1 **Modes of climate variability bridge proximate and evolutionary mechanisms of masting**

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8

9 **Abstract**

10 There is evidence that variable and synchronous reproduction in seed plants (masting) correlates to modes of

11 climate variability, e.g., El Niño-Southern Oscillation, North Atlantic Oscillation. In this perspective, we explore

12 the breadth of knowledge on how climate modes control reproduction in major masting species throughout

13 Earth's biomes. We posit that intrinsic properties of climate modes (periodicity, persistence, trends) drive

14 interannual and decadal variability of plant reproduction, as well as the spatial extent of its synchrony, aligning

15 multiple proximate causes of masting through space and time. Moreover, climate modes force lagged but in-

16 phase ecological processes that interact synergistically with multiple stages of plant reproductive cycles. This set

17 up adaptive benefits by increasing offspring fitness through either economies of scale or environmental

18 prediction. Community-wide links between climate modes and masting across plant taxa suggest an evolutionary

19 role of climate variability. We argue that climate modes may "bridge" proximate and ultimate causes of masting

20 selecting for variable and synchronous reproduction. The future of such interaction is uncertain: processes that

21 improve reproductive fitness may remain coupled with climate modes even under changing climates, but

22 chances are that abrupt global warming will affect Earth's climate modes so rapidly as to alter ecological and

23 evolutionary links.

24

25 **Keywords**

26 Climate change, disturbance ecology, ENSO, environmental prediction, Moran effect, reproduction

Introduction

In 1997-1998, major plant reproductive events took place in many regions of the world, including tropical forests in South-East Asia [1,2] and Central America [3,4], temperate forests of China and Japan [5,6], and boreal forests of North-West and North-East America [7,8]. The spatio-temporal synchrony of seeding in plants displaying variable reproduction (masting) has long interested ecologists [9]. Successful masting depends on the completion of consecutive stages of the reproductive process (i.e., resource uptake, floral induction, pollination, seed maturation), often spanning multiple seasons or years [10-13]. Weather can affect each stage by priming resource uptake, cueing floral bud formation, influencing pollination success or vetoing seed production [11,14]. Consequently, when favourable weather conditions are aligned in time and space over the entire reproductive process, i.e., the Moran effect [15,16], they lead to synchronous seed production in masting plants [13,17-19].

Many environmental patterns that play out over wide geographic areas are controlled by modes of climate variability, such as El Niño Southern Oscillation (ENSO) [20], the North Atlantic Oscillation (NAO) [21], and other modes that are integral components of Earth's climate system [22-25]. Different climate modes operate at different time scales, affecting weather patterns at frequencies from months to decades [20,21,26]. The spatio-temporal dynamics with which climate modes exert their influence has major implications for the synchronization of ecological processes and ecosystem functioning [22,25,27], including masting. Indeed, there is increasing evidence that masting events are associated with these modes of climate variability across all continents [3,2,28-31] but the existence of a causal link has yet to be ascertained.

In this perspective, we explore the breadth of knowledge on how climate modes control variable and synchronous seed production throughout Earth's biomes. Under the hypothesis that the intrinsic properties of climate modes (periodicity, persistence, and trend) drive proximate causes of seed production, we show that they coherently align, over multiple seasons, weather cues conducive to the success or failure of seed production in masting species. Furthermore, we assess the evidence that climate modes influencing the spatio-temporal combinations of proximate mechanisms drive the spatial synchrony/asynchrony of masting in several geographical regions.

Notably, modes of climate variability have tremendous cascading effects on multiple ecosystem processes, such as primary productivity [24,32], natural disturbance regimes [33,34], animal population dynamics [22], and have the potential to force in-phase ecological processes [27] that interact synergistically with multiple stages of plant reproduction. We explore the hypothesis that climate modes create such synergies via their autocorrelation structure, lagged effects on ecosystem dynamics, and density-dependent processes related to the extent of synchrony. From an evolutionary point of view, using climate modes as a pacemaker to time the production of large seed crops can increase the fitness of an individual plant by promoting the success of its offspring.

59 Finally, we discuss whether the widespread concordance between seed production and climate modes has

60 emerged by chance or is an evolved strategy, and to what extent it can be disrupted by global climate change.

61

62 **Correlation of seed production with climate modes: a widespread phenomenon**

63 Over the past three decades, studies have associated modes of climate variability and plant reproduction across

64 several continents (Figure 1), biomes and species (Supplementary Table S1). Most studies [3,30,35] have

65 analysed the correlation between time series of reproductive effort and large-scale climate indices [22] - often

66 defined as "teleconnection" indices. For example, the NAO is described via the NAO index [21], while ENSO is

67 characterized by the ONI index (see supplementary glossary for indexes description).

68 Seminal research first documented correlation between ENSO and mass fruiting in Dipterocarp tropical forests

69 of South-East Asia [28], where ENSO strongly influence weather patterns (Figure S1). ENSO has subsequently

70 been shown to correlate with seed production not only in South-East Asia [2,35-40], but also in New Zealand

71 [29], Africa [41], Western North America [7,31], South America [3,42,43], and in the Caribbean [4,44].

72 In the northern hemisphere, the NAO is one of the major climate modes concordant with plant reproduction

73 (Table S1), particularly in Europe (Figure 1) where the NAO index [21] correlates to the timing, variability and

74 synchrony of flowering, pollination and seed production of dominant forest species [13,30,45-50].

75 More generally, several episodes of community-wide mass flowering or fruiting have been tied to the main

76 climate modes influencing a given area [1,3,29,30,38,49,51,52], suggesting that species with disparate life traits

77 may all time their reproduction based on these modes.

78 The strength and direction of correlations between climate modes and seed production may vary in space and

79 time, following the spatial arrangement of each mode: dipolar or more complex patterns [2,27,31,52,53],

80 depending on the season (Figure S1) or on the time window considered [30], and being modulated by local

81 orographic features which can enhance, reduce or revert the large scale signal. Furthermore, modes interact

82 among each other [33,54-56]: higher-frequency climate modes such as ENSO or NAO are affected by lower-

83 frequency modes such as the Atlantic Multidecadal Variability (AMV) [57]. Such complex interactions appear to

84 be key in understanding cascading effects on linked ecological processes [33,58], including masting [7].

85

86 **Climate modes affect the (dis-)alignment of proximate mechanisms for variable reproduction**

87 Masting depends on the completion of multiple reproductive stages (i.e., resource priming, floral induction,

88 flowering, pollination, fruit maturation) that may occur over several seasons or years [13,18,59]. Numerous

89   studies linked reproductive success or failure to weather conditions experienced by plants during single

90   reproductive stages [12,17]. Other studies correlated favourable weather during these stages to modes of

91   climate variability [3,4,13,38,45] suggesting that climate modes are a key regulator of variable reproduction via

92   their direct effect on weather, and particularly on temperature (Figure S1).

93   However, we highlight evidence that climate modes can also synergistically align favourable weather conditions

94   during consecutive reproduction stages (Table S1). Climate modes are determined by quasi-oscillatory nonlinear

95   dynamics arising from the interaction of oceanic and atmospheric processes and influence the persistence of

96   circulation patterns over large portions of the globe across multiple seasons [20-22]. For example, ENSO

97   fluctuations between La Niña and El Niño phases display non-stationary periodicity [20]. Climate indices used to

98   represent ENSO, such as ONI (see glossary), display intrinsic autocorrelation (Figure S2a), positive at lags of 6

99   months (i.e., persistence of El Niño/La Niña) and negative at lags of 2 years (i.e., transition from the opposite

100   phase), with a periodicity ranging from 2 to 8 years (Figure S2b). These fluctuations have the potential for a multi-

101   seasonal alignment of proximate mechanisms, which would occur for example under increased resource

102   acquisition followed by favourable weather during flowering, pollination and fruit ripening.

103

104   *Aligned reproductive stages under ENSO*

105   In tropical forests of South-East Asia, cool and dry anomalies from December to February are believed to cue

106   mass flowering in Dipterocarp forests: in Malaysia general flowering typically occurs in March and in South-

107   Western Borneo in July [2,19,28,36,38,59]. Our analyses confirm significant negative temperature and

108   precipitation anomalies in the region prior to general flowering events in the last 60 years (Figure S3). Ushio et

109   al. (2020) and Satake et al. (2021) show that general flowering in the region is driven synergistically by low air

110   temperature and drought. Moreover, Chechina and Hamann (2019) suggest a cumulative-trigger model to

111   predict flowering in Dipterocarps that incorporates temporal accumulation of resources. Interestingly, these

112   regional masting events occur preferentially during the transition from La Niña (negative ENSO phase) to the

113   onset of El Niño (positive ENSO phase) (Figure S4) indicating a potential dynamic role of ENSO in aligning

114   cumulative and synergic cues. A wet period during La Niña stimulates resource priming [38,57] (Table S1), while

115   the onset of El Niño reduces cloud cover [57], leading to increased daytime radiation, lower night-time

116   temperatures (Figure S5a), and dry conditions (Figure S5b) over peninsular Malaysia, the Northern Sumatra and

117   western Borneo, approximately 12 months before the El Niño peak (usually from December to February). In these

118   Dipterocarp forests, ENSO temporally aligns increased resources and the dry-cool air cue of flowering. A similar

119   synergic alignment of resource availability and flowering cues during the onset of El Niño has been observed in

120   tropical moist forests in Central America [3].

Synergies caused by the transition from La Niña to El Niño also appear relevant for *Picea glauca* reproduction in Western [7] and Eastern North America (Figure S4). Masting of *P. glauca* in Eastern regions of North America is associated with temperature differences from the two prior summers [60], a cue known as ΔT [17]. Notably, over the last six decades the summer before the peak of El Niño showed negative anomalies in temperature throughout Eastern North America (Figure S5g), while the following summer after the El Niño winter peak, positive anomalies occurred across the same region (Figure S5h). This mechanism highlights how in Eastern North America the transition from La Niña to El Niño aligns the negative summer temperature cue two years before masting and the positive temperature cue the summer before masting, resulting in a significant positive ΔT cue (Figure S6).

Aligned reproductive stages under NAO

Another example of multi-seasonal synergies comes from Central Europe, where positive winter NAO and negative summer NAO during the resource priming stage correlate positively with reproduction in several tree species (Table S1), including *Fagus sylvatica*, *Picea abies*, *Quercus robur*, *Q. petraea*, *Betula pendula*, and *Pinus pinea* [13,30,46,49,61,62]. In *F. sylvatica* and *P. abies*, positive summer NAO during floral bud initiation is associated with masting in the following year [30,49,63]. Positive winter to spring NAO correlates with increased and synchronous pollen influx [45,48] and high seed crops in several species [30,49]. The explanation for these relationships lies in how seasonal NAO phases generate consecutive weather conditions that are optimal for reproduction, and thus promote masting (Figure 2). In Central Europe, positive NAO in December-February is associated with warm-wet winters (Figure S1) and earlier snowmelt [21], which promotes earlier leafing out [45]. Warm-wet winters also increase water availability in spring and the length of the growing season [46] with direct consequences on ecosystem productivity [32]. Positive summer NAO is associated with warm temperature in July-August (Figure S1), which induces floral bud differentiation in several species in Central Europe [18,49], while positive spring NAO is associated with warm, dry and windy weather (Figure S1) that favours pollination [30,49].

Several of these multi-seasonal reproductive cues align synergistically due to the intrinsic temporal structure of the NAO (Figure S7). The NAO index averaged over December to April is positively autocorrelated with a 1-year lag (Figure S7a), likely due to re-emergence of oceanic heat anomalies from one winter to another [64] and to decadal influences by the AMV [55]. Furthermore, the NAO shows a marked persistence from winter to early spring months, as shown by the correlation of the spring with the preceding winter NAO index (Figure S7b). In Central Europe periods of positive winter NAO phases are associated with increased resource uptake in European forests [24,32,65]. Importantly, the lag-1 positive autocorrelation of the winter NAO index (Figure S7a) means that a positive winter NAO can persist for consecutive years, thus promoting a prolonged resource gain.

153   Moreover, since positive spring NAO likely follows positive winter NAO (Figure S7b), this alignment promotes

154   earlier and synchronized flowering and associated release, dispersal, and transport of pollen [45] during a period

155   of increased resources [30].

156   Another interesting mechanism that links NAO properties to plant reproduction in Central Europe depends on

157   lagged effect of the winter-NAO on summer temperatures. Indeed, summer heat waves in Central-Northern

158   Europe are strong and wide-ranging when positive summer-NAO occurs in years of positive winter-NAO [66]. For

159   example, this was the case in 1994 before the beech masting in 1995, the largest event in the period 1952–2015

160   (Figure 2). This suggests a potentially higher sensitivity of beech masting to the summer cue during a positive

161   phase of the winter NAO [30]. Together with the higher probability of favourable conditions for pollination in

162   spring, this means that positive trends in winter NAO increase the likelihood of beech masting (Figure 2). On the

163   contrary, prolonged negative periods can result in poor resource uptake and vetoes to pollination (wet spring,

164   frost), leading to frequent reproductive failure and longer inter-mast periods, such as those occurred in Central

165   Europe in the 60s and 70s (Figure 2).

166

167   **Modes of climate variability affect reproductive synchrony through space and time**

168   The geographic extent of masting is one of its most impressive properties [67]. The spatial coherence of

169   proximate mechanisms of seed production (i.e., the Moran effect) plays a major role in synchronizing plant

170   reproduction over different scales [10,18,53,68]. Synchrony in reproduction occurs when conditions favourable

171   for each reproductive stage, from resource priming to fruit ripening, align not only in time, but also in space [30].

172   Likewise, large-scale reproductive vetoes affecting single stages may thwart reproduction over extended areas

173   [69].

174   Climate modes are implicated in synchronizing both resource dynamics [32,58] and weather cues of masting in

175   tropical [2,35], temperate [30,52], and boreal regions [7,8]. For example, in Central Europe the large-scale

176   synchronisation of resource dynamics [32] and weather cues [66] driven by NAO, results in spatially synchronized

177   resource priming, bud initiation [30] and timing of pollination at different sites [46]. This led to continent-wide

178   masting events such as those in 1990, 1992, and 1995 [18], which extended over an area of more than 1.3 million

179   km^2 (Figure 2). Conversely, in South-Eastern Europe the NAO has a more limited impact on local weather [21],

180   which is more driven by multiple interacting climate modes [25] and a complex geomorphology (e.g., water

181   bodies, orography). Greater local environmental variability differentiates weather patterns through space and

182   time, working against large-scale reproductive synchrony [68]. Similarly, in South-East Asia the complexity

183   created by the Malaysian Peninsula and Bornean and Sumatran coastlines and mountain ridges interacts with

184   the response of atmospheric circulation to ENSO and generates regional weather and masting patterns. In South-

185   Western peninsular Malaysia and Western Borneo, flowering and fruiting of Dipterocarp often occurs during the

186   transition from La Niña to El Niño (Figure S4). However, flowering starts in March in Peninsular Malaysia and in

187   July in South-Western Borneo, which mirrors the North-West to South-East shift of dry-cool air that precedes the

188   onset of El Niño (Figure S5a, c, g, i). Moreover, populations of Dipterocarps on Eastern sides of Borneo usually

189   flower and fruit after the onset of El Niño [35,70]. Indeed, the ENSO spatial impact is shaped by the geography

190   of the Indonesian archipelago, which drives opposite responses in sea surface temperatures and cascading

191   effects on weather patterns East and West of Borneo (Figure S5a, b, c, d). Still, the onset of particularly strong El

192   Niño events, such as those in 1959, 1977, or 1983, coincided with mass flowering throughout most of the region

193   [2,28].

194   Modes of climate variability often drive dipoles in the spatial synchrony of temperatures and precipitation and

195   hence induce dipolar masting patterns [8,53,71,72]. In Central Europe, the geographical divide exerted by NAO

196   on winter, spring, and summer temperatures extends along a ridge from 45°N-3°W to 50°N-26°E, termed the

197   "NAO node" (Figure S1). This ridge parallels the boundary between positive and negative synchrony in both

198   weather and large-scale masting of European beech [18,30,68]. Likewise, ENSO drives opposite effects on

199   precipitation over different areas of the Western United States, which are reflected by an asynchrony in seed

200   production by *Pinus edulis* in the Southern and Northern part of its distribution [31]. The onset of El Niño might

201   explain the peculiar spatial asynchrony that La Montagne et al. (2020) observed in *P. glauca* masting when

202   comparing Western and Eastern populations of Canada and Northern America. Indeed, positive surface

203   temperature anomalies appear in the West the summer before El Niño peaks, and negative in the East (Figure

204   S5g), thus cueing masting in the west [7]. However, the dipole switches the summer after El Niño (Figure S5h),

205   triggering masting in the East. The resulting West-East shift in the ΔT summer cue (Figure S6) is thus key to fully

206   understand why this masting dipole was observed in some periods (i.e., during the onset of El Niño) but not in

207   others.

208

209   **Climate modes drive synergies between masting and reproductive fitness of plants**

210   Climate modes do not only set the timing and extent of masting, but also influence the dynamics of ecosystem

211   processes that affect the success of offspring survival. In the few systems where this hypothesis has been

212   suggested [30,44,73] or tested [3,7], climate modes had concordant effects on proximate mechanisms of seed

213   production and on the environment into which seedlings grow. Such concordance may exist in several

214   geographical areas (Figure 3). As discussed, in tropical Dipterocarp forests of peninsular Malaysia, flower

215   initiation is associated with cool-dry air from January to March [2]. A recent study found a correlation between

216 the cool-dry weather cue and wet conditions favourable for seedling emergence a few months later, in October
217 to December [59]. Our analyses confirm such weather oscillation (Figure S3). Notably, in Malaysia and Western
218 Borneo this oscillation from cool-dry to wet conditions is associated with the transition from La Niña to El-Niño
219 (Figure S5), which synergistically aligns the flowering cue and precipitation that favours seed germination,
220 seedling emergence, and seedling establishment few months later (Figure S5i, q, d). The transition to El Niño
221 coincides with other advantageous mechanisms (Figure 3). Changes in large-scale weather during this transition
222 are tracked by long-distance mobile pollinators, which anticipates general flowering [74]. Drought brought by El
223 Niño can cause the formation of canopy gaps [73] and fire disturbance, which peaks six months before the El
224 Niño in Eastern Borneo, and during El Niño in Western Borneo [75], prior to seed dispersal. Similarly, in boreal
225 forests of Northern America the onset of El Niño leads to regional drought and heat pulses responsible for both
226 fire disturbance and floral bud initiation in *P. glauca* (Figure 4 - left), resulting in masting the ensuing year [7].
227 This alignment benefits spruce recruitment because seeds dispersed shortly after fire germinate more easily due
228 to partial litter consumption, and seedlings can establish in canopy openings [76]. Positive ENSO is also
229 responsible for extensive fires in tropical Amazon forests, with negative impacts on seed predators and positive
230 influences on *Bellucia* sp. fruit production [77].

231 Similarly, in Central Europe, the NAO has well-established links with both masting in multiple species (Table S1)
232 and natural disturbance regimes that may promote seedling establishment (Figure 3). For example, positive
233 winter NAO causes major windstorms in the area [34,78], which supports seedling establishment by creating
234 canopy gaps [79,80]. A large-scale climate cue similar to positive summer NAO is linked to both fire disturbance
235 [81] and beech masting the following year [63], with potential benefits for beech establishment in the post-fire
236 environment [82,83]. Also, a persistent positive NAO from winter to spring curbs populations of seed-eating
237 rodents because of lower snow cover and increased predation [22]. Notably, these seasonal NAO patterns also
238 promote dispersal dynamics. Positive winter NAO correlates with irruptions of key seed dispersers, such as
239 *Columba palumbus*, *Fringilla coelebs*, *Pica pica*, *Parus major*, and *Carduelis spinus* [84,85]. Similar synergies with
240 seed dispersers were described in North America, where a West-East dipole in temperatures, resembling the
241 pattern occurring in the summers before and after the peak of El Nino (Figure S5g, h), modulates both broad-
242 scale masting [8] and the irruption of seed-eating birds anticipating the resource pulse [52], with potential
243 benefits for seed dispersal.

244 In most other regions where the environment is under the influence of major climate modes, there is evidence
245 that ecosystem processes respond to them, and it will be interesting to see how often that results in an alignment
246 between drivers of seed production and other ecosystem processes improving reproductive fitness. For example,
247 negative phases of ENSO, Indian Ocean Dipole (IOD) and Southern Annular Mode (SAM) concurrently modulate

248 rainfall in central Australia, with direct effects on the productivity [58] and seed output [86-89] of Mulga (*Acacia*

249 *sp.)* and Spinifex (*Triodia sp.*) vegetation. Increased rainfall triggers multiple cascading processes such as ant

250 population dynamics [90] and wildfires [91]. Consequently, it is not surprising that synchronized flowering, ant

251 abundance, and fire in inland Australia have been correlated to La Niña [87,90,91]. In turn, landscape-scale fires

252 limit predators in Mulga species [92], and cue seed germination of both *Acacia* and *Triodia* [86,89]. The

253 interaction between ENSO-IOD-SAM acts thus as a large-scale mechanism that synchronizes resource priming,

254 flowering, seed dispersal by ants and large-scale fire disturbance with multiple adaptive benefits along the entire

255 plant reproduction sequence.

256

257 **Relevance of climate modes for the evolution of masting**

258 When considering the role of climate modes in the evolution of masting, we should ascertain whether these

259 modes have existed and maintained their properties (i.e., autocorrelation, periodicity, trends) for timeframes

260 relevant to the evolution of long-lived plants. There is evidence that modes of climate variability such as ENSO

261 have been acting for evolutionary-relevant time periods [93,94]. For example, annular modes of variability (as

262 the SAM) are observed in extremely idealized climate numerical simulations, pointing to the fact that such modes

263 of variability are an intrinsic feature of the Earth's climate system that have been existing for long time [95].

264 We highlight how climate modes drive reproduction and recruitment success not only directly, but also indirectly,

265 by forcing lagged but in-phase ecosystem dynamics conducive to favourable conditions for offspring. By

266 synergistically aligning the proximate mechanisms that cause masting and the processes that improve offspring

267 fitness (Figure 3), climate modes make favourable environmental conditions more "predictable" by plants [30],

268 a hypothesis known as "environmental prediction" [79,96]. Environmental prediction based on climate modes is

269 possible since they have predictable dynamics, i.e., inherent autocorrelations and periodicities, and because their

270 cascading effects lag in predictable ways.

271 The environmental prediction hypothesis has been regarded cautiously. Researchers have favoured adaptive

272 hypotheses related to economies of scale (EOSs) implied by large seed production events [96]. However, linking

273 reproduction to climate modes may also have implications on EOSs. The two major EOS hypotheses are predator

274 satiation and pollination efficiency. In predator satiation, occasional large seed crops satiate predators resulting

275 in higher per capita survival of seeds and seedlings [11,97]. In pollination efficiency, large flowering events lower

276 the upper threshold for pollen limitation [96,98,99]. The primary distinction between EOS and environmental

277 prediction is that EOSs are density-dependent, i.e., an individual plant benefits from pulsed flowering only when

278 other individuals are also flowering. In contrast, under environmental prediction, if an individual plant produces

279   seed based on cues that predict a favourable environment for seedlings, this would be enough to increase fitness.

280   Notably, climate modes have the potential to let both emerge.

281   A major implication of the link between climate modes and reproduction in plants is the spatial extent of

282   synchrony in flowering, pollination, and seed production, which is usually larger than a population. EOSs of seed

283   production emerge within a given range of extents in spatial synchrony. In some cases, it is sufficient for trees to

284   synchronize pollination within a stand [100], while avoidance of predation by nomadic vertebrates requires a

285   "regional escape" strategy by "community-wide" masting [1]. In the present study, we found evidence that

286   climate modes synchronize reproduction over different spatial extents, covering the full range of scales needed

287   for known EOSs to emerge. While adaptive benefits at smaller extents (i.e., individual, stand, population) have

288   been extensively studied [97,100], benefits emerging from synchrony at larger scales are understudied, and

289   mostly discussed in relation to pollen coupling [98,99]. However, synchrony at scales larger than a population,

290   peculiar of the climate mode-masting relationship, might imply adaptive benefits (Figure 5).

291   For example, although climate-driven disturbances are predictable in the time domain (i.e., environmental

292   prediction) by species that experience the same environmental cue (e.g., drought), they cannot be predicted in

293   the space domain (i.e., where a disturbed patch will occur). Large-scale and community-wide reproduction

294   increases the chances for a larger number of individuals to release seeds in favourable environments created by

295   disturbances [7,73,79,89]. Regional seed predators may also select for large-scale and community-wide

296   flowering/fruiting synchrony. The spatial scale at which synchrony in seed production effectively reduces losses

297   to predators is influenced by predator's mobility [101,102]. If a predator can move easily between plants, stands,

298   or regions, selection will favour synchrony among plants at a scale comparable to the predator's mobility [97].

299   For long-distance mobile predators, strategies that generate large-scale synchrony in seeding would be favoured

300   [103]. Relevant examples are the interaction between *Araucaria araucana* and the Austral parakeet, which is

301   highly mobile [104] and effectively satiated by seeding synchrony over distances of 10–100 km [105]. A similar

302   interaction occurs between Dipterocarps and large bodied, highly mobile generalist predators (*Pongo pygmaeus*,

303   *Sus barbatus*) in Borneo [1,106] (Figure 4). Over 800,000 pigs were observed migrating out of Northeast

304   Kalimantan after the 1983 Dipterocarp mast event and severe El Niño-associated drought [107]. Such ability to

305   move requires seeding synchrony over hundreds of kilometres for predator satiation to produce an effective

306   "regional escape" from predation [1], and is suggestive of similar interactions occurring in ecosystems with

307   similarly mobile predators (e.g., *Sus scrofa* in Eurasia). Other large-scale examples involve specialist birds like the

308   passenger pigeon, Carolina parakeet, and the Javanese finch [101]. Hence, testing the predator satiation

309   hypothesis at the tree or stand scale may only miss processes occurring at larger scales.

310 The extent of synchrony needed for pollination efficiency is debated [98,108]. In South-East Asia, minor and local

311 flowering events that precede mass-flowering in Dipterocarps [2}, do not lead to fruit development because of

312 low pollen density [109]. Synchronized flowering of many species in Dipterocarp forests causes an increase in

313 long-distance mobile pollinators through immigration [74], which directly affects pollination efficiency [110].

314 Synchronous flowering over large distances may also have evolutionary implications by contributing to the flow

315 of adaptive gene pools. Long-distance pollen dispersal contributes to a small percentage of pollination but is

316 highly relevant for gene flow between populations over evolutionary time scale [111,112]. Genetic similarities

317 among separated populations have been attributed to gene flow due to long-distance pollen dispersal [113],

318 which might occur only during synchronous flowering [114]. Intriguingly, the genetic structure of *P. glauca* in

319 Northern America [115], or of *Shorea macrophylla* in Borneo [116] resembles the West-East dipole in flowering

320 synchrony shaped by ENSO in both regions. Bogdziewicz et al. (2021) suggested that the spatial genetic structure

321 of *F. sylvatica* in Europe [117] resembles the divide in weather and pollination synchrony that is under the control

322 of the NAO. Interestingly, the same geographical divide in genetic structure is shared by other tree species in

323 Central Europe [118], raising the question whether the large-scale synchrony in pollination led by NAO plays a

324 role in shaping genetic similarities, in addition to legacies from post-glacial migration dynamics [117,113]. Gene

325 flow is a key process for increasing individual fitness since it allows exchange among diverse, separated, or

326 marginal populations, which continue to receive (and spread) genes with adaptive benefits. When masting

327 synchronizes over large scales, the higher chance for long-distance gene-flow might reinforce synchrony, since it

328 reduces in-breeding depression and increases local adaptation potential and fitness [119].

329

Climate change, climate modes, and masting

331 Anthropogenic climate change is having a strong impact on local weather in several regions on Earth, and masting

332 patterns appear to be shifting in response to these changes [120]. Climate change can also affect climate modes,

333 although their long-term response remains uncertain. ENSO is expected to remain the dominant mode in a

334 warmer world, but model projections do not agree over a systematic increase in ENSO variability, nor on future

335 changes in ENSO teleconnections [121,122]. However, most models show an increase in amplitude of ENSO

336 rainfall variability (therefore in the associated extreme events) ascribable to the increase in the mean sea surface

337 temperature and moisture [123]. The SAM is projected to become more positive [124] possibly intensifying the

338 Southern Hemisphere teleconnection with precipitation [33]. The positive phase of winter NAO is expected to

339 occur with higher frequency in a warmer world, following a strengthening and zonalization of the mid-latitude

340 westerly winds [125,126]. On the other hand, predicted future changes of the AMV are largely model dependent

341 [127].

342 These changes are impacting – and will further impact in the near future – the associated ecological processes

343 and their multiple spatio-temporal synergies [33,128], including masting [30]. In cases where weather influencing

344 proximate mechanisms anticipates weather during germination or seedling development, it is likely that these

345 processes will become decoupled as climates change [129]. Where lags in ecosystem processes result in

346 environmental prediction, it is possible that those processes may remain coupled even as Earth's climate systems

347 change considerably.

348

349 **Concluding remarks**

350 Studies testing for the influence of climate modes over variable and synchronous reproduction in seed plants

351 made use of correlation analyses between climate indices and time series of fruit and seed production. However,

352 in most cases the causal mechanisms behind those correlations were uncertain. In this perspective, we explain

353 the tight relationships between climate, weather patterns, and the physiology and ecology of plant species, and

354 we demonstrate that climate modes shape the spatio-temporal patterns of reproduction of major masting

355 species in most of Earth's biomes. We highlight how large scale modes of climate variability, such as ENSO or the

356 NAO, influence reproduction and recruitment both directly, through regional weather patterns that align

357 proximate mechanisms of seed production through time and space, and indirectly, by density-dependent EOSs

358 emerging at increasingly larger-scales, and by forcing lagged but in-phase ecosystem dynamics conducive to

359 favourable conditions for offspring. The observation that both ecosystem properties and seed production lag

360 considerably behind climate [22,84] might renew interest in the subject of the evolutionary emergence of

361 masting. We argue that climate modes have the potential to "bridge" proximate and ultimate causes of masting

362 selecting for variable and synchronous reproduction. To better understand the impacts of climate change on

363 plant reproduction, a deeper understanding of changes of climate modes and their relationship with global

364 warming will be critical. The future of such deep interaction is uncertain: processes that improve reproductive

365 fitness may remain coupled even under changing climates, but chances are that abrupt global warming will affect

366 Earth's climate modes so rapidly as to perturb ecological and evolutionary links.

367

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685 **Author's contribution**

686 A.D. led the overall study, formulated theses and drafted an initial manuscript. All authors participated in group
687 discussions about research ideas and provided considerable and meaningful contributions to writing the
688 manuscript and editing the figures. P.D. supervised and conducted climate data analysis. All authors gave final
689 approval for publication.

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Figures

Figure 1 - Regional distribution of selected published studies (extracted from Table S1) reporting correlations between climate indices and masting. Shading indicates regions where climate variability is influenced by the El Niño Southern Oscillation (orange) and the North Atlantic Oscillation (blue).

Figure 2 – Large-scale weather patterns associated with negative (left) and positive (right) phases of the North Atlantic Oscillation (NAO) during key reproductive stages (resource priming, floral induction, pollination) leading to *Fagus sylvatica* masting failure (left) or success (right). Positive NAO aligns consecutive mechanisms that promote successful seed production, such as warm-wet winters and extended wet growing seasons favouring resource uptake, hot summers triggering floral bud initiation, dry springs ensuring successful flowering, pollination, and fruiting (Table S1), leading to large-scale masting in Central Europe in 1995. The opposite occurs in 1966 during prolonged negative NAO phases. The December to March (DJFM) NAO index displayed in the bar plot was calculated using the NOAA index. The large-scale beech masting index in Central Europe was derived by Ascoli et al. (2017) and normalized (i.e., negative/positive values indicate higher/lower than average seed crops).

Figure 3 – Chord diagram showing the potential for climate mode phases (blue sector) to drive synergies between proximate (green sector) and ultimate (orange sector) mechanisms of masting in different geographical regions: Central Europe (left diagram, based on 45 sources), South-East Asia (right diagram, based on 35 sources). The sector size in the outer circle indicates the distribution of synergies, while the flows through the centre of the circle illustrate the relative importance of links between individual agents (as measured by the number of observations reporting on the respective link). Arrows point from the influencing climate mode to the mechanisms being influenced.

Figure 4 - Examples of density-independent (left) and density-dependent (right) mechanisms with adaptive benefits linked to models of climate variability. In North-West America (left) the onset of El Niño time spruce reproduction to anticipate favourable conditions for offspring early-life fitness due to fire disturbance. In South-East Asia (right) the transition from La Niña to El Niño synchronizes community-wide reproduction in Dipterocarp forest setting a "regional" escape from mobile animal predators such as *Sus barbatus* and *Pongo pygmaeus*.

726   Figure 5 – Theoretical scheme of the scale of reproduction synchrony covered by climate modes which is relevant

727   for different density-dependent economies of scale implying adaptive benefits. EOSs from left to right: seed

728   predation escape (grey), pollination efficiency (green), attraction of seed dispersers (blue), disturbance

729   intersection (red), gene-flow (violet). Escaping predation of low mobile predators (e.g., mice) occurs at the lower

730   spatial scale, the benefit increases sharply and remains constant at increasing spatial scales since the EOS is local.

731   Pollination efficiency benefits from a larger scale, although the cross-fertilization rate due to the outsource pollen

732   decreases at increasing distance of the pollen origin. Disperser attraction requires a spatial threshold of the

733   reproduction synchrony after which the irruption of long-distance disperser such as birds is triggered. The

734   encountering of a disturbed seedbed benefits linearly of the extent of the synchrony by increasing the likelihood

735   of intersecting a disturbed site but decreases after the regional scale since large-scales disturbances (e.g.,

736   megafires) affect negatively post-disturbance seed availability. Gene-flow benefits exponentially of reproduction

737   synchrony up to the larger scale when geographically separated population synchronize and exchange genes.