

Perspectives in Plant Ecology, Evolution and Systematics

Next-Gen Plant Clonal Ecology

--Manuscript Draft--

Manuscript Number:	PPEES-D-20-00091R1
Article Type:	Full length review
Keywords:	clonal, vegetative reproduction, ecology, evolution, review, plants
Corresponding Author:	Scott Franklin University of Northern Colorado Greeley, CO UNITED STATES
First Author:	Scott Franklin
Order of Authors:	Scott Franklin Peter Alpert Roberto Salguero-Gómez Zdeněk Janovský Tomáš Herben Jitka Klimešová Vladimir Douhovnikoff
Manuscript Region of Origin:	Europe
Abstract:	Some plants are capable of splitting into physically independent units, termed clonal growth. Clonal growth has a number of ecological and evolutionary implications, namely reproductive insurance, space monopolization, regeneration after injury, dormancy, and sharing resources among plant modules. Despite the commonness of the phenomenon and clear ecological implications for species that possess it, clonal growth and reproduction have received very little attention in plant ecology. Here, we outline a brief background of clonal plant ecology, its importance from evolutionary ecology to predicting climate change impacts on plant communities, and then focus on pressing questions. Our review and this special issue highlight both the obstacles and opportunities in explicitly incorporating clonal plant knowledge into mainstream plant ecology and evolution research.
Suggested Reviewers:	Fei-Hai Yu feihaiyu@126.com Clonal plant expert Sergio Roiloa sergio.roiloa@udc.es Clonal plant expert Petr Pyšek pysek@ibot.cas.cz Clonal plant invasion expert



Scott B. Franklin
(Scott.Franklin@unco.edu)
School of Biological Sciences
University of Northern Colorado
Ross Hall, Campus Box 92
Greeley, CO 80639-0017
Office (970) 351-2650; Fax (970) 351-2335

January 24, 2021

Claus Holzzapfel and Silke Dietz:

Thank you for allowing us to revise our introduction and review paper for the Special Issue on Clonal Plants. The resubmission specifically addresses the comments of the Editor (Claus), which we found insightful and worthy of response. In addition, Peter Alpert performed a thorough copy edit of the manuscript.

We hope you find are revision satisfactory for publication. We believe these few revisions improved the manuscript.

I would be happy to answer any questions or concerns,

Sincerely,

A handwritten signature in black ink, appearing to read "Scott B. Franklin".

Scott B. Franklin, Professor
Scott.Franklin@unco.edu

Response to Editor:

Claus: "what are "asi" and "si"? Are these formatting instructions?"

Response: "asi" is a typo; "si" stands for special issue, showing which of the cited publications in this intro were from this special issue. We changed this to an asterisk and provide context in headings.

Claus: "most?"

Response: changed as suggested

Claus: "I wonder whether one needs to include the "hidden cost of meiosis" namely the dilution (but not loss as implied here) of an individual's genetic material into the next generation through sexual reproduction. See a more recent discussion of this:

Gibson AK, Delph LF, Lively CM. The two-fold cost of sex: experimental evidence from a natural system. *Evol Lett.* 2017;1(1):6-15. doi:10.1002/evl3.1"

Response: We think we cover this a couple paragraphs later (lines 111-118) and have not added it at the comment location.

Claus: "There were a number of special issues that dealt with clonal biology/ecology. His would be a good place to cite them here. Just a suggestion."

Response: Since we see this as a review-style paper rather than a bibliographic source, we opted not to add but mention some at the end of section 2.

Claus: "Increased or decreased heterogeneity? Or just changes from the state before disturbance?"

Response: Actual changes in heterogeneity, so we left this alone.

Claus: "What about the possibility that clonal plants are more likely to establish after introduction as they do not need to "worry" about finding mates? Are there studies that look at differential rates of establishment success in clonal vs non-clonal plants? I recall that the now "infamous" 10s rule looked at that."

Response: Establishment rates are indeed hard to find, but this is incorporated into the exotics section of the, what little we have; especially lines 367-375.

Claus: "A potentially interesting side topic could be the reaction of plants to an often described and predicted pollinator shortage. Does the reduction of insect pollinators lead to an increase in clonal propagation?"

Response: We added a sentence to address this idea at the comment location and under research needs. "With the recent loss of pollinator species worldwide (Potts et al., 2010), the ability of asexual clonal plants to circumvent pollinator needs deserves scrutiny."

We hope you find are revision satisfactory for publication. We believe these few revisions improved the manuscript.

I would be happy to answer any questions or concerns,

Sincerely,



Scott B. Franklin, Professor
Scott.Franklin@unco.edu

TITLE: Next-Gen Plant Clonal Ecology

AUTHORS: Scott Franklin¹, Peter Alpert², , Roberto Salguero-Gómez^{3,4}, Zdeněk Janovský^{5,6}, Tomáš Herben^{5,6}, Jitka Klimešová^{5,6}, Vladimír Douhovnikoff⁷

AFFILIATIONS:

¹ School of Biological Sciences, University of Northern Colorado, 501 20th St., Greeley, CO 80639 USA

² Biology Department, University of Massachusetts, 611 North Pleasant Street, Amherst, MA 01003, USA.

³ Department of Zoology, 11a Mansfield Rd, University of Oxford, Oxford, OX1 3SZ, UK

⁴ Evolutionary Demography Laboratory, Max Planck Institute for Demographic Research, 1 Konrad zuße straße, Rostock, DE 18057, Germany

⁵ Institute of Botany, Czech Academy of Sciences, CZ-252 43 Průhonice, Czech Republic

⁶ Department of Botany, Faculty of Science, Charles University, Benátská 2, CZ-128 01 Praha 2, Czech Republic

⁷ Biology Department, Bowdoin College, 6500 College Station, Brunswick, ME 04011 USA

Corresponding Author: Scott Franklin

501 20th Street, School of Biological Sciences, University of Northern Colorado, Greeley, CO USA

scott.franklin@unco.edu

Highlights.

1. Despite the commonness of clonality and clear ecological implications for species that possess it, clonal growth and reproduction have received very little attention in plant ecology.
2. Clonal traits are related to climate, disturbance, species interactions, community assembly, and ecosystem function, thus increasing relative predictive power and improving models, albeit not without challenges.
3. Currently, we possess a number of novel tools, ranging from large trait databases through experimental approaches such as congeneric pair studies to phylogenetic and molecular techniques, to address the impact of clonality on community assembly, biological invasions, and the responses of plants to environmental factors.

1 **Next-gen plant clonal ecology**

2

3 Scott Franklin¹, Peter Alpert², Roberto Salguero-Gómez^{3,4}, Zdeněk Janovský^{5,6}, Tomáš

4 Herben^{5,6}, Jitka Klimešová^{5,6}, Vladimir Douhovnikoff⁷

5

6 ¹ School of Biological Sciences, University of Northern Colorado, 501 20th St., Greeley, CO

7 80639, USA

8 ² Biology Department, University of Massachusetts, 611 North Pleasant Street, Amherst, MA

9 01003, USA.

10 ³ Department of Zoology, 11a Mansfield Road, University of Oxford, Oxford, OX1 3SZ, UK

11 ⁴ Evolutionary Demography Laboratory, Max Planck Institute for Demographic Research, 1

12 Konrad Zübe Straße, Rostock, DE 18057, Germany

13 ⁵ Institute of Botany, Czech Academy of Sciences, CZ-252 43 Průhonice, Czech Republic

14 ⁶ Department of Botany, Faculty of Science, Charles University, Benátská 2, CZ-128 01 Praha 2,

15 Czech Republic

16 ⁷ Biology Department, Bowdoin College, 6500 College Station, Brunswick, ME 04011, USA

17

18 Corresponding Author: Scott Franklin, scott.franklin@unco.edu

19

20 Author contributions: TH, R S-G, and JK organized a special issue for this journal on clonal

21 plants; PA, SF, and VD organized a second special issue for the journal based on an international

22 conference on clonal plants; and all authors merged the two issues and contributed equally to this

23 introduction.

