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Unveil the unseen: Using LiDAR to capture time-lag dynamics in the herbaceous layer of European temperate forests

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2 **Unveil the unseen: Using LiDAR to capture time-lag dynamics in the**
3 **herbaceous layer of European temperate forests**

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21 **Abstract**

- 22 1. To understand time-lag dynamics in the response of biodiversity to **macro-environmental**
23 **changes (e.g., macroclimate warming and atmospheric pollution)**, we need to consider
24 other anthropogenic forcing factors such as land-use changes and changes in management
25 practices that can have both compounding and confounding effects. This is especially true
26 in European temperate forests, where legacies from past human activities have left strong
27 imprints on today's understory plant species composition, **generating long-term lagging**
28 **effects which can be mistakenly attributed to more recent macro-environmental changes.**
- 29 2. By combining the expertise of plant, soil, and historical ecologists together with remote
30 sensing scientists, we review the potential of light detection and ranging (LiDAR) to unveil
31 ghosts from the past in terms of former land uses and management practices.
- 32 3. We show that imprints from past land uses and management practices can still be captured
33 today throughout well-chosen LiDAR-derived variables describing, at sub-decimetre scale,
34 the vertical and horizontal micro-variations of vegetation and terrain structure hidden
35 below treetops.
- 36 4. *Synthesis.* We encourage plant and soil ecologists to use LiDAR data and to work with
37 historians, archaeologists, and remote sensing scientists in order to select meaningful
38 LiDAR-derived variables to account for time-lagged biotic responses to long-term macro-
39 environmental changes.

40 **Keywords**

41 Archaeology, biodiversity, climate change, climatic debt, disequilibrium dynamics, forest
42 management, historical ecology, legacy effects, microclimate, nitrogen deposition, remote
43 sensing, understory layer

44 *“When light encounters a strong magical field it loses all sense of urgency. It slows right down.” –*
45 *Terry Pratchett, The Light Fantastic (1986)*

46 **Introduction**

47 The current warming of the climate system is unprecedented in terms of its speed and spatial
48 extent within the context of the past 2,000 years (Neukom et al., 2019), leading to important
49 regional, continental, and global biodiversity changes: species range shifts (Lenoir et al., 2020);
50 shifts in the phenological synchrony of species interactions (Kharouba et al., 2018); community
51 thermophilization (i.e., increasing dominance of warm-adapted species) (Gottfried et al., 2012);
52 biotic homogenization (Staude et al., 2020); and even species extinction (Panetta et al., 2018). Yet,
53 the velocity at which these biotic responses happen is generally **lower than** the velocity at which
54 the macroclimate is warming (Bertrand et al., 2011; Dullinger et al., 2012; Rumpf et al., 2019;
55 Vitasse et al., 2021), leading to disequilibrium or lagging dynamics (Alexander et al., 2018;
56 Svenning & Sandel, 2013) sometimes also referred as the (macro)climatic debt in the scientific
57 literature (Bertrand et al., 2016; Devictor et al., 2012; Richard et al., 2021). **Likewise, delayed**
58 **recovery of plant species richness and composition in response to the decreased inputs of**
59 **atmospheric pollutants, after the peak in Europe during the 1970s for sulphur and during the**
60 **1980s for nitrogen, have been reported for both forest and grassland habitats (Riofrío-Dillon et al.,**
61 **2012; Storkey et al., 2015).**

62 **Lagging dynamics in response to macroclimate warming and the reduction in atmospheric**
63 **deposition, among other macro-environmental change drivers,** are especially pronounced within
64 the herbaceous layer of temperate deciduous forests (Bertrand et al., 2011, 2016; De Frenne et al.,
65 2013; Richard et al., 2021; Riofrío-Dillon et al., 2012; van Dobben & de Vries, 2017), which is the
66 most biodiversity-rich vegetation layer in these ecosystems (Gilliam, 2007; Landuyt et al., 2019). **In**
67 **terms of biotic responses to macroclimate warming,** thermophilization rates are ranging from 0.01

68 to 0.05°C per decade within understory plant communities of temperate forests, which is several
69 orders of magnitude lower (cf. greater lags) than the rates observed in other groups such as trees
70 (0.11°C per decade), bumblebees (0.14°C per decade), freshwater invertebrates (up to 0.22°C per
71 decade), or marine fishes and invertebrates (up to 0.38°C per decade) (see Table S5 in Richard et
72 al. (2021), and references therein, for a more exhaustive description). **For comparative purposes,**
73 **mean annual temperature increased at a rate of 0.23°C per decade between 1995 and 2015 in**
74 **France (Richard et al., 2021). As for the recovery time following the reduction in atmospheric**
75 **deposition in Europe, lagging effects seem also more pronounced in the herbaceous layer of**
76 **forests than in grassland communities (Schmitz et al., 2019; Storkey et al., 2015; van Dobben & de**
77 **Vries, 2017). However, whether or not the magnitude of these time-lagged biotic responses in**
78 **temperate forests can be attributed solely to macroclimatic warming or atmospheric deposition**
79 **remains an open question.** To resolve this, it is of utmost importance to also consider other
80 anthropogenic forcing factors such as past land-use changes and historical changes in forest
81 management practices that can have both **compounding and confounding effects with other more**
82 **recent environmental change drivers** (Forister et al., 2010; Guo et al., 2018; Larsen, 2012; Warren
83 et al., 2001). Indeed, the scientific literature is full of examples, detailed below, illustrating how
84 the history of forest management practices and land uses can interact, synergistically or
85 antagonistically, **with either macroclimate warming or atmospheric deposition,** to delay or
86 sometimes speedup changes in the understory of European temperate forests.

87 **As macroclimate warming accelerates, it is assumed that mean annual temperatures below**
88 **treetops increase as well but at lower rates than outside forests due to the lower coupling**
89 **between macroclimate and microclimate inside the forest understory (Lenoir et al., 2017).**
90 **Accordingly, De Lombaerde et al. (2021) predicted that maximum temperatures will, on average**
91 **for the 2060-2080 period, warm less inside (+0.27°C) than outside (+0.60°C) forests if the local**
92 **forest cover is maintained. However, maximum temperatures may also warm faster inside the**

93 forest understory than outside if canopy cover is reduced due to, for instance, management
94 interventions or forest dieback related to drought and pest damages. Such forest microclimate
95 dynamics driven by changes in canopy cover could explain part of what seems to be a delayed
96 biotic response to macroclimate warming, meaning that the so-called macroclimatic debt involves
97 microclimatic processes (De Frenne et al., 2021; Zellweger et al., 2020). Accordingly, Richard et al.
98 (2021) have recently demonstrated that lags in community thermophilization are accumulating
99 over time in the herbaceous layer of denser and older forest stands in France, while anthropogenic
100 and natural disturbances generating canopy gaps above the herbaceous layer tended to reduce
101 these lags. Hence, stand characteristics are important determinants of time-lag dynamics
102 observed in the herbaceous layer of temperate forests in response to macroclimate warming
103 (Brice et al., 2019; Richard et al., 2021). Besides, changes in stand characteristics over time interact
104 with long-term environmental changes through complex historical trajectories of forest
105 management practices and natural disturbances (e.g., fire, drought, wind storm). For instance, in
106 Europe, Perring et al. (2018) have shown that the trajectories of changes in forest plant
107 community composition over 40 years were clearly influenced by complex interactions between
108 management legacies from over 200 years ago and long-term environmental changes, in terms of
109 both the rate of nitrogen deposition and the rate of temperature change.

110 Time-lagged biotic responses that we attribute today to macroclimatic warming or to the
111 reduction in atmospheric deposition may also involve other long-term processes, such as legacy
112 effects of soil compaction due to mechanized timber harvesting as well as more ancient legacy
113 effects of past land uses (Bürgi et al., 2017), operating through microclimate and soil memory
114 effects. For instance, it has been recently demonstrated that old skid trails left by forestry vehicles
115 more than 50 years ago locally increase soil compaction and alter microclimatic conditions in the
116 soil (humidity and temperature), which leaves a strong imprint on contemporary community
117 composition and diversity in the herbaceous layer of temperate forests (Wei et al., 2015). More

118 precisely, by limiting water infiltration, skid trails locally increase the proportion of wetland plant
119 species in the community (Buckley et al., 2003), which alters community composition such that the
120 community may not only indicate wetter but also cooler conditions over time when analysed
121 through the lens of thermophilization indices solely. Indeed, a cooling effect is usually concomitant
122 with the humidifying effect of vegetation (Zhang et al., 2013). In such a case, time-lagged biotic
123 responses to soil compaction by skid trail may be mistakenly attributed to an inflated
124 macroclimatic debt.

125 The field of historical ecology (Szabó, 2015) is full of examples showing that current local
126 biodiversity continues to be influenced by past management practices and land uses, including fire
127 regimes, through complex biotic lags usually involving long-lasting effects of changes (or absence
128 of changes) in landscape configuration and soil abiotic conditions (Dambrine et al., 2007; Dupouey
129 et al., 2002; Jung et al., 2019; Metzger et al., 2009). For instance, time since afforestation, and thus
130 land-use history, has left a strong imprint on the herbaceous layer of temperate deciduous forests
131 in Europe, with several forest plant species (i.e., forest specialists) clearly associated with ancient
132 forests (land continuously forested for several centuries) (Rackham, 2008) as opposed to more
133 recent forests (Hermy et al., 1999; Peterken & Game, 1984; Valdés et al., 2015; Verheyen et al.,
134 2003). Similarly, historical landscape connectivity can strongly affect the present distribution
135 pattern of herbaceous forest plants in fragmented forests and hedgerows through changes in
136 habitat configuration and composition (Lenoir et al., 2021; Lindborg & Eriksson, 2004; Metzger et
137 al., 2009). Perhaps more surprisingly, former Roman agricultural practices throughout Europe can
138 still have irreversible impacts on forest biogeochemical cycles and biodiversity by increasing
139 today's soil pH, available phosphorus and nitrogen, and consequently the frequency of nitrogen-
140 demanding species (Dambrine et al., 2007; Plue et al., 2008; Vanwalleghem et al., 2004). In such a
141 case, without considering historical information on past land uses, one may mistakenly interpret
142 today's occurrence of nitrogen-demanding species in the community as a response to the high

143 nitrogen deposition during the 1980s while part of it may actually be due to longer-term lagging
144 effects induced by former Roman agricultural practices. By looking at terrain morphology and
145 micro-topographic variations in today's landscapes, archaeologists and geo-historians can read
146 such long-term legacies from past land uses, unearth artefacts of former human occupations, and
147 provide invaluable information to explain current biodiversity patterns (Briggs et al., 2006; Closset-
148 Kopp & Decocq, 2015; Dambrine et al., 2007; Dupouey et al., 2002; Plue et al., 2008). Hence, to
149 decipher the main determinants of time-lag dynamics in the herbaceous layer of temperate
150 forests it is necessary to analyse the response of species population and community dynamics to
151 contemporary macro-environmental changes (e.g., macroclimate warming or nitrogen deposition)
152 in the light of historical management practices and past land uses.

153 Vertical and horizontal micro-variations at sub-decimetre scale in both vegetation and terrain
154 structure can bear the imprints of historical management practices and land-use legacies which
155 are still contributing to today's biodiversity, and thus to time-lagged biotic responses to macro-
156 environmental changes, by locally altering microclimatic conditions near the soil surface as well as
157 edaphic conditions (**Fig. 1**). Light detection and ranging (LiDAR) data (**Box 1**) can capture these
158 vertical and horizontal micro-variations (i.e., structural traits) below treetops (**Fig. 2**). Indeed,
159 LiDAR data can provide quantitative metrics of both stand characteristics and micro-topographic
160 variations below the canopy at unprecedented detail, often impossible to perceive for the human
161 eye or to describe with traditional field measurement methods (Chase et al., 2012; Dassot et al.,
162 2011). To illustrate this, we first put on our plant-ecologist hat to show how LiDAR data can
163 capture detailed stand characteristics to unveil recent but also historical forest management
164 practices that affect current forest microclimates and thus the time-lag dynamics of understory
165 plants' responses to long-term environmental changes. Then, we put on our soil-ecologist hat to
166 illustrate how LiDAR data can unveil the imprints of former skid trails left by forestry vehicles that
167 are still affecting current plant community composition through soil compaction. Third, we take a

168 historical-ecologist viewpoint to demonstrate how LiDAR data can unveil long-term land use
169 history that may still affect contemporary plant community composition in the herbaceous layer.
170 Finally, we discuss research perspectives in light of the most recent advances in LiDAR technology
171 and its combination with other remote sensing technologies **as well as with recent developments**
172 **in computer science**. We conclude that LiDAR can be used as a tool to boost trans-disciplinary
173 research between plant ecologists, foresters, soil ecologists, archaeologists, historical ecologists,
174 and remote sensing scientists to advance our knowledge of time lags in the response of
175 understory plant communities to long-term macro-environmental changes.

Box 1: LiDAR principles*Measurement principles*

Light detection and ranging (LiDAR) is an active remote-sensing technology based on emission-reception of a laser beam. LiDAR can be divided into two main categories (Durrieu et al., 2015; Grotti et al., 2020): (1) time-of-flight LiDAR (**Fig. 2**) assessing distances by measuring the roundtrip time for a short laser pulse, in general emitted by a near-infrared or **visible (green)** laser, to travel between the sensor and a target; versus (2) phase-shift LiDAR emitting a continuous wave laser with intensity modulated at a series of frequencies to determine distances through shifts in phase of the returned modulations. Phase-shift LiDAR have higher measurement rates and can thus collect data at a much faster speed than time-of-flight LiDAR. They also measure distance with a precision of up to few millimetres against few centimetres for time-of-flight LiDAR. However, their maximum measurement range is much shorter, which makes phase-shift LiDAR more adapted for terrestrial LiDAR systems (TLS) than for airborne LiDAR systems (ALS) (**Fig. 2**). Additionally, phase-shift LiDAR is more prone to artefacts, for example those caused by range averaging, when a beam partially intercepts more than one object.

Scanning and geolocating principles

In order to acquire LiDAR data across a given area or landscape, a scanning system is used to deflect the emitted laser beams in different directions throughout the target scenery (**Fig. 2**). This is achieved thanks to: (1) the combination of a moving (e.g., rotating) mirror and the movement of either the scan head for static TLS or the vehicle on which the LiDAR is embedded for non-stationary systems like ALS (Tan et al., 2018); and (2) the multiplication of standpoints for TLS or flight lines for ALS. When both the scanning angles and the position of the LiDAR in a geographic reference system are known at the time of range measurements, the absolute position of the targets on the Earth's surface can be inferred. For mobile ALS, real-time sensor position and

200 orientation are obtained thanks to a differential global **navigation satellite system (DGNSS)** and an
201 inertial measurement unit on-board the platform. For static TLS, point cloud geolocation can be
202 achieved by measuring either scan positions or the positions of a set of high reflective targets
203 distributed in the field, which are clearly identifiable in the point clouds and used for the merging
204 of several scans. Positions can again be measured using a **DGNSS**. To improve location accuracy in
205 forest environments, it is recommended to use a **DGNSS** in a neighbouring open area as well **or**
206 **coupled with a total station (cf. tacheometer)**.

207 *Spatial distribution of LiDAR measurements and occlusions*

208 The spatial distribution of LiDAR measurements results from the combination of several factors,
209 such as laser emission rate, scanning system, and vector velocity for non-stationary ALS. However,
210 a major phenomenon impacts the spatial distribution of LiDAR measurements in forested
211 environments: occlusions. Like natural light, laser beams can penetrate through vegetation
212 openings but, when intercepted by vegetation elements, it is mostly reflected or absorbed,
213 generating shadows or occluded areas behind these elements (e.g., foliage, stems, flowers).
214 Besides, the quantity of light continuing its path through vegetation decreases each time part of a
215 laser beam hits a vegetation element. As a result, vegetation sampling is getting sparser when the
216 laser beam goes deeper inside the vegetation (**Fig. 2**). For TLS, point density decreases with the
217 distance from scan positions below the canopy, leading to sparser point clouds towards the top of
218 the canopy and generating occlusion areas behind large tree trunks located very close to the
219 scanning position. For ALS, the understory vegetation and the ground surface, including deadwood
220 and litter lying on the ground, are less densely measured than the top of the canopy, especially
221 after leaf-out and tree canopy closure in temperate deciduous forests.

222 **Using LiDAR-derived metrics of vegetation structure to capture time-lag dynamics in the**
223 **response of herbaceous plant communities to long-term environmental changes**

224 Forest structure is acknowledged to be a key factor to explain current plant species diversity and
225 community composition in the understory (Oettel & Lapin, 2021; Walter et al., 2021). LiDAR
226 technology allows the description of complex aspects of the forest structure that are
227 complementary to those observed by foresters during field surveys (**Box 2**) (Bouvier et al., 2015;
228 Venier et al., 2019). Primarily underpinned by objectives of forest resource inventory and
229 management, the capacity to remotely assess stand characteristics such as basal area, stem
230 density, dominant height, wood volume, and biomass distribution, has been widely studied and is
231 operationalized in a variety of forest contexts (Moeslund et al., 2019; White et al., 2016; Wulder et
232 al., 2013). Among those descriptors of stand attributes routinely used by foresters to assess forest
233 resources, some, like stand structure (e.g., basal area, diameter diversity, tree height),
234 management intensity, and tree species composition have proven to be useful to model current
235 plant diversity in the forest understory (Oettel & Lapin, 2021; Wei et al., 2020). However, many
236 other complementary metrics (e.g., canopy volume, vertical leaf density profile, understory shrub
237 cover), not routinely used by foresters to assess vegetation structure because they are difficult to
238 measure in the field, can be derived from LiDAR data (**Fig. 3**). In this **review**, we argue that LiDAR
239 data can be used to derive variables describing the complexity of the vertical layering of
240 vegetation in temperate forests, including subtle vertical structures bearing the imprints of
241 extreme weather conditions as well as the memory of past forest management practices for which
242 we have good records in Europe.

243 It is widely acknowledged that historical forest management practices, such as coppicing which
244 was widespread in European temperate forests before World War II (WWII), are major drivers of
245 current plant community composition and distribution in the forest understory (Bartha et al.,

246 2008; Becker et al., 2017a; Bricca et al., 2020; Decocq et al., 2004; Della Longa et al., 2020;
247 Müllerová et al., 2015). For instance, former coppice-with-standards (CWS) have left a visible
248 signature on current stand structure as well as on current plant species composition in the
249 herbaceous layer, even after conversion to high forests (HF), a very common practice in Europe
250 after WWII. Importantly, these changes in forest management practices in Europe happened
251 somewhat concomitantly with climate change and increased inputs of nitrogen via atmospheric
252 deposition, leading to complex compounding and confounding effects on the observed changes in
253 plant species composition in the herbaceous layer (Becker et al., 2017b; Perring et al., 2018).
254 Traditionally, CWS were managed as multi-storied stands consisting of a matrix of even-aged
255 stems (coppice) in the lower storey – cut down for firewood production in short rotations – and
256 single-stem (emergent) trees (i.e., standards) in the upper storey – left standing during longer
257 rotations for timber production. Whether or not CWS casts more shade at the forest floor than HF
258 remains unclear, but conversion from CWS to HF implies more regular thinning operations over
259 time, potentially leading to more frequent light pulses enhancing microclimate warming and
260 community thermophilization in the understory, ultimately compounding and confounding the
261 impact of macroclimate warming on understory plant communities (Zellweger et al., 2020).
262 Changing socio-economic conditions throughout history have also led to the complete
263 abandonment of active timber management in some regions of Europe (see Perring et al., 2018),
264 generating prolonged absence of high light conditions in the forest understory. Such trajectories
265 may have led to a loss of light-demanding plant species from open habitats and an increase of
266 typical shade-tolerant plant species (i.e., forest specialists) (Baeten et al., 2009), reducing
267 community thermophilization and contributing to the lagging response of understory forest plant
268 to macroclimate warming (Richard et al., 2021).

269 Using LiDAR technology to scan the vertical layering of vegetation **and better capture the**
270 **understory structure hidden below treetops (Box 2)**, as a mean to identify the complex trajectories

271 outlined above, holds untapped potential to understand time-lag dynamics that depends upon
272 past management legacies (Perring et al., 2018). For instance, a set of airborne LiDAR-derived
273 variables describing the vertical distribution of canopy height and cover was successfully applied
274 to identify old coppices in a Mediterranean context (Bottalico et al., 2014). **The most**
275 **straightforward metrics to describe the vertical structure of vegetation within a given spatial grid**
276 **cell include the mean and standard deviation of height values above the ground surface for all the**
277 **points classified as vegetation and belonging to the focal grid cell. Yet, these raw summary**
278 **statistics aggregated in a 2D pixelated space may not fully capture the complex layering of**
279 **vegetation in the understory (see **Box 2**). Refined approaches to assess the effective number of**
280 **vegetation layers below treetops consist in computing height percentiles and the number of**
281 **echoes or point density at several heights (Frey et al., 2016; Stickley & Fraterrigo, 2021). Using**
282 **airborne LiDAR data, Stickley & Fraterrigo (2021) summarized the vertical structure of temperate**
283 **deciduous forests in the Great Smoky Mountains National Park into five height classes and found**
284 **that variation in maximum temperature in the understory was best explained by the buffering**
285 **effects of the low-understory (below 5 m height) and low-canopy (from 10 to 15 m height) layers.**
286 **Finally, it is possible to compute more advanced LiDAR-derived metrics per unit of volume (see**
287 **Box 2) by relying on the resolution of the transmittance equation using the Beer-Lambert Law,**
288 **which relates the attenuation of light through a turbid medium – in this case, leaves and branches**
289 **– to the properties of that medium, or on the maximum likelihood theory (Soma et al., 2018). For**
290 **instance, plant area density (PAD) (in $\text{m}^2 \text{m}^{-3}$) can first be computed for each single voxel, a 3D cell**
291 **unit, from the local transmittance values by applying Beer-Lambert’s turbid medium**
292 **approximation (Vincent et al., 2017) (**Fig. 3e**). Thus, PAD values better reflect the amount of plant**
293 **material participating to light occlusion in the canopy than the above-mentioned metrics based on**
294 **point density. From vertical profiles of PAD values (**Fig. 3f**), it is then possible to summarize the**
295 **entire vertical structure of vegetation, including the understory, by computing the plant area index**

296 (PAI), which is the integral (area under the curve) of PAD profiles. Hence, PAI describes the entire
297 column of plant material participating to light occlusion and thus indirectly reflects the amount of
298 light reaching the forest floor. **Figure 4** shows that a denser forest with a complex shrub layer and
299 thus a higher PAI value (e.g., PAI = 6.28) than a less vertically complex and more open forest (e.g.,
300 PAI = 4.72) provides a higher buffering capacity during spring and summer, reducing daily mean
301 temperature by more than 5°C (against 3°C for the open forest). It is also possible to compute PAI
302 within a restricted vegetation layer, such as the shrub layer (e.g., below 7 m). This way, it is
303 possible to partition PAI values among vegetation layers and focus on the additional insulating
304 effect provided by shrubs (**Fig. 4**), which may bear the imprints of historical management practices
305 contributing to time-lag dynamics in the herbaceous layer. Spatially contiguous maps of forest
306 microclimate predictions (e.g., Frey et al., 2016; George et al., 2015) integrating the buffering
307 effects of the understory shrub layer through the use of PAI values are especially promising as they
308 may reflect the complex trajectories of forest management changes, and explain time-lag
309 dynamics in the response of the herbaceous layer to long-term environmental changes (Richard et
310 al., 2021; Zellweger et al., 2020).

311 **Box 2: The potential of LiDAR-derived variables to capture vertical structures in the understory**

312 Traditional forest inventory methods to measure forest structure in the field cannot be easily
313 applied contiguously at fine spatial resolutions and across large spatial extents. Moreover,
314 traditional forest surveys cannot extract the accurate three-dimensional structure of forests,
315 including tree cover rate, gap distribution, and a detailed vertical description of the understory.
316 **Using LiDAR data can help to overcome these limitations** (Almeida et al., 2019) (**Fig. 3**). Once the
317 digital terrain model (DTM) (**Fig. 3a**) of a given area has been computed from the set of points
318 classified as “ground”, it is possible to compute the exact height, relative to the ground surface, of
319 each point classified as “vegetation” across the area. This information can then be exploited to
320 extract very simple metrics of the vertical structure of vegetation, such as canopy density above a
321 specific height (**Fig. 3b**) or maximum canopy height (**Fig. 3c**). The level of details provided by LiDAR
322 data, and especially TLS data (**Figs. 3d**), to quantitatively describe the vertical layering of
323 vegetation in the understory of temperate forests (**Fig. 3e,f**) is unprecedented compared to
324 traditional field approaches (Venier et al., 2019). Foresters usually start recording and measuring
325 trees in the field above a minimum diameter at breast height (DHB) of 7.5 cm. Yet, individuals of
326 less than 7.5 cm DBH are also an important component of the understory shrub layer that can be
327 **partly captured depending on the quality of the raw LiDAR point cloud. The quality not only**
328 **depends on the point density, which can be high in case of TLS data (Fig. 3d-f), but also on the**
329 **intensity of the return and the number of echoes registered. For ALS data, full-waveform laser**
330 **scanning allows to digitize the complete waveform of each backscattered pulse and extract more**
331 **small echoes – even during leaf-on conditions – that may hold key information on the structure of**
332 **the understory shrub layer.** From the raw LiDAR point cloud, the most intuitive approach to
333 capture the understory shrub layer is to separate points classified as “vegetation” into different
334 vertical strata and extract summary statistics aggregated in a 2D pixelated space describing either

335 the mean, minimum, maximum, standard deviation, skewness, kurtosis, or relative percentage of
336 the distribution of the points within a vertical stratum (e.g., Frey et al., 2016; Stickley & Fraterrigo,
337 2021). To avoid using too many summary statistics for each vertical layer separately, LiDAR point
338 clouds classified as vegetation can also be aggregated in a 3D voxelated space to compute metrics
339 per unit of volume, like the 3D distribution of plant or leaf area density (PAD or LAD) (**Fig. 3e**). For
340 instance, Almeida et al. (2019) showed that LAD profiles have the capacity to track changes in
341 forest structure under different forest management practices. This biophysical information can be
342 further analysed to provide vertical vegetation profiles or information on gap size and distribution
343 (**Fig. 3f**). Vertical profiles and gap fraction together can better describe the 3D characteristics of
344 the forest. Venier et al. (2019) identified several metrics that are expected to directly capture
345 vegetation density in the understory: fractional cover (FRAC); plant or leaf area density (PAD or
346 LAD) profiles; voxel cover (VOX); and normalized cover (NORM). Additionally, the Gini coefficient is
347 a reliable descriptor of variation in tree sizes (Knox et al., 1989). Valbuena et al. (2016)
348 demonstrated the potential of LiDAR-derived estimations of the Gini coefficient to highlight
349 structural differences between forests that have been protected since the beginning of the 20th
350 century vs. forests presently under intense management.

351 **Using LiDAR data to highlight soil compaction from skid trails affecting current biodiversity**
352 **patterns in the forest understory**

353 Numerous studies have highlighted the long-lasting effects of heavy forestry vehicles on soil
354 processes and forest herb composition (Closset-Kopp et al., 2019; Godefroid & Koedam, 2004; Wei
355 et al., 2015). These effects include: (i) diaspore dispersal via the mud attached to tires and wheels
356 (i.e., agestochory) and air displacement induced by the vehicle's movements, which facilitates
357 anemochory; (ii) the creation of microreliefs within, beside, and between wheel tracks, generating
358 a complex mosaic of microenvironments; and (iii) local changes in soil abiotic (e.g., porosity,
359 microclimate, chemistry) and biotic (e.g., microbial activity) conditions. In particular, soil
360 compaction and the formation of deep ruts on the soil surface often impede water infiltration,
361 oxygen supply, nutrient bioavailability, as well as root development (Arocena, 2000; Cambi et al.,
362 2018; Kozłowski, 1999). This provides regeneration niches and suitable habitat conditions to a
363 range of (non-forest) plant species, such as aquatic weeds, sedges and rushes, as well as ferns
364 (Closset-Kopp et al., 2019) but on the other hand can negatively affect recruitment of other
365 species (e.g., trees). These three processes can lead to an increase in local species richness, yet
366 also a process of homogenization among forest habitats, by facilitating the colonization of the
367 same suite of wetland and ruderal species (Closset-Kopp et al., 2019; Godefroid & Koedam, 2004;
368 Kozłowski, 1999).

369 Ruts and soil compaction can be measured in the field, via rut depth, bulk density, or penetration
370 resistance, but the methods are time consuming to apply across large areas. Recently, several
371 studies highlighted the efficiency of remote sensing in the evaluation of rutting intensity and
372 spatial distribution (Marra et al., 2018; Mohieddinne et al., 2019; Niemi et al., 2017). Some of
373 them, using unmanned aerial vehicles equipped with digital cameras for high resolution
374 photogrammetry, returned a fine description of rut density associated with forest harvesting

375 (Marra et al., 2018; Talbot et al., 2018). However, this approach is only applicable to recently clear-
376 cut areas. In contrast, LiDAR data offers an interesting alternative to map skid trails below treetops
377 (**Fig. 5**) (Koren et al., 2015; Mohieddinne et al., 2019; Niemi et al., 2017). Indeed, points classified
378 as “ground” in the LiDAR point cloud can be used to generate a digital terrain model (DTM) at sub-
379 decimetre resolution so as to detect microrelief variations due to skid trails. The most
380 straightforward approach to highlight skid trails from a DTM is to use local relief models (LRMs)
381 that are widely used in archaeology to capture local, small-scale elevation differences after
382 removing the large-scale landscape forms from the data (Hesse, 2010). While TLS data can yield
383 LRMs at a very high accuracy over limited spatial extents (Koren et al., 2015), ALS data allows
384 assessing the impact of skid trails over much larger areas in a spatially contiguous manner (Niemi
385 et al., 2017). **Figure 5** clearly shows how ALS data can shed light on skid trails in the Compiègne
386 forest, a managed state forest in Northern France. The LRM reveals small-scale topographic
387 variations such as ruts, which sometimes appear as parallel paths following permanent skid trails
388 as delineated by forest managers (**Fig. 5a, bottom panels**) but also as numerous meandering paths
389 crossing each other (**Fig. 5b, bottom panel**). **Yet, LRMs only highlight ruts resulting from the traffic**
390 **intensity without providing the means for an automatic detection of these linear small-scale**
391 **topographic elements in the landscape. Indeed, one still needs to digitize, manually, the**
392 **illuminated ruts in the LRM image in order to analyse these elements afterwards. By doing so**
393 **across the entire Compiègne forest**, we found that the surface area covered by skid trails can
394 reach 40 to 80% in several of the forest management units. Noteworthy, in some of these units,
395 many ruts intersect (**Fig. 5b**). This suggests that either vehicles travel unevenly during a given
396 operation or that older ruts resulting from several successive forestry operations persist for a very
397 long time (at least 50 years) (Ebeling et al., 2016; Mohieddinne et al., 2019) with potential long-
398 lasting effects still visible on today’s plant species composition and diversity in the herbaceous
399 layer (Wei et al., 2015). **More specifically, the cumulated effect of soil compaction due to repeated**

400 traffic of heavy forest harvesters and forwarders contribute to local increases in the proportion of
401 wetland plant species in the community (Buckley et al., 2003) and to the homogenization of plant
402 communities in the forest understory (Closset-Kopp et al., 2019), most likely with a lagging effect.
403 Without considering skid trails, such time-lag dynamics can be misattributed to other concomitant
404 drivers of change in environmental conditions, such as nitrogen deposition known for being also
405 responsible for the biotic homogenisation of understory plant communities (Staute et al., 2020).
406 Currently, the main challenge to account for the impact of skid trails on understory vegetation at
407 large spatial extents is to automatize the detection of ruts from LRM images. More research is still
408 needed to achieve that but one possibility is to train a model with LRM data using machine
409 learning or deep learning algorithms such as convolutional neural networks (CNNs), which is
410 widely used in the field of computer vision (Ren et al., 2017).

411 **Using LiDAR data to unveil past land uses affecting current biodiversity patterns in the forest**
412 **understory**

413 One leading research question in historical ecology is (Plue et al., 2009): what did past human
414 societies leave behind and how does this influence present ecosystem functioning? For ecologists,
415 this question can be difficult to answer without a comprehensive knowledge of past interactions
416 between human societies and the environment at various spatial and temporal scales. LiDAR
417 technology has prompted an “archaeological revolution” by making it possible to identify, map,
418 and analyse hidden objects and structures (Costa et al., 2020; Hesse, 2010). In terms of historical
419 ecology, this is especially true for forested lands, where traditional remote sensing techniques
420 such as aerial photography cannot unveil archaeological features hidden below treetops. In such
421 situations, ALS can help to spot thousands of artefacts in a much shorter time frame than the
422 decades of pedestrian field surveys that would have been otherwise necessary to discover only the
423 most visible part of these artefacts (Chase et al., 2012; Štular et al., 2021). In many cases, ALS has
424 revealed previously unrecorded archaeological features. Spectacular examples of unexpected
425 findings are the medieval landscape planning by the classical Khmer civilization at Angkor (Evans et
426 al., 2013) and the early Maya metropolises in Guatemala (Canuto et al., 2018) and Mexico
427 (Inomata et al., 2020). Recent advances in deep learning algorithms may even allow to automatize
428 the inventory of archaeological remains (Oliveira et al., 2021; Trier et al., 2021). For instance,
429 Oliveira et al. (2021) applied CNNs on ALS data to automatically detect charcoal kilns dating back
430 to the industrial development period (17th-19th century) in North-eastern France. However,
431 remote and automatic detection still requires confirmation, either by field observations or through
432 the experienced eyes of archaeologists and geo-historians who can read and interpret images
433 processed from LiDAR data.

434 In Western Europe, many big woodlands have been continuously mapped or mentioned in
435 archives since the Middle Ages, so that they have long been considered as relicts of prehistoric
436 forests (Maury, 1850). This hypothesis was first challenged by the discovery of former Roman
437 settlements in these forests (Cauchemé, 1912; Desbordes, 1973; Laffite et al., 2002) and it is now
438 largely invalidated by ALS data which has revealed that these ancient forests were established on
439 former agricultural lands, often intensively cultivated during the Middle Ages and Antiquity (**Fig. 6**)
440 (Fruchart, 2020; Georges-Leroy et al., 2011; Rassat & Hugonnier, 2017). **Figure 6** illustrates this
441 phenomenon by unveiling past land uses hidden below treetops of the Compiègne forest in
442 Northern France, questioning the existence of prehistoric forest remnants in the Gallo-Roman
443 lowlands. With the increasing amount of land covered by ALS data (Fruchart, 2020), it becomes
444 obvious that what we today consider to be very ancient forests can result from **recolonization of**
445 abandoned Roman farmlands (Georges-Leroy et al., 2011). Also in Eastern Europe, ALS unveiled
446 more than 300 km of field boundaries and many (pre-)Roman settlements in the iconic “primary”
447 forest of Białowieża in Poland, indicating that the present forest **has** largely established on former
448 Celtic, Roman, and medieval fields, towards the 13th century AD (Stereńczak et al., 2020). Beyond
449 the reconstruction of the past landscapes, ALS renders it possible to assess the impact of past land
450 uses on current vegetation patterns and ecosystem processes. For example, buried former Roman
451 settlements typically host a species-rich, nitrogen-demanding understory, which often strongly
452 contrasts with the surrounding species-poor, acidophilous forest vegetation (Dambrine et al.,
453 2007; Dupouey et al., 2002; Plue et al., 2008). Interestingly, the soil seed bank in the Compiègne
454 forest indicates that plant communities associated with these former settlements can self-
455 perpetuate over time (Plue et al., 2008). This has been related to long-lasting alterations of
456 biogeochemical cycles, which extend far beyond the settlement, thereby creating strong ecological
457 gradients with different species assemblages (Dambrine et al., 2007).

458 Airborne LiDAR data also revealed the recurrence of certain human artefacts, **even outside ancient**
459 **settlements located in formerly cultivated land**, and highlight their possible ecological significance
460 in forests. We hereafter give three examples. Firstly, in North-eastern France, closed depressions
461 found on calcareous substratum have long been supposed to be of natural origin, but
462 archaeological research has suggested that they were rather artificial excavations from the late
463 Iron Age and Roman times, used to (i) extract marls (i.e., calcium carbonate or lime-rich mud) to
464 amend agricultural lands and/or to (ii) create local depression to collect water for livestock
465 (Etienne et al., 2011). Since this early publication, similar closed depressions have been recorded
466 thanks to ALS data in many “post-Roman” ancient forests elsewhere in Northern France (see **Fig. 6**
467 for an illustration in the Compiègne forest), suggesting that liming was a common practice during
468 Gallo-Roman times. Long-lasting effects on soil properties, plant communities, tree growth, and
469 forest health are thus expected (Brasseur et al., 2018; Dambrine et al., 2007; Dupouey et al., 2002;
470 Moore & Ouimet, 2021). **For instance, the effect of ancient liming practices is still visible on**
471 **today’s soil pH profile of post-agricultural forests, albeit this effect diminishes with the age since**
472 **afforestation (Brasseur et al., 2018). Being able to date the approximate age of the last agricultural**
473 **practices before afforestation makes it possible to estimate the magnitude of the imprint left by**
474 **former agricultural practices in the soil, and thus the effect on forest biodiversity and ecosystem**
475 **processes. The last agricultural practices are precisely those that most impacted the microrelief**
476 **preserved under the canopy of post-agricultural forests. Because of these microreliefs’ imprints,**
477 **geo-historians and archaeologists are able to read images from processed ALS data, such as a DTM**
478 **with hillshade (Fig. 6), and interpret characteristic microreliefs to identify Middle Ages strip fields**
479 **with cultivation ridges (Fig. 6b), Gallo-Roman linear agrarian fields (Fig. 6c), or even Celtic fields**
480 **(Meylemans et al., 2015). The approximate age since afforestation as well as the type of former**
481 **agricultural practices can be key explanatory variables to capture time-lag dynamics in the**

482 response of understory plant communities to the acidification rates of afforested soils that were
483 formerly cultivated (De Schrijver et al., 2012).

484 Secondly, another insight from ALS data is the evidence of an incredibly high density of former
485 charcoal kilns (i.e., chambers or ovens to turn wood into charcoal) in several forests across Europe,
486 from North-eastern France to Norway (Oliveira et al., 2021; Trier et al., 2021). This not only
487 indicates the huge intensity at which European forests used to be managed from the Middle Ages
488 to the end of the 19th century when humans started to mine and drill fossil fuels (Oliveira et al.,
489 2021), often as short-rotation coppice woodlands, but also that soils have been considerably
490 enriched in organic matter, carbon, and ash (Bonhage et al., 2020; Rutkiewicz et al., 2019). As a
491 result, these former “charcoal-producing coppices”, that are often managed as high forests
492 nowadays, harbour different plant communities and soil properties compared to woodlands that
493 have been continuously managed as high forests. For instance, the Bernadouze forest in the
494 French Pyrenees was initially managed as a beech coppice with fir standard before being
495 progressively transformed, during the 15th-17th century, into a monospecific beech coppice for
496 charcoal production, inducing long lasting effects on today’s biodiversity and soil processes
497 (Fouédjeu et al., 2021). Charcoal-producing coppices may contain an additional 4.9 to 8.9 Mg ha⁻¹
498 of soil carbon, and even more (Bonhage et al., 2020). In regions where former charcoal kilns were
499 associated with metal furnaces to forge weapons during medieval times, it may further explain
500 local soil pollution and its persisting effect on biodiversity and ecosystem processes (Karlsson et
501 al., 2015).

502 Thirdly, still in the Compiègne forest, ALS data also unveiled a number of raised, circular structures
503 that concentrated along a curved line into the forest, a few hundreds of meters from the current
504 edge. Field surveys identified them as rabbit warrens, that are artificial earth clods, also called
505 “mottes à conils” in French, erected at the end of the Middle Ages to rear rabbits for royal hunting

506 parties (Germond et al., 1988; Williamson, 2008; Zadora-Rio, 1986). This finding allows not only to
507 date the introduction of rabbit in Northern France somewhere between the 12th and 13th
508 century, and hence determine when forest dynamics started to be influenced by this invasive
509 rodent species, but also to locate the forest edge at that time (**Fig. 6**). It is therefore possible to
510 distinguish between the medieval forest and the modern one, providing an explanation for
511 differences of soil and vegetation characteristics.

512 In sum, LiDAR data not only prompted an “archaeological revolution” by revealing unexpected
513 past human activities and their intensity, but also play a crucial role to unravel the effects of these
514 (pre)historical activities on current biodiversity and ecosystem functioning. More than ever,
515 present ecosystems and landscapes must be viewed as a legacy of past interactions between
516 humans and their environment.

517 **Perspectives**

518 Although we focused our review on the lagging dynamics of vegetation changes in the understory
519 of European temperate forests, we suggest that the exact same suite of LiDAR-derived variables
520 can also be used to study time-lag dynamics in the response of other taxonomic groups to macro-
521 environmental changes. Indeed, plants in the understory layer provide food resources and
522 microhabitats (i.e., microclimatic conditions) for other organisms living in, on, or near the soil
523 surface. Therefore, time lags in vegetation changes can perpetuate and generate a domino effect
524 on other taxa and interaction networks throughout complex aboveground-belowground linkages
525 (Bardgett & Wardle, 2010). Such cascading effects not only involve bottom-up chain reactions
526 across trophic levels (e.g., from primary producers to primary consumers or soil decomposers)
527 (Valencia et al., 2018) but also top-down chain reactions. Indeed, changes in herbivore density or
528 composition (e.g., ungulates or insects), sometimes driven by macroclimate warming and
529 disrupted plant-herbivore interactions (Rasmann et al., 2014; Vitasse et al., 2021), can have long-
530 term biological legacies on aboveground plant community composition (Hamann et al., 2021;
531 Nuttle et al., 2014). For instance, Nuttle et al. (2014) showed that the initial density in white-tailed
532 deer (*Odocoileus virginianus*) in Pennsylvania still influences current understory vegetation in 30-
533 year-old, closed-canopy forests. In the meantime, LiDAR-derived variables have been successfully
534 incorporated as predictor variables into models of species diversity and distribution across a wide
535 range of taxonomic groups (de Vries et al., 2021; Farrell et al., 2013; Hattab et al., 2017; Moeslund
536 et al., 2019; Simonson et al., 2014), often as a mean to capture local processes such as
537 microclimates and biotic interactions (Lembrechts et al., 2019; Zellweger et al., 2019). Hence,
538 LiDAR-derived variables have the potential to significantly improve species distribution modelling
539 across a wide range of taxa, inform us on the structure of trophic webs, and therefore help us
540 better understand time-lag dynamics perpetuating across trophic levels.

541 Remote sensing science continues to innovate and thus some research perspectives should be
542 highlighted here. Innovations can come either from the LiDAR sensor itself, the combination with
543 other sensors (e.g., coupling LiDAR data with hyperspectral images) or from other technologies.
544 Typical LiDAR data retrieve discrete echoes in only one wavelength. Today, the two big new
545 innovations in LiDAR technology are (1) the analysis on the full-waveform laser information and (2)
546 the use of multispectral lasers, which bring both high resolution 3D point clouds and classical
547 multispectral information. The first one allows much more precise information of surfaces than
548 typical multi-echo LiDAR, especially for forest structure and composition (Fassnacht et al., 2016;
549 Koenig & Höfle, 2016). The second allows **the remote identification of tree species (Amiri et al.,**
550 **2019) as well as** the production of typical remote sensing indicators, such as normalized difference
551 vegetation index (NDVI), for understory conditions not easily accessible with classical multispectral
552 images that do not penetrate forest canopy cover. Additionally, data fusion remains one of the
553 main interests in remote sensing technology. For example, hyperspectral data has proven its
554 complementarity with LiDAR data to better understand ecosystem functioning (Ewald et al., 2018).
555 While LiDAR data gives precise information about the 3D structure of surfaces, hyperspectral
556 images give more precise information of surface reflectance (hundreds of spectral bands) than
557 classical multispectral images. **Hyperspectral data is thus more relevant than LiDAR data to provide**
558 **information on stand composition and can help detect foliar traits and leaf chemical composition**
559 **(Ewald et al., 2018).** For instance, in terms of lagging dynamics involving past land uses,
560 hyperspectral data could be used to locate particular pollutants **in the upper canopy layer** (for
561 example perchlorates that affect photosynthesis **and thus surface reflectance) as an indirect**
562 **indicator of pollutant concentration** in the soil (Wang et al., 2018) **likely affecting plant species**
563 **composition in the understory.** Coupling LiDAR and hyperspectral data could therefore be of high
564 interest and could give precious information of time-lag dynamics in biodiversity changes.
565 **Additionally,** it is possible to combine LiDAR data from a single survey with other types of

566 technologies to monitor changes in forest structure over time and thus better understand time-lag
567 dynamics in the forest understory. For example, photogrammetry can retrieve 3D surfaces to
568 generate digital surface models (DSMs) at different time periods using time series of RGB images.
569 Such time series of DSMs derived from photogrammetry could then be coupled with a single
570 LiDAR-derived DTM to monitor changes in maximum canopy height over time (Michez et al.,
571 2016). Pleiades satellites are interesting in this regard as they allow to produce DSMs across large
572 spatial extents at a relatively low price. In line with Pleiades, the CO3D mission is a pioneer
573 mission, planned to be launched by the CNES (the French Spatial Agency) in mid-2023. Ultimately,
574 the CO3D mission will provide a worldwide high (1-m) resolution DSM in 2025. Combining past
575 photogrammetric data sets, where available, with more recent time series of DSMs, from either
576 airborne or spaceborne data, would also allow obtaining the longer-term data necessary to
577 observe temporal dynamics.

578 Finally, there are exciting recent advances and open-source tools to overcome challenges
579 associated with LiDAR data handling and processing (Atkins et al., 2022). First, recent packages
580 developed for the R statistical software (R Core Team, 2021), such as the lidR (Roussel et al., 2020)
581 and forestr package (Atkins et al., 2018) for ALS and TLS data, respectively, have greatly advanced
582 the handling and processing of LiDAR data. Second, it is now possible to call programming
583 languages such as Python, which is chiefly used by the remote sensing community, directly within
584 the R environment, thanks to the reticulate package (Ushey et al., 2021). It is also possible and
585 quite usual to wrap C/C++ functions within R. Using a compiled language allows a speedier
586 execution when processing huge point cloud data sets. This, will allow ecologists – that are often
587 most familiar with R – to better access the recent open-source tools developed and used by the
588 remote sensing community. Third, recent advances in R and Python to use machine learning and
589 deep learning algorithms (e.g., the keras Python library) (Kalinowski et al., 2021) will help to lift
590 technical barriers in linking LiDAR data with ecological data from field observations. Finally, data

591 processing facilities continue to develop steadily, with increased access to data and computer
592 centres.

593 **Conclusion**

594 To conclude, LiDAR data can unveil past forest management interventions and even past land uses
595 within temperate deciduous forests. LiDAR technology has the capacity to monitor and determine
596 fine-grained structural information – namely: the vertical complexity of vegetation layering and
597 the micro-topographic variations at the ground surface – invisible to the naked eye, providing far
598 more information than conventional field surveys. Yet, LiDAR data alone is insufficient and still
599 requires to be coupled with field surveys to calibrate models, validate predictions, and correct
600 misclassifications of items. Besides, LiDAR technology needs a highly diverse set of expertise to
601 unveil any useful information hidden in the data. Hence, LiDAR is a transdisciplinary tool for plant,
602 soil, and historical ecologists as well as for foresters, archaeologists, and remote sensing scientists
603 to work together and help each other advance their respective fields of research. With this in
604 mind, we encourage plant and soil ecologists to work with historians, archaeologists, and remote
605 sensing scientists in order to use meaningful LiDAR-derived variables, such as the ones we
606 featured in this review (**Figs. 3-6**), as surrogates to capture time-lag dynamics in biotic responses
607 to long-term macro-environmental changes. Doing so will ultimately help us better predict the
608 current and future distribution of forest biodiversity.

609 *“Inside every sane person there's a madman struggling to get out,” said the shopkeeper. “That's*
610 *what I've always thought. No one goes mad quicker than a totally sane person.” –Terry Pratchett,*
611 *The Light Fantastic (1986)*

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622 **Conflict of interest**

623 No conflict of interest to declare.

624 Authors' contributions

625 JL conceptualized the project, designed the review paper, wrote the introduction and conclusion
626 sections, and led the writing. FZ and JIL co-led the writing of section 1 on using LiDAR to unveil
627 past forest management practices with contributions from PDF, KVM, CM, RM, EVG, and DR. HH
628 led the writing of section 2 on using LiDAR data to highlight soil compaction from skid trails with
629 contributions from BB and GD. GD led the writing of section 3 on using LiDAR data to unveil past
630 land uses with contributions from BB and JB. ML led the writing of section 4 on the perspectives
631 with contribution from RM. SD, led the writing of Boxes 1 and 2 with contributions from SA and
632 KD. EVG designed Fig. 1 with contribution from JL. SD designed Figs. 2 and 3 with contribution
633 from JL. CM designed Fig. 4 with contribution from JL. EGM designed Fig. 5 with contribution from
634 HH and JL. EGM & BB designed Fig.6 with contribution from JL. All authors significantly revised the
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636 **Data availability**

637 No data was used in this essay review.

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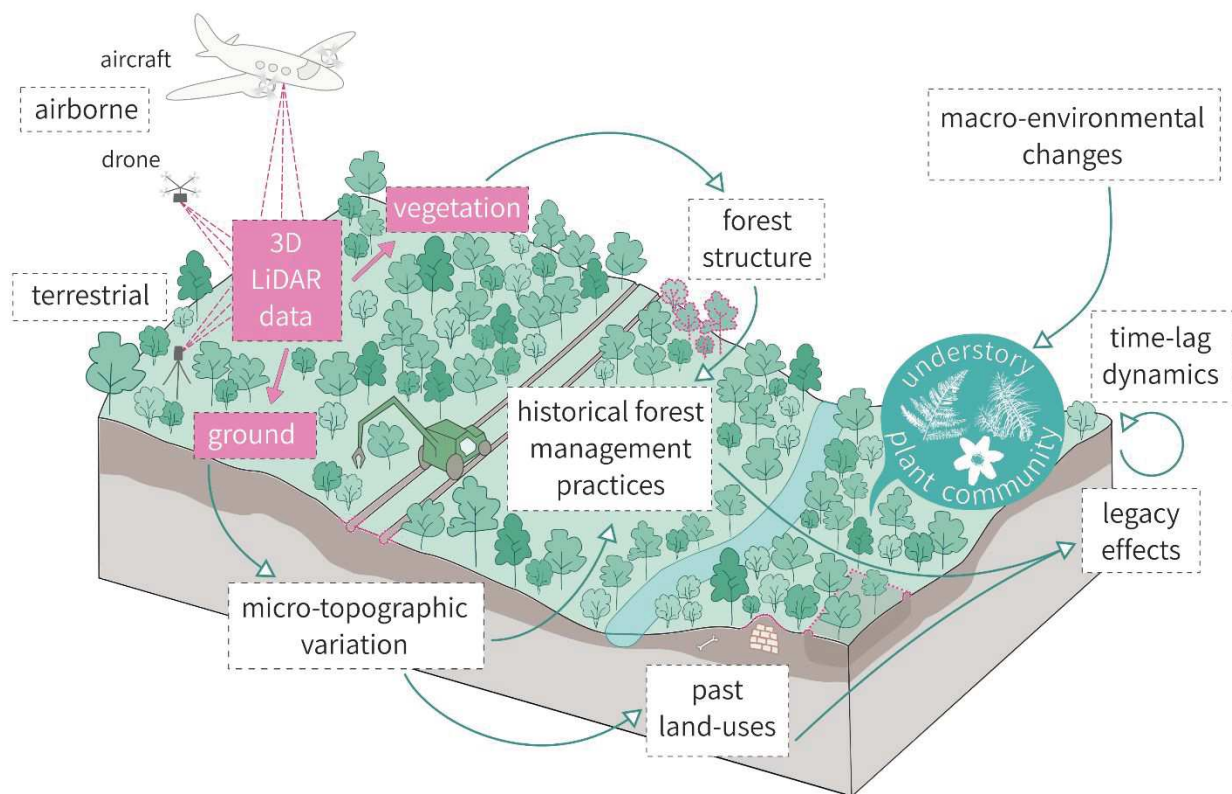
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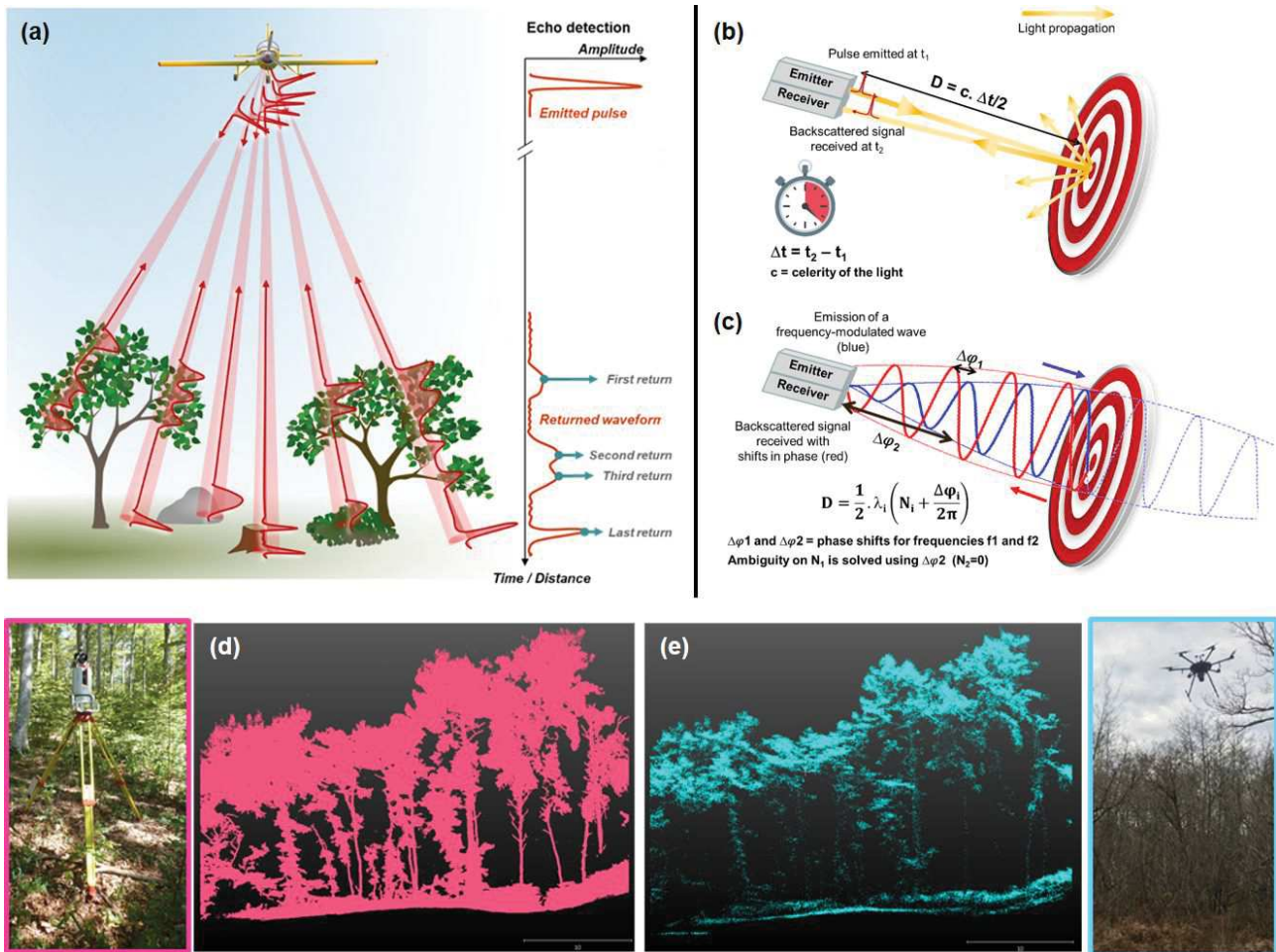
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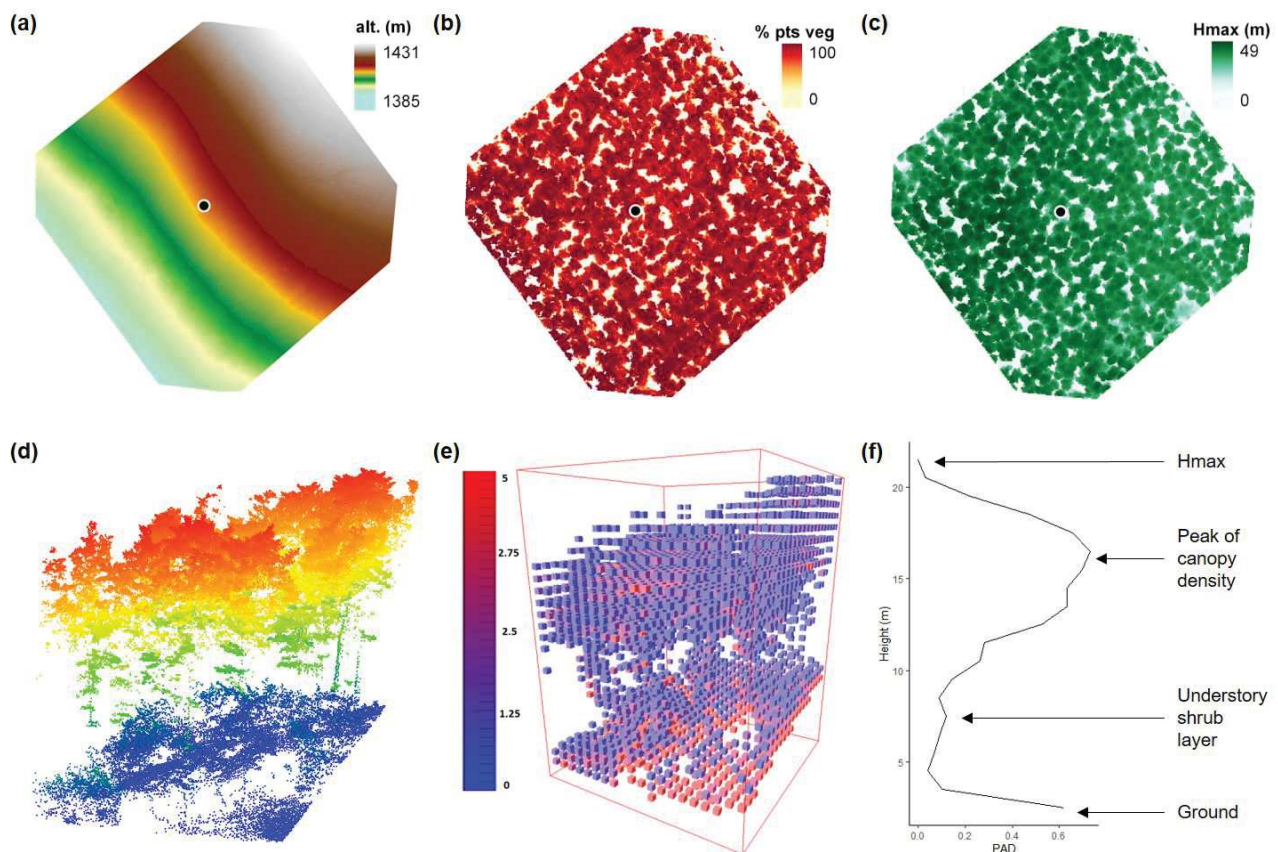
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1117 **Figure 1**

1118 **Fig. 1:** Conceptual figure illustrating how light detection and ranging (LiDAR) data can be used to
 1119 assess micro-topographic variation (e.g., skid trails) and forest structure (e.g., vertical layering of
 1120 vegetation) at a landscape level, and thus highlight legacy effects still affecting the current
 1121 composition of understory plant communities and their responses to macro-environmental
 1122 changes through time-lag dynamics. For instance, using well-chosen LiDAR-derived variables (see
 1123 the main text and subsequent figures), it is possible to not only capture the imprints of historical
 1124 forest management practices (e.g., ancient coppice-with-standards converted to high forests after
 1125 World War II or the more recent intensification of heavy vehicles' traffic to harvest timber) but
 1126 also to unveil past land uses (e.g., ancient settlements or agricultural fields).

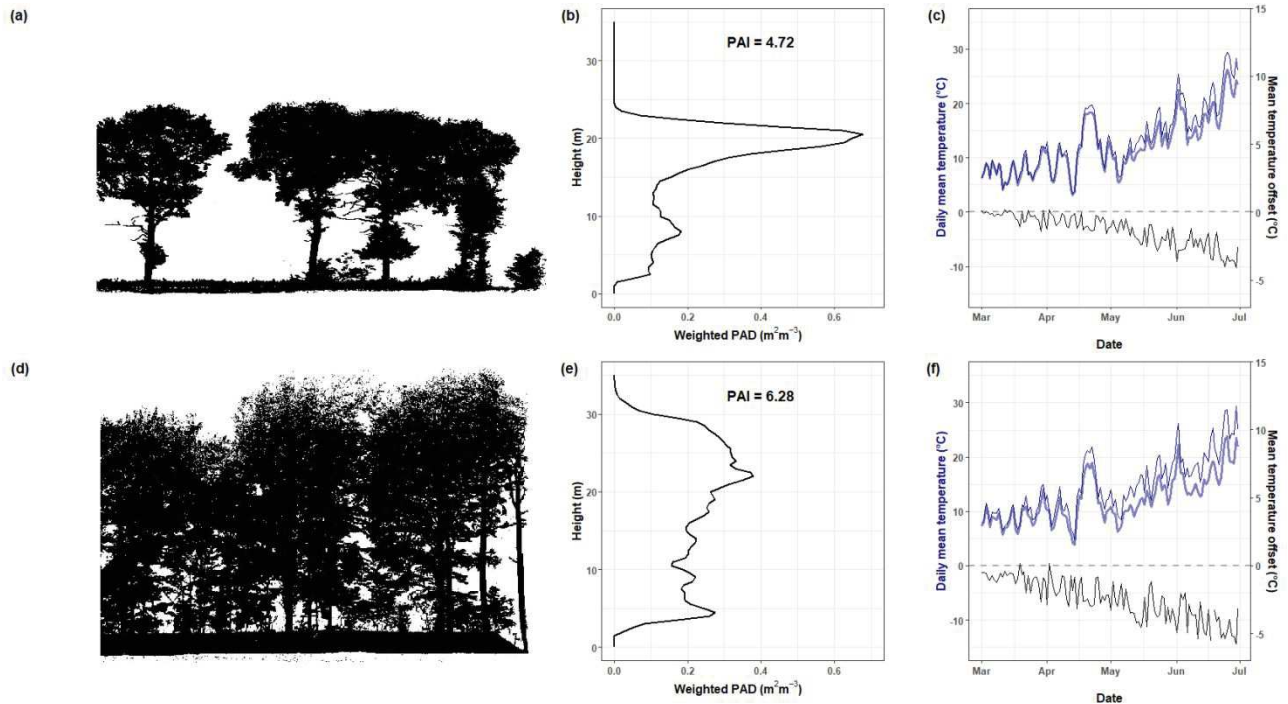
1127 **Figure 2**

1128 **Fig. 2:** How light detection and ranging (LiDAR) works (a, b, c) and the mean to acquire LiDAR data
 1129 from below or from above treetops (d, e). Upper-left panel (a): example of a non-stationary
 1130 airborne LiDAR system (ALS) on board an aircraft. Upper-right panels (b, c): basic principles of
 1131 time-of-flight vs. phase-shift LiDAR. Lower panels (d, e): data visualization of raw LiDAR point
 1132 clouds extracted from both a stationary terrestrial LiDAR system (TLS) (Riegl VZ400) and a non-
 1133 stationary ALS (YellowScan Vx20) covering the exact same study area in the Aigoual forest
 1134 (France).

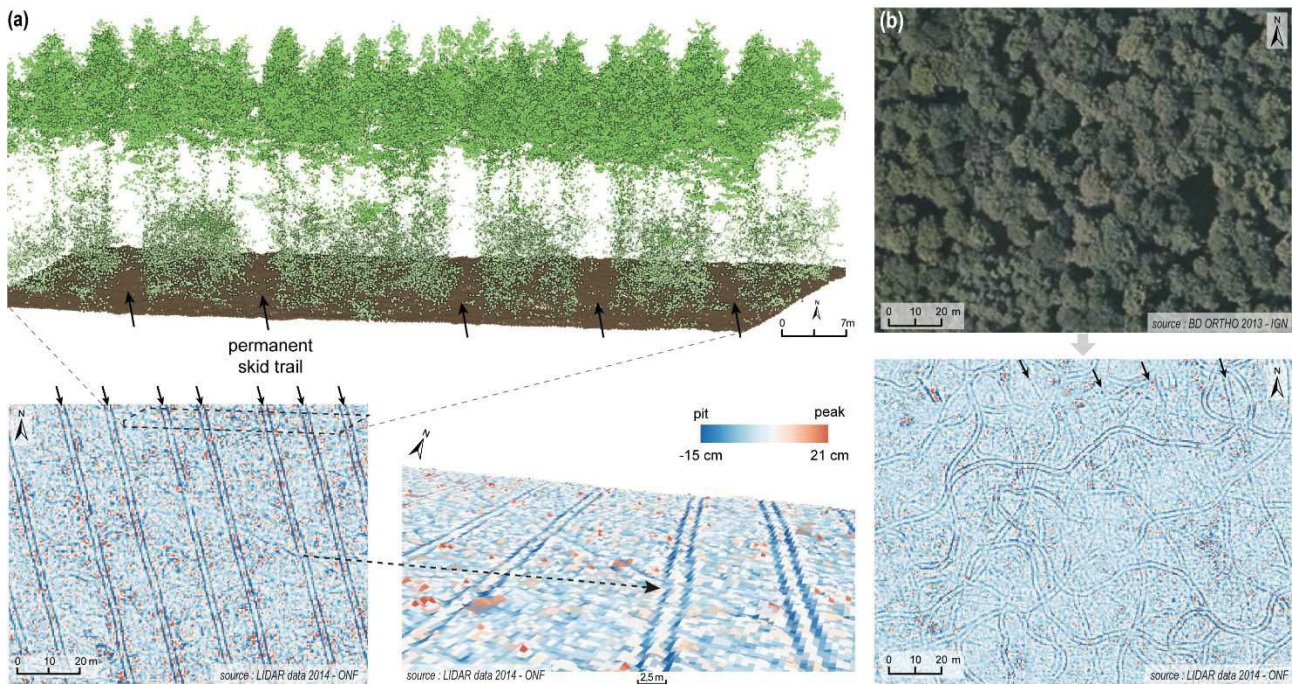
1135 **Figure 3**

1136 **Fig. 3:** Examples of LiDAR-derived variables to assess the vertical complexity below treetops.

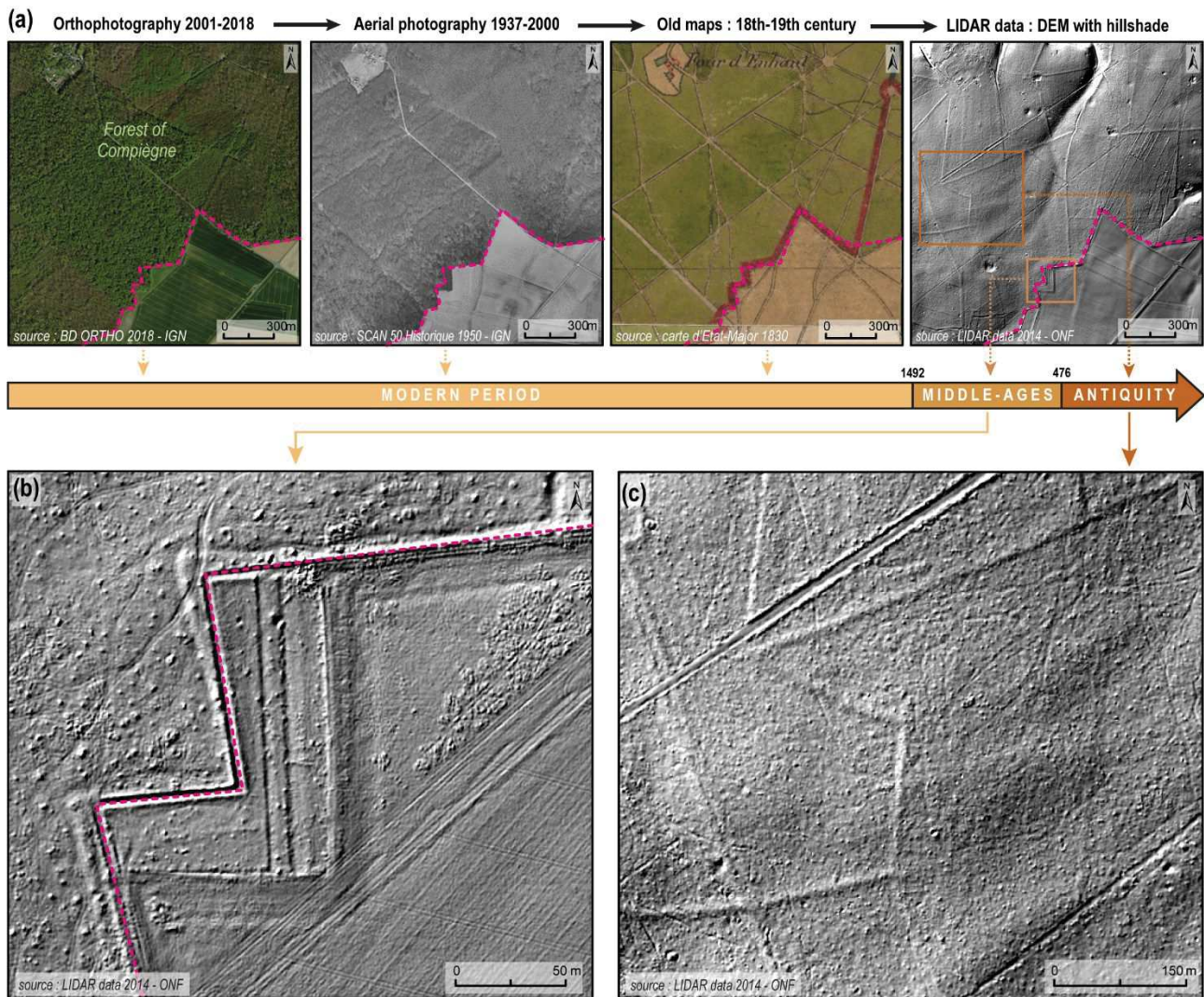
1137 Upper panels (a, b, c): raster layers, at 50 cm × 50 cm resolution, showing the digital terrain model
 1138 (DTM) (a), the percentage of points classified as “vegetation” (a proxy for canopy density) (b), and
 1139 maximum canopy height (Hmax) (c) across a 0.5 ha area (ca. 70 m × 70 m) in the Aigoual forest
 1140 (France). Lower panels (d, e, f): close-up on the raw 3D LiDAR point cloud across an area of 20 m ×
 1141 20 m size (d) to derive plant or leaf area density (PAD or LAD) computed for small volume units or
 1142 voxels of 50 cm × 50 cm × 50 cm size (e) further aggregated by height layer to generate a
 1143 vegetation profile of PAD values (f). Data were acquired with a non-stationary ALS (YellowScan
 1144 Vx20) (cf. **Fig. 2e**).

1145 **Figure 4**

1146 **Fig. 4:** Using terrestrial LiDAR systems (TLS) to derive variables explaining the variation in forest
 1147 microclimates in an open (a, b, c) vs. dense (d, e, f) oak forest located in Belgium. Left panels (a, d):
 1148 cross section of the raw lidar point cloud data. Central panels (b, e): vertical profiles of plant area
 1149 density (PAD) ($\text{m}^2 \text{m}^{-3}$) values as a function of the height of the same point clouds used to
 1150 compute the total plant area index (PAI), which is the integral of the PAVD-profile over the canopy
 1151 height. Right panels (c, f): daily mean temperature ($^{\circ}\text{C}$, blue lines) collected both inside (light-blue
 1152 lines) and outside (dark-blue lines) the respective forest stands. The daily mean temperature
 1153 offset, determined as the temperature inside the forest minus the temperature outside the forest,
 1154 is shown in black as well. The LiDAR data was acquired using a RIEGL VZ400 (RIEGL Laser
 1155 Measurement Systems GmbH, Horn, Austria). Single-scan position TLS was carried out in a dense
 1156 and open forest in Belgium during the summer of 2018.

1157 **Figure 5**

1158 **Fig. 5:** Using airborne LiDAR systems (ALS) to unveil regular (a) and irregular (b) skid trails below
 1159 treetops. A local relief model (LRM), at 50 cm resolution, was derived from the digital terrain
 1160 model (DTM) of the Compiègne forest in Northern France. Left panel (a): a 3D view of the raw
 1161 LiDAR point cloud with regular skid trails, illuminated in dark blue colors by the LRM, below the
 1162 canopy cover of a young forest stand. Right panel (b): irregular and meandering patterns of skid
 1163 trails, likely from different ages, below the canopy cover of a more mature forest stand. Green and
 1164 brown points represent points classified as vegetation and soil, respectively. Bluish and reddish
 1165 colours in the LRM refer to the micro-variation of the terrain microrelief and represent hollows
 1166 (ruts here) and bumps, respectively. The LiDAR data was acquired by the Office National des
 1167 Forêts (ONF) across the entire lowland forest of Compiègne (144 km²). The AERODATA Company
 1168 used a Riegl LMS-680i LiDAR installed on-board an aircraft and performed flights in February 2014
 1169 to get an average density of 12 points per m².

1170 **Figure 6**

1171 **Fig. 6:** Using airborne LiDAR systems (ALS) to extend a chronosequence (a) and unveil past land
 1172 uses (b, c). Upper panel (a): chronosequence of land uses at the southern edge of the Compiègne
 1173 forest in Northern France reconstructed with the help of modern orthophotography, historical
 1174 aerial photography, old archives from Cassini maps, and LiDAR data allowing us to extend the
 1175 chronosequence until the Middle Ages and Antiquity. We used a digital terrain model (DTM), at 50
 1176 cm resolution, with hillshade to unveil former agricultural practices inside the study area. The DEM
 1177 with hillshade on the right-hand side of panel (a) clearly highlights artificial excavations (i.e., see
 1178 the closed depressions) likely originating from the late Iron Age and Roman times and suggesting
 1179 marling/liming practices to enrich agricultural fields. Bottom panels (b, c): close-up across two
 1180 sites near the southern edge of the forest: evidence of (b) a typical late Middle Ages strip field

1181 with cultivation ridges and (c) linear microreliefs corresponding to a network of Gallo-Roman
1182 agrarian fields and secondary roads. The LiDAR data was acquired by the Office National des
1183 Forêts (ONF) across the entire lowland forest of Compiègne (144 km²). The AERODATA Company
1184 used a Riegl LMS-680i LiDAR installed on-board an aircraft and performed flights in February 2014
1185 to get an average density of 12 points per m².