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1 **Forum paper**

2 **Assisted migration in a warmer and drier climate: less climate buffering**
3 **capacity, less facilitation and more fires at temperate latitudes?**

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23 **Forum paper**

24 **Assisted migration in a warmer and drier climate: less climate buffering**
25 **capacity, less facilitation and more fires at temperate latitudes?**

26 **Summary**

27 Assisted tree migration has been proposed as a conceptual solution to mitigate lags in biotic
28 responses to anthropogenic climate change. The rationale behind this concept is that tree
29 species currently growing under warmer and drier climates will be more resistant and resilient
30 to the new climatic conditions than tree species naturally growing in currently wetter and
31 colder climates. However, we hypothesize that, by being more stress-tolerant to warmer and
32 drier conditions, translocated species should exhibit different functional attributes, which
33 could induce important ecological and societal costs and overcome the desired benefits of
34 maintaining wood production and other ecosystem services. We used principal component
35 analysis (PCA) to analyze variation in seven traits of 106 tree and tall shrub species from
36 contrasting latitudinal distributions in western North America and Europe to predict the
37 potential functional changes of forest ecosystems due to the translocation of tree species from
38 low to high latitudes. We show that species from both continents differed primarily by their
39 position on the leaf economy spectrum (LES) and their size traits. Even though, in Europe,
40 differences in LES were significantly correlated to species southern latitudinal positions, in
41 both continents differences in size traits were significantly correlated to latitude. These results
42 suggest that assisted migration by translocating more conservative species of shorter stature in
43 currently cooler climates should decrease the buffering capacity of forest canopies, decrease
44 facilitation for understory species, and increase wildfire risks, whose effects have the potential
45 to accelerate climate warming through negative atmospheric feedback processes. As an
46 alternative solution to assisted migration that may accelerate rather than mitigate climate

47 change, we recommend that foresters gradually diversify the vertical structure and layering of
48 the existing forest canopy to maintain a sustainable water cycle and energy balance between
49 the soil, the tree and the atmosphere without increasing the wildfire risk.

50 **Keywords:** buffering capacity, climate change, disturbance, drought stress, facilitation, forest
51 communities, microclimate, species migration, tree species traits, vegetation.

52

53 **INTRODUCTION**

54 Although plants have shifted their ranges across continents in response to changing climate
55 for millennia (Benneth 1983, Mottl et al. 2021), projections of contemporary climate change
56 have shown that several tree species and populations have migrated much slower than
57 predicted (Davis and Shaw 2001, Hoegh–Guldberg et al. 2008, Zhu et al. 2012). This is
58 particularly the case for long-lived woody species, such as trees and shrubs that have lower
59 abilities to shift their ranges and track suitable climate conditions as compared to short-lived
60 herbaceous species (Jump and Penuelas 2005, Lenoir et al. 2008). The current accelerating
61 pace of climate change prevents long-lived tree species from responding fast enough to
62 changing environmental conditions, which already has negative consequences for forest
63 growth, response to disturbances, and, ultimately, management and conservation (Chuine
64 2010, Chmura et al. 2011). Considering both the pace of climate warming and habitat
65 fragmentation hindering the capacity of trees to migrate fast enough, some foresters suggested
66 that, without human assistance, most tree species will be unable to adapt to climate change
67 (Williams and Dumroese 2013). For several decades, forest managers and stakeholders
68 proposed adaptation strategies, such as assisted migration (Peters and Darling 1985), which
69 can be defined as the translocation of species or populations (*sensu* Thomas 2011) to facilitate

70 natural range expansion through a direct management response to climate change (Vitt et al.
71 2010).

72 For some species, studies have found that seeding or planting trees from source
73 locations that are several degrees Celsius warmer than the translocation site may mitigate the
74 negative impacts of climate change on tree growth and survival (Martin-Alcon et al. 2016,
75 Carbajal-Navarro et al. 2019, Frischbier et al. 2019, Saenz-Romero et al. 2021). Gustafson et
76 al. (2023) showed that under slight changes in climate, assisted migration may indeed
77 increase biomass production through longer growing seasons and CO₂ fertilization. However,
78 they also showed that under more severe climatic scenarios, assisted migration strategies fail
79 to mitigate the deleterious effects of moisture stress and increase respiration to the detriment
80 of productivity (see also Newaz et al. 2017). They concluded that assisted migration was
81 increasingly unable to maintain ecosystem goods and services with the increasing severity of
82 climate change. Benito-Garzon et al. (2013) also highlighted that the uncertainty related to
83 extreme climate events, such as extreme low temperatures, could potentially make the search
84 for southern locations with climatic conditions similar to future of northern populations of
85 trees extremely difficult. A number of studies have also stressed the limitations of assisted
86 migration for conservation reasons, such as the introduction of exotic and invasive species
87 (Pedlar et al. 2012, Saenz-Romero et al. 2021) or novel disturbance regimes facilitated by
88 translocated species (Alfaro et al. 2014). Thus, a number of ecological reasons that are likely
89 to impede assisted migration success have already been documented.

90 In the present forum paper, we aim at highlighting other important functional and
91 ecosystem limitations that have been overlooked, such as (1) the potential decrease in the
92 microclimatic buffering capacity of forest communities due to the decrease in facilitative
93 effects of forest canopies with changing species traits; (2) the increasing risk of changes in
94 disturbance regimes, in particular the increase in forest flammability; and (3) the potential

95 negative feedbacks of environmental changes on the climate change due in part to the
96 concomitant decrease in transpiration and the increase in albedo. Note here that our focus will
97 be on the translocation of new species but not new populations of species already occurring at
98 the translocation site.

99

100 **THE BUFFERING CAPACITY AND FACILITATION EFFECT OF CANOPIES ON**
101 **UNDERSTORY MICROCLIMATES AND SPECIES: THE IMPORTANCE OF TREE**
102 **SPECIES TRAITS**

103 The buffering effect of temperature fluctuations under forest canopies is a well-known and
104 well-studied property of forest ecosystems (Aussenac 1973, 2000, Chen et al. 1995, 1999,
105 Morecroft et al. 1998, Grimmond et al. 2000, von Arx et al. 2012). More recently, it has
106 gained popularity due to its importance for local microclimate regulation under anthropogenic
107 climate change (De Frenne et al. 2021). At a global extent, it has been demonstrated that the
108 buffering capacity of forest canopies decreases maximum temperatures in the understory by
109 4.1°C on average, while it increases minimum temperatures by 1.1°C on average, compared
110 with temperature outside forests (De Frenne et al. 2019). However, this benefit comes at the
111 expense of a significant increase in water consumption by trees and vegetation in general. For
112 example, during the 2003 heatwave in Europe, Saccone et al. (2009) observed that the
113 buffering and facilitative capacity of Alpine mountainous deciduous forests collapsed in
114 convex slopes because the water flow from the upper slopes was interrupted, which ultimately
115 impeded tree transpiration and thus decreased the buffering effect of temperature. In contrast,
116 in concave slopes with greater water flow and influx from adjacent streams, understory vapor
117 pressure deficit (VPD) and temperature remained low, facilitating the survival of tree
118 seedlings.

119 For all vascular plants, roots, stems, and leaves are interconnected by a dense network
120 of xylem conduit (generally vessels and tracheids in angiosperms and only tracheids in
121 gymnosperms), ranging from 10 to 256 μm in diameter (Olson and Rosell 2013, Pittermann
122 and Sperry 2003), that ends with an even denser and refined network of apertures at the leaf
123 surface, i.e., stomata. This network of tiny tubes and apertures forms continuous water columns
124 allowing water to move to the canopy of tall trees and shrubs according to the tension-cohesion
125 theory (Dixon 1894). Transpiration is activated when stomata in the leaves open to assimilate
126 carbon during photosynthesis, which generates a tension (negative pressure) at the leaf surface
127 that pulls water from the roots up to the leaves. Hence, transpiration by trees and shrubs is the
128 main mechanism that redistributes water from the soil to the atmosphere such that during this
129 process it cools down temperature in the understory during warm periods but also warms up
130 temperature during cold periods.

131 The buffering capacity of forest canopies on understory temperature is highly dependent
132 on environmental conditions and the functional traits of canopy tree species. It varies greatly
133 from tropical to boreal latitudes in wet climates, such that the cooling of mean and maximum
134 temperatures is more pronounced in wet tropical forests, where water availability is less limited
135 (De Frenne et al. 2019). The buffering effect of temperature under forest canopies also varies
136 more locally, in space and time, according to changes in rock types and soil fertility or in stand
137 structure (Michalet et al. 2023a). For instance, Zellweger et al. (2019) showed that canopy cover
138 increases the cooling effect on maximum temperature, until it reaches a threshold at 89% cover,
139 during summer in temperate deciduous forests across Europe. Similarly, Gril et al. (2023) found
140 that stand height is an important driver of the buffering capacity of forest canopies on
141 understory temperatures during the leaf-on period in temperate forests, such that taller stands
142 have a greater buffering capacity (Michalet et al. 2023a). Additionally, broadleaved trees, like
143 beech (*Fagus* spp.) and oak (*Quercus* spp.), are in general more efficient than coniferous trees,

144 like pines (*Pinus* spp.), at cooling understory temperature during hot days in summer (von Arx
145 et al. 2012, Gril et al. 2023). For instance, von Arx et al. (2012) showed that broadleaved forests
146 can moderate daytime microclimate about twice as much as pine forests. This is partly the
147 consequence of angiosperm vessels being larger than gymnosperm tracheids (Olson and Rosell
148 2013), which is reflected by a higher sapwood-specific hydraulic efficiency (higher
149 conductivity, K_s) and transpiration rate. As a structural tradeoff, the angiosperm hydraulic
150 network is often more prone to air spreading between large vessels (i.e., cavitation-induced
151 embolism) and therefore to water stress than the hydraulic network of gymnosperms. Spread of
152 embolisms in woody plants is characterized by the hydraulic trait P50 (i.e., the xylem pressure
153 inducing 50% loss of K_s) and occurs through pore openings in angiosperms (Sperry and Hacke
154 2004) and through ruptures in pit membranes in gymnosperms (tracheid air-seeding; Domec et
155 al. 2006, Delzon et al. 2010). Consequently, the most stress-resistant tree species are generally
156 gymnosperms and in particular from the Cupressaceae family (e.g., *Callitris*, *Cupressus*,
157 *Juniperus*, *Tetraclinis*; Larter et al. 2017). Hence, tree and shrub species traits related to K_s and
158 P50 are key parameters that will affect water transport and the buffering capacity of forest
159 canopies on understory temperature.

160 The concomitant reduction in temperature due to shading and the increase in relative
161 humidity (RH) due to higher plant transpiration are expected to decrease atmospheric VPD
162 (Aguirre et al. 2021). The dampening of temperature extremes and the reduction in VPD
163 matters because it allows to maintain more stable climatic conditions under forest canopies
164 over time, which may then facilitate the survival of understory species from the adverse
165 effects of extreme climatic events. For instance, Renaud and Rebetez (2009) found that
166 maximum temperatures were on average up to 5.2°C cooler under the canopy during the 11-
167 day European heatwave event in August 2003. On the long term, depending on local forest
168 dynamics that encompass changes in stand structure, species composition, and species

169 interactions, the velocity at which microclimate is changing under forest canopies may totally
170 differ from the velocity at which macroclimate is warming outside forests (Zellweger et al.
171 2020). An increase in stand height and canopy cover over time following stand development
172 from early to mature forest stages may induce a local trajectory of more intense microclimate
173 cooling in the understory while macroclimate is warming, which may facilitate the survival of
174 forest specialist species amidst unfavorable regional climates: the climatic basis for
175 microrefugia (Dobrowski 2011). On the contrary, forest disturbances, either natural (e.g.,
176 windthrow) or induced by human activities (e.g., forest management practices), may create
177 large gaps in the upper canopy and speed up microclimate warming locally such that it
178 surpasses the velocity of macroclimate warming, leading to a complete state shift in
179 community composition that will pay off the so-called climatic debt (Richard et al. 2021). In
180 relation with the different buffering and microclimatic effects described above, forest
181 canopies are pivotal for the dynamics of tree regeneration and of all the vegetation present in
182 the understory. More specifically, many examples showed the important role of forest
183 canopies to facilitate and improve tree regeneration (Muhamed et al. 2013, Guignabert et al.
184 2020). Using such nurse trees or shrubs turned out to be an important forestry practice to
185 improve seed germination and seedling establishment (Gómez-Aparicio et al. 2004, Padilla
186 and Pugnaire 2006). However, such kind of facilitative interactions are not ubiquitous (but see
187 McIntyre and Fajardo 2014), which stresses the need to precise the context where such effects
188 are Important for forest dynamics.

189 Specific structural and functional traits provide fundamental insights on how trees can
190 potentially adapt to a changing climate (Violle et al. 2007, Gordo et al. 2010). Tree species
191 growing along climatic gradients generally exhibit different leaf trait values (Dong et al. 2020).
192 For example, in wetter climates, species tend to have higher Ks and lower specific stem wood
193 density (SSD) as well as larger and thinner leaves with bigger stomata, which reflect how much

194 photosynthetic tissue a plant has per unit of resource invested (Niimenets 2010). Inversely, in
195 warmer and drier climates tree species bear more conservative traits characterized by denser
196 wood or high SSD as well as smaller leaves: lower leaf area (LA) and lower leaf area index
197 (LAI) with higher dry matter content in their tissue, and low stomatal conductance, which
198 altogether provides a conservative water use strategy (Abrams et al. 1994). Specifically, species
199 with small leaves have a larger boundary-layer conductance and higher rate of heat exchange
200 with their surroundings, allowing more effective transpirational cooling in hot or dry climates
201 (Gates 1968). This trade-off leads to predictable biogeographical patterns in leaf size (Montero
202 et al. 2016). Similar to leaf traits, wood traits can also vary significantly along climatic gradients
203 due to adaptations to environmental conditions (Zwieniecki and Secchi 2015). A drought
204 tolerance strategy based on a xylem highly resistant to embolism (low P50) comes at the cost
205 of higher SSD to cope with extreme xylem tensions (Hacke et al. 2001). Along precipitation
206 gradients, trees in drier areas develop denser xylem tissue with more negative P50, which helps
207 to maintain water uptake during drought periods. This is achieved by having smaller conduit
208 diameters (thus inducing lower Ks) and thicker cell walls, which prevent air bubbles from
209 forming and spreading throughout the conductive tissues (Johnson et al. 2022). Additionally,
210 in cooler climates trees generally have denser wood with narrow vessels to prevent freezing
211 damages.

212 Since the pioneer proposal of the stress gradient hypothesis (SGH; Bertness and
213 Callaway 1994), plant ecologists have studied facilitative interactions in stressed and
214 constrained systems. The SGH proposed that the frequency of plant-plant interactions should
215 switch from dominantly negative to dominantly positive as stress increases. Therefore, many
216 examples of facilitation by nurse trees or shrubs are found in Mediterranean systems with
217 important summer aridity (Gómez-Aparicio et al. 2005, Rodriguez-Garcia et al. 2011,
218 Heydari et al. 2023) or continental climates (Michalet et al. 2003, Saccone et al. 2009).

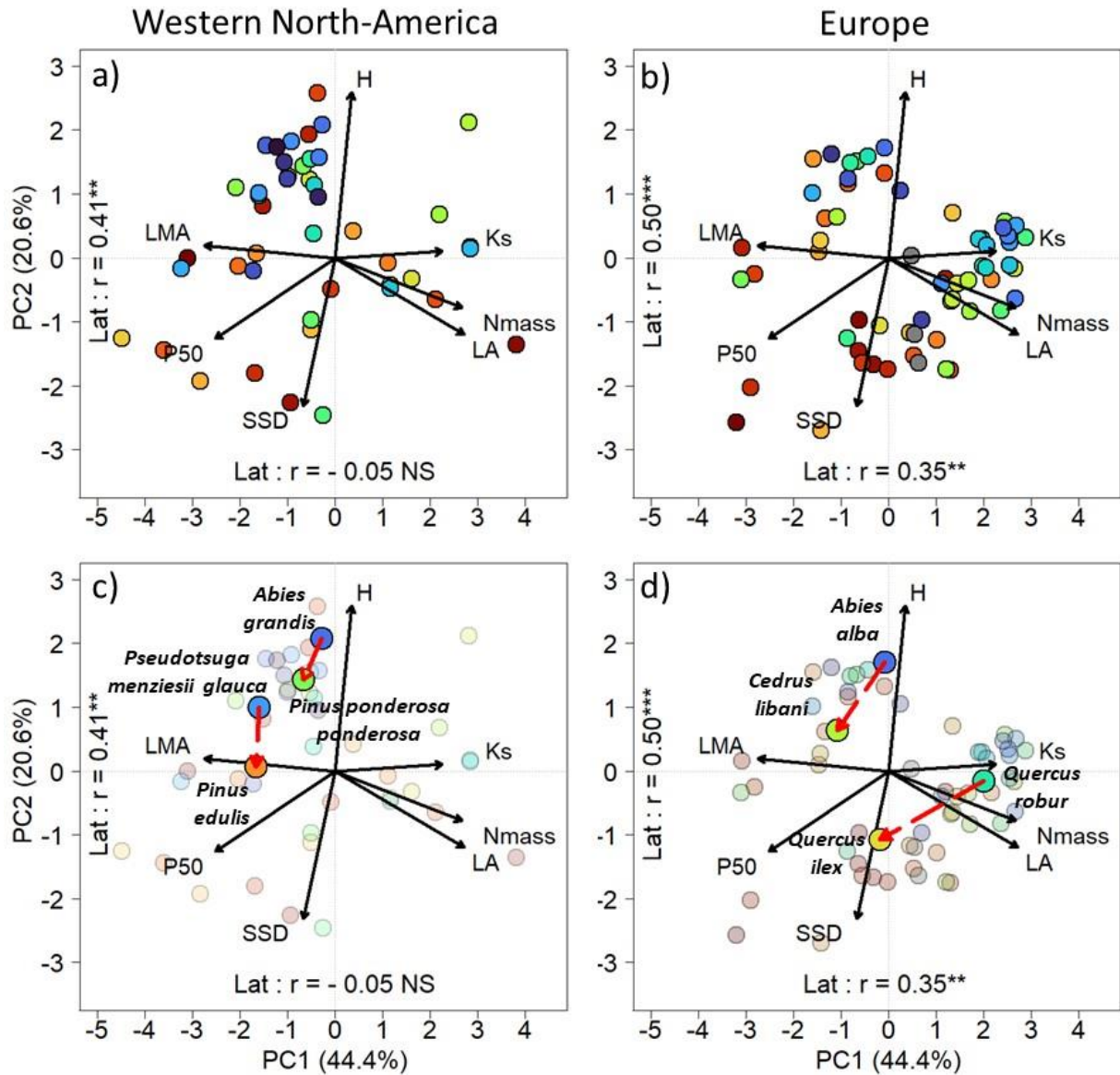
219 Nowadays, the ongoing climate change has several consequences regarding facilitative effects
220 in forest contexts. First, summer drought episodes are now common in more northern areas
221 and facilitation examples have started to accumulate in temperate climate regions (Pagès and
222 Michalet 2006, Martínez et al. 2010, Guignabert et al. 2020). Second, summer droughts
223 become more intense in southern areas, which raises the question of the maintenance of
224 facilitation in even more severe environments. Actually, in very dry systems or in case of very
225 important droughts, studies have shown a collapse of facilitation (Zhang et al. 2018), or even
226 a switch back to competition between species facing a very sparse water resource (Tielbörger
227 and Kadmon 2000, Maestre and Cortina 2004). Following these types of empirical evidence,
228 several authors proposed that facilitation should be the highest in moderately severe
229 environments, while competition or neutral interactions dominate in most severe
230 environments (Michalet et al. 2006, 2014, Holmgren and Scheffer 2010). Therefore, in the
231 northern hemisphere, it is possible to assume that facilitation would migrate northward with
232 climate change, being increasingly important for temperate forests with moderate summer
233 drought, and less frequent southwards in areas with more severe aridity (Saccone et al. 2009;
234 Holmgren and Scheffer 2010). Consequently, translocating tree and shrub species from
235 warmer and drier locations towards milder locations may disrupt and decrease facilitation
236 processes.

237 During the last two decades we also have strongly increased our knowledge of the
238 main ecological processes that drive facilitation in forest communities. Likely because
239 pioneer studies have recurrently found that facilitation was chiefly represented in dry
240 climates, there was a general tendency to consider that facilitation processes below trees and
241 shrubs were mostly driven by the increase in water availability, in particular through
242 mechanisms like soil hydraulic lift (Zou et al. 2005, Brooks et al. 2006, but see Ludwig et al.
243 2004, Prieto et al. 2011) or decreasing soil evaporation in the shade (Callaway 1995,

244 Holmgren et al. 1997, Castro et al. 2002, Gomez-Aparicio et al. 2004, Butterfield et al. 2016).
245 However, these mechanisms have not always been demonstrated in field studies since
246 evapotranspiration (in presence of shrub or trees) is expected to be higher than evaporation
247 alone without shrubs or trees. The active transpiration of shrubs and trees in the upper layers
248 of forest canopies is another pivotal mechanism to understand facilitative effects that we have
249 already mentioned earlier in the text. The active transpiration decreases VPD and temperature
250 extremes, as acknowledged by several studies focusing on facilitation processes (Gomez-
251 Aparicio et al. 2005, Saccone et al. 2009, Muhamed et al. 2013, Guignabert et al. 2020,
252 Aguirre et al. 2021, Michalet et al. 2023a). This understanding of facilitation processes in
253 forest ecosystems allows to predict that facilitation in temperate climates will likely depend
254 on the ability of trees species to mitigate understory microclimate, i.e., to decrease VPD and
255 cool down high temperatures. Therefore, the translocation of tree species from Mediterranean
256 climates that might have a lower ability to buffer understory microclimates than temperate
257 species would therefore decrease such facilitative effects, in relationships with their functional
258 traits and syndromes – see paragraph below regarding the functional difference of species
259 from warmer and drier climates.

260

261 **THE FUNCTIONAL BIOGEOGRAPHY OF SPECIES TRAITS WILL LIKELY**
262 **DETERMINE CHANGES IN FOREST BUFFERING CAPACITY AND**
263 **FACILITATIVE EFFECTS WITH ASSISTED MIGRATION**



265

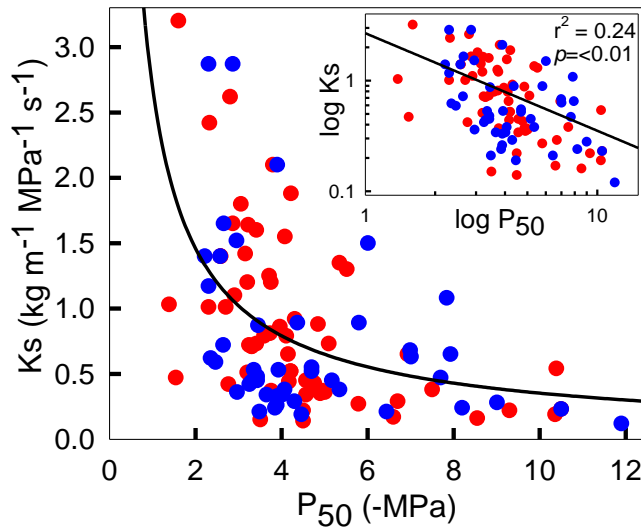
266 **Figure 1.** Outputs of the principal component analysis (PCA) conducted on seven functional
 267 traits of 106 species from western North America (**a** and **c**, 45 species) and Europe (**b** and **d**,
 268 61 species). Upper panels (**a**, **b**) show all species of each continent, whereas lower panels (**c**,
 269 **d**) show two examples of functional trajectories induced by possible assisted migration per
 270 continent; (**c**) For western North America: *Abies grandis* replaced by *Pinus ponderosa* var.
 271 *ponderosa* in the coastal mountains, and *Pseudotsuga menziesii* var. *glauca* replaced by *Pinus*
 272 *edulis* in the Rocky Mountains; (**d**) For Europe: *Abies alba* replaced by *Cedrus atlantica* or
 273 *Cedrus libani* in the highlands and *Quercus robur* replaced by *Quercus ilex* or *Quercus*

274 *rotundifolia* in the lowlands. In the four panels each dot corresponds to a different species and
275 arrows show correlations of traits with PCA axes. A single PCA was performed for all species
276 but results for the two continents are split on different panels. The first principal component
277 (PC1) opposes conservative species (high Leaf Mass Area-LMA, low leaf N concentration-
278 Nmass) having lower Ks on the left to acquisitive species on the right. The second principal
279 component (PC2) opposes taller species (high H values) with low wood density (i.e., specific
280 stem density, SSD) on the top to short species with high SSD on the bottom of the panels.
281 Resistance to cavitation (P50) and leaf area (LA) are correlated to both PC1 and PC2. The
282 color gradient used for species symbols indicates the latitude of the southern limit of each
283 species distribution range (purple is for the lowest latitudes and dark blue for the highest
284 latitudes, see Supplementary Information SI-1 for precise color legend and species list with
285 traits values). Pearson correlation coefficients for American and European species between
286 their southern latitude limits and each PC are shown on the bottom (first component) and left
287 (second component) with corresponding statistical significance (***, $P < 0.001$; **, $P < 0.01$).
288 Correlation tests with the latitude of their northern limits or central position of their
289 distribution range gives similar results. Traits data are extracted from the TRY database
290 (Kattge et al. 2016) for H, LA, LMA, Nmass, and from Hammond et al. 2020 and Domec's
291 personal database for Ks and P50. The PCA and correlations were run with R version 4.0.4 (R
292 core team, 2020).

293 Previously, we showed that forest buffering capacity and facilitative effects are highly
294 dependent on climate conditions and the functional traits of canopy tree species. Thus, we may
295 infer potential changes in the buffering capacity and facilitation of forest ecosystems through
296 assisted migration by knowing the biogeographical origin of the translocated tree species and
297 their traits. We chose to assess the variation of functional traits of dominant trees and tall shrubs
298 from western North America and Europe because most assisted migration studies have been

299 conducted in these two continents. Additionally, these two biogeographical regions are known
300 to have different tree functional compositions despite very similar latitudes (from subtropical
301 to boreal latitudes) and close climatic conditions due to their similar positions on the east side
302 of the Pacific and Atlantic Oceans, respectively (Waring and Franklin 1979, Michalet et al.
303 2021). The outcomes of the PCA we performed on seven functional traits from 106 species
304 from western North America and Europe (including North-Africa and the Near East) indicated
305 the existence of two strong independent dimensions of trait variation (Fig. 1), consistent with
306 the literature regarding plant traits (Diaz et al. 2004, 2016, Maynard et al. 2022, Michalet et al.
307 2023b). Regardless of the continent, the first principal component (PC1) represented the leaf
308 economic spectrum (LES; Wright et al. 2004) opposing on the negative side of the axis
309 conservative strategies characterized by high LMA and low P50 from acquisitive plants having
310 fast returns on investment of nutrients *versus* plant physiology (high N_{mass}, LA, and K_s) on
311 the positive side of the axis. Note that LMA and LA were closely negatively correlated because
312 the structural component of LMA is highly dependent on LA. The PCA also showed that P50
313 and K_s were clearly represented and diverging along PC1, indicative of a negative feedback
314 between hydraulic safety and hydraulic efficiency, with a similar trend between both continents
315 (Fig. 2). For the present species, the migration of more drought resistant species would then be
316 accompanied by a sharp decrease in hydraulic efficiency. Because plant hydraulic efficiency
317 controls plant water use (Domec et al. 2017; Johnson et al. 2022), we can then expect a negative
318 impact of these new species on transpiration rates. When transpirational water is released from
319 the leaves and evaporates, it absorbs heat energy from the surrounding environment, leading to
320 a cooling effect. Even though newly planted drought-resistant species will use less water and
321 transpire less, they will then also limit the regulation of canopy energy. For example, in urban
322 settings, air temperature gradient between outside and inside tree canopy dropped by 1.6°C in
323 *Tilia cordata* trees compared to less than a degree for the more drought resistant species *Robinia*

324 *pseudoacacia* (Rahman et al. 2019). This difference was due to *Tilia cordata* transpiring more
 325 than *Robinia pseudoaccacia* as a consequence of higher LA and a more efficient water transport
 326 system.



327

328 **Figure 2.** Hydraulic safety–efficiency relationship for all 106 species used in the principal
 329 component analysis (PCA) (see Fig. 1). Efficiency is represented by sapwood-specific
 330 hydraulic efficiency (K_s) and safety by the pressure at which 50% loss of K_s occurs (P_{50}) for
 331 western North American (blue, ●) and European species (red, ●), respectively. Insert shows
 332 the log-transformed relationships.

333 The second principal component (PC2) was related to species size with tall species on
 334 the positive side and short species on the negative side of the axis. This plant-size axis is also
 335 certainly correlated to stem diameter, bark thickness, crown surface and LAI, all these metrics
 336 being interconnected by allometric relationships (Smith et al. 1991, Turner et al. 2000;
 337 Fréjaville et al 2018). The strong negative correlation between plant height and SSD is likely
 338 driven by species with very high wood density such as *Juniperus* or *Quercus* which are also
 339 shorter species in stature, and by species with low wood density such as *Abies* or *Populus*,
 340 that are generally taller.

341 Interestingly, correlation values between species scores along PC1 or PC2 and the
342 southern latitudinal limits of their expansion ranges were high in both continents, at least for
343 PC2, while the correlation was only significant in Europe for PC1. The reduction of plant size
344 (and LAI) with decreasing latitude observed in both continents from temperate to
345 Mediterranean climates (Fig. 1) was expected because plant size is strongly modified and
346 reduced in drier climates (Joswig et al. 2022). Noteworthy, all microclimatic effects
347 mentioned above are certainly related to plant size: a taller tree having a higher LAI will
348 intercept more light, transpire more and generate a higher buffering capacity. Actually, plant
349 effects and especially plant facilitative effects through microclimate improvement are known
350 to be related to plant size (Peláez et al. 2019, Guignabert et al. 2020, Randé et al. 2022).

351 In contrast, for PC2, we found a significant correlation between latitude and the LES
352 only in Europe (Fig 1b), with species from southern areas in Europe being more conservative
353 regarding resource acquisition and species from northern areas in Europe being more
354 acquisitive (Wright et al. 2004, Reich 2014). This corresponds to a shift from deciduous
355 temperate forests to evergreen Mediterranean forests from northern to southern latitudes in
356 Europe. This shift was not observed in western North America because of the dominance of
357 evergreen forests at both latitudes on the west side of the North American continent (both in
358 coastal oceanic mountains and the continental Rocky Mountains, Michalet et al. 2021). We
359 thus may expect stronger functional shifts and changes in buffering capacity and facilitation
360 processes of forest canopies with assisted migration in Europe than in western North America.
361 Indeed, in Europe both plant size and growth traits will be affected, whereas only plant size
362 traits will change in western North America. These differences in functional shift between
363 both continents under assisted migration frameworks can be expected and clearly visible in
364 Fig. 1c and Fig. 1d (vector changes in the functional space of the PCA). Indeed, we found
365 mostly vertical shifts in western North America (from *Abies grandis* to *Pinus ponderosa* var.

366 *ponderosa* in the coastal mountains and *Pseudotsuga menziesii* var. *glauca* to *Pinus edulis* in
367 the Rocky Mountains), *versus* oblique shifts in Europe (from *Abies alba* to *Cedrus libani* in
368 the highlands and even more for *Q. robur* to *Quercus ilex* in the lowlands). Because
369 conservative species have lower metabolic rates and photosynthetic activity, their
370 transpiration is reduced (Wright et al. 2004, Sack et al. 2013), which strengthens the lower
371 buffering capacity of southern European species to improve air temperature and relative
372 humidity (RH) in the understory of future northern forests. Having smaller surface area (lower
373 LA and thicker leaves, i.e., higher LMA; Fig. 1) would also limit hydraulic efficiency (lower
374 Ks), water transport capacity and, thus, decrease the cooling effect by transpiration, more in
375 Europe than in western North America. The differences in traits of tree species transferred to
376 wet and cold climates will probably not acclimate fast enough to new conditions, which
377 would probably have significant negative implications on climate buffering effect of future
378 forest canopies, in particular in Europe.

379 In summary, in temperate forests, canopy effects provide an array of positive effects
380 by the direct modification of important factors such as light, temperature, VPD and nutrients
381 (Muhamed et al. 2013, Blondeel et al. 2020). These effects likely contribute to the resilience
382 of forest systems in face of the ongoing climate change marked by more frequent and intense
383 summer droughts. Using assisted migration focusing only on criteria based on cultivated tree
384 productivity can jeopardize these effects, leading to lighter and thus drier forest systems. In
385 Europe, the more conservative status of southern species regarding the LES may increase
386 these negative effects and raises also the question of litter quality, nutrient cycling and
387 productivity on the long term.

388 In addition, the outcome of plant-plant interactions not only depends on plants
389 producing the facilitative effects, but also on the sensitivity of beneficiary plants to these

390 facilitative effects (Delerue and Michalet 2022). It is generally agreed in the literature that
391 there is a tradeoff between light requirements and drought tolerance for temperate forest
392 species (Niinemets and Valladares 2006). Light-demanding species develop in more open
393 areas and, depend less on climate stress mitigation by a dense canopy cover. Reversely,
394 shade-tolerant species are able to develop under the cover of nurse plants and benefit more
395 from drought stress mitigation for their growth (Gómez-Aparicio et al. 2008). Therefore,
396 shade-tolerant and drought-intolerant species are rationally found in forests with denser
397 canopies, i.e, made of bigger trees with important LAI, such as in northern temperate forests
398 across several continents. This eco-evolutionary strategy stresses the risk of a decrease in
399 understory plant facilitation when using species originating from warmer and drier climates in
400 the context of assisted migration because of the reduction of the facilitative effects of canopy
401 trees acting as benefactor species.

402

403 **TREE SPECIES TRANSLOCATION FACILITATES THE FLAMMABILITY OF** 404 **ECOSYSTEMS AND LANDSCAPE THROUGHOUT PLANT TRAITS**

405 The deliberate translocation of tree species for assisted migration indirectly adds to the
406 complexity of climatic changes. Trees are translocated between regions or imported from
407 other continents or realms because it is assumed they are better adapted to future climate to
408 maintain ecological services. In addition, climate change also modifies the interactions
409 between forest ecosystems and disturbances (e.g., windthrow, insect outbreak, wildfire),
410 which can in turn be transformed by new or altered disturbance regimes facilitated by the
411 translocated species through changes in tree traits (Alfaro et al. 2014, Coop et al. 2020). The
412 disturbance regime involves the frequency of events, but also the intensity, duration, and
413 extent of such events. These parameters control the severity, which is the ecological aftermath

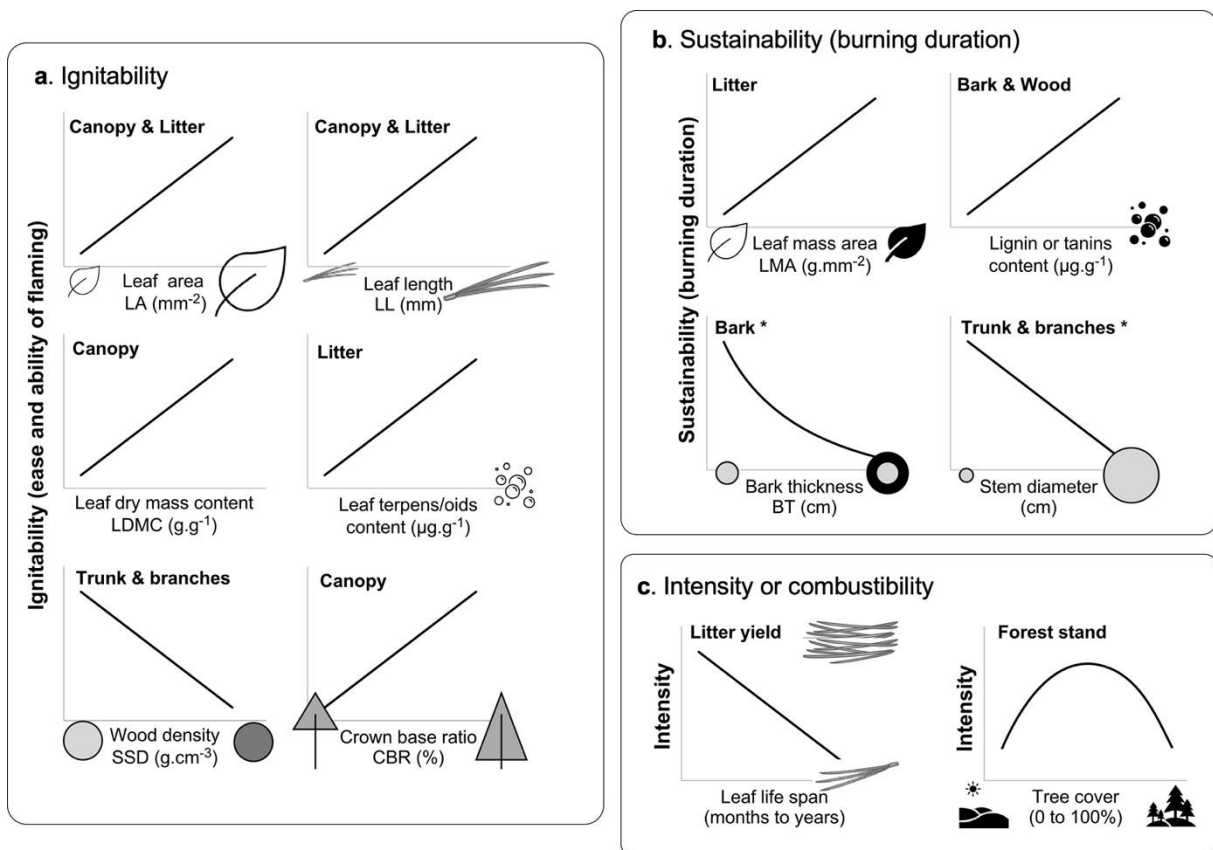
414 of a disturbance. Therefore, ecosystems transformed by the novel climates and translocated
415 tree species are also altered by the new disturbance regime, therefore producing novel forest
416 ecosystems.

417 The issue of new disturbance regime, such as wildfire (SI-2) is rarely considered by
418 studies on assisted migration. When considered, the aftermaths of disturbances are almost
419 never assessed in the framework of assisted migration (Buma and Wessman 2013, Yazzie et
420 al. 2018). Wildfire, that is the main disturbance on Earth (Bond et al. 2005, Bowman et al.
421 2009) with decadal to centennial consequences (Overpeck et al. 1990, Genries et al. 2009,
422 Fletcher et al. 2014), worries stakeholders and forest managers since the burning risk rises
423 with changes in climate and land uses (Moritz et al. 2014, Sayedi et al. 2023).

424 Popovic et al. (2021) have synthesized the traits within the ‘plant economic spectrum’
425 (Reich 2014) that promote flammability, notably ignition and sustainability (burning
426 duration), which are helpful traits to assess fire risks (Fig. 3). In short, trees facilitating
427 flammability present high LA, leaf length (LL), and leaf dry mass content (LDMC), and
428 present elevated terpenoids’ content (“terpenes”), as well as tall length crown (or canopy)
429 relative to total tree height (i.e., the crown base ratio, CBR). Traits such as LA, LL, LDMC,
430 and terpenes stimulate the ignition of canopy or litters. The sustainability of fire, central for
431 fire spread, depends on (i) abundant but also ventilated litter layer composed of leaves with
432 high LMA and LL, (ii) high tannins in the fine fuel component (Cornelissen et al. 2017), and
433 (iii) low bark thickness (BT) and SSD of fine fuel and understory of trees and shrubs (Fig. 3).
434 The leaf life span (LLife) also indirectly acts on the quality of the litter layer: the shorter the
435 LLife (a few months *versus* several years), the more the litter yield, everything else being
436 equal (Blarquez et al. 2012). Importantly, LLife and LMA covary in the same way (Harper et
437 al. 2016). Stand flammability increases with high LDMC, LMA, terpenes, fine fuel, and

438 intermediate tree-cover but decreases with high BT, SSD and stem diameter (Fréjaville et al.
 439 2013, 2018; Fig. 3).

440 These tree traits generally correspond to needleleaf species often used in assisted
 441 migration programs, for instance *Pinus species*, which have high flammability traits (LL,
 442 terpenes, LDMC, SSD, LLS), as well as Mediterranean *Abies species*, *Cedrus atlantica*,
 443 *Pseudotsuga menziesii* (CBR, LDMC, SSD, BT), or *Cupressus arizonica* (terpenes, CBR,
 444 BT). Broadleaved species abundantly translocated and presenting a high fire risk are for
 445 instance *Eucalyptus species* (LMA, LL, Terpenes, LDMC, BT, SSD, CBR). Independently
 446 from species, the flammability also depends on stand age (McCarthy et al. 2001, Zylstra et al.
 447 2018) and tree density (Archibald et al. 2009, Fréjaville et al. 2016).



448
 449 **Figure 3.** Theoretical framework linking ‘plant economic spectrum’ to flammability
 450 components of canopy (live leaves), litter (dead leaves), stems (wood, bark) and tree stand
 451 traits: (a) ignitability; (b) burning sustainability; and (c) burning intensity. When it comes to

452 stem, it is not tree trunks that generally burn, but woody debris and chiefly the fine woody
453 debris; the finer the debris (stem diameter) and lower stem wood density (SSD), the better the
454 flammability. To sum-up, fire spread is fueled by fine woody debris (twigs) and well-
455 ventilated leaf litter of needleleaf species in intermediate stand density, with crown connected
456 to the ground (i.e., creating a fuel continuum).

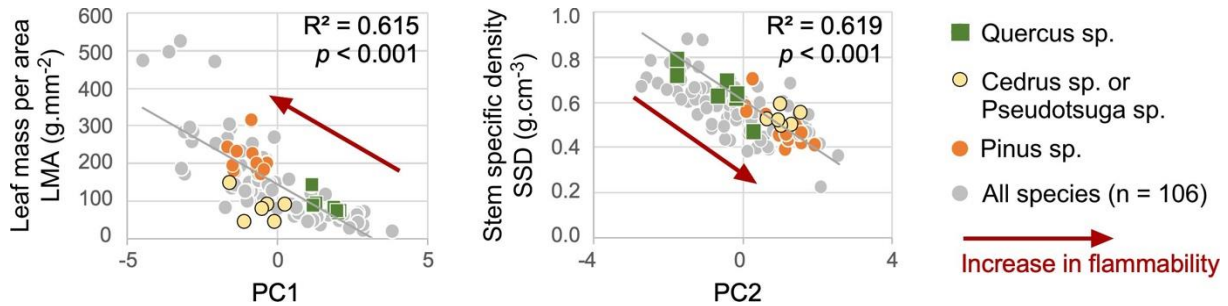
457 *Pinus* species are iconic because some are fire-prone, meaning that they both facilitate
458 wildfire and are resilient to wildfire. These fire-prone pines (e.g., *P. contorta*, *P. pinaster*, *P.*
459 *radiata*, *P. brutia*) were broadly introduced in many countries long before the emerging
460 concept of assisted migration. Model-based studies questioning the consequences of
461 translocated pines have included fire in the equation and demonstrated that planted fire-prone
462 trees can lead to abrupt non-linear environmental changes, notably for fire risks (Higgins and
463 Richardson 1998; Stevens and Beckage 2009, C3bar-Carranza et al. 2014). Interestingly, in
464 boreal ecosystems, it has been shown that preferring low flammable trees (i.e., broadleaved,
465 e.g., *Populus tremuloides* or *Betula papyrifera*, instead of needleleaf, e.g., *Pinus banksiana* or
466 *Picea mariana*) could mitigate the climate effect on fire regimes (Girardin and Terrier 2015),
467 which is supported by empirical paleoecological studies in Canada (Girardin et al. 2013) or in
468 Scandinavia (Ohlson et al. 2011). *Pinus banksiana*, *Picea mariana* and *Populus tremuloides*
469 are recommended by programs of assisted migration in Canada (e.g., Savva et al. 2007, Gray
470 et al. 2011, Huang et al. 2013), and the forest industry have different interests in these species
471 for plywood, pupwood, timber or ligno-chemistry. Industrial choices of translocated species
472 should result unimportant, massive and contrasting socio-environmental issues for decades, at
473 least, in terms of fire risks and their aftermaths (e.g., CO₂ release) knowing that 76% of
474 burned boreal forests in North America are those dominated by *Pinus banksiana* or *Picea*
475 *mariana* (Flannigan 2015).

476 There are frequent fires in *Pinus pinaster* plantations of southwestern France, notably
477 in 2002, where this species was translocated from southern latitudes in the nineteenth century
478 for improving forest productivity on very poor drained sandy soils (Carcaillet et al. 2022).
479 Such fires enhanced by warmer climatic conditions globally and favored by historic
480 translocations of the highly flammable *Pinus* species before the onset of climate change
481 illustrates the increasing facilitation of fire risk by flammability enhancement of ecosystems
482 and landscapes (Fig. 4) towards higher latitudes if very flammable *Pinus* species are used to
483 replace deciduous *Quercus* forests in the name of sustainable biomass production in response
484 to climate change, as proposed by French foresters (Bouillie 2021). This flammability
485 facilitation is particularly exacerbated in Europe, due to the strong correlation existing
486 between latitude and LMA (see PC1 in Fig. 4). The risk of increasing flammability is
487 certainly much lower in western North America due to the absence of such significant
488 correlation, and because North American ecosystems already coevolved with more intense
489 fire regimes than in Europe (Rogers et al. 2015). The increase in SSD with decreasing latitude
490 (towards more negative values along PC2; Fig. 1 and Fig. 4) may instead decrease
491 flammability in both continents. We thus predict that assisted migration will poorly modify
492 flammability in western North America due to the overwhelming dominance of evergreen
493 forests both in coastal and continental mountains (Waring and Franklin 1979, Michalet et al.
494 2021). In contrast, in Europe, increasing LMA and decreasing SSD in plantations will have
495 negative effect by facilitating ecosystem and landscape flammability notably when *Pinus* is
496 translocated further north (Fig. 4).

497 Assisted migration and wildfire are mentioned together in papers questioning the
498 adaptation of land cover to climatic changes (SI-2). Yet, the risk of changes in disturbance
499 regimes resulting from assisted migration is still a gap of knowledge (Yazzie et al. 2018). The
500 concept progresses blindly by offering a solution of ‘sorcerer's apprentice’ to forest managers

501 and stakeholders, with unassessed potential environmental risks (e.g., wildfires, diseases) and,
502 finally, a risk of providing less ecosystem services than expected to cope with future climate
503 changes.

504



505

506 **Figure 4.** Example of translocation effects of needleleaf species (*Pinus*, *Cedrus*,
507 *Pseudotsuga*), frequently used in assisted migration, in place of deciduous *Quercus* species
508 threatened by global warming. Species were selected from the dataset used for the PCA (cf.
509 Fig. 1; 106 species); the chosen traits (LMA, SSD) were selected because of data availability
510 from the TRY dataset and because these traits are well correlated to the PCA axes ($p < 0.001$)
511 (see Fig.1). The arrows show that the translocation of *Pinus* in place of *Quercus* should
512 produce more flammable forest stands (higher LMA, KS-test, $p < 0.001$; lower SSD,
513 $p < 0.001$). The use of *Cedrus* or *Pseudotsuga* instead of *Pinus* is intermediate because wood
514 density (SSD) would result in outputs close to *Pinus* (KS-test, $p = 0.07$) but LMA would
515 remain unchanged compared to *Quercus* ($p = 0.80$). Planting *Pinus* to substitute *Quercus*
516 poses facilitates wildfires (risk), but planting *Cedrus* or *Pseudotsuga* to substitute *Quercus*
517 would be less risky, based on these two canopy and litter flammability traits (see Fig. 3).

518

519 POTENTIAL FEEDBACKS ON CLIMATE CHANGE INDUCED BY ASSISTED 520 MIGRATION

521 The potential feedbacks induced by assisted migration on climate change, throughout biotic
522 and environmental modifications, are complex and can vary depending on many factors,
523 including the specific species involved during translocation and the location and the timing of
524 the assisted migration (Aubin et al. 2011). Natural ecosystems are coupled to the land–
525 atmosphere exchanges through important biogeophysical mechanisms that control the
526 partitioning of the surface energy fluxes into latent (plant transpiration) and sensible fluxes
527 and the development of convective cloud formation and regional precipitation patterns
528 (Manoli et al. 2016). Changes in LAI alone can have a direct impact on plant transpiration
529 (Brown et al. 2005) and on canopy water storage capacity linked to rainfall, and thus on the
530 seasonality of the direct evaporation of the plant-intercepted precipitation, which can
531 represent up to 35% of an ecosystem water balance (van Dijk et al. 2015). As describe before,
532 rear-edge populations (i.e., low latitude and warm) are water stress-adapted and fire-tolerant,
533 and as mentioned before generally bear sparse canopy characterized by high LMA (Fig. 4),
534 low LA and LAI (Dong et al. 2020).

535 Weather parameters are sensitive to the vegetation state and particularly to the albedo
536 (i.e., the measure of how much more or less solar radiation is reflected from vegetation
537 surfaces), that is a function of LAI and the optical properties and geometric arrangement of
538 leaf and wood tissues (Bright et al. 2015). Climatic feedback involving the albedo is one of
539 the important parameters that affects the available surface energy within the canopy and thus
540 controls the land surface radiative balance (Pielke and Avissar 1990, Chen et al. 2016).
541 Because albedo varies between different species due to variations in canopy morphology and
542 leaf-surface properties, it is expected that the deliberate translocation of tree species to new
543 geographic locations to help mitigation under changing environmental conditions would
544 change the reflectivity of forest canopies, which can in turn affect the amount of sunlight
545 absorbed by the Earth's surface. There is limited research on the specific impacts of assisted

546 tree migration on the reflectivity of forest ecosystems, but we know that changes in vegetation
547 types and cover through the introduction of non-native tree species can alter the albedo of
548 forest ecosystems (Myhre and Myhre 2003). For example, enhanced surface albedo by
549 deforestation, fires or by increasing the proportion of broadleaf tree species through forest
550 management (such as *Populus tremuloides* in North America) resulted in positive feedbacks
551 to climate change (Lee et al. 2011, Bright et al. 2017; Sayedi et al. 2023). Reversely, if new
552 species with a higher LAI or lower SLA (= high LMA) are translocated, the albedo of the
553 ecosystem is expected to decrease because the denser canopy will modify the shortwave
554 radiation budget (Räsänen and Smolander 2008). Results from the PCA indicated that
555 moving species to higher latitudes in western North America would not change traits
556 associated with the LES, whereas in Europe we should expect a switch in several key traits
557 (Fig. 1). Therefore, in Europe, the introduction of stress-tolerant species such as for example
558 *C. libani* or *C. atlantica* bearing thicker and darker-colored leaves (higher LMA) to replace *A.*
559 *alba* (Fig. 1d) is expected to decrease not only the tree cooling effect as discussed previously,
560 but also the overall albedo because more sunlight would be absorbed, leading to a lesser
561 reflection of solar radiation and a warming effect on canopy surfaces, which could be
562 considered an inefficient mitigation measure. However, it is important to note that the effects
563 of assisted migration on physical and structural properties are complex and can vary
564 depending on the species involved, the environmental conditions of the new habitat, and the
565 interactions between the introduced exotic species and the native species (Prater and DeLucia
566 2006). Reforestation projects inducing a positive radiative forcing from an albedo decrease
567 could also potentially cool the surface due to an increase in transpiration and turbulent mixing
568 of air (Rotenberg and Yakir 2010). Therefore, the potential impacts of assisted migration on
569 albedo and other ecosystem processes should be carefully evaluated on a case-by-case basis
570 before any management decisions are made.

571 We have shown in the previous part that assisted migration is very likely to increase
572 forest flammability, particularly in Europe because North American forests are generally
573 more naturally adapted to intense and frequent fires (Rogers et al. 2015). Broadleaved tree
574 species are less likely to burn than species with thick leaves (high LMA) and more drought-
575 adapted species (Bernier et al. 2017). Consequently, there could be a risk to replace deciduous
576 broadleaved-stands by evergreen coniferous forests that are about 24 times more likely to
577 burn (Girardin et al. 2015). Increasing the risk of wildfires (wildfire frequency and spread)
578 through decreased deciduous broadleaved trees composition would then be detrimental to
579 reducing greenhouse-gas emissions (Kasischke et al. 2010).

580 Finally, assisted migration and the changes in species composition could potentially
581 impact the carbon cycle by changing the rate of ecosystem carbon uptake and respiration
582 (Jandl et al. 2007) or fire-based mineralization (Kasischke et al. 2010). Changes in species
583 composition by translocating species with higher LMA values and lower canopy size should
584 result in lower K_s (Fig. 1) and photosynthetic rates, thereby impacting forest productivity and
585 carbon sequestration. Again, because of the strong correlation between the latitude and the
586 LES axis (PC1) of Fig. 1, assisted migration is expected to have a stronger negative effect on
587 carbon uptake in Europe than in western North America. Finally, studies suggesting that
588 carbon sinks should increase as forests currently growing under warmer climates expand into
589 cold climates assume that forest productivity would increase under future climate (White et al.
590 2000). However, it seems that in the short term, the growth of new species could be
591 negatively affected if traits such as LMA or N_{mass} are not adapted to the areas targeted by
592 tree translocations (Poorter and Bongers 2006, O'Neill et al. 2008), and the climate advantage
593 at the translocated sites may actually accelerate the decrease in forest cover and productivity
594 therein (Morin et al. 2018).

595

613 change and the time span that is needed for trees to migrate through natural dispersal will
614 have important negative consequences on the buffering capacity of forest canopies on
615 understory microclimates and, thus, likely decrease facilitation of understory species that
616 ultimately may have strong consequences on tree regeneration. These negative effects are
617 expected to be the strongest in Europe because of both decreasing tree size and the increasing
618 conservation strategy of tree species towards lower latitudes (Fig. 5). In contrast, in west
619 North America only tree size should be affected by the translocation of southern species,
620 because of the scarcity of deciduous species at temperate latitudes. For example, translocating
621 broadleaved tree species from lower latitudes (such as in Europe *Q. robur* by *Q. ilex* or
622 *Quercus rotundifolia*, see Fig. 1d and Fig. 5) with leaf and hydraulic traits that are adapted to
623 warmer and drier conditions (e.g., thicker leaves and thinner xylem vessels) is likely to
624 reduce, on the long term, the Ks of the novel forest canopy at the translocated site, thus,
625 limiting the redistribution of water towards the upper atmospheric layer through transpiration,
626 which in turn may locally decrease the buffering effect of temperature under forest canopies.
627 Not only will this reduce the cooling effect on understory temperature that facilitates the
628 survival of understory species, but it may also alter the general circulation of water and
629 precipitation regimes by potentially reducing the local amount of precipitations.

630 This difference between continents may explain why assisted migration has first been
631 proposed by North American foresters, resulting abundant scientific literature in USA and
632 Canada (Benomar et al. 2022), and should warn European foresters to adapt their
633 management strategy to the specificity of European forests. Additionally, assisted migration is
634 very likely to increase fire risks, notably in Europe due to the increase in LMA (a trait
635 strongly involved in plant flammability) with decreasing latitude. Finally, changing canopy
636 species traits, forest buffering and facilitative abilities and increasing fire risks may have
637 strong feedback effects on global change, particularly due to increasing forest albedo and CO₂

638 emissions and modifying the water cycle through changing evapotranspiration rates. Hence,
639 by being too much proactive in trying to adapt tree species composition of tomorrow's forests
640 to future climate, we may initiate a positive feedback loop that will render the translocated
641 sites drier on the long term while the initial motivation was to save water by reducing tree
642 transpiration.

643 Instead of trying to establish novel forest canopies by translocating tree species and
644 populations adapted to warmer and drier conditions with a risk to accelerate climate change,
645 an alternative solution would consist in managing the vertical structure and layering of the
646 existing forest canopy to maintain a sustainable water cycle between soil and the atmosphere.
647 For instance, a more complex vegetation layering of the upper canopy that not only includes
648 several tree species but also mixes young with old adult trees together with rich shrub and
649 herb layers in the understory may increase stand resistance and resilience to climate change
650 and extreme events such as droughts. Recently, Au et al. (2022) showed that young adult trees
651 are less resistant but more resilient to droughts than their older counterparts, suggesting that a
652 good mixture of young and adult trees may provide a good balance for forest stands to both
653 resist and be resilient to droughts. In general, complexifying forest canopy structure will help
654 to maintain a sustainable buffering effect of temperature and water balance under forest
655 canopies which will then facilitate the survival of local populations amidst unsuitable regional
656 climate and potentially buy more time for forest biodiversity to adapt to climate change. In
657 short, because of plant size reduction (in both continents) and occurrence of more
658 conservative species (in Europe only) in southern latitudes, assisted migration will likely
659 decrease the ability of dominant tree to provide buffering and facilitative effects leading
660 ultimately to a lower resilience of forest systems to the ongoing climate change.

661

662 **AUTHORS' CONTRIBUTIONS**

663 RM conceived the paper. FD and JCD collected plant traits from databases. CC, FD and JCD
664 conducted statistical analyses. JL led the section on the buffering capacity of forest canopies.
665 CC led the section on the changes in disturbance regimes. JCD led the section on tree
666 physiology. RM, CC, FD, JCD and JL wrote the manuscript, and all approved the final text.

667

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678

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