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The Neglected Belowground Dimension of Plant Dominance

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The neglected belowground dimension of dominance

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Abstract:	Dominants are key species shaping ecosystem functioning. Plant dominance is typically assessed on aboveground appearance but aboveground-belowground dominance of individual species may not scale proportionally. This is especially important in biomes where most biomass is allocated belowground, and includes areas accounting for >60% of biomes' land cover worldwide.

Dear Dr Andrea Stephens, Editor of *Trends in Ecology and Evolution*,

On behalf of all the co-authors, I here submit the revision of our Forum piece entitled **“The neglected belowground dimension of dominance”** [TREE-D-20-00095] to your Journal. We have addressed all the concerns and suggestions made by you and the two reviewers in the dedicated response letter appended to this submission. In there, we have indicated where and how we have tackled each issue, reporting the corresponding line numbering in the main text referring to the implemented change. We believe that all comments greatly helped us to improve the clarity of our message.

Thanking you for your time, I look forward to receiving news. Please, do not hesitate to contact me if you would need further information or details (gianluigi.ottaviani@ibot.cas.cz).

With best regards,

Dr Gianluigi Ottaviani

Třeboň, 9 May 2020

Dear Dr Andrea Stephens, Editor of *Trends in Ecology and Evolution*,

On behalf of all the co-authors, I here submit the revision of our Forum piece entitled “**The neglected belowground dimension of dominance**” [TREE-D-20-00095] to your Journal. Below, we have addressed all the concerns and suggestions made by you, and the two reviewers. We believe that all comments helped us to significantly improve the quality and clarity of our manuscript. Our replies are reported in blue-text, and we indicated the line numbering [yellow-highlighted to facilitate the identification] where the change has been implemented in the paper.

Editor

ED: As you can see from reading the reviewer reports below, you'll see that the both reviewers thought the topic timely and important. The most pressing concern was raised by Reviewer 1, who thought that there was a conflation in the article between (1) species dominance within and ecosystem and (2) differences in above vs. below ground allocation across ecosystems. Reviewer 2's comment about Ln 104-107 should help you in thinking this through and addressing this.

AUT: We thank the Referees and the Editor for asking this important clarification. We have provided examples of species that are characterized by discrepant behaviors in their aboveground vs belowground dimension of dominance in relation to biomass allocation. We tried to make this point clearer in the main text [L38-57; L66-111] as well as in the Fig. 1 where four examples of species are now reported [an in its caption; L241-246]. We have referred to possible issues related to estimating specific ecosystem functions that can be biased by not considering the belowground dimension of dominance – an issue particularly relevant in those biomes [i.e. seasonal and disturbance-prone grassy and shrubby systems] where a community as a whole allocate most of their biomass belowground but not necessary all plant species in the community behave the same. This may lead to different levels of dominance of individual species in aboveground vs belowground space due to allocation discrepancy [L66-111].

ED: I have provided a marked up copy of your manuscript with comments and suggestions that I would like you to follow. Therefore, I encourage you to prepare a revised version of your article, taking into account the referees' and my suggestions as far as possible - but taking care not to increase the length of the text or reference list beyond that recommended in the instructions to authors.

AUT: We have addressed all the comments in this response letter, and we have implemented most of the suggestions in the main text and in the figure – we acknowledge the thoughtful contribution of the Referees and Editor in the dedicated section.

Reviewer #1

Rev#1: In this forum article, the authors highlight the importance of considering the belowground component of species dominance in ecosystems. This is indeed a largely neglected dimension with important implications for many aspects of ecosystem functioning, making the article timely and relevant. However, that having been said, I must say I found the manuscript as it is currently written rather underwhelming, with a lot of inconsistencies.

AUT: We thank the Reviewer for highlighting a few sections that required a better explanation and a clearer formulation. We have tackled the main concerns, and as a result we believe that the robustness and logic flow of the story has greatly improved.