24 **Abstract**

25 Plants with clonal growth can produce multiple potentially independent units, termed ramets.
26 Clonal growth can have important ecological and evolutionary consequences, such as by
27 increasing probability of reproduction, space monopolization, and regeneration after injury; and
28 by permitting physiological integration of connected ramets. Although clonal growth is
29 widespread among species and habitats, it has received relatively little attention in plant ecology.
30 To introduce this special issue on clonal plant ecology, we first provide a brief background on
31 the topic, noting its importance in areas ranging from evolution to the impacts of climate change
32 on plant communities. We then focus on a set of pressing questions, to highlight both the
33 obstacles and opportunities to more explicitly incorporate clonal growth in research on plant
34 ecology and evolution.

35

36 Keywords: Clonal plant; Community assembly; Demography; Disturbance; Invasive species;
37 Population genetics

38

39 **1. Purpose** (* indicates papers in the special issue)

40 Clonal growth in plants is the ability to produce multiple potentially physiologically
41 independent units, termed ramets, of the same genetic individual, or genet, via vegetative growth
42 of stems, roots, or leaves. Although about two-thirds of plant species are capable of clonal
43 growth (Herben and Klimešová, 2020), clonality is often overlooked in plant research (but see
44 Larson and Funk, 2016; Salguero-Gómez, 2018) due to factors such as unfamiliarity with the
45 differential responses of clonal and non-clonal plants, lack of attention to plant architecture and

46 morphology, and the difficulty of studying the belowground organs responsible for much clonal
47 growth. Spreading knowledge about the role of clonality in plant ecology is therefore crucial.

48 The importance of clonal growth in plant ecology and evolution is illustrated by the
49 breadth of the 17 contributions to this special issue on the ecology and evolution of clonal
50 growth. These papers cover transgenerational effects (Dong et al., 2019a*), species interactions
51 (Wang et al., 2019*; Bittebiere et al., 2020*; Duchoslavová and Herben, 2020*), invasion
52 biology (Roiloa 2019*; Wang et al. 2019*), life history (Janovsky and Herben, 2020*),
53 allocation (Goldberg et al., 2020*), biodiversity conservation (Amor et al, 2020*), population
54 structure (Ricono et al., 2020*), and responses to environmental stress (Huebner et al., 2019*)
55 and disturbance (Huebner et al., 2019*; Vesk and Yen, 2019*; Escandón et al., 2020*; Franklin
56 et al., 2020*; Martínková et al., 2020*). Understanding of clonal plant ecology is needed to
57 adequately model plant community assembly and ecosystem function (Bittebiere et al. 2020*)
58 and responses to climate change (Chelli et al. 2019*; Lubbe and Henry, 2019*; Watts et al.
59 2019*) and environmental heterogeneity (Franklin et al., 2020*). To introduce the special issue,
60 we begin with a brief review of previous work on clonal plants and then consider some key
61 current questions and challenges.

62

63 **2. Background**

64 In contrast to most animals, nearly all plants are modular (Harper and Bell, 1979): they
65 maintain meristems with indeterminate growth that produce new shoot and root modules which
66 add to or replace old ones (Ottaviani et al., 2017). In many plants, sets of modules can become
67 physiologically independent. How clonality affects plant architecture has been stressed many
68 times (see review by Oborny, 2019). However, the ecological and evolutionary consequences of

69 clonal growth have not received sufficient attention. Clonal growth can provide reproductive
70 insurance when sexual reproduction is not possible (Herben et al., 2015); facilitate
71 monopolization of space (Zheng et al., 2019), regeneration after injury (Martinkova et al.,
72 2020*), and vegetative dormancy (Shefferson, 2009; Ott et al., 2019); and permit physiological
73 integration between connected ramets (Qureshi and Spanner, 1971, 1973; Alpert and Stuefer,
74 1995; Jaafrey et al., 2016; Liu et al., 2016) and even potential immortality of genotypes
75 (Eriksson, 1993; Klimešová et al., 2015). Since some of these properties are lacking in species
76 that reproduce asexually only via vagile propagules such as apomictic seeds, bulbils, or plantlets,
77 the term clonal growth, and its synonym clonality, are commonly used to refer only to asexual
78 reproduction via non-vagile propagules.

79 Clonality is widespread in the plant kingdom, but it is by no means universal. It is more
80 common in herbaceous species than in woody species (Aarssen, 2008). A recent phylogenetic
81 analysis found that clonality, while showing distinct phylogenetic patterns in angiosperms, has
82 been repeatedly evolved and lost (Herben and Klimešová, 2020), implying that selective
83 pressures can favor or disfavor clonality. This suggests that clonality has advantages but also
84 costs, and that these are likely to be determined by the biotic and abiotic environment.

85 Clonal growth plays a role in the ecology of some economically important plant groups.
86 Some important crops are clonal, such as banana, potato, sweet potato, and manioc (Denham et
87 al., 2020; McKey et al., 2010). Clonal growth has long been explored as a means to quickly
88 increase world production of key crop species (Allaby, 2019; Denham et al., 2020), albeit with
89 the risk of reduced genetic diversity (Kenei et al., 2012). Clonal plants, especially those with
90 extensive systems of rhizomes or roots, can be important in the prevention of soil erosion
91 (Guerrera-Campo et al., 2008). One economic cost of clonality may be promotion of biological

92 invasions; clonal species are disproportionately represented among introduced, invasive plants in
93 some floras (Pyšek et al., 2015).

94 Existing data show that different forms of clonal growth are associated with key
95 environmental factors, including disturbance and stress. Different types of disturbance
96 respectively favor clonal and non-clonal plants (Clarke et al., 2015; Bellingham and Sparrow,
97 2000), mainly due to regeneration potential and bud banks. Prevalance of clonality is affected by
98 water availability (Ye et al., 2014; Klimešová et al., 2016), possibly due to aeration potentials of
99 clonal growth organs or to ease of production of new roots (Sosnová et al., 2010). Proportions of
100 different clonal growth forms (e.g., root- or stem-based) and of clonal plants overall change
101 along environmental gradients, often nonlinearly (Herben et al., 2018).

102 Clonality in plants can be attained by several morphological means. New ramets may be
103 produced along stems, roots, or even leaves (Klimeš et al., 1997) and clonal species differ in bud
104 bank and other clonal growth traits (Klimešová et al., 2019). Experimental data clearly link these
105 traits to the functioning of clonal plants (Liu et al., 2016; Martínková et al., 2020*). For example,
106 plants with different clonal growth organs differ in the ability to share resources between
107 connected ramets, which can strongly affect clonal fitness (Martínková et al., 2020*). We also
108 know that clonal plants forage for nutrients by roots in heterogenous soil less than non-clonal
109 counterparts (Weiser et al., 2016); such differences may help explain coexistence of different
110 growth strategies in one community (Vojtkó et al., 2017).

111 Clonal growth can affect evolution in a variety of ways. Clonality tends to increase
112 generation time, which can save costs of meiosis but slow adaptation (Vallejo-Marín et al., 2010;
113 Gibson et al., 2017; Salguero-Gomez, 2018). Number of meiotic divisions is also hypothesized
114 to be an important driver of non-adaptive molecular evolution in plants (Lanfear, 2013). Some

115 types of clonality may confer a direct microevolutionary advantage in some contexts by reducing
116 probabilities of speciation or extinction (Figueiredo et al., 2019). Different types of clonality are
117 associated with different reproductive systems, generation times, and dispersal strategies, all of
118 which influence rates of diversification (e.g., Roquet, 2013; Van Drunen and Husband, 2019).

119 Much of the literature on clonal plants has been produced by two informal groups of
120 researchers, one centered in Europe and a newer one centered in China. Research presented in
121 association with the conferences held by these groups over the past several decades has been
122 published as books and special issues of journals (e.g., de Kroon and van Groenendahl, 1995;
123 Dong et al., 2014, Gross et al., 2017). We are pleased to continue this tradition with this special
124 issue based on "Clones in Context", the international conference on clonal plants held in August
125 2018 at Bowdoin College in Brunswick, Maine, USA, and on a combined special issue on clonal
126 ecology.

127

128 **3. Moving Forward with Clonal Ecology – Pressing Questions**

129

130 *3.1. What can population genetics tell us about clonal plant ecology?*

131

132 3.1.1. What We Know

133 Clonal plants call for an added dimension of analysis that can capture the horizontal and
134 temporal distribution of genotypes across the landscape. As extremely modular organisms, clonal
135 plants, whether large integrated clones or fragmented into numerous independent units, challenge
136 our notions of individuality and population genetics. Ultimately, the genetic footprint of a clonal
137 genotype can be considerably broader than that of a non-clonal genotype. Replicated across the

138 landscape, a large genotype can have a multiplier effect on traits such as fecundity. The potential
139 longevity of clonal plants strains temporal concepts such as cohorts and generations. Genetic
140 individuals can range over hundreds of kilometers and live for thousands of years. Each
141 additional ramet is potentially an added source of pollen and seeds; thus, fitness is likely to
142 increase with the spatial and temporal extent of the genotype (de Witte and Stöcklin, 2010).
143 Special care is required when applying fundamental non-clonal theory and models such as the
144 Hardy-Weinburg Equilibrium to clonal systems. Cautious interpretation is required for
145 population genetic metrics such as heterozygosity or genetic diversity that could impact
146 scientific, management, and conservation efforts, as these values will vary greatly depending on
147 the extent of clonality and the definition of the individual (Douhovnikoff and Leventhal, 2016).

148 Due to less frequent sexual reproduction and potential interbreeding across multiple
149 generations, it has been hypothesized that clonal plant populations should have lower genetic
150 diversity than non-clonal plant populations and that genetic diversity may be lost over time as
151 thinning reduces the population to a few large individuals. However, there are few examples of
152 genetic erosion. In fact, observations of higher than anticipated diversity are not unusual and may
153 be due to the great longevity of genotypes (de Witte and Stöcklin, 2010) as well as microsite
154 heterogeneity. Also, many clonal plant species are polyploid, and the additional sets of
155 chromosomes could potentially balance relatively low levels of inter-genet diversity with
156 relatively high levels of intra-genet diversity. In effect, each individual has a deeper pool of
157 genetic diversity to draw upon.

158 Recent work has also indicated that epigenetic variation may play a role in compensating
159 for possible reduced reliance on sexual recombination among clonal genotypes (Dong et al.,
160 2019b). Epigenetic mechanisms can allow for the acclimation of optimal phenotypes and the

161 transfer of those optimizations to daughter ramets. In this way, heritable acclimation can
162 supplement adaptation (Douhovnikoff and Dodd, 2015; González et al., 2018). For example,
163 Dong et al. (2019b) point out that epigenetic regulation may be an explanation for the
164 transgenerational effects they observed to be transmitted to non-integrated offspring ramets of
165 *Alternanthera philoxeroides*.

166

167 3.1.2. Research Needs

168 Our exploration of the extent and role of clonality in plant population genetics is still at
169 an early stage. More species are now recognized as clonal (e.g., Herben and Klimešová, 2020),
170 but, as observed by several authors in this issue, our ability to predict clonal structure and to
171 understand the variables that influence clonal diversity is still limited (Huebner et al., 2019*;
172 Watts et al., 2019*; Ricono et al., 2020*). These studies are good examples of the work that is
173 necessary to better understand the influence of clonality on population genetics and on evolution
174 of clonal species. New technologies that provide for higher genotyping resolution will be needed
175 to facilitate and improve these studies going forward. Amor et al. (2020*) describe one such
176 innovation in next generation sequencing. Better insights into clonal plant population ecology
177 and evolution, more *in situ* data at high resolution and across species, and novel approaches to
178 concepts such as fitness, fecundity, heterozygosity, and diversity are required to improve upon
179 standard ecological and evolutionary models developed with marginal consideration for clonal
180 plants (but see Winkler et al., 1999; Tuomi and Vuorisalo, 1989).

181

182 *3.2. How does a clonal plant allocate resources?*

183

184 3.2.1. What we know

185 Most clonal plants have two modes of reproduction: they produce sexual offspring via
186 seeds and asexual offspring by vegetative growth. As both reproductive modes have their costs,
187 we can expect a tradeoff of investments between sexual and asexual reproduction, although
188 experimental results on intraspecific variability are equivocal (Chaloupecká and Lepš, 2004;
189 Coelho et al., 2005). One comparative study of seed production per area in nearly 500 species
190 concluded that clonal plants have lower seed production than non-clonal plants and that the
191 difference is especially pronounced in clonal plants with long rhizomes (Herben et al., 2015).

192 Most of the organs of clonal growth are positioned belowground and often function in
193 storage. Building extensive belowground structures that are not directly involved in resource
194 acquisition but enable clonal growth and regeneration after damage or seasonal rest incurs costs.
195 However, these costs have not been fully studied, and investments into clonal growth versus
196 investment into regeneration ability are rarely separated. For example, in fire-prone areas, so-
197 called resprouters relying on regeneration from belowground organs after fire have lower
198 competitive ability and seed production compared to species that rely on seed regeneration
199 (Midgley, 1996; Bellingham and Sparrow, 2000). Similarly, perennial herbs of temperate regions
200 invest more in belowground biomass than annual plants due to storage of carbohydrates and
201 building of bud banks for regeneration after seasonal rest. This calls for a more detailed analysis
202 of costs due solely to resource storage, which is common also in nonclonal species, and costs
203 specifically associated with clonal reproduction.

204 Martínková et al. (2020*) showed that clonal herbaceous perennials invest relatively
205 more in belowground biomass than non-clonal ones do. We also know that biomass of rhizomes,
206 the most common clonal growth organ, in grassland communities ranges from 30% to nearly

207 100% of aboveground biomass depending on productivity and management (Klimešová et al.,
208 2018). Similar values were obtained for single clonal plant genets in experiments (Fiala, 1978;
209 Jitka Klimešová, unpublished data). The comparison of clonal and non-clonal perennial herbs
210 and their investments can provide useful information when clonality is provided by belowground
211 organs. However, quantification of investments into aboveground clonal growth organs like
212 stolons that do not have a regeneration function is not straightforward, partly because they are
213 green and obtain at least part of their necessary resources themselves.

214 Different clonal growth organs clearly have different costs to produce, and we can
215 speculate that these costs, apart from usually considered functions of the organs, might be partly
216 responsible for their distribution along environmental gradients. For example, long,
217 hypogeogenous rhizomes are more common in wetter and more nutrient-rich soils. This might be
218 at least partly due to the large costs of these rhizomes (Craine et al., 2001).

219

220 3.2.2. Research needs

221 To obtain a more complete understanding of clonal growth strategies, quantifying the
222 investments into clonal growth organs is necessary and must cover not only resource allocation
223 in individuals but also consequences for dynamics of population subject to different
224 perturbations or situations. For example, low seed production in clonal plants may be
225 compensated by clonal regeneration in an established population (Herben et al., 2012) but might
226 result in failure to establish new populations. To obtain reliable and comparable data for different
227 clonal species despite their high morphological diversity, a standardized method for measuring
228 investments was proposed by Goldberg et al. (2020*) for plants with hypogeogenous rhizomes,
229 one of the most common clonal growth organs. Methods for evaluating the investments in other

230 types of clonal growth organs are still waiting to be developed. These methods will allow us to
231 understand only a part of the story about resource allocation concerning clonal growth but will
232 represent an important step forward. Finally, clonal growth, in particular that based on
233 belowground organs, should be recognized as a general strategy of resource storage, an
234 important dimension of plant life often overlooked (but see Iwasa and Kubo, 1997; Fischer et al.,
235 2011; Klimešová et al., 2018).

236

237 *3.3. How do clonal plants respond to disturbance?*

238

239 3.3.1. What we know

240 Disturbances are contextualized by two key elements: disturbance to the plant itself (removal or
241 destruction of plant biomass; Grime, 1979) and disturbance to the environment of the plant
242 (changes in competitors, nutrient pools, etc.; Battisti et al., 2016). Both of these aspects likely
243 lead to the evolution of clonal plant traits and to allocation to vegetative reproduction over sexual
244 reproduction. Interaction between clonal plants and disturbance has long been suggested (Sebens
245 and Thorne, 1985), and change to the disturbance regime is a strong factor controlling clonal
246 plant response (Herben et al., 2018). Bellingham and Sparrow (2000) suggested an advantage of
247 asexual versus sexual reproduction under intermediate frequency and low intensity of
248 disturbance. Typical heterogeneity of landscapes likely offers advantage to both reproductive
249 modes.

250 There are four responses or behaviors that clonal plants are especially capable of,
251 compared to non-clonal organisms: (1) resource sharing among physiologically integrated
252 ramets, (2) ability to track resources through foraging behavior, (3) short-range dispersal using

253 competitively superior ramets, and (4) longevity enhancing genet persistence (Svennson et al.,
254 2013). Such traits confer advantages of clonal plants over non-clonal plants with respect to
255 physical disturbances to the plant itself such as herbivory (Bitterbiere et al., 2020*) and flooding
256 (Martínková et al., 2020*) and to alterations to the environment due to disturbance, such as
257 heterogeneity (Franklin et al., 2020*). However, it is unclear if these traits help following all
258 disturbances. Clonal plants tend to be less dominant following disturbance (Klimeš et al., 1997),
259 and clonal plant response to disturbance has known costs (Martínková et al., 2020*).

260 In an examination of plant traits related to disturbance regime in predominantly
261 herbaceous flora, the traits of life span, clonal growth, and resprouting showed a stronger
262 relationship with the environment than leaf, height, or seed traits (Herben et al., 2018). Clonal
263 plants are expected to allocate more resources to seeds when long-distance dispersal is
264 advantageous and when probability of establishing seeds in newly formed gaps or local ramet
265 density are high (Janovský and Herben, 2020*; Bitterbiere et al., 2020*). High frequency
266 disturbances lead to colonization opportunities that favor long-distance dispersal and high seed
267 production, and thus clonal plants are less dominant under more frequent disturbance (Janovský
268 and Herben, 2020*). Indeed, on the slow-fast life history continuum (Salguero-Gómez et al.,
269 2016), clonal plants in general are slower than non-clonal ones (Janovský and Herben, 2020*),
270 which tends to make sense given the strategy of investing in belowground structures that allow
271 individuals to both recover from injury (Martínková et al., 2020*) and overcome negative effects
272 of environmental heterogeneity (Escandón et al., 2020*). However, this advantage comes with a
273 cost, and it likely takes time to acquire this advantage (Martínková et al., 2020*). Thus, based on
274 the life history and traits of clonal plants, we would not expect clonal plants to dominate

275 frequently disturbed areas although they still may be present (Herben et al., 2018). What about
276 areas of low disturbance?

277 In general, low disturbance means increased competition or harsh abiotic environments
278 (Grime 1977); the latter are not discussed here. Bittebiere et al. (2020*) provide an excellent
279 review of clonal plants and competition in which they elucidate that clonal types differ in their
280 competitive ability and that competition is mostly among connected parts of a clone (i.e.,
281 fragments), not disconnected ramets or genets. Phalanx types, clumping types in which few or
282 short internodes result in closely packed ramets (Lovett-Doust, 1981), tend to be more common
283 in homogenous environments than guerrilla types, spreading types with many or long internodes
284 resulting in widely spaced ramets. Clumped growth structure may help competitive ability by
285 decreasing interspecific competition and using size as a type of priority effect. Larger individuals
286 exploit more resources and thus compete better, but this advantage again takes time. In a
287 comparison of 17 congeneric pairs of clonal and non-clonal herbs, clonal individuals were
288 generally larger than non-clonal ones (Martínková et al., 2020*). Guerilla types tend to be more
289 rapid colonizers and to be found in heterogenous environments, and are able to take advantage of
290 their disjunct resources through integration (Franklin et al., 2020*). However, guerilla types are
291 poorer competitors than phalanx types in the colonization-competition trade-off. Increased
292 competition can lead to either increased sexual reproduction or increased allocation to reserve
293 organs (i.e., to storage), and the latter is perhaps a bet-hedging strategy as the individual awaits
294 some form of disturbance. The increased storage in belowground organs allows persistence and
295 recovery (Roiloa, 2019*; Escandon et al., 2020*). Thus, as Martínková et al. (2020*)
296 hypothesize, clonal plant dominance should be in intermediately disturbed areas; and as

297 Janovský and Herben (2020*) suggest, the main advantage of clonality may be that it relaxes
298 adaptative constraints of the fecundity versus longevity trade-off.

299

300 3.3.2. Research needs

301 Scale is always an issue when discussing disturbance. While relationships between, say,
302 climate and clonal traits may be evident at the biogeographic scale (Chelli et al., 2019*; Vesk
303 and Yen, 2019*), and generalities may also be found among disturbance and traits (Herben et al.
304 2016, 2018; Janovský and Herben, 2020*), plant response to disturbance may be on a more local
305 scale, that of competition and integration. Studies at multiple scales could help elucidate the most
306 meaningful traits and growth strategies for modeling vegetation dynamics and separate the direct
307 impacts of disturbance on plants, such as herbivory, from the indirect impacts, such as increasing
308 or decreasing heterogeneity.

309 Studies on congeneric pairs of clonal and non-clonal species (e.g., Martínková et al.,
310 2020*) are needed to determine the effect size of being clonal (Vesk and Yen, 2019*), and such
311 studies need to follow standardized protocols of data collection (Goldberg et al., 2020*).

312 Categories of clonal plant organs have helped elucidate the differing importance of traits such as
313 integration and storage, but we do not fully understand their relative advantages in different
314 environments. The colonization-competition tradeoff requires further scrutiny, as we are
315 hindered by a lack of knowledge of the relative amounts of sexual and vegetative reproduction of
316 many species (Huebner et al, 2019*) and by conflicting results on how species respond
317 reproductively to disturbance (Martínková et al., 2020*) and competition (Bittebiere et al.,
318 2020*).

319

320 *3.4. Does clonal growth promote invasiveness?*

321

322 3.4.1. What we know

323 Invasiveness can be defined as propensity to spread into new places and negatively affect
324 things already there, and is of particular ecological concern in introduced species, those
325 intentionally or unintentionally transported outside their native range by human action (Alpert et
326 al., 2000). Evidence to date suggests that clonal growth is associated with invasiveness in
327 introduced plants (Cadotte et al., 2006a). For example, clonal species are overrepresented among
328 introduced, invasive plant species in the Czech Republic (Pyšek et al., 1995), invasive woody
329 plants in New England (Herron et al., 2007) and North America (Reichard and Hamilton, 1997),
330 introduced species in Ontario (Cadotte et al., 2006b), invasive species in China (Liu et al., 2006),
331 and neophytes in Germany (Küster et al., 2008). Worldwide, clonal introduced species reduce
332 richness of natives more than non-clonal introduced species worldwide (Vilà et al., 2015).

333 The association between invasiveness and clonality does appear to have limits. For
334 instance, it is confined in some cases to specific habitats within a region, such as those disturbed
335 by humans (Lloret et al., 2005; Holmes and Matlack, 2019), and studies of some regions have
336 found no association (Gassó et al., 2009; Tecco et al., 2010). Moreover, no study appears to have
337 systematically and quantitatively shown that clonality explains more than a small proportion of
338 the invasiveness of introduced plant species (e.g., Pyšek et al., 2015).

339 If clonal growth significantly promotes invasiveness, which properties of clonal growth
340 are responsible? There is little evidence so far that capacity for resource sharing between
341 established, adult ramets, a signature property of clonal growth, is involved. Comparisons of
342 more to less invasive, introduced, clonal species within genera have found no clear evidence that

343 more invasive species have greater capacity for integration (Portela and Roiloa, 2017; Roiloa et
344 al., 2019). A meta-analysis of studies on clonal integration in various species likewise failed to
345 find that integration increased clonal performance more in more invasive species although
346 integration did increase performance of individual ramets with relatively low access to resources
347 more in more widespread introduced species (Song et al., 2013). Roiloa et al. (2016) similarly
348 found that integration benefited apical ramets but not whole groups of ramets more in introduced
349 than in native clones of *Carpobrotus edulis*. A different type of comparison, between introduced
350 invasive species and congeneric native species, did find that clonal integration increased
351 accumulation of mass more in the introduced species (Wang et al., 2017).

352 However, resource sharing in the form of support of new offspring ramets by parental
353 ramets seems likely to contribute to invasiveness. Resource sharing from parent to offspring
354 ramets increases their probability of survival, which could increase the spread and thus
355 invasiveness of clones. Several studies have concluded that invasiveness increases with capacity
356 for clonal spread (Suehs et al., 2004; Burns, 2006) and that introduced populations show more
357 clonal growth than native populations of the same species (Jakobs et al., 2004; Douhovnikoff and
358 Hazelton, 2014; Shah et al., 2014). Parental support could explain why tall but not short clonal
359 species often increase in dominance when nutrient levels increase in grasslands (Dickson et al.,
360 2014): when adult ramets overtop neighbors but juveniles do not, support facilitated by high
361 nutrient availability allows juveniles to survive and grow up into the light. Canavan et al. (2019)
362 found that grasses more than 2 m tall were about three times more likely to naturalize following
363 introduction than shorter grasses, and tall clonal grasses account for much of the loss of diversity
364 in some grasslands after long-term addition of nutrients. More generally, resource sharing may

365 promote competitiveness when juvenile but not adult ramets are subject to asymmetric
366 competition (Wang et al. 2021).

367 Reproduction is a key factor involved in the successful establishment and spread
368 following long-distance dispersal (e.g., Moravcová et al., 2015). Asexual reproduction might be
369 favored under unreliable conditions, providing reproductive assurance and persistence of small
370 populations and adaptive genotypes (see review by Vallejo-Marín et al., 2010). Combined
371 reproduction by seed and clonal growth can enable species to spread on two scales at once,
372 distances of meters to hundreds of meters by seeds and over centimeters to meters by clonal
373 growth, analogous to the spread of wildfire by airborne sparks that set small individual fires. For
374 example, the invasive, clonal species *Acroptilon repens* and *Phragmites australis* can produce an
375 advancing front of growing patches (Duncan et al., 2017; Gaskin and Littlefield, 2017).

376 In aquatic habitats, individual ramets or small groups of connected ramets fragmented
377 from larger groups by disturbance may serve the dispersal function of seeds (Vilas et al., 2017;
378 Uya et al., 2018). In two highly invasive, aquatic clonal species provisioning of ramets by
379 resource sharing before fragmentation greatly increased their subsequent growth (Dong et al.
380 2019a*; Adomako et al. 2021). Very limited evidence suggests an association between
381 probability of establishment of fragmented ramets and invasiveness in aquatic species: fragments
382 of the invasive, introduced species *Elodea nutallii* showed a higher probability of forming roots
383 than co-occurring native species in German streams (Heidbüchel et al., 2019). Cultivated fields
384 may be another type of habitat where fragmentation of clones leads to wide dispersal
385 (Klimešová, 2011)

386 Physiological integration between connected ramets might also promote invasiveness
387 through signaling for responses such as division of labor. For example, Roiloa et al. (2019)

388 documented greater induction of division of labor in the more invasive of two introduced species
389 of *Carpobrotus*, and Chao et al. (2020) reported greater effects of integration on allocation of
390 mass, consistent with greater capacity of division of labor, in introduced than in native genotypes
391 of *Hydrocotyle vulgaris*.

392 One obvious consequence of clonal growth is that clonal offspring are genetically
393 identical. This could preclude post-introduction adaptation, although epigenetic variation might
394 partly compensate (e.g., Gaurino et al., 2019; Shi et al., 2019). On the other hand, clonal growth
395 could perpetuate particularly invasive genotypes. Populations of introduced, invasive, clonal
396 species in a region sometimes consist of a single clone (e.g., Canavan et al., 2017). This might
397 just be because only one clone has been introduced and conditions permit clonal but not sexual
398 reproduction (Ferrero et al., 2020). Alternatively, some invasive clones may have exceptionally
399 high fitness in their introduced range. For instance, numerous clones of the highly invasive
400 species *Arundo donax* (Canavan et al., 2017) and *Eichhornia crassipes* (Zhang et al., 2010) have
401 been introduced but one clone clearly dominates the introduced range of each worldwide.

402 Selective placement of offspring is another potential advantage of clonal growth. Chen et
403 al. (2019) recorded that invasive clonal species grew fewer but larger ramets in low-nutrient
404 patches than native, clonal congeners. A novel study by Reijers et al. (2019) concludes that
405 spread of the clonal grasses *Ammophila arenaria* and *A. breviligulata* on coastal sand dunes can
406 be modeled as a random walk with high variability. The spatial pattern of spread of the former
407 species, which builds higher dunes and has been more invasive, traps more sand per unit of
408 clonal growth.

409 Besides testing for links between invasiveness and individual, special properties of clonal
410 growth, researchers have asked if clonality is associated with properties linked to invasiveness in

411 plant species in general. Many invasive species show relatively great increases in growth in
412 response to high nutrient availability (Alpert et al., 2000). Wang et al. (2019*) report that a set of
413 invasive clonal species responded more to high nitrogen than co-occurring native clonal species.
414 In a rare study of evolution of clonal traits following introduction, Bock et al. (2018) conclude
415 that the positive effect of high water availability on the clonal spread of *Helianthus tuberosus*
416 increased following introduction.

417 High competitive ability is another obvious mechanism of spread in native communities
418 after introduction. Clones of *Phragmites australis* introduced from Europe have displaced native
419 clones in parts of North America, and Pyšek et al. (2020) show that European clones in both
420 Europe and North America have greater competitive ability than native North American clones.
421 Competitiveness and response to nutrients could combine to promote invasiveness, but recent
422 studies have variously reported that higher nutrient levels increased (Liu et al., 2019; Liang et al.,
423 2020) or decreased (Wang et al., 2019*) the competitive ability of invasive clonal species.

424

425 3.4.2. Research needs

426 Investigations of the link between clonal growth and invasiveness in plants so far suggest
427 that clonal growth is among the plant traits that promote invasiveness. More research is needed
428 on two main fronts. First, we need to know more about how habitat and introduction history
429 may interact with clonal traits to make species invasive following introduction. For example, do
430 certain disturbance regimes favor invasion by clones?

431 Second, we need to better understand which traits of clonal growth confer invasiveness.
432 Comparisons between more and less invasive, introduced clonal species or between more and
433 less invasive genotypes within species seem especially promising. In particular, demographic,

434 morphological, and physiological comparisons between the genotypes that dominate very
435 widespread invasion by some clone species and other introduced genotypes in the same species
436 could tell us if these dominant clones share common features that make fitness remarkably high.
437 Comparison between introduced and source populations of invasive clonal species could show
438 whether introduced populations have evolved greater propensity for clonal growth and suggest if
439 this has traded off with reduced sexual reproduction.

440 More studies of interactive effects of clonal and other traits may reveal effects of
441 clonality on invasiveness not apparent when clonal species are considered as a whole. The prime
442 case of this so far seems to be the spread of clonal species that are also relatively tall and that
443 place new ramets relatively far from parents within grasslands following increase in soil nutrient
444 availability. Finally, few studies have documented or modeled the combined effects of
445 fragmentation and clonal growth on the spread of introduced species.

446

447 *3.5. How does clonal multiplication affect our understanding of plant demography?*

448

449 3.5.1. What we know

450 Demographic approaches of clonal plants provide an ideal platform on which to identify
451 the role that clonality as an ecological strategy plays in the life cycle of plants, their viability, and
452 thus the selective forces that underlie evolution of clonality and its loss (Klimeš et al., 1997;
453 Salguero-Gómez, 2018; Janovský and Herben, 2020*). Indeed, population ecology must
454 inevitably deal with the hierarchical nature of individuality in clonal plants, ranging from ramets
455 through clonal fragments (i.e., connected and potentially physiologically integrated sets of
456 ramets) to genets. From a demographic perspective, clonal growth can be considered as a type of

457 reproduction during which new independent units arise; from the evolutionary perspective,
458 clonality is a form of individual growth that enlarges the genet in space and consequently in time
459 (Aarssen, 2008) through ramet turnover. Indeed, clonal species seem to have traded the
460 postponing of ramet senescence for the postponing of genet senescence (Salguero-Gómez, 2018),
461 decelerating recombination rates and evolutionary changes as a side effect (Bousquet et al.,
462 1992; Smith and Donoghue, 2008; Orive et al., 2017). However, the relationship between
463 evolutionary rates and zygote formation may be blurred by somatic mutations taking place in the
464 extensive vegetative tissues of clonal plants (Schoen and Schultz, 2019).

465 Demographic analyses have shown that clonal growth can act as an effective means of
466 maintaining diversity in disturbed ecosystems. For instance, the turnover of ramets in genets
467 enables clonal species to occupy habitats with stronger disturbance regime than permitted by
468 sexual reproduction only (Klimeš et al., 1997; Herben et al., 2018; Janovský and Herben, 2020*
469 Clonal growth also increases variation in ramet population growth rates of clonal species,
470 permitting the species to exploit "windows of opportunity" under favourable conditions
471 (Janovský and Herben, 2021*). Moreover, clonal growth seems to relax to some extent the
472 demographic constraints imposed by a plant's developmental and architectural constraints and
473 allow plants to evolve different life history strategies than those available to non-clonal plants.
474 For instance, with short-lived ramets and clonal growth it is possible to maintain both short and
475 long genet generation times, while in non-clonal species ramet and genet life span cannot be
476 decoupled (Eriksson and Bremer, 1993; Salguero-Gómez, 2018).

477 Besides the trade-off between clonal growth and sexual reproduction, clonal growth can
478 affect plant species' demography through further decreases of reproduction by seeds due to
479 pollen limitation (Barrett, 2015), especially in self-incompatible clonal species (Honnay and

480 Jacquemyn, 2008). This is mainly due to production of new ramets increasing the abundance of
481 sources of self-pollen in a ramet's surroundings and thus possibly affecting the quality of
482 generative offspring (Harder and Barrett, 1995; Vallejo-Marín et al., 2010) through increased
483 risk of self-pollination (e.g. Hu et al., 2015). With the recent loss of pollinator species worldwide
484 (Potts et al., 2010), the ability of asexual clonal plants to circumvent pollinator needs deserves
485 scrutiny.

486

487 3.5.2. Research needs

488 The existing knowledge of demographic characteristics of ramets is relatively good,
489 though for a rather limited number of clonal plant species (e.g. Eriksson, 1988; Carlsson and
490 Callaghan, 1990; Jongejans and de Kroon, 2005; Černá and Münzbergová, 2013). This
491 knowledge gap is particularly obvious when considering that two thirds of the Plant Kingdom
492 has clonal abilities (Herben and Klimešová, 2020). Of greater concern is that similar information
493 about genets is even rarer, which precludes general evolutionary comparisons of demography of
494 non-clonal and clonal plants (Janovský et al., 2017). While studies on genet demography do exist
495 (Eriksson and Bremer, 1993; Fair et al., 1999; Araki and Ohara, 2008; Czarnecka, 2008; de Witte
496 et al., 2011; Matsuo et al., 2018), they rarely provide sufficient detail to integrate ramet within
497 genet dynamics. The much-needed integration of both biological levels of organisation in clonal
498 plants would allow for a much deeper understanding of the evolutionary pressures, ecological
499 strategies, and conservation biology outcomes of this prominent plant trait.

500 A possible solution for this gap could be to derive genet demographic characteristics by
501 simulating genet life histories from the existing demographic models of populations of ramets
502 (Janovský et al., unpublished). However, such an approach cannot be applied to species with

503 strong integration of ramets within the genet because of differing vital rates for ramets of
504 different types (e.g. Carlsson and Callaghan, 1990; Munzbergova et al., 2005; Wikberg and
505 Svensson, 2006), and whole genets need to be followed in a way that does not damage them and
506 so jeopardise the long-term monitoring necessary in most demographic studies of plants.
507 Demography of whole genets thus seems to be an obvious choice for compact tussock-forming
508 species and may work well in the short term; however, clear delimitation of working units may
509 become problematic as clonal fragments disintegrate over longer time periods. For such species,
510 we therefore need more studies coupling demography with genetic techniques (such as Harada et
511 al., 1997; Amor et al., 2020*; Ricono et al., 2020*; Tsujimoto et al., 2020).

512 The way plant demographers define individuals of clonal plants (ramets or genets) to be
513 observed and modelled largely depends on plant species' architecture, mainly type of branching
514 and shoot cyclicity. Plant architecture also affects the probability of recording clonal growth;
515 e.g., demographers more frequently fail to record clonality in species with monocyclic shoots
516 (see Serebriakova, 1977, for definition) where ramets emerge at different positions each season
517 (Fig. 1). There is a general lack of studies on species with very low (due to frequent omissions of
518 recording clonal growth) and very high intensities of clonal growth (due to difficulties in
519 tracking ramet identity in such species; Janovský et al., 2017). This especially holds true for
520 species possessing extensive rhizome systems and featuring a rich bud bank such as most grasses
521 (e.g. Mortimer, 1983; Ott and Hartnett, 2015). In general, we need to differentiate among clonal
522 species more according to their architecture in future studies reflecting thus the multitude of
523 events (and possibly selection pressures) in which clonality has evolved, as well as
524 sexual/asexual ratios and changes to those ratios resulting from environmental factors.

525

526 3.6. *Does clonality affect community assembly?*

527

528 3.6.1. What we know

529 In 1995, a review by Oborny and Bartha (1995) reflected on the fact that clonal
530 reproduction seemed to be a prevalent process in many plant communities but had not been
531 systematically examined as a process structuring communities. Similarly, they posited that
532 differences in clonal traits (not yet denoted by this term then) are likely to be important for
533 driving species coexistence. Since then, a number of studies on the topic have been published,
534 but these existing papers are more a haphazard collection of separate studies than a systematic
535 foray into a single phenomenon.

536 Clonality has generally been an overlooked trait in studies of community assembly.
537 While it has been argued that trait space is incomplete without traits on resource storage,
538 clonality, and resprouting (Ottaviani et al., 2017; Klimešová, 2018; Klimešová et al., 2018), most
539 trait-based studies on community assembly have failed to take these traits into account.
540 Important to note, clonality is not a single trait, in spite of references to a non-clonal versus
541 clonal dichotomy in many papers. Plants reproducing clonally may have long or short inter-ramet
542 distances, with very different bearing on species interactions, coexistence, and resulting
543 community assembly. There may be less difference between a non-clonal plant and a plant with a
544 slowly growing, epigeogenous rhizome than between two clonal plants that differ strongly in
545 inter-ramet distances and multiplication rates. It is worth noting here that these traits have
546 generally low phylogenetic conservatism (Herben and Klimešová, 2020), implying that their
547 variation cannot be easily proxied by phylogenetic data and must be approached directly.

548 The few existing studies on clonal traits have almost always found signals of
549 convergence in traits of clonal growth, often stronger than convergence in leaf, height, and seed
550 traits such as height at maturity, specific leaf area, or seed mass (de Bello et al., 2011; Ye et al.,
551 2014, Vojtkó et al., 2018; Chelli et al., 2019*), which has generally been interpreted as
552 environmental filtering. It is worth noting that most of these studies with the exception of Ye et
553 al. (2014) have collected data on a fairly narrow range of community types, indicating strong
554 environmental effects. On the other hand, most studies have also found that clonal and non-
555 clonal species coexist in almost all community types and that variation in clonal trait values
556 within a community can still be large (de Bello, 2011; Vojtkó et al., 2017). Demographic
557 differentiation of coexisting species involves an important axis of clonal dispersal even at the
558 small scale (Herben et al., 2019). Longitudinal data also show that it does not need to change
559 substantially through time (Duchoslavová and Herben, 2020*). This phenomenon is too common
560 to be due to simple sampling phenomenon from a larger species pool (de Bello, 2011; Vojtkó et
561 al., 2018), indicating that differences in clonal growth are one of the patterns in multispecies
562 communities and elucidating its potential role in species assembly.

563 However, analysis of community traits structure has its obvious limitations; namely, very
564 different mechanisms may produce indistinguishable trait patterns (Mayfield and Levine, 2010;
565 Kraft et al., 2015; Münkemüller et al., 2020). In particular, trait convergence as a putative
566 signature of environmental filtering is difficult to distinguish from resource competition (Kraft et
567 al., 2015). It is therefore essential to link functional traits with recognized assembly mechanisms
568 (Adler et al., 2007), namely differences in fitness and stability.

569 Current data show that differences in clonality per se are unlikely to contribute to fitness
570 differences. Clonality is, as a rule, associated with large belowground structures used for

571 resource storage and resprouting. Building storage clearly constrains investment into
572 aboveground organs, which play the key role in asymmetric competition for light (Suzuki and
573 Hara, 2001; Martínková et al., 2020*). This is likely to make competition more symmetric and
574 thus reduce fitness differences among species; as a result, niche differences necessary for
575 coexistence should be weaker. However, this is not restricted to clonal plants only, as all species
576 in habitats where large belowground storage is necessary for survival (e.g., due to frequent,
577 unpredictable disturbance) show similar patterns. Fitness effects of clonality may change with
578 environmental conditions: clonality interacts with plant height for fitness response to fertilization
579 (Eilts et al., 2011; Gough et al., 2012), and the role of clonal integration for coexistence differs
580 among habitats (Pennings and Callaway, 2000).

581 It is less obvious whether and how clonality can affect niche differences. Here it is
582 important to note that the role of clonality in coexistence is intimately linked with spatial
583 processes (Oborny and Bartha, 1995; Gigon and Leutert, 1996) which to an important degree
584 modify interactions predicted by nonspatial models (Bolker et al., 2003). Clonal plants tend to
585 position their offspring close to their parental individuals, resulting in strong spatial structure that
586 constrains, often in a nontrivial way, how individual species can coexist (see e.g. Stoll and Prati,
587 2001; Lenssen et al., 2005 for experimental demonstrations). In principle, there are three
588 important mechanisms by which clonality may affect species coexistence through spatial
589 processes. First, founder-controlled communities in spatially explicit systems can, in contrast to
590 nonspatial systems, remain diverse in spite of potential competitive exclusion of one species by
591 the other, essentially due to an equalizing mechanism that prevents fitness differences from
592 prevailing (Molofsky et al., 2002; Bolker et al., 2003). Although this mechanism does not
593 account for stable-state coexistence (Chesson and Huntly, 1997), time to extinction is far too

594 long in realistic settings, making it effectively a mechanism of coexistence. Second, clonality
595 may strongly contribute to fast occupancy of space in open patches in the community by a
596 process that has been termed spatial successional niches (Bolker et al., 2003; see e.g. Vítová et
597 al., 2017, for an experimental demonstration). This process would take place only in moderately
598 disturbed systems; differences in traits of spatial spreading do not generate niche differentiation
599 in model systems with no disturbance. Third, spatial dynamics due to clonal growth may be
600 linked with negative plant-soil feedback (Bever, 2003; Bever et al., 2015).

601

602 3.6.2. Research needs

603 Most important, we need to know how clonality and different values of clonal traits
604 contribute to the key processes of species coexistence, namely niche differences and differences
605 in fitness, taking into account the multidimensionality of clonal traits. At the same time, we need
606 to know relationships between clonal traits and other sets of traits, namely those known to affect
607 species interactions, such as plant height and root foraging, as well as the relationship between
608 clonality and growth form. Existing data support the contention that woody species are less
609 clonal and show morphologically and functionally different types of clonality. We need to be
610 sure that this pattern is general; if it is, it can be indicative of the role of clonality both in
611 environmental response and interactions with neighbours. We also need to know more about the
612 relationship of clonality and clonal traits to regeneration strategies; while it is commonly
613 assumed that regeneration is associated with clonality (Bellingham and Sparrow, 2000), many
614 non-clonal species are able to regenerate, and the link between clonality and disturbance is
615 weaker than often assumed (Herben et al., 2018; Martínková et al., 2020*).

616 Phylogenetic analyses have shown that clonality is a trait that is fairly easily acquired and
617 lost; this indicates that individual species respond to selective forces in favour of and against
618 clonality (Herben and Klimešová, 2020). While these forces may not necessarily be due to
619 coexistence-related processes (e.g., they may be due to a link between clonality with sexual
620 reproduction), we clearly need to know the role of environmental effects, both abiotic and of
621 neighbours. This can hardly be attained without comparative experimental approaches,
622 examining response to competition of sets of species differing in their clonal traits.

623

624 **4. Conclusion**

625 This introductory overview and this special issue highlight both the obstacles and
626 opportunities for incorporating clonal plant knowledge into mainstream plant ecology and
627 evolution studies. Clonal plants take modularity to another level, offering both novel traits and
628 responses to a variety of environmental biotic and abiotic factors. This seemingly easy to gain or
629 lose strategy is related to climate, disturbance, species interactions, community assembly, and
630 ecosystem function. Including clonality will increase predictive power and improve models,
631 albeit not without challenges.

632 One major challenge includes the continued lack of tools that capture the hierarchical
633 nature of an individual in clonally growing plants, so we need studies utilizing more genetic
634 demographic information and studies at the whole genet scale. Studies have concentrated on
635 relatively few species, and studies on species with very high intensities of clonal growth are
636 largely lacking. A second major challenge is lack of a standardized way of measuring allocation
637 in various clonal types and of comparing resulting architectures. Despite these challenges,
638 similarity of questions and importance of clonal plants to overall biomass and diversity of

639 ecosystems implies an easy incorporation into mainstream plant studies. Currently, we possess a
640 number of novel tools, ranging from large trait databases through experimental approaches such
641 as congeneric pair studies to phylogenetic and molecular techniques, to address the impact of
642 clonality on community assembly, biological invasions, and the responses of plants to
643 environmental factors. With land use impacting communities and ecosystems as much as climate
644 change, we need to link colonization and resilience traits to disturbance regimes and to scale up
645 to communities and ecosystems.

646

647 **5. Acknowledgements**

648 JK and TH were supported by the Grant Agency of the Czech Republic (GA19-13103S and 19-
649 13231S), ZJ was supported by the Ministry of Education, Youth and Sports of the Czech
650 Republic (LTT20003). We give special thanks to the Alan Irving Memorial Fund of
651 Bowdoin College for financial support of Clones in Context, the international symposium
652 on clonal plants held at the college in August 2018.

653

654 **6. Literature cited** (asterisks indicate papers in the special issue on clonal plants)

655 Aarssen, L.W., 2008. Death without sex - the 'problem of the small' and selection for

656 reproductive economy in flowering plants. *Evol. Ecol.* 22, 279-298.

657 Adler P.B., HilleRisLambers J., Levine J.M., 2007. A niche for neutrality. *Ecol. Lett.* 10, 95–

658 104.

659 Adomako, M.O., Alpert, P., Du, D.L., Yu, F.H., 2021. Effects of fragmentation of clones

660 compound over vegetative generations in the floating plant *Pistia stratiotes*. *Ann. Bot.*

661 127, 123-133.

662 Allaby R. 2019. Clonal crops show structural variation role in domestication. *Nature Plants* 5,
663 915-916.

664 Alpert, P., Bone, E., Holzapfel, C., 2000. Invasiveness, invasibility, and the role of
665 environmental stress in preventing the spread of non-native plants. *Perspect. Plant Ecol.*
666 *Evol, Syst.* 3, 52-66.

667 Alpert, P., and Stuefer, J.F., 1997. Division of labour in clonal plants. In Pages 137-154 in H. de
668 Kroon, H., van Groenendael, J. (Eds.), *The Ecology and Physiology of Clonal Plants*.
669 Backhuys Publishers, Leiden, The Netherlands, pp. 137-154.

670 *Amor, M.D., Johnson, J.C., James, E.A., 2020. Identification of clonemates and genetic
671 lineages using next-generation sequencing (ddRADseq) guides conservation of a rare
672 species, *Bossiaea vomkata* (Fabaceae). *Perspect. Plant Ecol. Evol. Syst.* 45, 125544.
673 [https://https://doi: 10.1016/j.ppees.2020.125544](https://doi.org/10.1016/j.ppees.2020.125544).

674 Araki, K., Ohara, M., 2008. Reproductive demography of ramets and genets in a rhizomatous
675 clonal plant *Convallaria keiskei*. *J. Plant Res.* 121, 147-154.

676 Barrett, S.C.H., 2015. Influences of clonality on plant sexual reproduction. *Proc. Nat. Acad. Sci.*
677 USA 112, 8859-8866.

678 Battisti C., Poeta G., Fanelli G., 2016. The concept of disturbance. In: [needs eds.] *An*
679 *Introduction to Disturbance Ecology, Environmental Science and Engineering*. Springer,
680 [Cham??], pp. [needs pages]. [https://https://doi.org/10.1007/978-3-319-32476-0_2](https://doi.org/10.1007/978-3-319-32476-0_2).

681 Bellingham P.J., Sparrow A.D., 2000. Resprouting as a life history strategy in woody plant
682 communities. *Oikos* 97, 409-416.

683 Bever, J.D., 2003. Soil community feedback and the coexistence of competitors: conceptual
684 frameworks and empirical tests. *New Phytol.*, 157, 465–473.

685 Bever, J.D., Mangan, S.A., Alexander, H.M., 2015. Maintenance of plant species diversity by
686 pathogens. *Ann. Rev. Ecol. Evol. Syst.*, 46, 305–325.

687 *Bittebiere, A-K., Benot, M-L., Mony, C., 2020. Clonality as a key but overlooked driver of
688 biotic interactions in plants. *Perspect. Plant Ecol. Evol. Syst.* 43, 125510.
689 [https://https://doi: 10.1016/j.ppees.2020.125510](https://doi.org/10.1016/j.ppees.2020.125510).

690 Bock, D.G., Kantar, M.B., Caseys, C., Matthey-Doret, R., Rieseberg, L.H., 2018. Evolution of
691 invasiveness by genetic accommodation. *Nat. Ecol. Evol.* 2, 991.

692 Bolker, B.J., Pacala, S.W., Neuhauser, C., 2003. Spatial dynamics in model plant communities:
693 what do we really know? *Am. Nat.* 162, 135-148.

694 Bousquet, J., Strauss, S.H., Doerksen, A.H., Price, R.A., 1992. Extensive variation in
695 evolutionary rate of *rbcL* gene sequences among seed plants. *Proc. Nat. Acad. Sci.* 89,
696 7844-7848.

697 Burns, J.H., 2006. Relatedness and environment affect traits associated with invasive and
698 noninvasive introduced *Commelinaceae*. *Ecol. Appl.* 16, 1367-1376.

699 Cadotte, M.W., Murray, B.R., Lovett-Doust, J., 2006a. Ecological patterns and biological
700 invasions: using regional species inventories in macroecology. *Biol. Invasions* 8, 809-
701 821.

702 Cadotte, M.W., Murray, B.R., Lovett-Doust, J., 2006b. Evolutionary and ecological influences of
703 plant invader success in the flora of Ontario. *Écoscience* 13, 388-395.

704 Canavan K., Paterson, I.D., Hill, M.P., 2017. Exploring the origin and genetic diversity of the
705 giant reed, *Arundo donax* in South Africa. *Invasive Plant Sci. Manag.* 10, 53-60.

706 Canavan, S., Meyerson, L.A., Packer, J.G., Pyšek, P., Maurel, N., Lozano, V., Richardson, D.M.,
707 Brundu, G., Canavan, K., Ciccattelli, A., Cuda, J., Dawson, W., Essl, F., Guarino, F., Guo,

708 W. Y., van Kleunen, M., Kreft, H., Lambertini, C., Pergl, J., Skalova, H., Soreng, R.J.,
709 Visser, V., Vorontsova, M.S., Weigel, P., Winter M., Wilson, J.R.U., 2019. Tall-statured
710 grasses: a useful functional group for invasion science. *Biol. Invasions* 21, 37-58.

711 Carlsson, B.Å., Callaghan, T.V., 1990. Programmed tiller differentiation, intraclonal density
712 regulation and nutrient dynamics in *Carex bigelowii*. *Oikos* 58, 219-230.

713 Černá, L., Münzbergová, Z., 2013. Comparative population dynamics of two closely related
714 species differing in ploidy level. *PloS One* 8.

715 Chaloupecká, E., Lepš, J., 2004. Equivalence of competitor effects and tradeoff between
716 vegetative multiplication and generative reproduction: case study with *Lychnis flos-cuculi*
717 and *Myosotis nemorosa*. *Flora* 199, 157-167.

718 Chao, S., Alpert, P., Zhang, J.-F., Lin, J., Wang, Y.-Y., Hong, M.-M., Roiloa, S., Yu, F.-H.,
719 2020. Capacity for clonal integration in introduced versus native clones of the invasive
720 plant *Hydrocotyle vulgaris*. *Sci. Total Environ.* 745, 141056.

721 *Chelli, S., Ottaviani, G., Simonetti, E., Wellstein, C., Canullo, R., Carnicelli, S., