
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46 371 °C/decade (95 % CI: 0.20-0.42, $t = 5.51$, $P < 0.001$; **Fig. 2b**) during 1995–2017. Over
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48 372 the same time periods, the velocities of CTI changes were weaker, but similar trends
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51 373 and magnitudes were observed in both the five-year (0.10 ± 0.03 °C/decade, 95 %
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3 374 CI: 0.04-0.15, $t = 3.62$, $P < 0.001$; **Fig. 2a**) and yearly (0.08 ± 0.03 °C/decade, 95 %
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5 375 CI: 0.01-0.14, $t = 2.15$, $P = 0.031$; **Fig. 2b**) datasets. No significant differences were
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7 376 observed in CTI trends between inside and outside of the fenced area. Further, the
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9 377 difference between MAT and CTI values showed a tendency to increase steadily over
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11 378 time (**Fig. 2**): the lag in the response of herbaceous plant communities to climate
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13 379 warming increased linearly over time. Although we found a significant effect of time,
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15 380 it contributed weakly to the overall variation in MAT and CTI values: $R^2_m \leq 0.01$
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17 381 while R^2_c ranged between 0.92 to 0.96.
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23 382 *Factors contributing to the climatic debt*

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26 383 For both the yearly and five-year datasets, the model averaging procedure to explain
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28 384 the climatic debt (MAT – CTI) selected 4 and 3 candidate models ($\Delta AIC_c < 2$),
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30 385 respectively. The best candidate models explained 55% and 70% of the total
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32 386 variation in the difference between MAT and CTI values for the five-year ($R^2_m =$
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34 387 0.33 ; $R^2_c = 0.55$) and yearly ($R^2_m = 0.46$; $R^2_c = 0.70$) datasets, respectively. The best
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36 388 candidate model for the five-year dataset contained 6 variables including the year of
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38 389 sampling, stand age, the anteriority of the last disturbance, the cumulative number
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40 390 of anthropogenic disturbances, stand basal area, and baseline temperature
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42 391 conditions. For the yearly dataset, the best candidate model included the same 6
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44 392 variables together with **the type of dominant tree species** (*Supporting Information*
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46 393 *App. Tables 3 & 4 and App. Fig. 9 & 10*).
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3 394 Irrespective of the dataset considered in our analyses, we found very
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5 395 consistent and similar trends in the factors contributing to the climatic debt (**Fig. 3**).
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8 396 For instance, the year of sampling had a positive effect on the magnitude of the
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10 397 difference, confirming an increasing climatic debt of understory plant communities
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12 398 over time (five-year dataset = 0.06 ± 0.03 SE, *Fig. 3a*; yearly dataset = 0.31 ± 0.04
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14 399 SE, *Fig. 3b* and *Fig. 4a*).

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18 400 Baseline temperature conditions had the strongest positive influence on the
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20 401 climatic debt (five-year dataset = 0.77 ± 0.04 SE, *Fig. 3a*; yearly dataset = $0.72 \pm$
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22 402 0.10 SE, *Fig. 3b*), indicating greater lags in plots with warmer baseline temperature
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24 403 conditions during the period 1961–1990. We also found a positive effect of stand
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26 404 characteristics, through the variables stand age in 1995 and basal area during the
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28 405 year of monitoring, on the magnitude of the lag. More specifically, the lag was larger
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30 406 in denser (five-year dataset = 0.22 ± 0.04 SE, *Fig. 3a*; yearly dataset = 0.35 ± 0.05
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32 407 SE, *Fig. 3b* and *Fig. 4b*) and older (five-year dataset = 0.15 ± 0.04 SE, *Fig. 3a*;
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34 408 yearly dataset = 0.46 ± 0.07 SE, *Fig. 3b* and *Fig. 4c*) forests. We found no clear
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36 409 differences in the climatic debt between coniferous and deciduous forests as well as
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38 410 between inside and outside of the fenced area.

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45 411 In contrast, forest disturbance had a negative effect on the climatic debt (*Fig.*
46
47 412 *3*). Notably, the magnitude of the lag was negatively correlated with the anteriority
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49 413 of the last disturbance event (five-year dataset = -0.12 ± 0.02 SE, *Fig. 3a*; yearly
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51 414 dataset = -0.10 ± 0.03 SE, *Fig. 3b*), revealing that lags decrease in plots recently
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53 415 disturbed. Moreover, the cumulative number of anthropogenic disturbances were
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3 416 negatively correlated to the climatic debt (five-year dataset = -0.17 ± 0.04 SE, *Fig.*
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5 417 *3a*; yearly dataset = -0.19 ± 0.07 SE, *Fig. 3b*), indicating that lags decrease in the
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7 418 most frequently disturbed plots, following logging events. The cumulative number of
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9 419 natural disturbances was only retained in the models based on the five-year dataset,
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11 420 albeit its tendency towards a negative effect did not differ from zero (-0.04 ± 0.04
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13 421 SE, *Fig. 3a*).
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19 422 Discussion

20 21 22 423 *Velocities of thermophilization*

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25 424 Irrespective of the temporal resolution in the data (i.e. the yearly vs. five-year
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27 425 dataset), we show a very similar increase in temperature conditions inferred from
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29 426 understory plant communities over the period 1995–2017, consistent with a
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31 427 thermophilization process. This finding adds to a growing body of evidence
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33 428 describing thermophilization of plant communities across many forest ecosystems
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35 429 around the globe (e.g. in temperate, boreal and tropical ecosystems; Lenoir *et al.*,
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37 430 2010; Bertrand *et al.*, 2011; De Frenne *et al.*, 2013; Savage & Vellend, 2015;
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39 431 Fadrique *et al.*, 2018; Zellweger *et al.*, 2020), as well as across other ecosystems and
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41 432 taxonomic groups (e.g. in mountain plant communities, Gottfried *et al.*, 2012;
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43 433 marine fishes and invertebrates, Cheung *et al.*, 2013; birds and butterflies, Devictor
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45 434 *et al.*, 2012; bumblebee communities, Fourcade *et al.*, 2018). The velocities of
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47 435 thermophilization we report here (ranging from 0.08 to 0.10 °C/decade) are broadly
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49 436 in the range of those reported in the scientific literature (from 0.03 to 0.38
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3 437 °C/decade; *Supporting Information App. Table. 5*), but also are among the highest
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5 438 rates recorded for plant communities (maximum value of 0.27 °C/decade; Duque *et*
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8 439 *al.*, 2015). Specifically, we show velocities that are twice as fast as the average
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10 440 thermophilization rate estimated for understory plant communities across
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12 441 temperate deciduous forests in Europe (i.e. 0.041 °C/decade; De Frenne *et al.*, 2013).
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15 442 Nevertheless, these rates are still much lower than those found in marine
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17 443 ecosystems, where environmental constraints may weakly limit the dispersal of
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20 444 species in response to rising temperatures (Lenoir *et al.*, 2020).
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23 445 Our findings consist in the most recent updates supporting and consolidating
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25 446 previous reports of plant community thermophilization which happened across the
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28 447 same study area (France) (Bertrand *et al.*, 2011; Martin *et al.*, 2019). Focusing on a
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30 448 completely independent dataset from the period 1965–2008, Bertrand *et al.* (2011)
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33 449 were the first to highlight a thermophilization of understory plant communities in
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35 450 the French forests. More recently, Martin *et al.* (2019) have described a similar
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38 451 thermophilization trend extending to other plant communities at national and
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40 452 regional scales in France over the period 2009–2017. Unlike these previous studies
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42 453 relying either on massive collection of opportunistic surveys over time (Bertrand *et*
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44
45 454 *al.*, 2011) or citizen science data (Martin *et al.*, 2019), our study is the first that used
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47 455 a long-term monitoring program based on strictly permanent plots intensively
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50 456 monitored over time (up to every year), providing a very detailed time series of
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52 457 changes in understory plant community composition. Hence, we argue that the
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55 458 velocities we report here do not suffer from biases due to space-for-time
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3 459 substitutions and are thus likely to be more accurate than those previously reported
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5 460 (Elmendorf *et al.*, 2015), which matters for informing our society on future scenarios
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8 461 of biodiversity changes (IPBES, 2019). Furthermore, our yearly resurveys over a
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10 462 period of 25 years confirm that the thermophilization rate of understory plant
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12 463 communities in temperate forests is following a linear trajectory over time. This is
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15 464 an important and novel finding that helps us to understand the temporal dynamic of
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17 465 the biotic responses to anthropogenic climate change. Yet, time alone had a very
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20 466 minor contribution to explain the variation in temperature conditions inferred from
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22 467 understory plant communities. This suggests that other abiotic and biotic
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25 468 determinants, such as the macroclimatic context as well as local stand
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27 469 characteristics influenced by anthropogenic disturbances may potentially explain
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30 470 local variations in temperature conditions.

31 32 33 471 *The climatic debt and its potential determinants*

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36 472 One of our most striking results is that the velocity at which atmospheric air
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38 473 temperatures are rising is twice faster, on average, than the velocity at which
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41 474 understory plant communities are responding, generating a climatic debt that is
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43 475 steadily growing over time, even after accounting for the relative contribution of
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46 476 several abiotic and biotic determinants modulating it. Although the idea of an
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48 477 increasing climatic debt over time has already been suggested (Bertrand *et al.*,
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51 478 2011), we provide the first evidence that the climatic debt of understory plant
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53 479 communities in response to the ongoing climate change is steadily increasing over
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55 480 time. This contrasts with a previous report showing no clear temporal signal in the

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3 481 climatic debt of herbaceous plant communities in French forests (Bertrand *et al.*,
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5 482 2016). Considering the velocity of the predicted future climate change (Loarie *et al.*,
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7 483 2009), this is an important result because it raises the question whether the lag will
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9 484 continue to steadily accumulate and approach a potential critical breakpoint for
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11 485 understory biodiversity and forest ecosystem functioning. Interestingly, the linear
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13 486 increase of the climatic debt over time is clearer and more pronounced (higher effect
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15 487 size) in the yearly dataset than in the five-year dataset. This is probably because the
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17 488 long-term increasing trend in the climatic debt was better separated from inter-
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19 489 annual variations in the yearly dataset than in the five-year dataset. Inter-annual
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21 490 variations tend to play a bigger role in blurring the long-term response of understory
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23 491 plant communities when the frequency between resurveys is lower.
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30 492 Importantly, we demonstrate that forest stand characteristics and
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32 493 anthropogenic disturbances significantly matter in modulating the climatic debt, by
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34 494 either increasing (positive effect) or mitigating (negative effect) the lag. For
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36 495 instance, both the anteriority of the last disturbance event and the cumulative
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38 496 number of anthropogenic disturbances have a negative effect on the climatic debt.
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40 497 Such findings are in accordance with recent works indicating that local disturbances
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42 498 speed up the process of thermophilization in plant communities (Stevens *et al.*,
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44 499 2015; Brice *et al.*, 2019; Zellweger *et al.*, 2020). However, it remains to be
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46 500 investigated in more details whether the thermophilization of understory plant
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48 501 communities following anthropogenic disturbances is due to warm-adapted species
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50 502 that are: (i) replacing more mesophilous species (pure turnover); (ii) increasing the
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3 503 local species pool (nestedness); or both simultaneously. For instance, Closset-Kopp
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5 504 *et al.* (2018) have shown that understory plant communities in heavily managed
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8 505 forest stands had the tendency to be richer in warm-adapted species in 2015 than in
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10 506 1970, mostly due to an increase in local species richness but no species turnover. In
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12
13 507 our study, both processes seem to occur. Indeed, while the total number of species
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15 508 per plot increases over time, suggesting a process of nestedness, the set of warm-
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18 509 adapted species that are colonizing (i.e. species gain) the plots of our monitoring
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20 510 network between 1995 and 2015 are also replacing relatively more mesic species
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22 511 that are disappearing (i.e. species loss) (*Supporting Information, App. Fig. 11*),
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25 512 suggesting a process of turnover. Not only the richness of warm-adapted species
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27 513 increases at the expense of cold-adapted species, but this effect is concomitant with
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30 514 a relative increase in the richness of light- and nitrogen-demanding species at the
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32 515 expense of species tolerating shade conditions and nitrogen-poor soils (*Supporting*
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34 516 *Information, App. Fig. 12*). **These trends further confirm the importance of local**
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36 517 **disturbances as key factors modulating the lag between macroclimatic conditions**
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38 518 **and plant community thermophilization.** Noteworthy, our results contrast with
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41 519 those from Bertrand *et al.* (2016), who reported non-significant effects of
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44 520 anthropogenic disturbances on the climatic debt of understory plant communities.
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46 521 Looking at the effects of stand characteristics, our results underline the key role of
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48
49 522 stand age and basal area to modulate the climatic debt. Older and denser (high
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51 523 basal area) forest stands provide particular microclimatic conditions (e.g. cooler
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54 524 ground-level temperatures due to increased shading and humidity conditions) that
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56 525 are likely to buffer the adverse effects of macroclimatic warming on understory
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3 526 plant communities thus providing thermal microrefugia for species persistence
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5 527 (Lenoir *et al.*, 2017; De Frenne *et al.*, 2019; Zellweger *et al.*, 2020). In contrast,
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8 528 repeated disturbances are likely to create canopy openings in forest stands,
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10 529 modifying the microhabitat and associated microclimate that strongly exacerbate
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12 530 the impact of macroclimate temperature warming for understory vegetation
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15 531 (Vanderwel & Purves, 2014; Zellweger *et al.*, 2020). This can in turn lead to drastic
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17 532 changes in the overall composition of the plant community (i.e. by increasing the
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19 533 proportion of warm-adapted species through either species turnover or an increase
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21 534 in local species richness) that will reduce the climatic debt. Paying off the climatic
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23 535 debt of understory plant communities in temperate forests implies to break off this
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25 536 microclimate stability, which can consequently reduce the microrefugia capacity of
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27 537 forest habitats for the survival of forest-dwelling species under anthropogenic
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29 538 climate change (Lenoir *et al.*, 2017). Accepting the idea that the climatic debt of
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31 539 understory plant communities might be a positive sign of local adaptation has
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33 540 significant implications on the concept of climatic debt itself, which might be
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35 541 interpreted as a macroclimatic debt but not a microclimatic debt.
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42 542 Contrary to our initial expectation that large herbivores should contribute to
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44 543 the climatic debt by further increasing the lag in the response of understory plant
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46 544 communities to macroclimate warming, we found no difference in the observed
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48 545 climatic debt between outside and inside the fenced area. This suggests that the
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50 546 climatic debt generated by the buffering effect of microclimate in the understory
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52 547 may mostly stem from the canopy layer and independently from the shrub layer, as
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3 548 large herbivores are mostly impacting woody species from the understory shrub
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5 549 layer (Olofsson *et al.*, 2009; Boulanger *et al.*, 2018). The indirect effects of herbivores
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8 550 on vegetation responses to climate warming can be highly dependent on the
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10 551 ecological context, as pointed out by Vuorinen *et al.*, (2020).

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13 552 Together with previous studies, our results show that the climatic debt in
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15 553 understory plant communities seem to be much more pronounced in situations
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17 554 where temperature conditions were warmer during the period preceding the
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19 555 baseline surveys (Bertrand *et al.*, 2016), such as in the lowlands (Bertrand *et al.*,
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21 556 2011). However, the fact that warmer baseline conditions increase the climatic debt
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23 557 of understory plant communities could also stem from a bias towards an
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25 558 underestimation of CTI values in communities where immigrating species can only
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27 559 come from even warmer regions likely outside the calibration range used to compute
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29 560 the CTI values. This could therefore lead to a systematic overestimation of the
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31 561 observed climatic debt in the warmest part of the study area. This hypothesis is
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33 562 supported by the extreme values observed in the distribution of indicator values
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35 563 (IVs) from the EcoPlant database (*Supporting Information App. Fig. 5*), which may
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37 564 indicate that the model calibration range is too limited and should be extended to
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39 565 other environmental conditions (i.e. here, the Mediterranean regions to capture the
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41 566 pool of immigrating species coming from for warmer conditions). This potential bias
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43 567 supports general recommendations to take into account existing differences in
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45 568 sensitivity between species pools when assessing temporal changes in CTI values
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47 569 (Burrows *et al.*, 2019; Williams *et al.*, 2020). More data on species IVs, either expert-

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3 570 based or biogeographically-derived IVs, are needed from warmer regions to improve
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5 571 estimates of CTI values in the current context of global warming.
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9 572 Conclusion

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12 573 This study shows that the thermophilization of understory plant communities in
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14 574 French forests continued during the last two decades with rapid but insufficient
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16 575 rates to track the velocity of current climate warming, leading to a steadily increase
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18 576 in the climatic debt. Additionally, we report that forest stand structure and
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20 577 anthropogenic disturbances can be modulated to increase or decrease the climatic
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22 578 debt. For instance, the positive effect of denser and older canopy layers on forest
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24 579 microclimate dynamics could inflate the climatic debt of understory plant
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26 580 communities and provide more time for understory plant communities to locally
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28 581 adapt. However, it remains uncertain how big the climatic debt can grow over time
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30 582 before a tipping point is reached such that the climatic debt will suddenly be paid
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32 583 off. For instance, repeated drought events leading to extensive tree dieback and
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34 584 massive crown defoliation could exceed this tipping point by suddenly recoupling the
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36 585 understory layer with macroclimatic conditions prevailing outside forests. Such a
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38 586 quick recovery of the climatic debt will have drastic consequences on forest
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40 587 biodiversity and ecosystem functioning.
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For Peer Review

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3 **792 Data Accessibility Statement**
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7 793 Datasets on CTI values are provided in Supporting Information, and will be
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9 794 archived in an appropriate public repository after the process of review and
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11 795 acceptance of the manuscript.
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For Peer Review

797 **Figures**

798 *List and captions*

799 **Figure 1.**

800 Workflow implemented in the study. The 102 plots of the RENEFOFOR network are
801 mapped, and the two datasets used in our analyses are represented in color (in red
802 and blue for the five-year and yearly datasets, respectively). Analyses of temporal
803 trends in mean annual temperature (MAT) and the community temperature index
804 (CTI) and factors contributing to the lag between MAT and CTI (MAT-CTI) are
805 conducted on the two datasets separately. For more details, see the Materials and
806 Methods section.

807 **Figure 2.**

808 Temporal trends for mean annual temperature (MAT) and the community
809 temperature index (CTI) in (a) the five-year dataset from 1995 to 2015 and (b) the
810 yearly dataset from 1995 to 2017. Linear trends (dashed lines) with standard errors
811 (ribbons) of estimated MAT or CTI values are shown. For CTI, the values for
812 enclosure or enclosure are plotted separately. Observed values for temperatures
813 (MAT or CTI) are represented with their associated standard errors and symbol
814 sizes are proportional to sample size (number of plots).

815 **Figure 3.**

816 Coefficient estimates and 95% confidence intervals extracted from linear mixed-
817 effects models testing the relative contribution of several potential abiotic and biotic
818 determinants on the magnitude and direction of the lag between mean annual

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3 819 temperature (MAT) and the community temperature index (CTI) values in (a) the
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5 820 five-year dataset and (b) yearly dataset. Points (with 95% confidence intervals)
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8 821 represent the standardized mean coefficients averaged from the selected models (Δ
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10 822 $AICc < 2$) in the model-averaging procedure. Colors show the magnitude and
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12 823 significance of effects (red: significant amplification of the lag; blue: significant
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14 824 mitigation of the lag; light grey: non-significant).

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18 825 **Figure 4.**

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20 826 Plots of partial residuals illustrating the contribution of three factors in explaining
21
22 827 the magnitude and direction of the lag between mean annual temperature (MAT)
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24 828 and the community temperature index (CTI) for the yearly dataset. These plots
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26 829 indicate the effects of each of the three factors when all others factors in the model
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28 830 are accounted for and set to their mean value for quantitative variables. Qualitative
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30 831 variables were set to deciduous stands and to outside the fence area here. The
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32 832 factors (a) 'Years', (b) 'Stand Basal Area' and (c) 'Stand Age in 1995' were extracted
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34 833 from the best model (in the model-averaging procedure) explaining the lagged
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36 834 responses of forest plant communities in the yearly dataset. Solid lines and ribbons
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39 835 represent the linear trend and associated standard errors, respectively.
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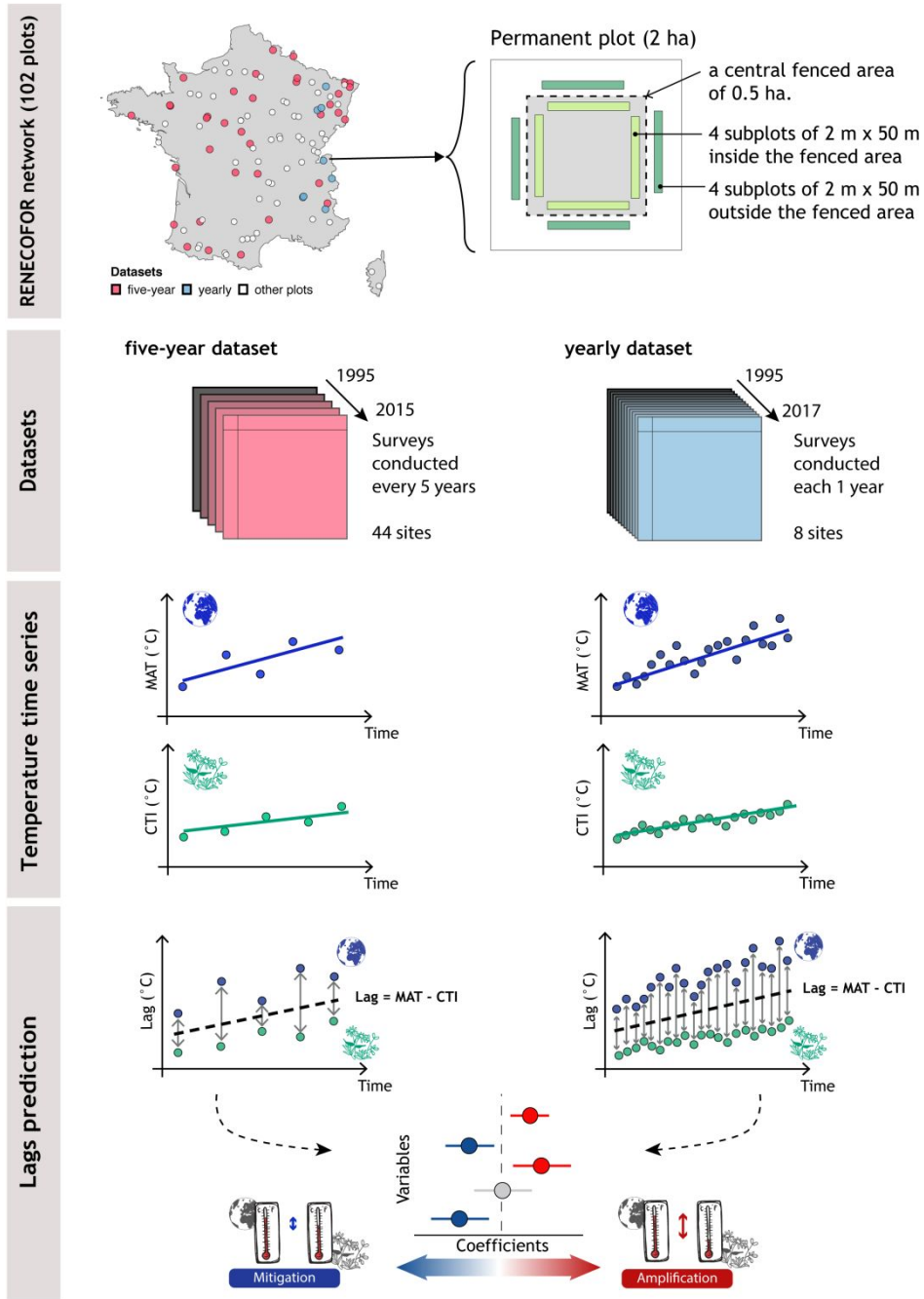


Figure 1.

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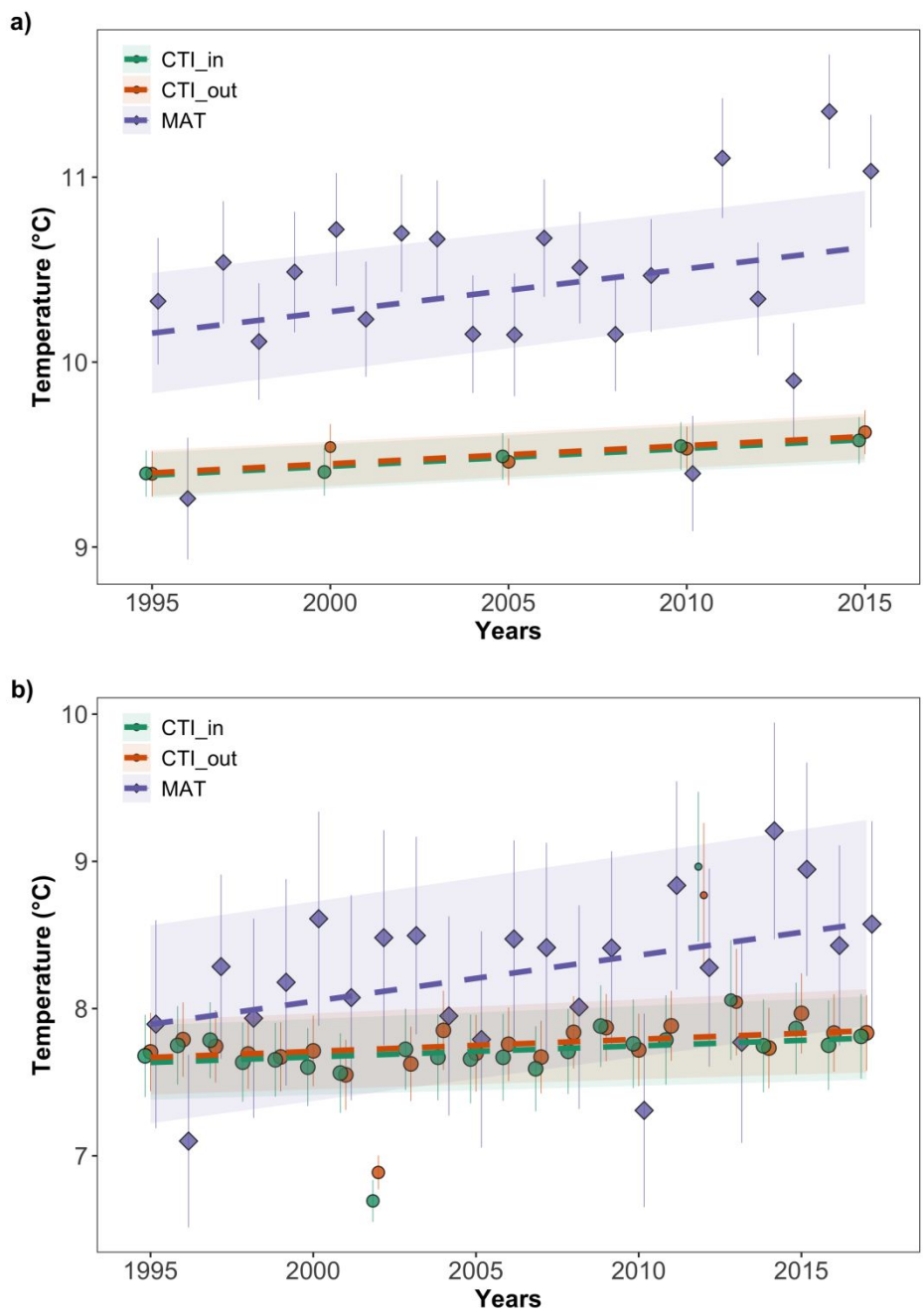


Figure 2.

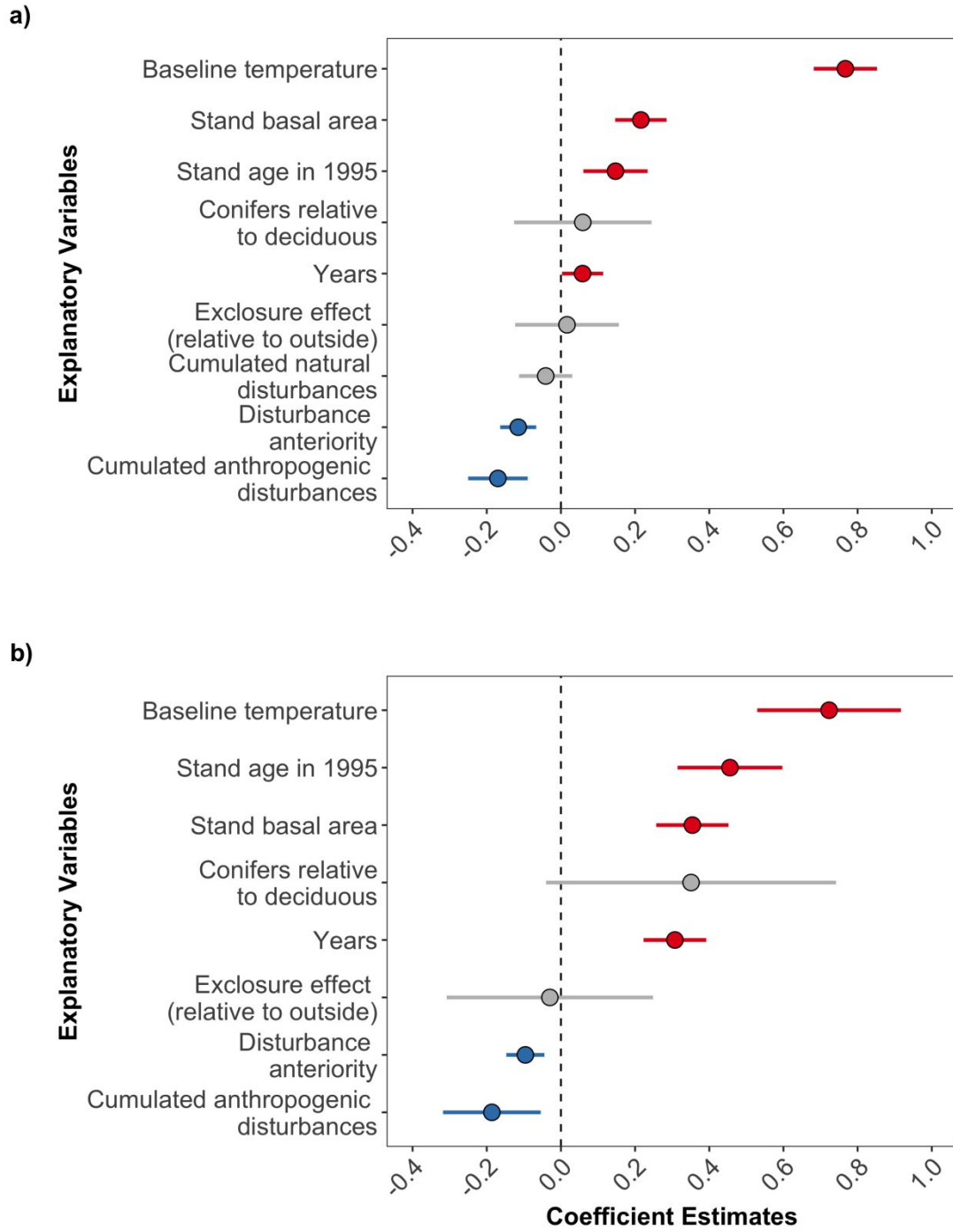
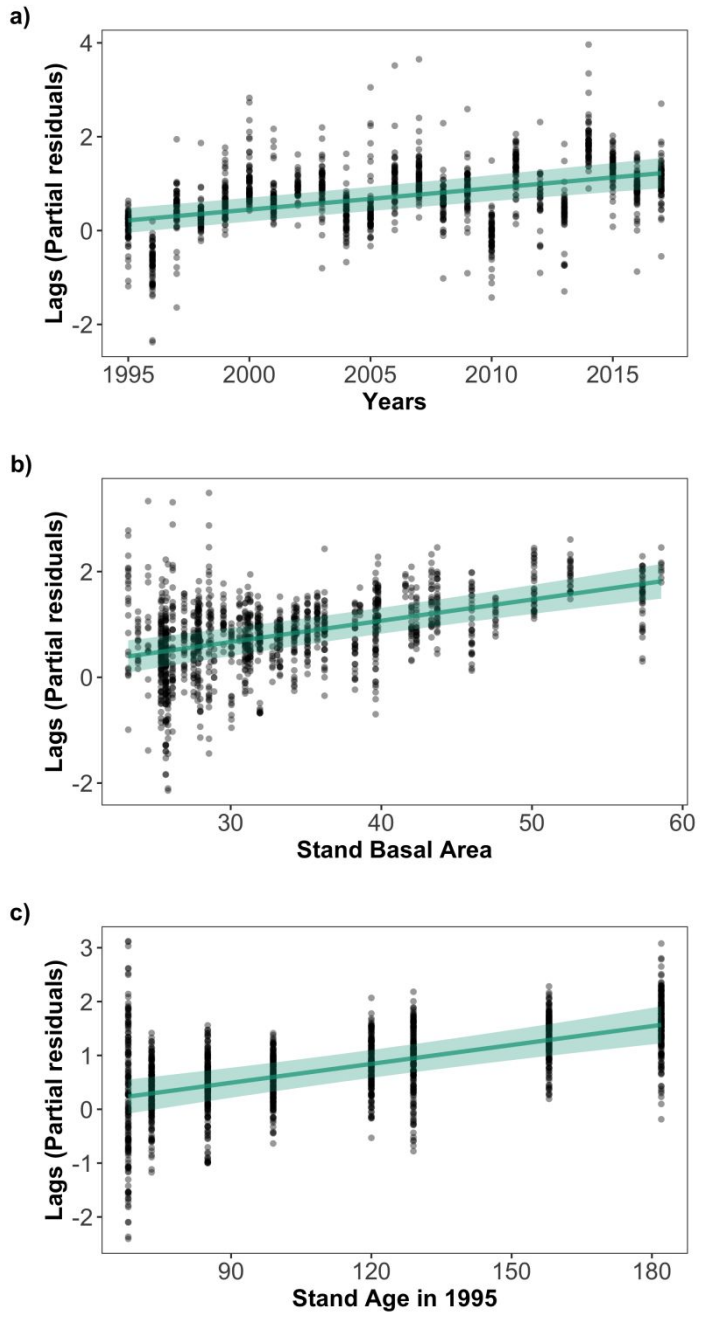


Figure 3.



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Figure 4.

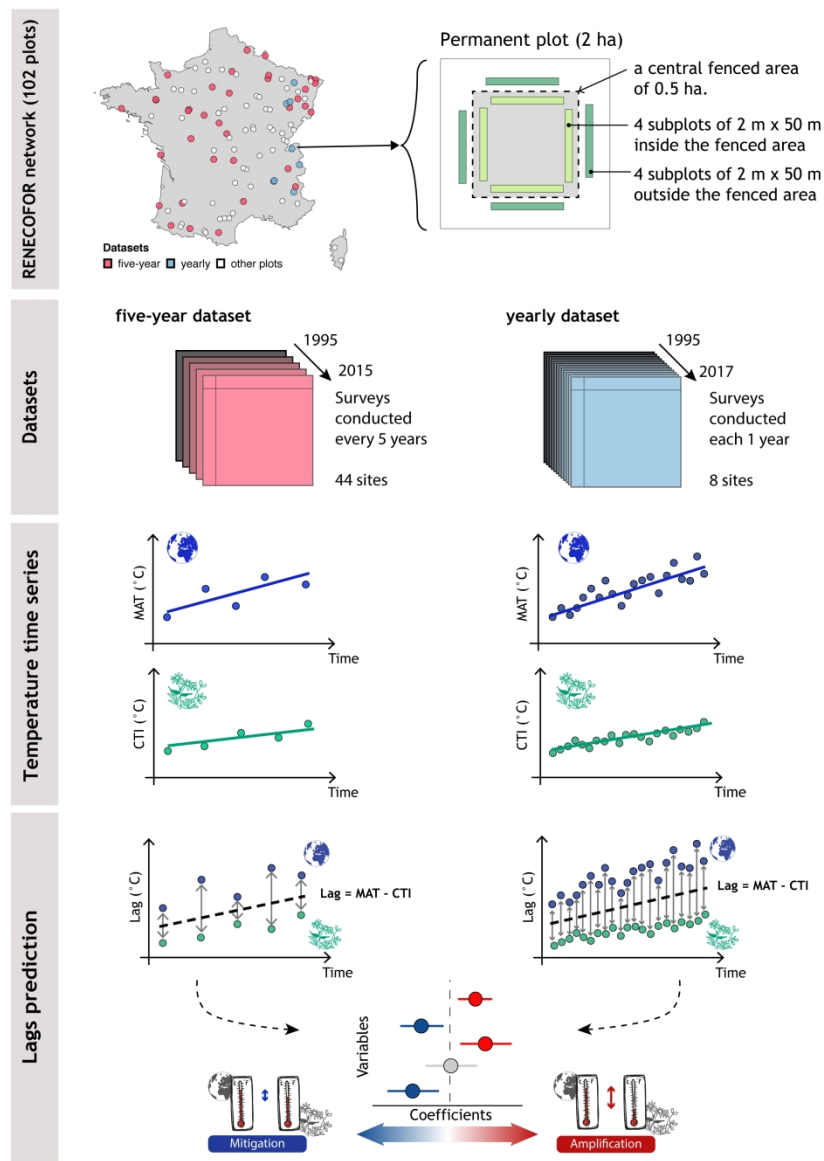


Figure 1. Workflow implemented in the study. The 102 plots of the RENEFOR network are mapped, and the two datasets used in our analyses are represented in color (in red and blue for the five-year and yearly datasets, respectively). Analyses of temporal trends in mean annual temperature (MAT) and the community temperature index (CTI) and factors contributing to the lag between MAT and CTI (MAT-CTI) are conducted on the two datasets separately. For more details, see the Materials and Methods section.

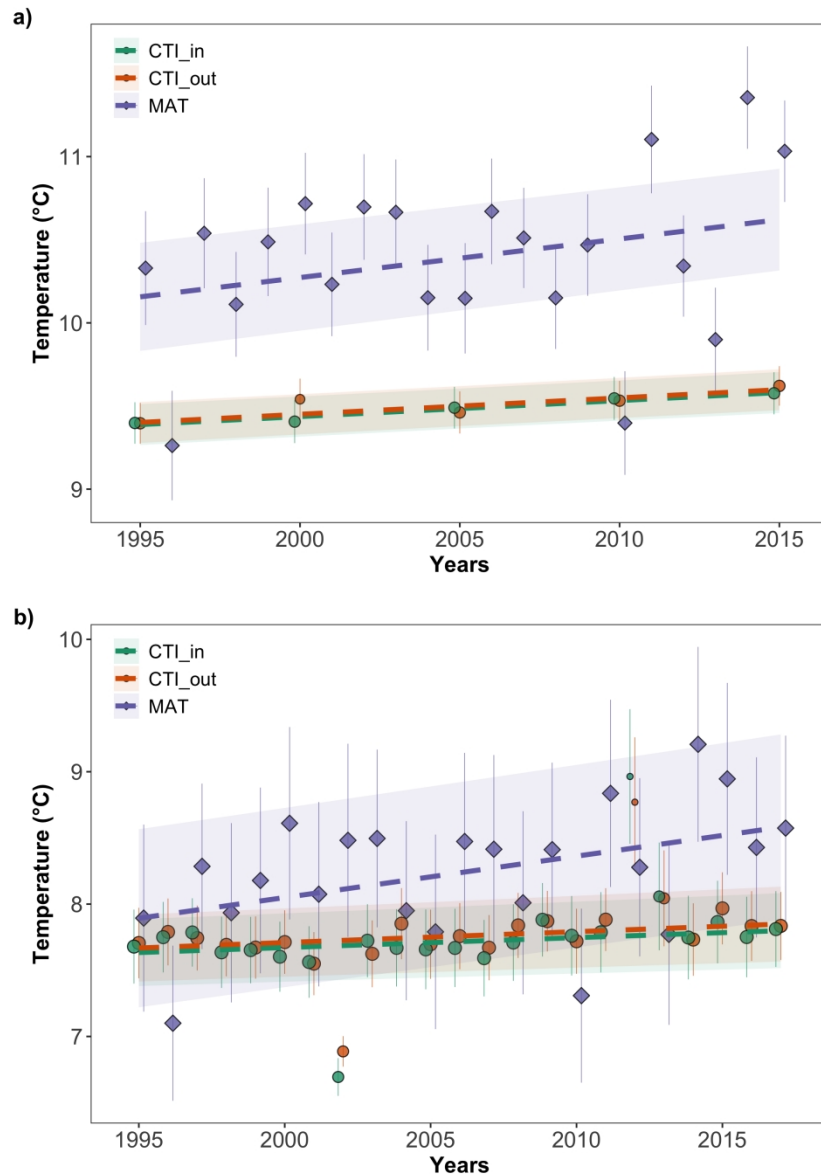


Figure 2. Temporal trends for mean annual temperature (MAT) and the community temperature index (CTI) in (a) the five-year dataset from 1995 to 2015 and (b) the yearly dataset from 1995 to 2017. Linear trends (dashed lines) with standard errors (ribbons) of estimated MAT or CTI are shown. For CTI, the values for enclosure or enclosure are plotted separately. Observed values for temperatures (MAT or CTI) are represented with their associated standard errors and symbol sizes are proportional to sample size (number of plots).

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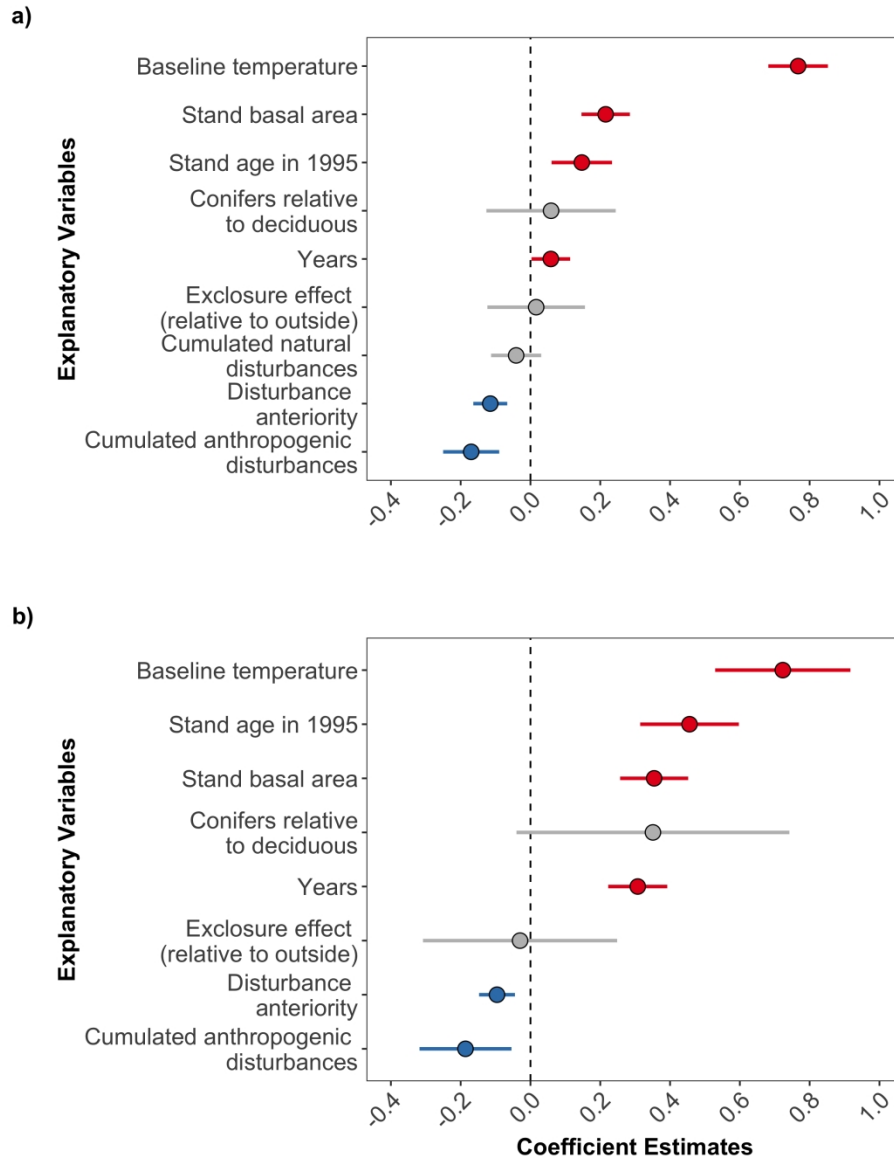


Figure 3. Coefficient estimates and 95% confidence intervals extracted from linear mixed-effects models testing the relative contribution of several potential abiotic and biotic determinants on the magnitude and direction of the lag between mean annual temperature (MAT) and the community temperature index (CTI) values in (a) the five-year dataset and (b) yearly dataset. Points (with 95% confidence intervals) represent the standardized mean coefficients averaged from the selected models ($\Delta AICc < 2$) in the model-averaging procedure. Colors show the magnitude and significance of effects (red: significant amplification of the lag; blue: significant mitigation of the lag; light grey: non-significant).

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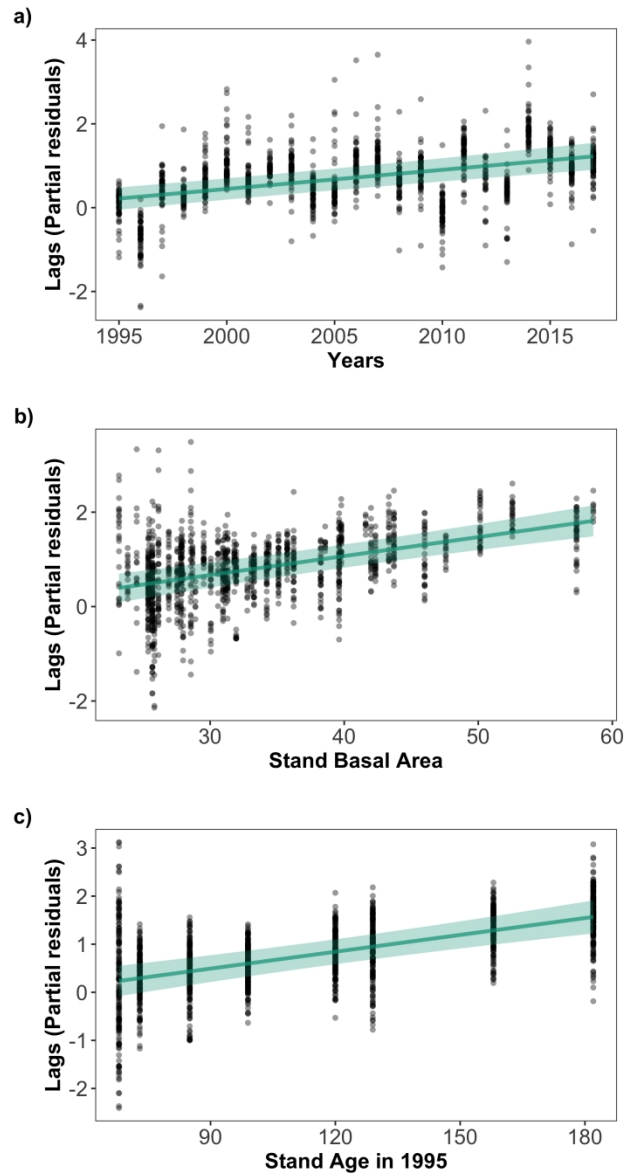


Figure 4. Plots of partial residuals illustrating the contribution of three factors in explaining the magnitude and direction of the lag between mean annual temperature (MAT) and the community temperature index (CTI) for the yearly dataset. These plots indicate the effects of each of the three factors when all others factors in the model are accounted for and set to their mean value for quantitative variables. Qualitative variables were set to deciduous stands and to outside the fence area here. The factors (a) 'Years', (b) 'Stand Basal Area' and (c) 'Stand Age in 1995' were extracted from the best model (in the model-averaging procedure) explaining the lagged responses of forest plant communities in the yearly dataset. Solid lines and ribbons represent the linear trend and associated standard errors, respectively.

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Supplementary Information

Title:

1. **The climatic debt is growing in the understory of temperate forests: stand characteristics matter**
2. **Running title: Explaining** the climatic debt of temperate forests

List of appendices (figures and tables):

1. **App. Fig. 1** | Location of the monitored plots throughout France and the time-sequence of resurveys for each plot.
2. **App. Fig. 2** | Comparison between different dataset sources for macroclimate temperature time series.
3. **App. Fig. 3** | Trends in mean annual temperatures anomalies from 1958 to 2017 across the 44 study plots.
4. **App. Fig. 4** | Construction of the Community Temperature Indices (CTIs) and the transfer function.
5. **App. Fig. 5** | Information used to construct the transfer function for calculating CTI values.

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3 17 6. **App. Fig. 6** | Illustration of the indices created to account for disturbance and
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5 18 forest management.
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9 19 7. **App. Fig. 7** | Plots of disturbance and forest management indices with data
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11 20 from each studied plot.
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14 21 8. **App. Fig. 8** | Correlation matrix plots for explanatory variables used in our
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16 22 models.
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20 23 9. **App. Fig. 9** | Partial residuals plots for variables explaining lags in the best
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22 24 model in the five-year dataset.
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25 25 10. **App. Fig. 10** | Partial residuals plots for variables explaining lags in the best
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27 26 model in the yearly dataset.
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31 27 11. **App. Fig. 11** | Average of species richness over time (a), number of species
32
33 28 gained or lost between survey years (b), and mean of IV for Temperature over
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35 29 time in group of species gained or lost between survey years (c).
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39 30 12. **App. Fig. 12** | Trends over time of species richness within each class of IV for
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41 31 Temperature, Light and Nitrogen.
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45 32 13. **App. Table 1** | Informations on sites characteristics.
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48 33 14. **App. Table 2** | List of 751 forest species found in the herbaceous layer in our
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50 34 study.

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3 35 15. **App. Tables 3 & 4** | Results of the model-averaging procedures and selected
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5 36 models.

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8 37 16. **App. Table 5** | Review of some scientific publications studying the
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10 38 thermophilization rates (expressed in °C/decade) in different ecosystems and
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12 39 taxonomic groups.
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41 *Captions:*

42 **App. Figure 1.** Location of the monitored plots throughout France (a) and the time-
43 sequence plot for the repeated surveys (b). The two datasets are distinguished by
44 color (in black and light blue for the five-year dataset and yearly dataset,
45 respectively). Seasonal relevés are represented by different symbols (◦, Spring; +,
46 Summer; ×, Autumn) and grouped by year. Labels refer to the names of plots in the
47 RENECOFOR network. The baseline TerraClimate temperature conditions over the
48 1960–1990 period is used as background raster.

49 **App. Figure 2.** Comparisons between three sources of time-series for macroclimate
50 temperatures (TerraClimate, CHELSA and local meteorological stations). For
51 comparisons, only 13 sites from the RENECOFOR network were used because they
52 had local meteorological stations nearby. a) Location of the 13 sites from the
53 RENECOFOR network used for comparisons. b) Time-series of macroclimate
54 temperatures provided by TerraClimate, CHELSA, and the meteorological stations.
55 Shaded ribbon (in grey) and dotted line show the beginning of vegetation surveys in
56 the RENECOFOR monitoring program.

57 **App. Figure 3.** Trends in mean annual temperatures anomalies from 1958 to 2017 in
58 the 44 permanent plots studied. Temperature anomalies are computed for each
59 permanent plot as the difference between yearly temperatures and the mean
60 temperature over the period 1958–2017. The black line depicts a 5-year moving
61 average of MAT. Mean of temperature anomalies and standard errors are

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3 62 represented, red and blue colors correspond to positive and negative values,
4
5 63 respectively. Shaded ribbon in grey and arrow show the beginning of vegetation
6
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8 64 surveys in the RENEFOFOR monitoring program.
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11 65 **App. Figure 4.** Workflow conducted to calculate the Community Temperature
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13 66 Indices (CTIs) through the transfer function.
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17 67 **App. Figure 5.** Supporting information for the construction of Community
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19 68 Temperature Indices (CTIs) using the transfer function.
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22 69 a) Venn diagram depicting the number of taxa recorded in the CATMINAT and
23
24 70 EcoPlant databases for species indicator value of temperature. Our dataset
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26
27 71 includes a total of 877 taxa (all strata of vegetation combined).
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30 72 b) Relationship between the IVs of temperature of CATMINAT and EcoPlant at
31
32 73 the species level.
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36 74 c) Map of the sites where the NFI floristic surveys have been performed, and
37
38 75 which have been used to model the transfer function.
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41 76 d) Hexagonal binning plot between the CTIs calculated with CATMINAT and
42
43 77 EcoPlant at the community level, and the transfer function fitted to obtain CTI
44
45 78 values from CATMINAT in degrees Celsius.
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49 79 *Text details for App. Figure 5 :* To infer temperature from plant species
50
51 80 assemblages, we used an approach based on Community Temperature Indices
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53 81 (CTIs) with species Indicator Values (IVs), and a transfer function to model the
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3 82 relationship of two databases : CATMINAT (Julve, 1998) and EcoPlant (Gégout et
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5 83 al., 2005). These two databases were chosen, because CATMINAT contains almost
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7
8 84 all of species recorded in our dataset and EcoPlant, poorer in species, has the
9
10 85 advantage to allow the direct computation of CTI values in degrees Celsius.
11
12 86 CATMINAT (Julve, 1998) is based on expert knowledge similarly to Ellenberg IVs
13
14
15 87 (Ellenberg et al., 1992), with temperature preferences of plant species coded along
16
17 88 an ordinal scale from cold (1) to warm (9) environments. While the CATMINAT
18
19
20 89 database contains almost all of the species sampled in the RENECOFOR monitoring
21
22 90 program (858 out of the 877 species recorded within all strata of vegetation; **App.**
23
24 91 **Fig. 5a**), CTI values estimated with these species IVs are unitless and direct
25
26 92 comparisons with macroclimatic temperatures are not possible. On the other hand,
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28
29 93 EcoPlant allows the computation of CTI values in degrees Celsius. EcoPlant is a
30
31 94 phyto-ecological database which provides information about ecological optimum for
32
33 95 key variables of forest plant species based on their distribution over the French
34
35 96 territory. In EcoPlant, species IV for temperature are expressed in degrees Celsius
36
37 97 as they are estimated using logistic regression models based on climatic data **from**
38
39 98 **AURELHY dataset** for the historical period (1961–1990). Nevertheless, the EcoPlant
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41
42 99 database covers much less species from our dataset (396 out of 877 species).
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46 100 Therefore, we calibrated a transfer function to transform the unitless CTI values
47
48 101 from the CATMINAT database into a CTI value expressed in degrees Celsius. By
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51 102 regressing CTI values from EcoPlant against CTI values from CATMINAT, we can
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54 103 obtain predicted CTI values from CATMINAT expressed in degrees Celsius (see
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3 104 Lenoir et al., 2013 for a similar approach). To improve the quality of the fit, we used
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5 105 the community level and not directly the species level **App. Fig. 5b-d**).

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8 106 To construct the transfer function, we processed as follows:

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11 107 1. We used an independent dataset of floristic surveys gathered from the French
12
13 108 National Forest Inventory (NFI) for the 2005–2016 period to calibrate our
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15 109 transfer function. Homogenization procedures were performed to avoid
16
17 110 taxonomic and nomenclatural issues between our dataset, the NFI data and the
18
19 111 IV databases. We selected only the floristic surveys from NFI performed during
20
21 112 the growing season and surveys recording at least 2 species. This yielded a total
22
23 113 of 45 379 surveys covering the whole French territory (**App. Fig. 5c**).
- 24
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26 114 2. Then, we computed the CTI values for each floristic survey both with
27
28 115 CATMINAT and EcoPlant, using species presence/absence to give the same
29
30 116 weight to common and rare species. The relationship between CTI values from
31
32 117 the two IV datasets was also analyzed with species abundance and results were
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34 118 similar (Pearson' correlation between occurrence and abundance data = 0.88, $t =$
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36 119 386, $df = 45\ 377$, $P < 0.001$).
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39 120 3. To model the relationship between CTI values from CATMINAT and CTI from
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41 121 EcoPlant, we used a Generalized Additive Model (GAM) with a
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43 122 calibration/training procedure to select the best smoothness parameter λ . The
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45 123 dataset was split into a training set and a test set (i.e. proportion of 70/30,
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3 124 respectively). The final GAM was adjusted with $\lambda = 6$ (model with the lowest
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5 125 RMSE) and it explained 72.9% of the total deviance (**App. Fig. 5d**).

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9 126 **App. Figure 6.** Illustrative examples of the indices created to account for disturbance
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11 127 and forest management. Two cases are presented : a) A site with two anthropogenic
12
13 128 events that occurred during several vegetation surveys ; and b) A site with one
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16 129 anthropogenic event and two natural events that occurred during several vegetation
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18 130 surveys. For survey year, we recorded informations about : (i) Cumulated disturb.,
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20 131 as the cumulative number of disturbance known in a forest stand since the plot
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22 132 establishment, whatever its nature (anthropogenic or natural event); (ii) the Type of
23
24 133 last event (anthropogenic or natural event); (iii) Anteriority, as the anteriority in
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26 134 year of the last disturbance whatever its nature; (iv) the Cumulated disturb. of
27
28 135 anthropogenic events : (v) the Cumulated disturb. of natural events. Only the
29
30 136 columns filled in grey were used in our analyses. Anthropogenic events include
31
32 137 mainly silvicultural operations such as thinning, logging, tree extraction, cleaning
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34 138 brush and forestry machine passage. Natural events include for example, windfalls
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36 139 and tree uprooting after a storm event.
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43 140 **App. Figure 7.** Cumulative number of disturbance events along time for each studied
44
45 141 plot. The type of disturbance is distinguished by different symbols, and the
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47 142 anteriority (in years) of the last disturbance is shown by a color scale.
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51 143 **App. Figure 8.** Correlation matrix plots between explanatory variables used in our
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53 144 analyses, showing scatterplots, density curves and Pearson correlation coefficients
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55 145 for the explanatory variables tested in the models. 'lags': difference MAT – CTI;
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3 146 'Years': Year of survey; 'Baseline T°C': the baseline temperature conditions during
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5 147 the 1961–1990 period; 'Age in 1995': Age of forest stand in 1995 (year of the first
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7 148 field campaign); 'Disturb. anterior': Anteriority (in years) of the last disturbance
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9 149 which occurred in the plot ; 'Cum.anthr.disturb.': cumulative sum of the number of
10
11 150 annual anthropogenic disturbances; 'Cum.nat.disturb.': cumulative sum of the
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13 151 number of natural disturbances ; 'Basal area': forest stand basal area. See Materials
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15 152 and methods for further details.

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21 153 **App. Figure 9.** Partial residuals plots for factors contributing to lags in the best
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23 154 model selected by the model averaging procedure in the five-year dataset. Partial
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25 155 residuals are the residuals that remain after removing the effect of all other
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27 156 covariates in the model.

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31 157 **App. Figure 10.** Partial residuals plots for factors contributing to lags in the best
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33 158 model selected by the model averaging procedure in the yearly dataset. Partial
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35 159 residuals are the residuals that remain after removing the effect of all other
36
37 160 covariates in the model.

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41 161 **App. Figure 11.** Species richness changes over time (a), Number of species gained or
42
43 162 lost between survey years (b), and Temporal changes over time for averages of IVs
44
45 163 for Temperature within the group of species gained or lost between survey years (c).
46
47 164 Points and error bars correspond to the average of values between the 44 studied
48
49 165 sites and the standard errors, respectively. For the temporal changes, we compared
50
51 166 the species lists between the first survey in 1995 and the later surveys of each plot
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54 167 to identify the pools of species gained and lost between each pair of surveys. In

1
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3 168 particular, these two pools are used to calculate temporal β -diversity between two
4
5 169 surveys of a given plot (Legendre, 2019). Then, we computed the average of IVs for
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8 170 Temperature within the gained and lost species.
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11 171 **App. Figure 12.** Temporal changes over time in species richness within each class of
12
13 172 IV for Temperature, Light and Nitrogen (from CATMINAT, Julve, 1998). Each class
14
15 173 of IV are detailed in the online version of CATMINAT
16
17 174 (<http://philippe.julve.pagesperso-orange.fr/catminat.htm>). Species richness per
18
19 175 classes are expressed in pourcentage of the total species richness in a given plot.
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21 176 Points correspond to the average of species richness between the 44 studied sites,
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23 177 and only significant linear regressions are displayed ($P < 0.05$).
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29 178 **App. Table 1** Informations on sites characteristics detailing the name of
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31 179 RENECOFOR plots, the dominant tree species in the forest stands, the altitude, the
32
33 180 geographical coordinates (latitude and longitude in WGS84), and the dataset(s) in
34
35 181 which they occurred (see Materials and Methods for details on the yearly or five-
36
37 182 year datasets).
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41 183 **App. Table 2** List of 751 forest species inventoried in the herbaceous layer. Species
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43 184 retained for analyses are marked with a “1” in the éponymous column.
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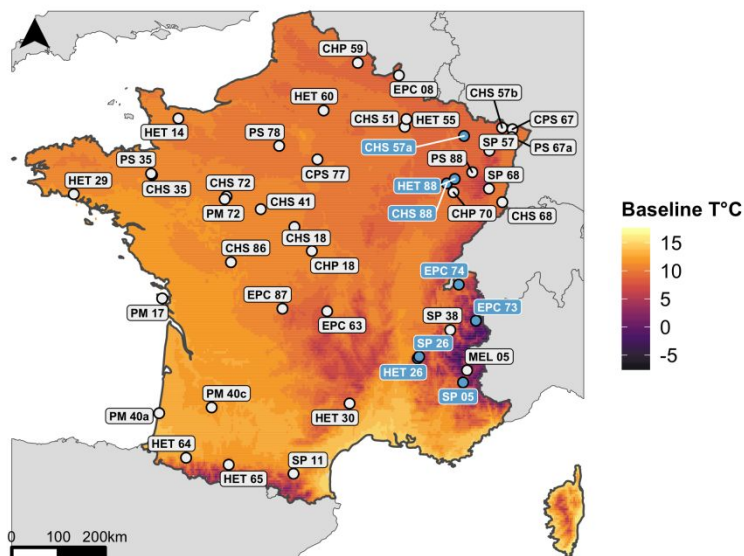
47 185 **App. Tables 3 & 4** Results of the model-averaging procedures and selected models
48
49 186 for the study of the effects of different variables on lag (difference between MAT
50
51 187 and CTI). Only the top 20 models are presented. Coefficients of variables were
52
53 188 estimated using linear mixed-effects models (LMMs including ‘plot’ and ‘nested
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3 189 subplots' as random effects) in a model-averaging procedure. All variables were
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5 190 standardized (z -score) to interpret estimates as relative effect sizes. Coefficient
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8 191 estimates for predictor variables, marginal R^2_m and conditional R^2_c are shown. R^2_m
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10 192 and R^2_c describe the variation explained by fixed effects only and variation
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13 193 explained by the fixed and random effects, respectively. Only models with ΔAIC_c
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15 194 values < 2 were used to estimate coefficients.

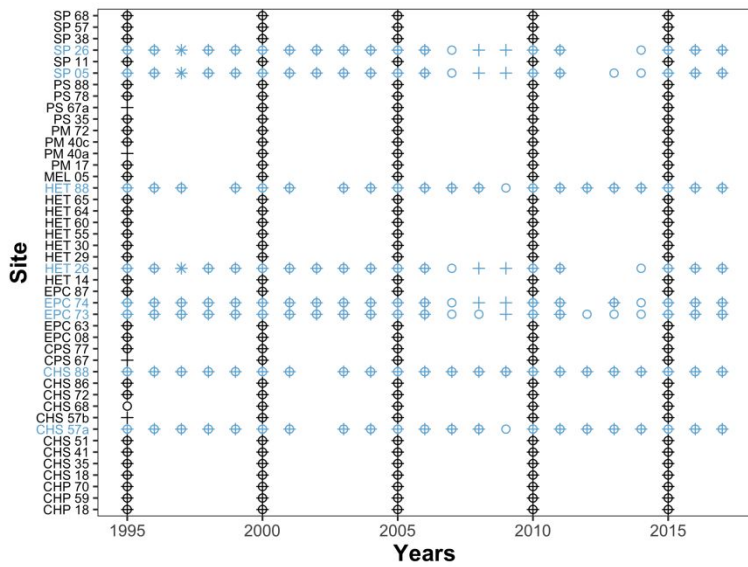
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18 195 **App. Table 5** Review of some scientific publications studying the thermophilization
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20 196 rates (expressed in $^{\circ}\text{C}/\text{decade}$) in different ecosystems and taxonomic groups.
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198 *Appendices:*

a)



b)



Sampling_period ○ Spr. + Sum. × Aut.

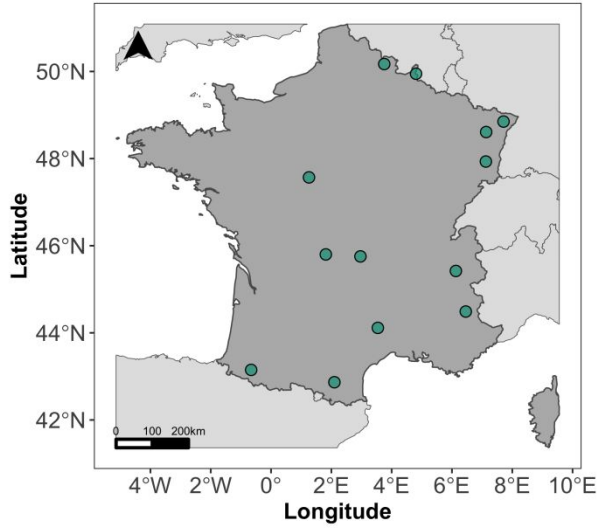
Dataset ● five-year ● yearly

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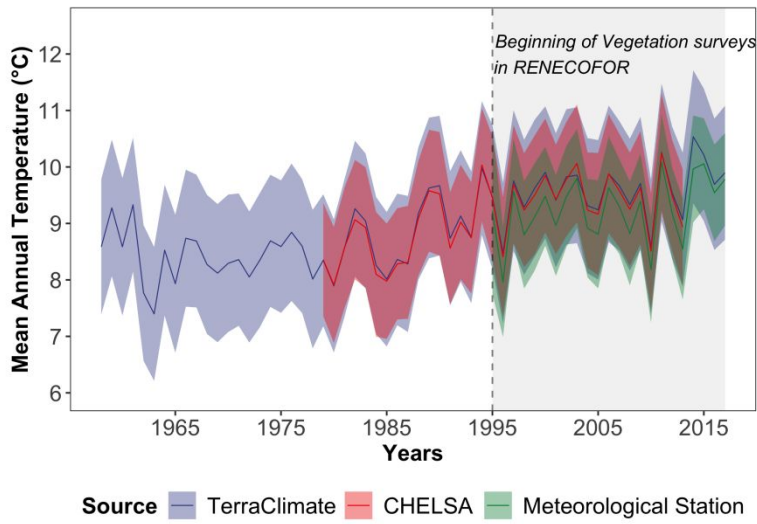
200 App. Figure 1.

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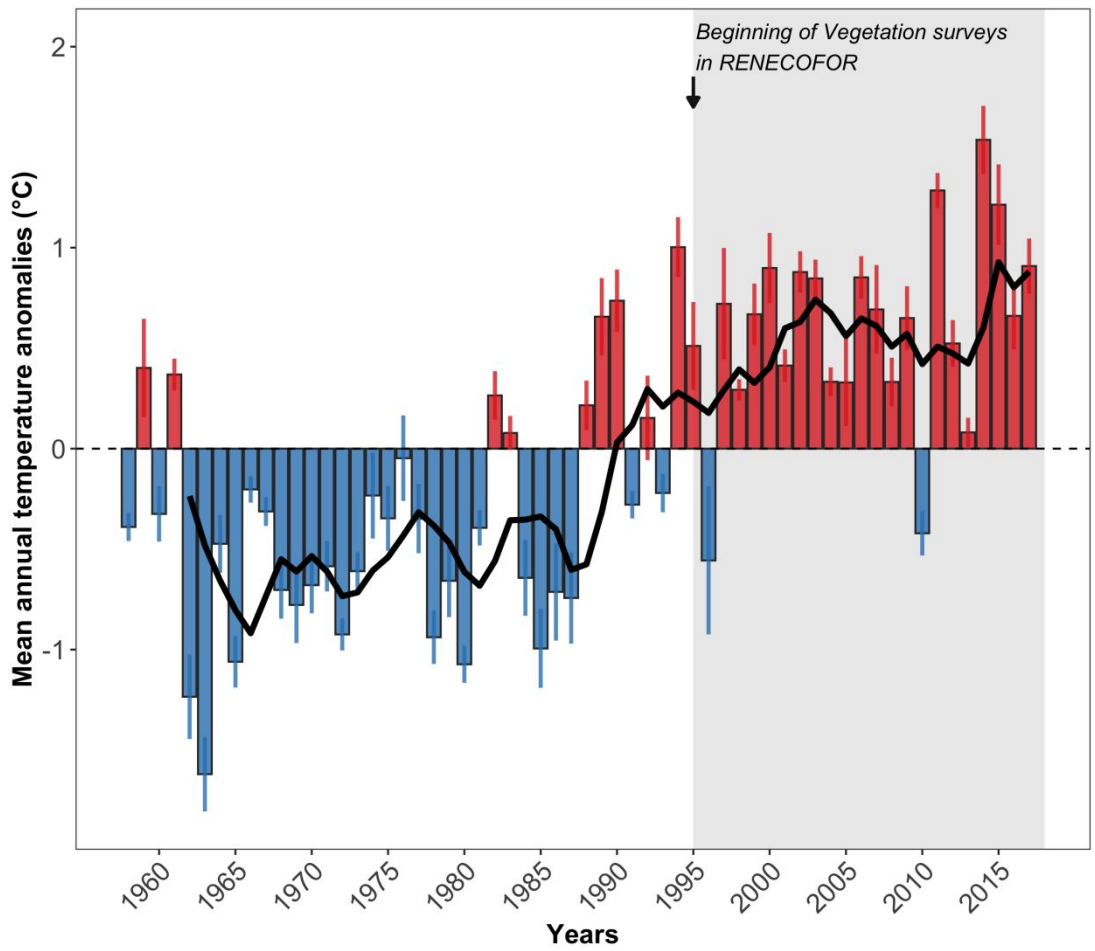
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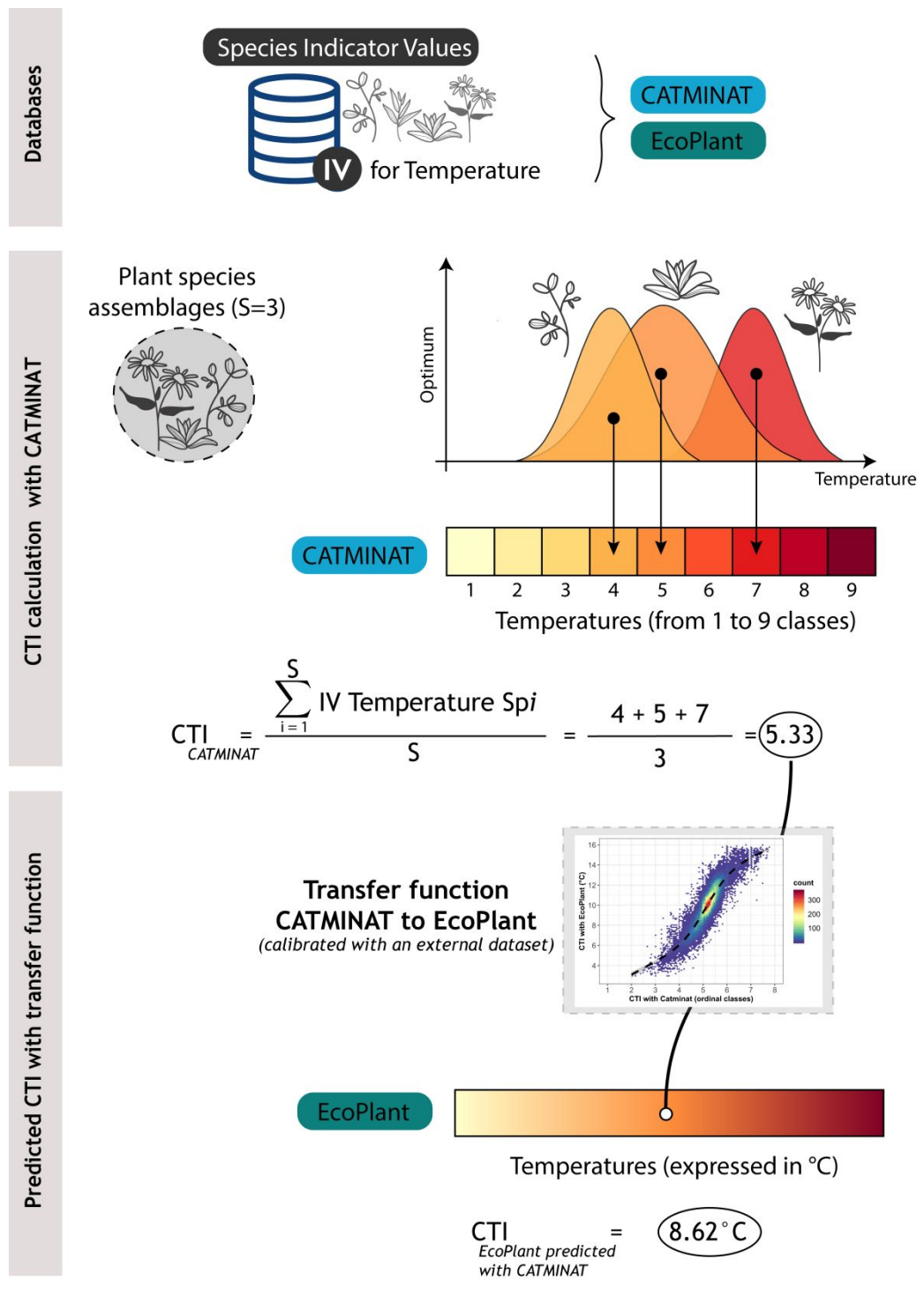
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App. Figure 2.



App. Figure 3.

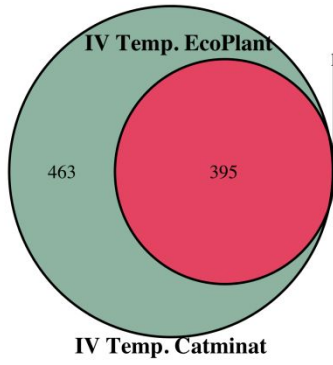


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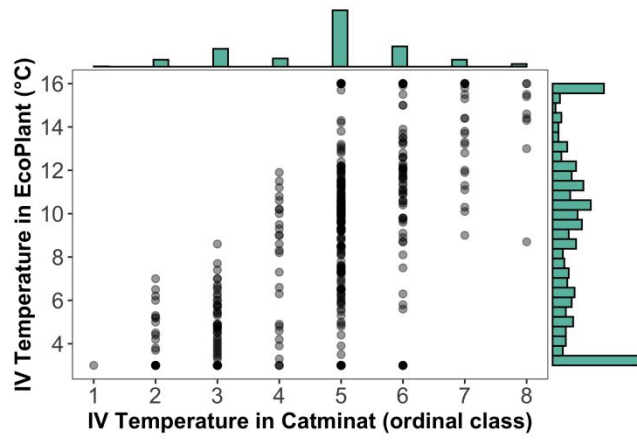
209 App. Figure 4.

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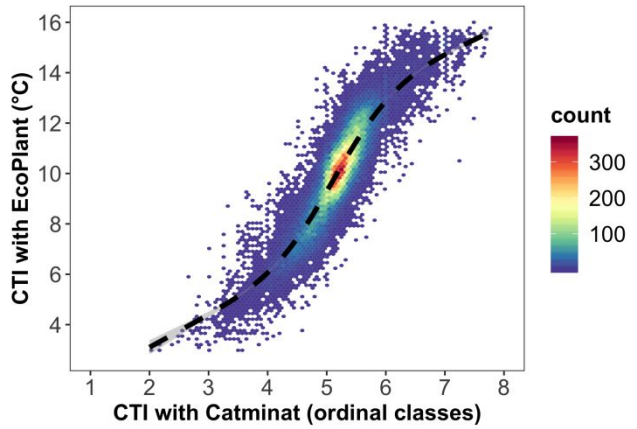
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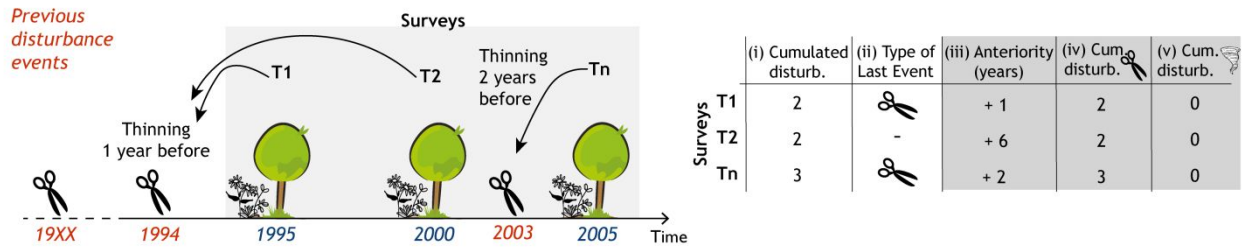
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211 **App. Figure 5.**

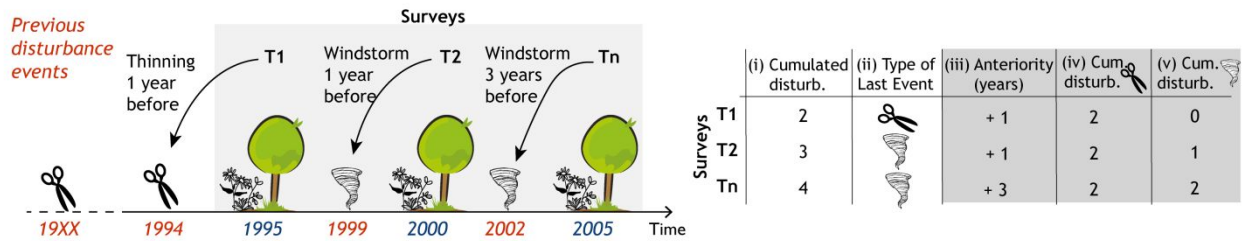
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Disturbance and Forest management indices

a) Illustrative Case for Anthropogenic events (2 events)



b) Illustrative Case for Anthropogenic and Natural events (1 and 2 events, respectively)

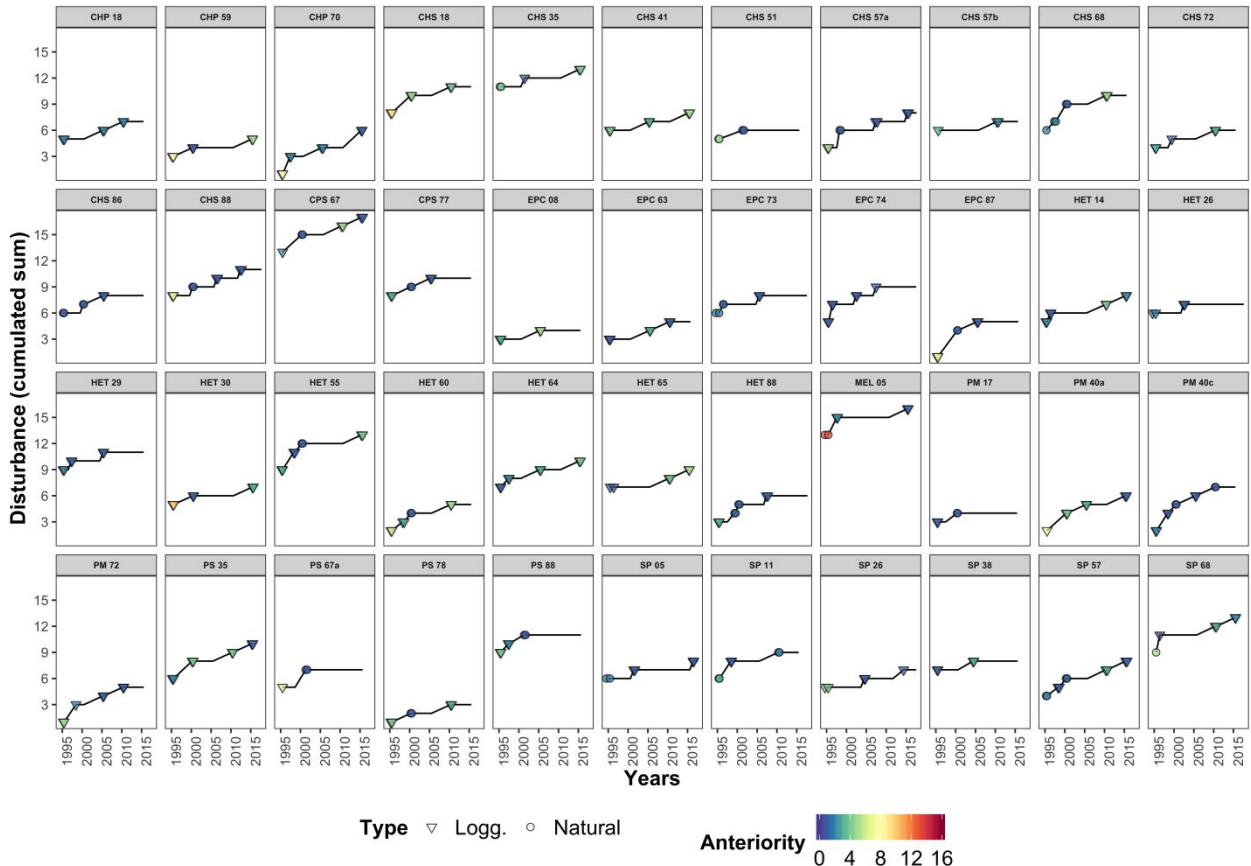


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214 App. Figure 6.

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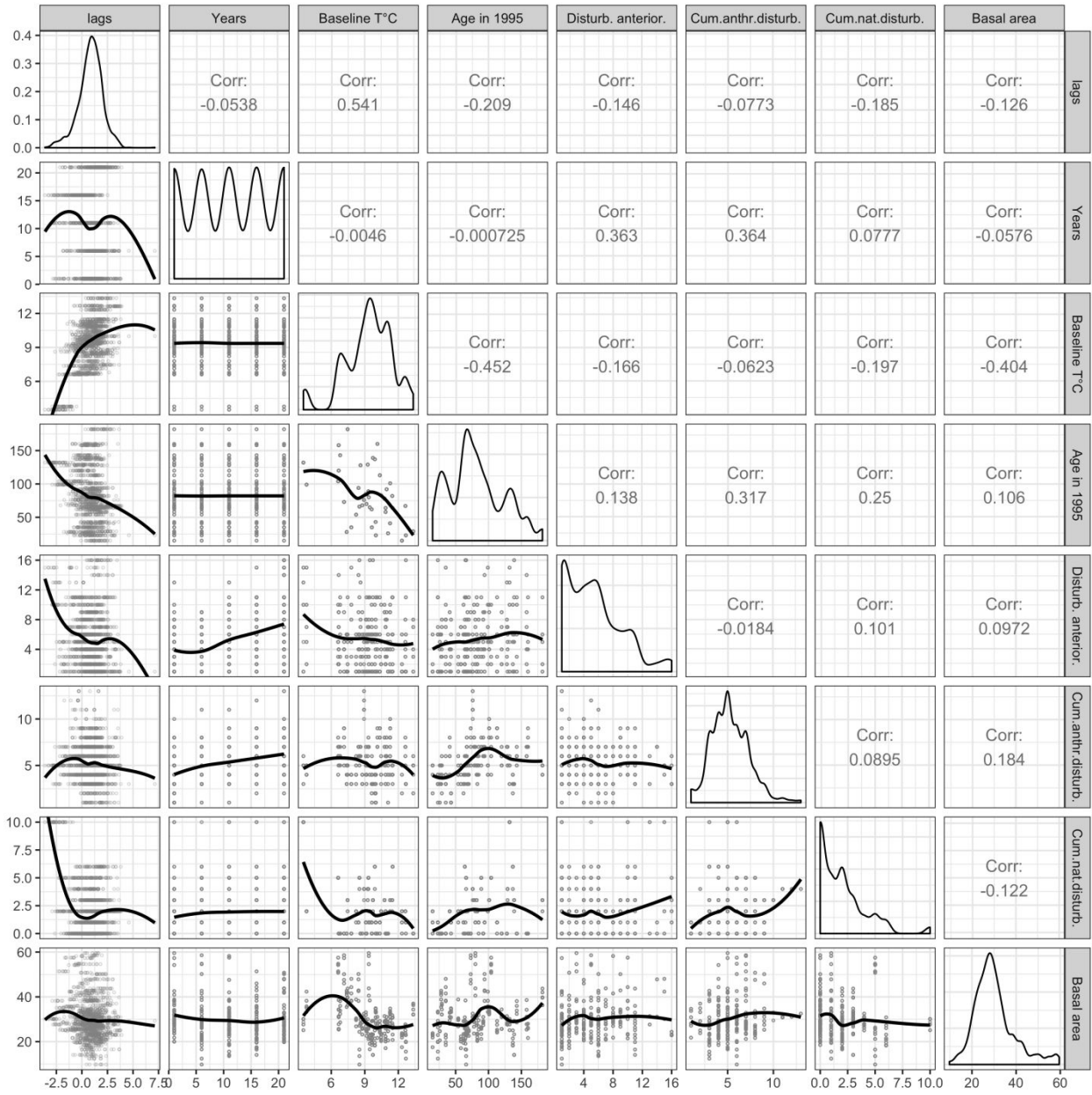
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App. Figure 7.

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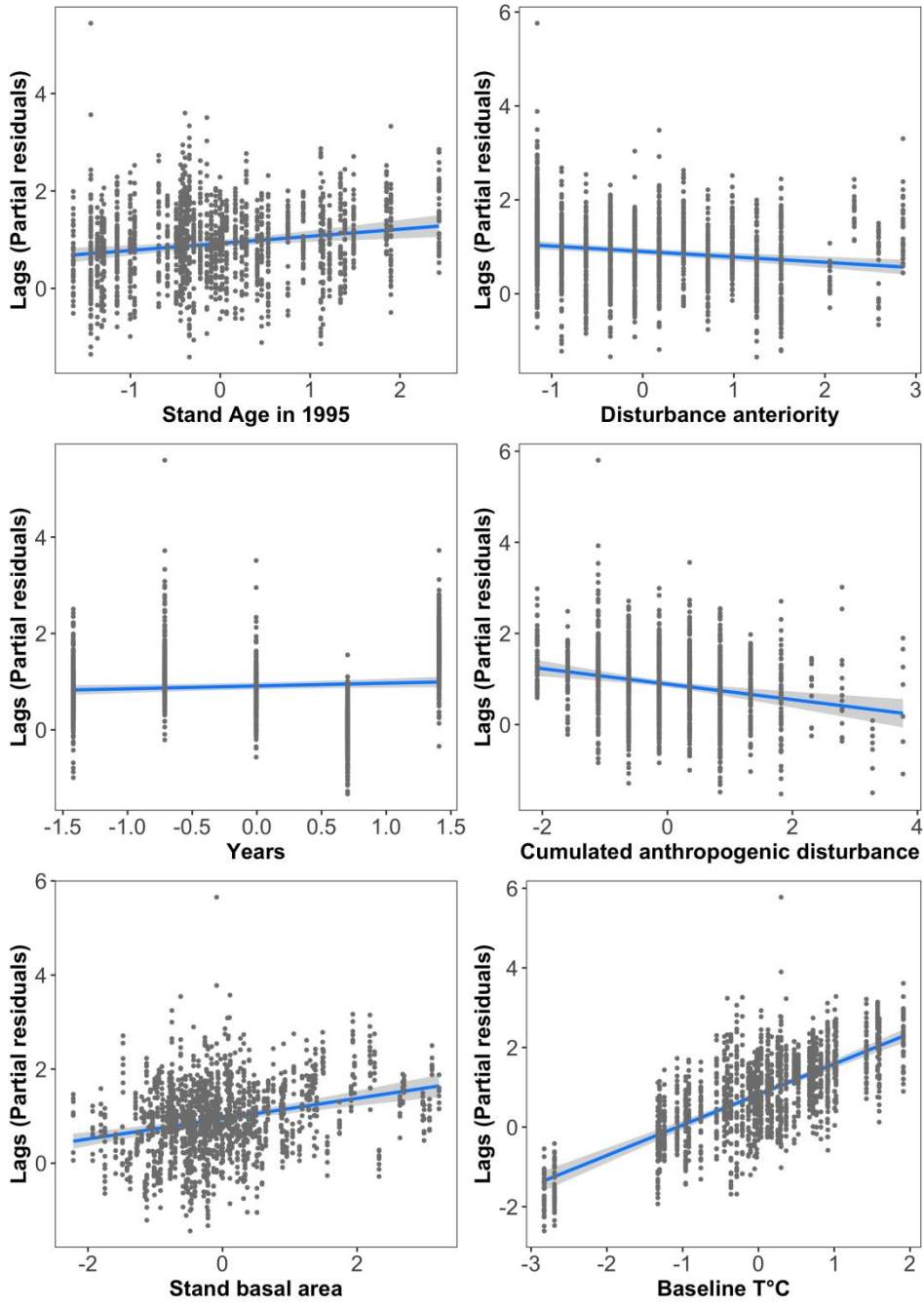
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220 App. Figure 8.

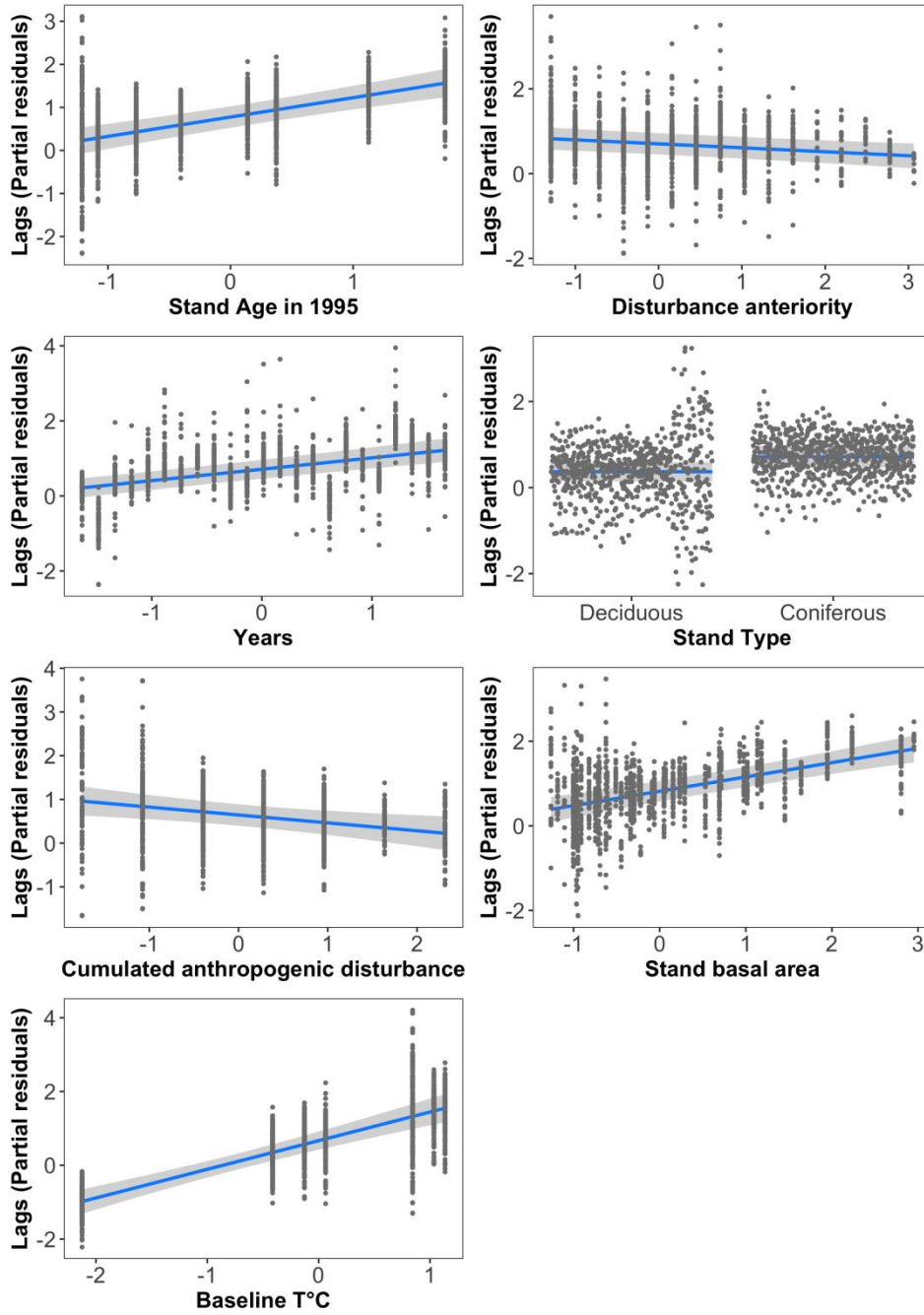
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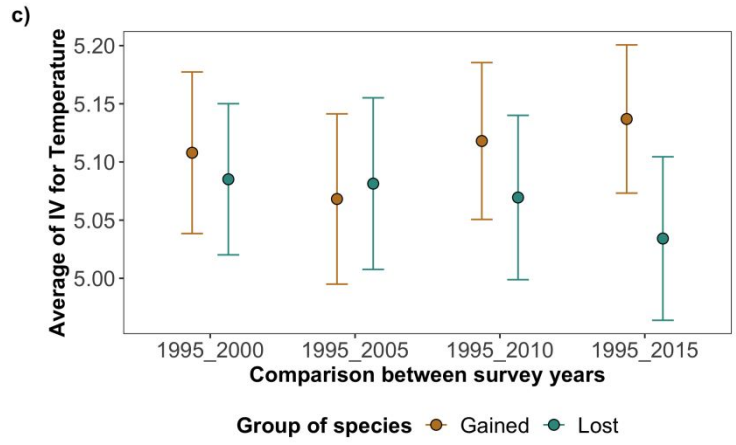
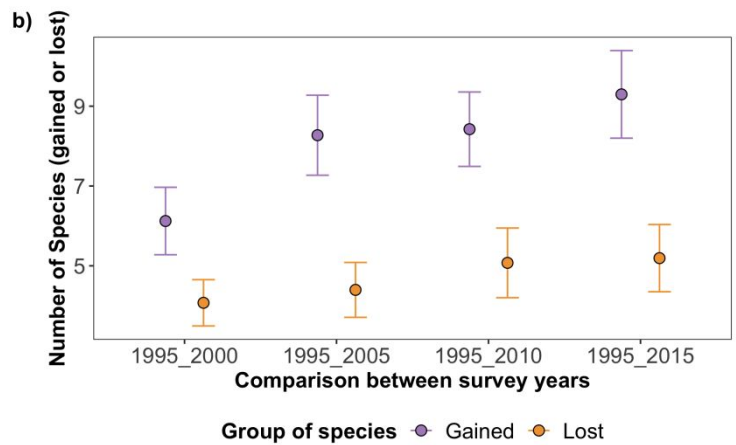
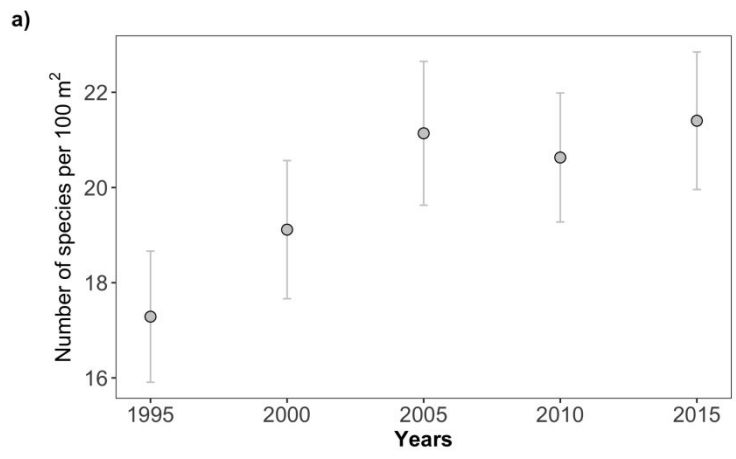
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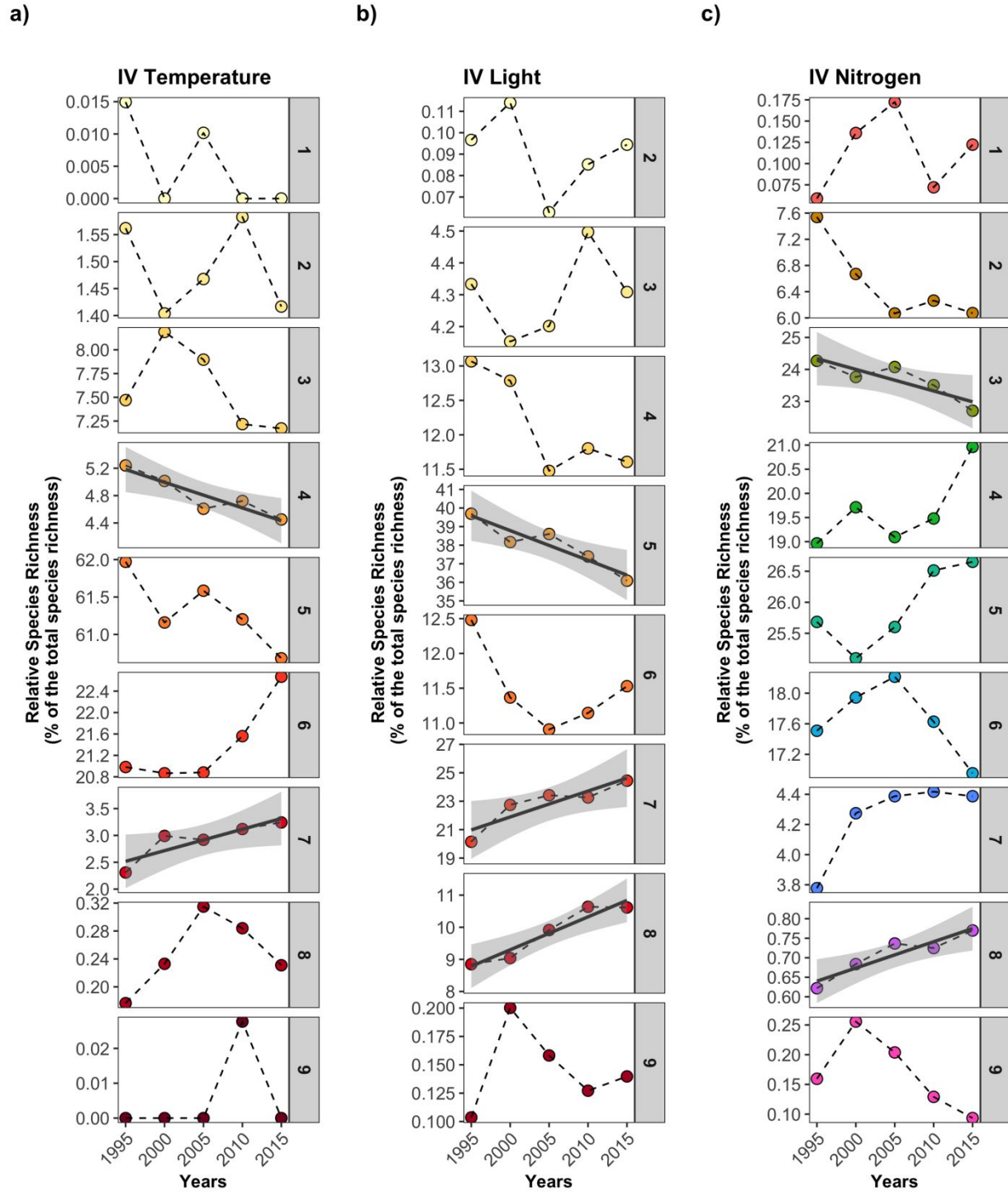
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App. Figure 11.



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232 App. Figure 12.

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234 **App. Table 1** cf. Excel file

235 **App. Table 2** cf. Excel files

236 **App. Tables 3 & 4** cf. Excel files

237 **App. Tables 5** cf. Excel files

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255 Northern Europe. *Global Change Biology*, 19(5), 1470–1481.
256 <https://doi.org/10.1111/gcb.12129>

	Site name	Dominant tree species	Altitude	Latitude_WGS84	Longitude_WGS84	Dataset(s)
1						
2						
3	CHP 18	Pedunculate oak	175	46.825	2.573	five-year
4	CHP 59	Pedunculate oak	149	50.171	3.754	five-year
5	CHP 70	Pedunculate oak	240	47.87	6.211	five-year
6						
7	CHS 18	Sessile oak	176	47.254	2.125	five-year
8	CHS 35	Sessile oak	80	48.177	-1.536	five-year
9	CHS 41	Sessile oak	127	47.569	1.259	five-year
10	CHS 51	Sessile oak	180	49.032	4.959	five-year
11	CHS 57a	Sessile oak	315	48.871	6.482	five-year; yearly
12	CHS 57b	Sessile oak	320	49.016	7.461	five-year
13						
14	CHS 68	Sessile oak	256	47.693	7.466	five-year
15	CHS 72	Sessile oak	170	47.796	0.379	five-year
16	CHS 86	Sessile oak	116	46.626	0.494	five-year
17	CHS 88	Sessile oak	330	48.026	6.039	five-year; yearly
18						
19	CPS 67	Sessile or pedunculate oa	350	48.99	7.728	five-year
20	CPS 77	Sessile or pedunculate oa	80	48.454	2.716	five-year
21	EPC 08	Norway spruce	480	49.948	4.809	five-year
22	EPC 63	Norway spruce	950	45.754	2.965	five-year
23	EPC 73	Norway spruce	1700	45.586	6.789	five-year; yearly
24	EPC 74	Norway spruce	1200	46.228	6.348	five-year; yearly
25						
26	EPC 87	Norway spruce	650	45.8	1.816	five-year
27	HET 14	Beech	90	49.182	-0.858	five-year
28	HET 26	Beech	1320	44.917	5.294	five-year; yearly
29	HET 29	Beech	50	47.836	-3.545	five-year
30	HET 30	Beech	1400	44.114	3.542	five-year
31						
32	HET 55	Beech	250	49.17	5.004	five-year
33	HET 60	Beech	138	49.324	2.875	five-year
34	HET 64	Beech	400	43.149	-0.66	five-year
35	HET 65	Beech	850	43.026	0.435	five-year
36	HET 88	Beech	400	48.106	6.244	five-year; yearly
37						
38	MEL 05	European larch	1850	44.704	6.561	five-year
39	PM 17	Maritime pine	15	45.982	-1.273	five-year
40	PM 40a	Maritime pine	27	43.942	-1.352	five-year
41	PM 40c	Maritime pine	150	44.045	-0.004	five-year
42						
43	PM 72	Maritime pine	153	47.746	0.333	five-year
44	PS 35	Scots pine	80	48.201	-1.558	five-year
45	PS 67a	Scots pine	175	48.85	7.71	five-year
46	PS 78	Scots pine	170	48.695	1.732	five-year
47	PS 88	Scots pine	500	48.225	6.695	five-year
48						
49	SP 05	Silver fir	1360	44.489	6.458	five-year; yearly
50	SP 11	Silver fir	950	42.866	2.101	five-year
51	SP 26	Silver fir	1150	44.947	5.331	five-year; yearly
52	SP 38	Silver fir	1100	45.42	6.13	five-year
53	SP 57	Silver fir	400	48.609	7.134	five-year
54	SP 68	Silver fir	680	47.933	7.124	five-year
55						
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57						
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60						

1	Species	Species retained for analyses
2		
3	<i>Abies alba</i>	1
4	<i>Abies grandis</i>	1
5	<i>Acer campestre</i>	1
6	<i>Acer platanoides</i>	1
7	<i>Acer pseudoplatanus</i>	1
8	<i>Acer sp.</i>	0
9		
10	<i>Aceras anthropophorum</i>	1
11	<i>Achillea macrophylla</i>	1
12	<i>Achillea millefolium</i>	1
13	<i>Aconitum lycoctonum</i> subsp. <i>vulparia</i>	1
14	<i>Aconitum sp.</i>	0
15	<i>Aconitum variegatum</i> subsp. <i>paniculatum</i>	1
16	<i>Actaea spicata</i>	1
17	<i>Adenostyles alliariae</i>	1
18	<i>Adenostyles alpina</i>	1
19	<i>Adoxa moschatellina</i>	1
20	<i>Aegopodium podagraria</i>	1
21	<i>Aetheorhiza bulbosa</i>	1
22	<i>Aethusa cynapium</i> subsp. <i>cynapioides</i>	1
23	<i>Agrimonia eupatoria</i>	1
24	<i>Agrimonia procera</i>	1
25	<i>Agrostis agrostiflora</i>	1
26	<i>Agrostis canina</i>	1
27	<i>Agrostis capillaris</i>	1
28	<i>Agrostis curtisii</i>	1
29	<i>Agrostis sp.</i>	0
30	<i>Agrostis stolonifera</i>	1
31	<i>Ajuga pyramidalis</i>	1
32	<i>Ajuga reptans</i>	1
33	<i>Ajuga sp.</i>	0
34	<i>Alchemilla alpina</i>	1
35	<i>Alchemilla coriacea</i>	1
36	<i>Alchemilla glaucescens</i>	1
37	<i>Alchemilla xanthochlora</i>	1
38	<i>Alliaria petiolata</i>	1
39	<i>Alnus glutinosa</i>	1
40	<i>Alnus viridis</i>	1
41	<i>Alopecurus pratensis</i>	1
42	<i>Anchusa officinalis</i>	1
43	<i>Anemone apennina</i>	1
44	<i>Anemone nemorosa</i>	1
45	<i>Angelica sylvestris</i>	1
46	<i>Antennaria dioica</i>	1
47	<i>Anthoxanthum odoratum</i>	1
48	<i>Anthoxanthum sp.</i>	0
49	<i>Anthriscus sylvestris</i>	1
50	<i>Anthyllis vulneraria</i>	1
51	<i>Aquilegia vulgaris</i>	1
52	<i>Arabis brassica</i>	1

1		
2	<i>Arabis hirsuta</i>	1
3	<i>Arbutus unedo</i>	1
4	<i>Arctium nemorosum</i>	1
5	<i>Arenaria montana</i>	1
6	<i>Arnica montana</i>	1
7	<i>Arrhenatherum elatius</i>	1
8	<i>Arum italicum</i>	1
9	<i>Arum maculatum</i>	1
10	<i>Arum sp.</i>	0
11	<i>Aruncus dioicus</i>	1
12	<i>Aruncus sp.</i>	0
13	<i>Asparagus officinalis</i>	1
14	<i>Asphodelus albus</i>	1
15	<i>Asplenium trichomanes</i>	1
16	<i>Asplenium trichomanes-ramosum</i>	1
17	<i>Astrantia major</i>	1
18	<i>Athyrium distentifolium</i>	1
19	<i>Athyrium filix-femina</i>	1
20	<i>Atropa bella-donna</i>	1
21	<i>Avena sativa</i>	1
22	<i>Avena sp.</i>	0
23	<i>Betula pendula</i>	1
24	<i>Betula pubescens</i>	1
25	<i>Betula sp.</i>	0
26	<i>Blackstonia perfoliata</i>	1
27	<i>Blechnum spicant</i>	1
28	<i>Brachypodium pinnatum</i>	1
29	<i>Brachypodium sp.</i>	0
30	<i>Brachypodium sylvaticum</i>	1
31	<i>Briza media</i>	1
32	<i>Bromus benekenii</i>	1
33	<i>Bromus ramosus</i>	1
34	<i>Bromus sp.</i>	0
35	<i>Buxus sempervirens</i>	1
36	<i>Calamagrostis epigejos</i>	1
37	<i>Calamagrostis sp.</i>	0
38	<i>Calamagrostis varia</i>	1
39	<i>Calamagrostis villosa</i>	1
40	<i>Calamintha grandiflora</i>	1
41	<i>Calamintha sylvatica</i>	1
42	<i>Callitriche sp.</i>	0
43	<i>Calluna vulgaris</i>	1
44	<i>Caltha palustris</i>	1
45	<i>Campanula barbata</i>	1
46	<i>Campanula cervicaria</i>	1
47	<i>Campanula latifolia</i>	1
48	<i>Campanula rapunculoides</i>	1
49	<i>Campanula rhomboidalis</i>	1
50	<i>Campanula rotundifolia</i>	1
51	<i>Campanula trachelium</i>	1

1		
2	<i>Cardamine flexuosa</i>	1
3	<i>Cardamine heptaphylla</i>	1
4	<i>Cardamine hirsuta</i>	1
5	<i>Cardamine impatiens</i>	1
6	<i>Cardamine pentaphyllos</i>	1
7	<i>Cardamine pratensis</i>	1
8	<i>Cardamine sp.</i>	0
9		
10	<i>Carduus carlinifolius</i>	1
11	<i>Carduus defloratus</i>	1
12	<i>Carex acutiformis</i>	1
13	<i>Carex alba</i>	1
14	<i>Carex arenaria</i>	1
15	<i>Carex bohémica</i>	1
16	<i>Carex brizoides</i>	1
17	<i>Carex caryophyllea</i>	1
18	<i>Carex curta</i>	1
19	<i>Carex demissa</i>	1
20	<i>Carex digitata</i>	1
21	<i>Carex divulsa</i>	1
22	<i>Carex echinata</i>	1
23	<i>Carex ferruginea</i> subsp. <i>australpina</i>	1
24	<i>Carex flacca</i>	1
25	<i>Carex flava</i>	1
26	<i>Carex hallerana</i>	1
27	<i>Carex hirta</i>	1
28	<i>Carex laevigata</i>	1
29	<i>Carex montana</i>	1
30	<i>Carex muricata</i>	1
31	<i>Carex muricata</i> subsp. <i>lamprocarpa</i>	1
32	<i>Carex ornithopoda</i>	1
33	<i>Carex ovalis</i>	1
34	<i>Carex pallescens</i>	1
35	<i>Carex panicea</i>	1
36	<i>Carex pendula</i>	1
37	<i>Carex pilosa</i>	1
38	<i>Carex pilulifera</i>	1
39	<i>Carex remota</i>	1
40	<i>Carex sp.</i>	0
41	<i>Carex strigosa</i>	1
42	<i>Carex sylvatica</i>	1
43	<i>Carex umbrosa</i>	1
44	<i>Carlina acaulis</i>	1
45	<i>Carpinus betulus</i>	1
46	<i>Carum verticillatum</i>	1
47	<i>Castanea sativa</i>	1
48	<i>Centaurea montana</i>	1
49	<i>Centaurea nigra</i>	1
50	<i>Centaurea uniflora</i>	1
51	<i>Centaureum erythraea</i>	1
52	<i>Cephalanthera damasonium</i>	1
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1		
2	<i>Cephalanthera longifolia</i>	1
3	<i>Cephalanthera rubra</i>	1
4	<i>Cephalanthera</i> sp.	0
5	<i>Cerastium arvense</i>	1
6	<i>Cerastium fontanum</i>	1
7	<i>Cerastium fontanum</i> subsp. <i>vulgare</i>	1
8	<i>Cerastium glomeratum</i>	1
9	<i>Cerastium</i> sp.	0
10	<i>Ceratocapnos claviculata</i>	1
11	<i>Chaerophyllum aureum</i>	1
12	<i>Chaerophyllum hirsutum</i>	1
13	<i>Chaerophyllum</i> sp.	0
14	<i>Chaerophyllum villarsii</i>	1
15	<i>Chenopodium album</i>	1
16	<i>Chenopodium bonus-henricus</i>	1
17	<i>Chrysosplenium alternifolium</i>	1
18	<i>Chrysosplenium oppositifolium</i>	1
19	<i>Cicerbita alpina</i>	1
20	<i>Cicerbita plumieri</i>	1
21	<i>Circaea alpina</i>	1
22	<i>Circaea lutetiana</i>	1
23	<i>Circaea x-intermedia</i>	1
24	<i>Cirsium arvense</i>	1
25	<i>Cirsium eriophorum</i>	1
26	<i>Cirsium oleraceum</i>	1
27	<i>Cirsium palustre</i>	1
28	<i>Cirsium</i> sp.	0
29	<i>Cirsium spinosissimum</i>	1
30	<i>Cirsium vulgare</i>	1
31	<i>Cistus salvifolius</i>	1
32	<i>Clematis alpina</i>	1
33	<i>Clematis vitalba</i>	1
34	<i>Clinopodium vulgare</i>	1
35	<i>Colchicum autumnale</i>	1
36	<i>Conopodium majus</i>	1
37	<i>Convallaria majalis</i>	1
38	<i>Conyza canadensis</i>	1
39	<i>Corallorhiza trifida</i>	1
40	<i>Cornus mas</i>	1
41	<i>Cornus sanguinea</i>	1
42	<i>Cornus</i> sp.	0
43	<i>Corylus avellana</i>	1
44	<i>Cotoneaster nebrodensis</i>	1
45	<i>Crataegus laevigata</i>	1
46	<i>Crataegus monogyna</i>	1
47	<i>Crataegus</i> sp.	0
48	<i>Crepis biennis</i>	1
49	<i>Crepis conyzifolia</i>	1
50	<i>Crepis paludosa</i>	1
51	<i>Cynoglossum germanicum</i>	1

1		
2	<i>Cytisus scoparius</i>	1
3	<i>Cytisus</i> sp.	0
4	<i>Dactylis glomerata</i>	1
5	<i>Dactylis</i> sp.	0
6	<i>Dactylorhiza maculata</i>	1
7	<i>Danthonia decumbens</i>	1
8	<i>Danthonia</i> sp.	0
9	<i>Daphne cneorum</i>	1
10	<i>Daphne gnidium</i>	1
11	<i>Daphne laureola</i>	1
12	<i>Daphne mezereum</i>	1
13	<i>Daucus carota</i>	1
14	<i>Deschampsia cespitosa</i>	1
15	<i>Deschampsia flexuosa</i>	1
16	<i>Digitalis grandiflora</i>	1
17	<i>Digitalis lutea</i>	1
18	<i>Digitalis purpurea</i>	1
19	<i>Draba</i> sp.	0
20	<i>Dryopteris affinis</i>	1
21	<i>Dryopteris affinis</i> subsp. <i>borreri</i>	1
22	<i>Dryopteris carthusiana</i>	1
23	<i>Dryopteris dilatata</i>	1
24	<i>Dryopteris filix-mas</i>	1
25	<i>Dryopteris remota</i>	1
26	<i>Dryopteris</i> sp.	0
27	<i>Elymus caninus</i>	1
28	<i>Elymus</i> sp.	0
29	<i>Epilobium angustifolium</i>	1
30	<i>Epilobium collinum</i>	1
31	<i>Epilobium hirsutum</i>	1
32	<i>Epilobium montanum</i>	1
33	<i>Epilobium obscurum</i>	1
34	<i>Epilobium</i> sp.	0
35	<i>Epilobium tetragonum</i>	1
36	<i>Epipactis atrorubens</i>	1
37	<i>Epipactis helleborine</i>	1
38	<i>Epipactis microphylla</i>	1
39	<i>Epipactis</i> sp.	0
40	<i>Epipogium aphyllum</i>	1
41	<i>Equisetum arvense</i>	1
42	<i>Equisetum palustre</i>	1
43	<i>Equisetum ramosissimum</i>	1
44	<i>Equisetum sylvaticum</i>	1
45	<i>Erica ciliaris</i>	1
46	<i>Erica cinerea</i>	1
47	<i>Erica scoparia</i>	1
48	<i>Erica tetralix</i>	1
49	<i>Erigeron alpinus</i>	1
50	<i>Erigeron annuus</i>	1
51	<i>Euonymus europaeus</i>	1

1		
2	<i>Euonymus latifolius</i>	1
3	<i>Eupatorium cannabinum</i>	1
4	<i>Euphorbia amygdaloides</i>	1
5	<i>Euphorbia cyparissias</i>	1
6	<i>Euphorbia dulcis</i>	1
7	<i>Euphorbia hyberna</i>	1
8	<i>Euphorbia portlandica</i>	1
9	<i>Euphorbia serrulata</i>	1
10	<i>Fagus sylvatica</i>	1
11	<i>Festuca altissima</i>	1
12	<i>Festuca curvula</i>	1
13	<i>Festuca flavescens</i>	1
14	<i>Festuca gigantea</i>	1
15	<i>Festuca glauca</i>	1
16	<i>Festuca heterophylla</i>	1
17	<i>Festuca ovina</i>	1
18	<i>Festuca pratensis</i>	1
19	<i>Festuca rubra</i>	1
20	<i>Festuca rubra</i> subsp. <i>pruinosa</i>	1
21	<i>Festuca</i> sp.	0
22	<i>Festuca tenuifolia</i>	1
23	<i>Festuca trichophylla</i>	1
24	<i>Festuca vasconensis</i>	1
25	<i>Filipendula ulmaria</i>	1
26	<i>Fragaria</i> sp.	0
27	<i>Fragaria vesca</i>	1
28	<i>Frangula alnus</i>	1
29	<i>Fraxinus excelsior</i>	1
30	<i>Fraxinus</i> sp.	0
31	<i>Galeopsis tetrahit</i>	1
32	<i>Galium album</i>	1
33	<i>Galium aparine</i>	1
34	<i>Galium arenarium</i>	1
35	<i>Galium aristatum</i>	1
36	<i>Galium boreale</i>	1
37	<i>Galium glaucum</i>	1
38	<i>Galium mollugo</i>	1
39	<i>Galium odoratum</i>	1
40	<i>Galium palustre</i>	1
41	<i>Galium pumilum</i>	1
42	<i>Galium rotundifolium</i>	1
43	<i>Galium saxatile</i>	1
44	<i>Galium</i> sp.	0
45	<i>Galium sylvaticum</i>	1
46	<i>Galium uliginosum</i>	1
47	<i>Galium verum</i>	1
48	<i>Genista anglica</i>	1
49	<i>Genista pilosa</i>	1
50	<i>Gentiana acaulis</i>	1
51	<i>Gentiana lutea</i>	1

1		
2	<i>Gentiana purpurea</i>	1
3	<i>Gentiana verna</i>	1
4	<i>Gentianella ciliata</i>	1
5	<i>Geranium columbinum</i>	1
6	<i>Geranium nodosum</i>	1
7	<i>Geranium robertianum</i>	1
8	<i>Geranium sylvaticum</i>	1
9	<i>Geum montanum</i>	1
10	<i>Geum rivale</i>	1
11	<i>Geum sp.</i>	0
12	<i>Geum urbanum</i>	1
13	<i>Glechoma hederacea</i>	1
14	<i>Glechoma hirsuta</i>	1
15	<i>Glyceria fluitans</i>	1
16	<i>Glyceria striata</i>	1
17	<i>Gnaphalium sp.</i>	0
18	<i>Goodyera repens</i>	1
19	<i>Gymnocarpium sp.</i>	0
20	<i>Halimium alyssoides</i>	1
21	<i>Hedera helix</i>	1
22	<i>Helictotrichon sedenense</i>	1
23	<i>Helleborus foetidus</i>	1
24	<i>Helleborus viridis</i>	1
25	<i>Helleborus viridis subsp. occidentalis</i>	1
26	<i>Hepatica nobilis</i>	1
27	<i>Heracleum sphondylium</i>	1
28	<i>Hieracium bifidum</i>	1
29	<i>Hieracium juranum</i>	1
30	<i>Hieracium laevigatum</i>	1
31	<i>Hieracium murorum</i>	1
32	<i>Hieracium pilosella</i>	1
33	<i>Hieracium prenanthoides</i>	1
34	<i>Hieracium rapunculoides</i>	1
35	<i>Hieracium sp.</i>	0
36	<i>Hieracium umbellatum</i>	1
37	<i>Hieracium vulgatum</i>	1
38	<i>Hippocrepis comosa</i>	1
39	<i>Holcus lanatus</i>	1
40	<i>Holcus mollis</i>	1
41	<i>Holcus sp.</i>	0
42	<i>Homogyne alpina</i>	1
43	<i>Hordelymus europaeus</i>	1
44	<i>Hordeum vulgare</i>	1
45	<i>Humulus lupulus</i>	1
46	<i>Hyacinthoides non-scripta</i>	1
47	<i>Hypericum androsaemum</i>	1
48	<i>Hypericum hirsutum</i>	1
49	<i>Hypericum humifusum</i>	1
50	<i>Hypericum maculatum</i>	1
51	<i>Hypericum montanum</i>	1

1		
2	<i>Hypericum perforatum</i>	1
3	<i>Hypericum pulchrum</i>	1
4	<i>Hypericum richeri</i>	1
5	<i>Hypericum</i> sp.	0
6	<i>Hypochoeris maculata</i>	1
7	<i>Hypochoeris radicata</i>	1
8	<i>Hypochoeris</i> sp.	0
9	<i>Ilex aquifolium</i>	1
10	<i>Impatiens noli-tangere</i>	1
11	<i>Impatiens</i> sp.	0
12	<i>Inula conyza</i>	1
13	<i>Iris foetidissima</i>	1
14	<i>Isopyrum thalictroides</i>	1
15	<i>Jasione montana</i>	1
16	<i>Juglans regia</i>	1
17	<i>Juncus acutiflorus</i>	1
18	<i>Juncus bufonius</i>	1
19	<i>Juncus bulbosus</i>	1
20	<i>Juncus conglomeratus</i>	1
21	<i>Juncus effusus</i>	1
22	<i>Juncus inflexus</i>	1
23	<i>Juncus</i> sp.	0
24	<i>Juncus tenuis</i>	1
25	<i>Juniperus communis</i> subsp. <i>alpina</i>	1
26	<i>Knautia arvensis</i>	1
27	<i>Knautia dipsacifolia</i>	1
28	<i>Knautia dipsacifolia</i> subsp. <i>gracilis</i>	1
29	<i>Lactuca serriola</i>	1
30	<i>Lactuca virosa</i>	1
31	<i>Lamiastrum galeobdolon</i>	1
32	<i>Lamiastrum</i> sp.	0
33	<i>Lamium album</i>	1
34	<i>Lapsana communis</i>	1
35	<i>Larix decidua</i>	1
36	<i>Laserpitium halleri</i>	1
37	<i>Laserpitium siler</i>	1
38	<i>Laserpitium</i> sp.	0
39	<i>Lathyrus laevigatus</i> subsp. <i>occidentalis</i>	1
40	<i>Lathyrus montanus</i>	1
41	<i>Lathyrus niger</i>	1
42	<i>Lathyrus pratensis</i>	1
43	<i>Lathyrus</i> sp.	0
44	<i>Lathyrus sphaericus</i>	1
45	<i>Lathyrus tuberosus</i>	1
46	<i>Lathyrus vernus</i>	1
47	<i>Leontodon hispidus</i>	1
48	<i>Leontodon pyrenaicus</i> subsp. <i>helveticus</i>	1
49	<i>Leontodon</i> sp.	0
50	<i>Leucanthemum vulgare</i>	1
51	<i>Ligustrum vulgare</i>	1

1		
2	<i>Lilium martagon</i>	1
3	<i>Linaria repens</i>	1
4	<i>Lithospermum officinale</i>	1
5	<i>Lobelia urens</i>	1
6	<i>Lolium perenne</i>	1
7	<i>Lonicera alpigena</i>	1
8	<i>Lonicera caerulea</i>	1
9	<i>Lonicera nigra</i>	1
10	<i>Lonicera periclymenum</i>	1
11	<i>Lonicera xylosteum</i>	1
12	<i>Lotus corniculatus</i>	1
13	<i>Lotus sp.</i>	0
14	<i>Lotus uliginosus</i>	1
15	<i>Lunaria rediviva</i>	1
16	<i>Luzula campestris</i>	1
17	<i>Luzula forsteri</i>	1
18	<i>Luzula luzulina</i>	1
19	<i>Luzula luzuloides</i>	1
20	<i>Luzula multiflora</i>	1
21	<i>Luzula multiflora subsp. congesta</i>	1
22	<i>Luzula nivea</i>	1
23	<i>Luzula pilosa</i>	1
24	<i>Luzula sieberi</i>	1
25	<i>Luzula sp.</i>	0
26	<i>Luzula sylvatica</i>	1
27	<i>Lycopus europaeus</i>	1
28	<i>Lysimachia nemorum</i>	1
29	<i>Lysimachia nummularia</i>	1
30	<i>Lythrum salicaria</i>	1
31	<i>Maianthemum bifolium</i>	1
32	<i>Malus sylvestris</i>	1
33	<i>Marrubium sp.</i>	0
34	<i>Medicago lupulina</i>	1
35	<i>Medicago sp.</i>	0
36	<i>Melampyrum nemorosum</i>	1
37	<i>Melampyrum pratense</i>	1
38	<i>Melampyrum sylvaticum</i>	1
39	<i>Melica nutans</i>	1
40	<i>Melica uniflora</i>	1
41	<i>Melittis melissophyllum</i>	1
42	<i>Mentha aquatica</i>	1
43	<i>Mentha arvensis</i>	1
44	<i>Mercurialis perennis</i>	1
45	<i>Mercurialis sp.</i>	0
46	<i>Mespilus germanica</i>	1
47	<i>Milium effusum</i>	1
48	<i>Minuartia laricifolia</i>	1
49	<i>Moehringia muscosa</i>	1
50	<i>Moehringia trinervia</i>	1
51	<i>Molinia caerulea</i>	1

1		
2	<i>Molinia caerulea</i> subsp. <i>arundinacea</i>	1
3	<i>Monotropa hypopitys</i>	1
4	<i>Mycelis muralis</i>	1
5	<i>Myosotis alpestris</i>	1
6	<i>Myosotis scorpioides</i>	1
7	<i>Myosotis sylvatica</i>	1
8	<i>Myosoton aquaticum</i>	1
9	<i>Narcissus bulbocodium</i>	1
10	<i>Nardus stricta</i>	1
11	<i>Neottia nidus-avis</i>	1
12	<i>Odontites verna</i>	1
13	<i>Orchis purpurea</i>	1
14	<i>Oreopteris limbosperma</i>	1
15	<i>Origanum vulgare</i>	1
16	<i>Ornithogalum pyrenaicum</i>	1
17	<i>Ornithopus perpusillus</i>	1
18	<i>Orobanche lutea</i>	1
19	<i>Orobanche rapum-genistae</i>	1
20	<i>Orobanche</i> sp.	0
21	<i>Orthilia secunda</i>	1
22	<i>Osmunda regalis</i>	1
23	<i>Osyris alba</i>	1
24	<i>Oxalis acetosella</i>	1
25	<i>Oxalis europaea</i>	1
26	<i>Paris quadrifolia</i>	1
27	<i>Pastinaca sativa</i>	1
28	<i>Petasites albus</i>	1
29	<i>Peucedanum gallicum</i>	1
30	<i>Peucedanum ostruthium</i>	1
31	<i>Phalaris arundinacea</i>	1
32	<i>Phegopteris connectilis</i>	1
33	<i>Phleum alpinum</i>	1
34	<i>Phyteuma betonicifolium</i>	1
35	<i>Phyteuma ovatum</i>	1
36	<i>Phyteuma</i> sp.	0
37	<i>Phyteuma spicatum</i>	1
38	<i>Phytolacca americana</i>	1
39	<i>Picea abies</i>	1
40	<i>Picris hieracioides</i>	1
41	<i>Picris</i> sp.	0
42	<i>Pimpinella major</i>	1
43	<i>Pimpinella saxifraga</i>	1
44	<i>Pinus cembra</i>	1
45	<i>Pinus pinaster</i>	1
46	<i>Pinus pinaster</i> subsp. <i>atlantica</i>	1
47	<i>Pinus</i> sp.	0
48	<i>Pinus sylvestris</i>	1
49	<i>Plantago alpina</i>	1
50	<i>Plantago lanceolata</i>	1
51	<i>Plantago major</i>	1

1		
2	<i>Plantago maritima</i>	1
3	<i>Plantago media</i>	1
4	<i>Plantago sp.</i>	0
5	<i>Poa alpina</i>	1
6	<i>Poa annua</i>	1
7	<i>Poa bulbosa</i>	1
8	<i>Poa chaixii</i>	1
9	<i>Poa compressa</i>	1
10	<i>Poa nemoralis</i>	1
11	<i>Poa pratensis</i>	1
12	<i>Poa sp.</i>	0
13	<i>Poa supina</i>	1
14	<i>Poa trivialis</i>	1
15	<i>Poa trivialis subsp. sylvicola</i>	1
16	<i>Polygala serpyllifolia</i>	1
17	<i>Polygonatum multiflorum</i>	1
18	<i>Polygonatum sp.</i>	0
19	<i>Polygonatum verticillatum</i>	1
20	<i>Polygonum bistorta</i>	1
21	<i>Polygonum mite</i>	1
22	<i>Polygonum persicaria</i>	1
23	<i>Polygonum sp.</i>	0
24	<i>Polypodium vulgare</i>	1
25	<i>Polystichum aculeatum</i>	1
26	<i>Polystichum lonchitis</i>	1
27	<i>Polystichum setiferum</i>	1
28	<i>Polystichum sp.</i>	0
29	<i>Populus sp.</i>	0
30	<i>Populus tremula</i>	1
31	<i>Potentilla erecta</i>	1
32	<i>Potentilla grandiflora</i>	1
33	<i>Potentilla reptans</i>	1
34	<i>Potentilla sterilis</i>	1
35	<i>Prenanthes purpurea</i>	1
36	<i>Primula elatior</i>	1
37	<i>Primula veris</i>	1
38	<i>Prunella grandiflora</i>	1
39	<i>Prunella vulgaris</i>	1
40	<i>Prunus avium</i>	1
41	<i>Prunus laurocerasus</i>	1
42	<i>Prunus padus</i>	1
43	<i>Prunus serotina</i>	1
44	<i>Prunus sp.</i>	0
45	<i>Prunus spinosa</i>	1
46	<i>Prunus virginiana</i>	1
47	<i>Pseudarrhenatherum longifolium</i>	1
48	<i>Pseudorchis albida</i>	1
49	<i>Pseudotsuga menziesii</i>	1
50	<i>Pteridium aquilinum</i>	1
51	<i>Pulmonaria affinis</i>	1

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2	<i>Pulmonaria longifolia</i>	1
3	<i>Pulmonaria montana</i>	1
4	<i>Pulmonaria obscura</i>	1
5	<i>Pulmonaria saccharata</i>	1
6	<i>Pulsatilla alpina</i> subsp. <i>apiifolia</i>	1
7		
8	<i>Pyrola media</i>	1
9	<i>Pyrola minor</i>	1
10	<i>Pyrus pyraeaster</i>	1
11	<i>Quercus ilex</i>	1
12	<i>Quercus petraea</i>	1
13	<i>Quercus pubescens</i>	1
14	<i>Quercus pyrenaica</i>	1
15	<i>Quercus pyrenaica</i>	1
16	<i>Quercus robur</i>	1
17	<i>Quercus rubra</i>	1
18	<i>Quercus sp.</i>	0
19		
20	<i>Quercus suber</i>	1
21	<i>Ranunculus aconitifolius</i>	1
22	<i>Ranunculus acris</i>	1
23	<i>Ranunculus aduncus</i>	1
24	<i>Ranunculus auricomus</i>	1
25	<i>Ranunculus ficaria</i>	1
26	<i>Ranunculus ficaria</i>	1
27	<i>Ranunculus flammula</i>	1
28	<i>Ranunculus lanuginosus</i>	1
29	<i>Ranunculus montanus</i>	1
30	<i>Ranunculus platanifolius</i>	1
31	<i>Ranunculus platanifolius</i>	1
32	<i>Ranunculus pyrenaicus</i>	1
33	<i>Ranunculus repens</i>	1
34	<i>Ranunculus serpens</i> subsp. <i>nemorosus</i>	1
35	<i>Ranunculus sp.</i>	0
36		
37	<i>Rhamnus catharticus</i>	1
38	<i>Rhododendron ferrugineum</i>	1
39	<i>Ribes alpinum</i>	1
40	<i>Ribes rubrum</i>	1
41	<i>Ribes uva-crispa</i>	1
42		
43	<i>Rosa arvensis</i>	1
44	<i>Rosa canina</i>	1
45	<i>Rosa pendulina</i>	1
46	<i>Rosa pimpinellifolia</i>	1
47	<i>Rosa villosa</i>	1
48		
49	<i>Rubia peregrina</i>	1
50	<i>Rubus caesius</i>	1
51	<i>Rubus canescens</i>	1
52	<i>Rubus fruticosus</i>	1
53	<i>Rubus idaeus</i>	1
54	<i>Rubus questieri</i>	1
55	<i>Rubus saxatilis</i>	1
56	<i>Rubus saxatilis</i>	1
57	<i>Rubus sp.</i>	0
58	<i>Rubus ulmifolius</i>	1
59	<i>Rubus vestitus</i>	1
60	<i>Rumex acetosa</i>	1

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2	<i>Rumex acetosella</i>	1
3	<i>Rumex alpestris</i>	1
4	<i>Rumex alpinus</i>	1
5	<i>Rumex obtusifolius</i>	1
6	<i>Rumex sanguineus</i>	1
7	<i>Rumex scutatus</i>	1
8	<i>Rumex sp.</i>	0
9		
10	<i>Ruscus aculeatus</i>	1
11	<i>Salix atrocinerea</i>	1
12	<i>Salix caprea</i>	1
13	<i>Salix cinerea</i>	1
14	<i>Salix elaeagnos</i>	1
15	<i>Salix repens</i>	1
16	<i>Salix sp.</i>	0
17		
18	<i>Sambucus ebulus</i>	1
19	<i>Sambucus nigra</i>	1
20	<i>Sambucus racemosa</i>	1
21	<i>Sambucus sp.</i>	0
22		
23	<i>Sanguisorba minor</i>	1
24	<i>Sanicula europaea</i>	1
25	<i>Saxifraga cuneifolia</i> subsp. <i>robusta</i>	1
26	<i>Saxifraga granulata</i>	1
27	<i>Saxifraga rotundifolia</i>	1
28	<i>Scilla bifolia</i>	1
29	<i>Scirpus sylvaticus</i>	1
30	<i>Scorzonera humilis</i>	1
31	<i>Scrophularia alpestris</i>	1
32	<i>Scrophularia nodosa</i>	1
33	<i>Scutellaria minor</i>	1
34	<i>Scutellaria sp.</i>	0
35		
36	<i>Sedum anacampseros</i>	1
37	<i>Sedum montanum</i>	1
38	<i>Sempervivum arachnoideum</i>	1
39	<i>Sempervivum tectorum</i>	1
40	<i>Senecio adonidifolius</i>	1
41	<i>Senecio jacobaea</i>	1
42	<i>Senecio nemorensis</i> subsp. <i>fuchsii</i>	1
43	<i>Senecio sp.</i>	0
44		
45	<i>Senecio sylvaticus</i>	1
46	<i>Senecio viscosus</i>	1
47	<i>Senecio vulgaris</i>	1
48	<i>Serratula tinctoria</i>	1
49	<i>Seseli montanum</i>	1
50	<i>Sesleria albicans</i>	1
51	<i>Setaria sp.</i>	0
52		
53	<i>Silene dioica</i>	1
54	<i>Silene nutans</i>	1
55	<i>Silene rupestris</i>	1
56	<i>Silene vulgaris</i>	1
57		
58	<i>Simethis planifolia</i>	1
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2	<i>Sison amomum</i>	1
3	<i>Sisymbrium orientale</i>	1
4	<i>Solanum dulcamara</i>	1
5	<i>Solanum nigrum</i>	1
6	<i>Soldanella alpina</i>	1
7	<i>Solidago canadensis</i>	1
8	<i>Solidago gigantea</i>	1
9	<i>Solidago sp.</i>	0
10	<i>Solidago virgaurea</i>	1
11	<i>Sonchus arvensis</i>	1
12	<i>Sonchus asper</i>	1
13	<i>Sonchus oleraceus</i>	1
14	<i>Sonchus sp.</i>	0
15	<i>Sorbus aria</i>	1
16	<i>Sorbus aucuparia</i>	1
17	<i>Sorbus domestica</i>	1
18	<i>Sorbus sp.</i>	0
19	<i>Sorbus torminalis</i>	1
20	<i>Stachys alpina</i>	1
21	<i>Stachys officinalis</i>	1
22	<i>Stachys sylvatica</i>	1
23	<i>Stellaria graminea</i>	1
24	<i>Stellaria holostea</i>	1
25	<i>Stellaria media</i>	1
26	<i>Stellaria nemorum</i>	1
27	<i>Stellaria uliginosa</i>	1
28	<i>Succisa pratensis</i>	1
29	<i>Tamus communis</i>	1
30	<i>Taraxacum officinale</i>	1
31	<i>Taraxacum sp.</i>	0
32	<i>Taxus baccata</i>	1
33	<i>Teucrium scorodonia</i>	1
34	<i>Thalictrum aquilegifolium</i>	1
35	<i>Thalictrum sp.</i>	0
36	<i>Thesium alpinum</i>	1
37	<i>Thlaspi alpestre</i>	1
38	<i>Tilia cordata</i>	1
39	<i>Tilia platyphyllos</i>	1
40	<i>Tilia platyphyllos</i> subsp. <i>cordifolia</i>	1
41	<i>Torilis japonica</i>	1
42	<i>Tragopogon pratensis</i>	1
43	<i>Trifolium alpestre</i>	1
44	<i>Trifolium alpinum</i>	1
45	<i>Trifolium badium</i>	1
46	<i>Trifolium medium</i>	1
47	<i>Trifolium pratense</i>	1
48	<i>Trifolium repens</i>	1
49	<i>Trifolium sp.</i>	0
50	<i>Trisetum flavescens</i>	1
51	<i>Trochiscanthes nodiflora</i>	1
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2	<i>Trollius europaeus</i>	1
3	<i>Tussilago farfara</i>	1
4	<i>Ulex europaeus</i>	1
5	<i>Ulex minor</i>	1
6	<i>Ulmus glabra</i>	1
7	<i>Ulmus minor</i>	1
8	<i>Urtica dioica</i>	1
9	<i>Vaccinium myrtillus</i>	1
10	<i>Vaccinium vitis-idaea</i>	1
11	<i>Valeriana montana</i>	1
12	<i>Valeriana officinalis</i>	1
13	<i>Valeriana officinalis</i> subsp. <i>sambucifolia</i>	1
14	<i>Valeriana tripteris</i>	1
15	<i>Veratrum album</i>	1
16	<i>Verbascum lychnitis</i>	1
17	<i>Verbascum nigrum</i>	1
18	<i>Verbascum sinuatum</i>	1
19	<i>Verbascum thapsus</i>	1
20	<i>Veronica anagallis-aquatica</i>	1
21	<i>Veronica beccabunga</i>	1
22	<i>Veronica chamaedrys</i>	1
23	<i>Veronica hederifolia</i>	1
24	<i>Veronica hederifolia</i> subsp. <i>lucorum</i>	1
25	<i>Veronica montana</i>	1
26	<i>Veronica officinalis</i>	1
27	<i>Veronica serpyllifolia</i>	1
28	<i>Veronica serpyllifolia</i> subsp. <i>humifusa</i>	1
29	<i>Veronica sp.</i>	0
30	<i>Veronica urticifolia</i>	1
31	<i>Viburnum lantana</i>	1
32	<i>Viburnum opulus</i>	1
33	<i>Vicia cracca</i>	1
34	<i>Vicia disperma</i>	1
35	<i>Vicia hirsuta</i>	1
36	<i>Vicia pisiformis</i>	1
37	<i>Vicia sativa</i>	1
38	<i>Vicia sativa</i> subsp. <i>nigra</i>	1
39	<i>Vicia sepium</i>	1
40	<i>Vicia sp.</i>	0
41	<i>Vicia sylvatica</i>	1
42	<i>Vicia tetrasperma</i>	1
43	<i>Vinca minor</i>	1
44	<i>Vincetoxicum hirundinaria</i> subsp. <i>intermediur</i>	1
45	<i>Viola biflora</i>	1
46	<i>Viola canina</i>	1
47	<i>Viola hirta</i>	1
48	<i>Viola mirabilis</i>	1
49	<i>Viola odorata</i>	1
50	<i>Viola reichenbachiana</i>	1
51	<i>Viola riviniana</i>	1

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2	Viola sp.	0
3	Viola tricolor	1
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For Peer Review

	(Intercept)	Age_1995	Disturbanc	Years	Stand_Type	Exclosure	eCumulated	Cumulated	Stand basa
3	0.838	0.145	-0.115	0.058			-0.17		0.216
4	0.838	0.152	-0.113	0.059			-0.167	-0.042	0.207
5	0.811	0.16	-0.113	0.055	+		-0.165		0.208
6	0.83	0.145	-0.115	0.058		+	-0.17		0.216
8	0.805	0.17	-0.11	0.055	+		-0.161	-0.045	0.196
9	0.838	0.121	-0.087				-0.114		0.195
10	0.83	0.152	-0.113	0.059		+	-0.167	-0.042	0.207
11	0.838	0.127	-0.085				-0.111	-0.04	0.185
12	0.797	0.145	-0.087		+		-0.111		0.184
14	0.803	0.16	-0.113	0.055	+	+	-0.165		0.208
15	0.792	0.154	-0.084		+		-0.107	-0.044	0.172
16	0.797	0.17	-0.11	0.055	+	+	-0.161	-0.045	0.196
17	0.83	0.121	-0.087			+	-0.114		0.195
18	0.83	0.127	-0.085			+	-0.111	-0.04	0.185
20	0.789	0.145	-0.087		+	+	-0.111		0.184
21	0.784	0.154	-0.084		+	+	-0.107	-0.044	0.172
22	0.837		-0.084				-0.09		0.185
23	0.837		-0.099	0.033			-0.118		0.196
24	0.877		-0.104	0.041	+		-0.133		0.211
25	0.862		-0.085		+		-0.094		0.193

For Peer Review

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	Baseline te df	logLik	AICc	delta	weight	R2_marg	R2_cond
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3	0.766	11	-2304.28	4630.707	0 0.214	0.329	0.549
4	0.757	12	-2303.63	4631.446	0.738 0.148	0.331	0.547
5	0.778	12	-2304.07	4632.328	1.621 0.095	0.33	0.549
6	0.766	12	-2304.25	4632.681	1.974 0.08	0.329	0.549
7							
8	0.77	13	-2303.34	4632.881	2.173 0.072	0.332	0.547
9	0.754	10	-2306.41	4632.955	2.248 0.07	0.325	0.543
10	0.757	13	-2303.61	4633.42	2.713 0.055	0.331	0.547
11	0.745	11	-2305.83	4633.804	3.097 0.046	0.326	0.541
12	0.773	11	-2305.95	4634.042	3.335 0.04	0.327	0.544
13							
14	0.778	13	-2304.05	4634.305	3.597 0.035	0.33	0.549
15	0.765	12	-2305.22	4634.617	3.909 0.03	0.329	0.541
16	0.77	14	-2303.31	4634.858	4.15 0.027	0.332	0.547
17	0.754	11	-2306.39	4634.927	4.22 0.026	0.325	0.543
18							
19	0.745	12	-2305.8	4635.777	5.07 0.017	0.326	0.541
20	0.773	12	-2305.92	4636.016	5.309 0.015	0.327	0.544
21	0.765	13	-2305.19	4636.592	5.884 0.011	0.329	0.541
22	0.698	9	-2310.65	4639.41	8.703 0.003	0.32	0.545
23	0.698	10	-2309.94	4640.008	9.301 0.002	0.322	0.548
24							
25	0.691	11	-2309.39	4640.939	10.232 0.001	0.322	0.548
26	0.694	10	-2310.43	4640.978	10.271 0.001	0.32	0.545
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References	Years	Journal	Methods to compute the CTI
Bertrand et al.	2011	Nature	CTI reconstructed using a combination of weighted averaging partial least squares and Breiman's random forest with transfer function
Brice et al.	2019	Global Ecology and Biogeography	CTI computed with the average of species temperature distributions (i.e. Wordclim) based on tree occurrence data (Forest inventory databases of eastern North America)
Cheung et al.	2013	Nature	CTI based on the average of temperature preferences of marine fishes and invertebrates in fisheries catch
De Frenne et al.	2013	PNAS	CTI computed with temperature preference distributions of species (during growing season April to September) in permanent or semipermanent plots
Devictor et al.	2008	PNAS	CTI calculated as the average of species thermal preferences
Devictor et al.	2012	Nature Climate Change	CTI calculated as the average of species thermal preferences
Devictor et al.	2012	Nature Climate Change	CTI calculated as the average of species thermal preferences
Fadrique et al.	2018	Nature	CTI calculated as the average of species thermal preferences
Flanagan et al.	2019	Ecography	CTI calculated as the average of species thermal preferences
Fourcade et al.	2018	Biodiversity and Conservation	CTI calculated as the average of species thermal preferences
Gotfried et al.	2012	Nature Climate Change	Temperature index with ecological indicator
Haase et al.	2019	Science of the Total Environment	CTI calculated as the average of species thermal preferences
Lindström et al.	2013	Ecography	CTI calculated as the average of species thermal preferences

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Savage et al.	2015	Ecography	CTI calculated as the average of species thermal preferences
Elmendorf et al.	2015	PNAS	CTI calculated as the average of species thermal preferences ; Repeated sampling of historical studies and warming experiments
Duque et al.	2015	PNAS	CTI calculated as the average of species thermal preferences
Zellweger et al.	2020	Science	CTI calculated as the average of species thermal preferences

For Peer Review

Methods to compute the velocity of changes

	Period
Differences between CTI from between 1965-1986 and 1987-2008 periods	1965-1986 and 1987-2008
Comparison between historical and contemporary periods	1970 - 2016
Slope of linear regression	1970 - 2006
Comparison between historical and contemporary periods	depending on forest plots and regions; overall, from 1940 (minimum) to 2009 (maximum)
Slope of linear regression	1989 - 2006
Slope of linear regression	1990 - 2008
Slope of linear regression	1990 - 2008
Slope of linear regression	2000 - 2015
Slope of linear regression	1990 - 2014
Comparison between historical and contemporary periods	1960 - 2011
Comparison between historical and contemporary periods	2001 - 2008
Slope of linear regression	1990 - 2014
Slope of linear regression	1975 - 2009

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Comparison between historical and contemporary periods	1970 - 2012
Slope of linear regression	1970 - 2012

Rates calculated as the annualized change in the CTI values for each plot over the entire census period	2006-2014
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Comparison between baseline surveys and resurveys	depending on forest plots and regions; overall, from 1934 (minimum) to 2017 (maximum) ; median time interval between two surveys of 38 years
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For Peer Review

Taxonomic groups	Regions	Thermophilization rates
Forest understorey vegetation	France	$\Delta 0.02^{\circ}\text{C}$ and $\Delta 0.54^{\circ}\text{C}$ between 1965-1986 and 1987-2008 in lowland and highland, respectively.
Tree communities	Canada, Québec	0.03°C / decade
Marine fishes and invertebrates	Global	0.19°C / decade
Forest understorey vegetation	29 regions of Europe and North America	0.041°C / decade
Birds	France	0.044°C / decade
Birds	Europe	0.044°C / decade
Butterflies	Europe	0.051°C / decade
palms, tree ferns and lianas (Trees (including	The Andes (Peru, Colombia, Argentina, Ecuador)	0.066°C / decade
Marine fishes and invertebrates	Northeast U.S. continental shelf	in fall: 0.25°C / decade; in spring: 0.38°C / decade
Bumblebees	Norway	0.14°C / decade
Mountain vegetation	Europe	-
Stream invertebrate communities	Central Europe	0.22°C / decade (abundance data); 0.15°C / decade (occurrence data)
Birds	Norway	0.031°C / decade (Old monitoring scheme); 0.096°C / decade (New monitoring scheme)

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Forest understorey vegetation	Canada, Québec	0.05° C / decade
Tundra vegetation	Canada, Québec	0.199° C / decade
Tree communities	Northern tropical Andes	adult trees: 0.11°C / decade; juvenile trees: 0.27°C / decade
Forest understorey vegetation	Europe	0.01°C / decade

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