Rev#1: For one, the authors conflate discussions of dominance with patterns of overall allocation belowground in many places. That there are scaling discrepancies between aboveground and belowground biomass across ecosystems (typically across climatic and rainfall gradients) is well-established and hardly novel. What is more interesting (and what I believe is the main premise of the paper based on the initial few paragraphs) is whether the relative contribution of different species to biomass or abundance within an ecosystem (dominance) is the same above- and below-ground, and whether these patterns change in any consistent manner across environmental gradients and biomes. However, this aspect is rather poorly developed in the paper, with the bulk of the discussion focusing on differences in overall biomass allocation above and belowground across systems, rather than on how the relative contribution of species to these components changes in any consistent manner across systems. These differences need to be more clearly articulated in the paper.

AUT: We thank the Referee for noting this. Our aim was indeed to point out differences in biomass allocation among species [i.e. biomass scaling discrepancy] causing different level [or lack] of dominance in aboveground vs belowground space, and how this may affect ecosystem functioning. Biomes were instrumental for stressing this point as we consider the biomass scaling discrepancy is especially important in biomes known for high belowground: aboveground biomass ratio [at the community level]. Dominance studies however are typically focused on species level, and this leap [i.e. from community to individual species] constitutes a challenge that we aim to highlight, and propose viable ways forward. In the edited version, we provide examples [i.e. of species that are behaving as subordinate aboveground and as dominant belowground + dominant aboveground but not belowground] in the main text [L66-111] as well as 4 examples in the Figure 1 [L241-246].

Rev#1: I also don't think the authors make a convincing case for WHY understanding belowground dominance (as opposed to overall biomass allocation belowground) is important, and what we miss out by not quantifying it. At present, the justification is largely in the form of a few broad sweeping statements - i.e. it can affect a number of ecosystem functions and properties such as nutrient cycling, biomass turnover etc. and so it is worth studying. While I am in no way contesting that understanding belowground dominance is important, I would have liked to see the authors parse out the benefits of doing so in a little more detail. Many of the functions and processes the authors discuss are impacted to a large extent by just total belowground allocation, irrespective of which species is contributing to this allocation. What further insights can we gain by more explicitly quantifying belowground dominance, and what exactly are ecologists missing by not doing so?

AUT: We have added links to specific ecosystem functions that we risk to miss out or getting a biased view upon by not considering the belowground dimension of dominance [L66-111; L125-130]. Knowing plant species identity and its contribution to belowground biomass is not trivial as different species can affect ecosystem functioning differently, especially if very abundant and accounting for a large portion of biomass. We added reasons why this should be the case, primarily by considering interspecific differences in belowground traits, including for example i) lignin content affecting belowground litter decomposability and nutrient cycling, and ii) concentration of storage carbohydrates and bud bank linked to resprouting ability and carbon sequestration [L75-111].

Rev#1: Along the same lines, under what conditions and in what systems is belowground dominance (and not total allocation at the system level) likely to differ from aboveground dominance, i.e. are there conditions under which species that dominate aboveground within any given system are likely to differ from those that dominate belowground? What traits of the constituent species can provide us insights into this?

AUT: We know that, for example, temperate grassland herbs characterized by long-lived belowground organs coexist with herbs having short-lived belowground organs. Long-lived belowground organs accumulate more biomass over years, contain more lignin, and are more recalcitrant to decomposition than short-lived belowground organs [L95-102]. Another example relates to seeder and resprouter species in fire-prone areas. In these regions, species that invest considerably to seed production and seed bank [usually not surviving fire and have strategies to effectively seed, release and germinate after fire] co-occur with species with contrasting strategies, i.e. that accumulate carbohydrates and buds belowground forming bulky organs. Different seeder and resprouter species provide therefore ecosystems with plants responding differently to fire [L102-111]. Looking only at how plants appear aboveground is largely misleading for detecting dominance as well as for assessing ecosystem functioning since e.g. resprouters store carbon and buds belowground in coarse organs. These examples were present also in the previous version, and now should be clearer from the additional examples [in text; L66-111, and figure; L241-246].

Rev#1: I think the manuscript would have also benefitted from a more in-depth discussion or synthesis of the methods available to quantify species contributions belowground. At present, the authors just refer to previous work - a brief synthesis here would be a very valuable contribution.

AUT: We agree with the Referee that expanding this practical part [synthetically reported in Box 1 with some key references] would be interesting. However, the format and target of the paper does not allow to add many details along this line so that we concentrated more on conceptual issues and left this topic to future publications.

Rev#1: Finally, I think there is a fair bit of repetition in the text that can be reduced to free up space for more in-depth discussions of the points raised above. For example, much of the first 2 paragraphs can be significantly condensed.

AUT: We agree that the text was at places a bit repetitive, such as the initial sections [largely edited; L33-61]. We aimed at streamlining the overall message through a careful overhaul of the manuscript using the handy suggestions offered by the Referees and the Editor.

Reviewer #2

Rev#2: Overall I found it to be an important paper reminding every (plant) ecologist that there's more than meets the eye and measuring only the aboveground characteristics is not enough. In addition, the authors highlight ways how to account for the belowground dominance, by DNA-based methods and/or trait databases. I thought that the piece is mostly well-written, the glossary with extra explanations was informative and the level of detail in the figure is impressive. However, more clarity can be achieved in some parts, which I have pointed to below.

AUT: We thank the Referee for appreciating our effort and for providing useful insights.

Rev#2: Abstract: „Dominants are keystone species..." perhaps you mean key species, since „keystone species" has a slightly different definition than dominant species (disproportionate vs proportionate impact).

AUT: We agree, and we have changed the word accordingly [L25].

Rev#2: Line 40-42 „In fact, species abundance is assessed based on plant aboveground appearance which may have important implications for the understanding of species dominance" - this sentence could be developed further - what's wrong with assessing abundance based on aboveground appearance (or do you mean occurrence?), what important

information are we missing out or what new understanding does including the belowground portion give us to understand the causes and consequences of dominant species?

AUT: This issue should be now solved after we have heavily edited and re-focused this entire section. Also, the examples related to forested vs grassy and shrubby biomes should help in making this point clearer [L37-61].

Rev#2: Line 47-52 „These criteria may effectively detect overall dominance (i.e. aboveground and belowground; Fig. 1) when biomass scaling between aboveground and belowground biomass is known, yet such scaling is highly context-dependent..." and „Therefore, while aboveground characteristics can be used as reliable proxy for overall dominance in forested biomes, they may lead to biased estimations in grassy and shrubby ones (Fig. 1)." I don't follow the logic here- if we know the biomass scaling for grassy and shrubby vegetation (e.g. something like the the biomass ratios in Fig1) and can take this into account, why does it lead to more biased estimations (more than for forests for instance)? Or in other words, if the BGB:AGB ratio for any given biome/site is known, is it then ok to use the aboveground characteristics as long as we scale it accordingly?

AUT: We thank the Referee for spotting this. We agree that the sentencing and logic flow deserved improvement. In fact, without specifying that aboveground-belowground biomass scaling can be largely discrepant at the species as well as the community level and that this is particularly relevant [and problematic] in those biomes where plants allocate most of their biomass belowground, the point was not clear. We have therefore heavily edited and re-focused this entire section [L33-61], using also comments made by the Editor and Rev#1 related to the same part.

Rev#2: Line 54-58 It's not clear if and why are you making a distinction between fine roots and coarse roots. It's mostly the fine roots which are related to turnover and acquisitive traits and in several parts of the paper what you say about roots, e.g. mycorrhizal interactions, apply for fine roots. My point is that perhaps it's not necessary to exclude fine roots?

AUT: We agree, however that sentence has been deleted in the new version.

Rev#2: Line 89: „Why and where should we 'bother' about the belowground dimension of dominance?" perhaps „need to consider" instead of „bothered", since you would not want to bother people with this topic, but you want to convince them it's important.

AUT: In this occasion, we disagree with the Reviewer – we intentionally used a thought-provoking heading and sentencing, and that was why we stated 'bother'. We are indeed acknowledging and aware that working belowground is generally more time-consuming and challenging than is aboveground. This has brought to a far less research attention directed belowground than aboveground – but this trend is finally changing in recent years! Here, we want to stress priority research areas and biomes where ecologists and biogeographers should be focusing – hence the word pun 'bother', as we suggest researchers should at least start to conceptually considering the belowground dimension of dominance even if this is challenging. This way, we may maximize the future research effort where would be more needed, i.e. seasonal and disturbance-prone grassy and shrubby biomes rather than forested biomes. Therefore, we would like to maintain our formulation.

Rev#2: Line 104-107: would it be worth providing an example of a well-known species that based on aboveground abundance could be considered a subordinate species, but most likely is a dominant based on belowground abundance/traits?

AUT: We thank the Referee for pointing this out, which greatly assisted in tackling the main concern of Rev#1. We have amended the text [L92-111] and Figure 1 reporting examples where

aboveground vs belowground dimensions of dominance are [or are expected to be] discrepant [L241-246]. Please, refer also to related comments and replied above.

Rev#2: Line 131: „Also, many species are characterized by associations with mycorrhizas and other organisms (e.g. N₂ fixing bacteria) that may influence species fitness and dominance potential" Here mycorrhizal fungi instead of mycorrhizas since you provide examples of organisms that form associations with plant roots.

AUT: We agree and we have changed the text accordingly [L120].

Rev#2: Lines 134-136: „They therefore constitute priority research areas in dominance-related studies, deserving further exploration especially in highly seasonal and disturbance-prone biomes." Definitely not only in dominance-related studies.

AUT: The sentence has been deleted in the edited version as not needed anymore.

Rev#2: Lines 200-203: „Scaling discrepancy in aboveground vs belowground dominance may be caused by the relaxation of certain physical limitations (e.g. gravity). Belowground coarse, non-acquisitive organs are linked to such scaling discrepancy as they account for most of the biomass in grassy and shrubby biomes" I don't quite get the gravity example? Please explain more or provide another example of biomass scaling discrepancy.

AUT: We agree that the phrasing here was not very clear and adding potential confusion. Also, the biomass scaling discrepancy concept is explained in the main text, so we have decided to delete the last two sentences.

Rev#2: Line 238: The „DNA-based methods" should be „DNA sequencing-based methods" as real-time PCR is also a DNA-based method.

AUT: We have edited the text accordingly [L253].

1 **The neglected belowground dimension of dominance**

2

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19

20 **Keywords:** Belowground organs; Biomass allocation; Biomass scaling; Ecosystem
21 functioning; Local abundance

22

23 **Abstract**

24

25 Dominants are key species shaping ecosystem functioning. Plant dominance is typically
26 assessed on aboveground appearance but aboveground-belowground dominance of
27 individual species may not scale proportionally. This is especially important in biomes
28 where most biomass is allocated belowground, and includes areas accounting for >60%
29 of biomes' land cover worldwide.

30

31 **Aboveground vs belowground dimension of dominance**

32

33 **Dominant plant species** (see Glossary) can greatly affect ecosystem functions such as
34 biomass production, nutrient cycling and carbon sequestration [1]. So far, studies
35 focused on dominance are heavily biased towards its aboveground dimension, a pattern
36 also present in plant functional ecology, community ecology and global change science
37 [2,3]. The most important criteria used to assess species dominance are indeed
38 aboveground abundance (e.g. cover, frequency, local density, biomass). Belowground,
39 however, the dominance may not mirror the aboveground behaviour as plant species
40 differ in their relative biomass investments into belowground organs. This 'biomass
41 scaling discrepancy' can largely vary in different **biomes**. The identification of which
42 biomes and ecosystem functions would benefit from considering the belowground
43 dimension of dominance is therefore compelling.

44

45 In forested biomes (i.e. rainforest, temperate forest, taiga) plants invest up to ~80% of
46 biomass in their aboveground parts, and dominant species generally do not differ in
47 their aboveground-belowground biomass scaling (Fig. 1). Therefore, aboveground
48 characteristics can be used as reliable proxies for species dominance (aboveground
49 and belowground). Conversely, in seasonal and disturbance-prone grassy and shrubby
50 biomes (i.e. savanna, shrubland, temperate grassland, tundra) biomass allocation is
51 notably directed into belowground organs at the community level [2-5]. Additionally,
52 individual species may substantially differ in their biomass scaling; this is because
53 different species vary in their allocation to belowground structures such as thick roots,

54 **lignotubers, rhizomes** and other organs that enable survival during unfavourable
55 seasons and recovery after major disturbances [3,4]. As a consequence, basing the
56 identification of species dominance on aboveground characteristics can lead to biased
57 estimates of dominance in grassy and shrubby biomes. We here identify that the
58 belowground dimension of dominance can be relevant to >60% of terrestrial biomes'
59 cover (Fig. 1), and we exemplify how neglecting this striking figure can translate into
60 biased understanding of species dominance and ecosystem functioning, indicating
61 approaches that can be used to fill this gap (Box 1).

63 **Why and where should we 'bother' about the belowground dimension of** 64 **dominance?**

65
66 Grassy and shrubby biomes are characterized by high belowground-aboveground
67 biomass ratio (**BGB:AGB**; Fig. 1) [2]. In these biomes, the preferential allocation of
68 biomass belowground into coarse (resource-storage and bud-bearing) organs reflects
69 plant survival strategies under recurrent disturbance (e.g. herbivory, frost, fire) that
70 removes aboveground biomass [3-5]. Conversely, in forested biomes, low BGB:AGB
71 values are driven by aboveground competition for light that, due to the lack or scarcity of
72 disturbance events, shapes plant strategies and promotes investments in height growth
73 (Fig. 1) [5].

74
75 These BGB:AGB figures were obtained at the community level, while identifying
76 dominance implies considering single species' contribution to total biomass [1].
77 Generally, species-level BGB:AGB studies have been carried out in pots where only
78 young individuals are included [e.g. 6]. This constitutes a bias towards the aboveground
79 dimension; biomass allocation to perennating belowground organs is indeed highly
80 dependent on plant age [7]. This concern is particularly relevant for grassy and shrubby
81 biomes where species can be characterized by long-lived individuals, perennating
82 belowground organs associated with a marked aboveground-belowground biomass
83 scaling discrepancy. Therefore, especially in these biomes, field-collected data are
84 required. Species identification (and the excavation it requires), however, is difficult

85 when looking at plants belowground, and only few studies have attempted to identify
86 species and their biomass belowground [8]. As a result, our understanding of
87 dominance, especially in grassy and shrubby biomes, remains limited. In order to
88 overcome this hurdle, we suggest the approach proposed by [1] be implemented
89 belowground in conjunction with direct and indirect methods for recognizing species
90 identity and quantifying species' biomass allocation (Box 1).

91
92 One could legitimately ask why to make all the effort to identify a species identity, its
93 biomass allocation and functional role belowground so to confirm or reject the species
94 dominance whether working at the community level may already provide insights into
95 ecosystem functioning [2]. To clarify this key point, we make two examples. In
96 temperate grasslands, herbaceous species characterized by long-lived belowground
97 organs coexist with species having short-lived belowground organs [3]. Species with
98 long-lived belowground organs (e.g. *Iris lutescens*; Fig. 1) compared to species with
99 short-lived ones (e.g. *Bromus erectus*) accumulate more belowground biomass over
100 years, contain larger pools of storage carbohydrates and lignin and therefore are more
101 recalcitrant to decomposition. These species' functional differences directly affect soil
102 carbon sequestration. Another example relates to fire-prone savannas and shrublands.
103 In these biomes, species that tend to preferentially invest into seed production and seed
104 bank and only little into belowground organs are usually killed by fire (seeders). Seeders
105 co-occur with species distinguished by contrasting strategies, i.e. accumulating
106 carbohydrates and buds belowground forming bulky organs adapted to cope with fire
107 (resprouters, e.g. *Eucomis autumnalis*; Fig. 1) [4,5]. As a result, coexisting seeder and
108 resprouter species contribute differently to aboveground vs belowground biomass of the
109 entire community, and respond differently to fire. A striking and well-known case of
110 resprouter species which abundantly allocate their biomass belowground is constituted
111 by **geoxyles** in the so-called 'underground forests' [5].

112
113 Additionally, species may interact with their neighbours belowground differently than
114 they do aboveground – this can be illustrated by the spatial distribution of belowground
115 organs (Fig. 1). For instance, belowground organs (e.g. roots, rhizomes) of different

116 species can be tightly intermingled and occupy broader areas belowground than
117 aboveground [3,9]. Moreover, belowground organs may provide species with enhanced
118 abilities related to space occupancy, and resource acquisition and sharing over large
119 areas, so affecting species competitive abilities [3,8,9]. Also, many species are
120 characterized by associations with mycorrhizal fungi and other organisms (e.g. N₂ fixing
121 bacteria) that influence fitness and dominance potential [8-10]. All these ecological
122 interactions that are linked with and affected by the belowground dimension of
123 dominance remain poorly studied in relation to ecosystem functioning.

124

125 Finally, different species play different functional roles in communities, and dominant
126 species are considered the major drivers in the functioning of any ecosystem [1].

127 Examples of important functions exerted by different belowground organs that may be
128 largely affected by the belowground dimension of dominance include i) carbon
129 sequestration and nutrient cycling through biomass accumulation and turnover, ii) soil
130 stabilization via mechanical support, iii) recovery after disturbance (resprouting) [3,4].

131 We argue that by neglecting the belowground dimension of dominance we risk to get a
132 partial and potentially biased picture of dominance and of impacts that dominant
133 species may have on key functions.

134

135 **What is next? Start digging in grassy and shrubby biomes**

136

137 Sampling plants belowground is generally a challenging and laborious procedure. This
138 is why belowground plant ecology is still lagging behind its aboveground counterpart
139 [3,11]. This gap is even larger for dominance-related studies. Remarkably, we noticed
140 how the role of the belowground dimension of dominance may be highly relevant to
141 seasonal and disturbance-prone grassy and shrubby biomes (accounting for >60% of
142 land cover) where allocating biomass belowground may constitute an adaptive strategy
143 facilitating species persistence [3-5]. This striking figure exemplifies the global relevance
144 of the knowledge gap related to the belowground dimension of dominance.

145

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147

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151 Editor Dr Andrea Stephens for providing thoughtful insights during the revision process.

152

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191

192 **Glossary**

193

194 **BGB:AGB ratio** (typically but misleadingly termed root:shoot ratio): quotient between
195 belowground and aboveground biomass, typically without discriminating between
196 different plant organs [2,3]. For instance, the term “root” incorporates acquisitive fine
197 roots, non-acquisitive thick roots, stem-derived rhizomes and tubers.

198

199 **Biomass scaling**: relationships between biomass of different organs (e.g. leaves vs
200 fine roots), parts (i.e. aboveground vs belowground biomass) forming an individual plant
201 (usually in pot experiments) or across plant species forming a community (commonly in
202 field studies). Generally, the scaling ratio is dependent on plant size and longevity, and
203 is limited by gravity, transpiration flow from roots to leaves [6,7].

204

205 **Biome**: ecological and biogeographical concept used to define biotic and functional
206 community types worldwide based on climate, evolutionary history and disturbance
207 regime [2].

208

209 **Dominant plant species:** a species that is locally abundant in relation to its co-
210 occurring species (e.g. accounting for large proportion of biomass), affecting ecosystem
211 functioning proportionally to its abundance [1]. The identification of dominant species is
212 a context-dependent matter, e.g. based on spatial scale involved and focal biome.

213

214 **Geoxyle:** a growth form typical of fire-prone regions, forming the so-called 'underground
215 forests' [5]. Species belonging to this group are able to resprout from their belowground
216 organs, generally from a woody rhizome or lignotuber.

217

218 **Lignotuber:** an enlarged belowground woody structure of root and stem origin that
219 serves as bud and resource storage in woody plants. Lignotubers enable resprouting
220 after disturbance and are commonly found in fire-prone regions [11].

221

222 **Rhizome:** a belowground horizontal stem with adventitious roots that operates as bud
223 and resource storage in herbaceous and woody plants [11]. Rhizomes enable clonal
224 multiplication, space occupancy, resprouting, resource foraging, storing and sharing. In
225 certain biomes, e.g. temperate grassland, rhizomes may account for a considerable
226 proportion of belowground biomass.

227

228 **Figure 1. Scaling Between Belowground And Aboveground Biomass Across**
229 **Terrestrial Biomes.** Belowground (BGB) vs aboveground (AGB) biomass allocation for
230 eight main terrestrial biomes. Biome definition follows [2] from which data on biomass
231 scaling have been gathered (BGB:AGB; colours indicate biome-specific average ratio).
232 BGB:AGB values: Tundra = 4.8, Temperate grassland = 4.3, Desert = 2.6, Shrubland =
233 2.3, Savanna = 1.3, Taiga = 0.4, Rainforest = 0.3, Temperate forest = 0.3. Pie-chart
234 represents biomes' land cover. Scale bar indicates 1m. Inset panels exemplify profiles
235 of aboveground-belowground biomass allocation across biomes, especially where the
236 belowground dimension of dominance and scaling discrepancy are expected to be
237 particularly relevant (with rainforest reported for comparison). Drawings are simplified
238 plant communities with plant organs and their distribution illustrated in real size and

239 proportion. Inspiration for drawings: Tundra, South American Andes; Temperate
240 grassland, Central Europe; Desert, Central America; Savanna (humid), Southern Africa;
241 Rainforest, Central Africa. Examples of plant species showing discrepant aboveground-
242 belowground biomass scaling are reported, i.e. behaving as subordinate aboveground
243 and dominant belowground for Tundra (1; *Eriophorum angustifolium*), Temperate
244 grassland (2; *Iris lutescens*) and Savanna (4; *Eucomis autumnalis*) whereas an example
245 of a species appearing dominant aboveground and subordinate belowground is
246 illustrated for Desert (3; *Geraea canescens*).

247

248 **Box 1. Methods To Identify The Belowground Dimension Of Dominance**

249 In highly seasonal and disturbance-prone biomes (Fig. 1), a candidate dominant
250 species aboveground should be confirmed as a belowground dominant based on its
251 contribution to total biomass [1]. Three methods to identify species identity and biomass
252 allocation belowground exist. These are (1) digging out a species' belowground organs
253 [11]; (2) molecular and DNA sequencing-based techniques [9], including real-time PCR
254 [8] and DNA-metabarcoding [10]; and (3) indirectly, by examining species traits that may
255 serve as proxy of biomass allocation [3,11,12].

256

257 Traits related to coarse non-acquisitive organs have great potential to detect the
258 belowground dimension of dominance. For example, the trait 'persistence of rhizome'
259 may provide insights on biomass allocation and turnover [3,11]. Trait databases
260 providing species-specific functional information on belowground coarse organs exist for
261 certain biomes, e.g. CLOPLA for temperate grassland [12]. Scattered information occur
262 for other biomes, therefore knowledge is largely incomplete – but see [4] for shrubland.
263 This gap is especially relevant where the belowground dimension of dominance is
264 expected to be key, e.g. tundra, savanna (Fig. 1). Another important, context-dependent
265 factor is the recommended sampling depth which largely varies across biomes, yet
266 reliable thresholds have been proposed [2].

Figure 1

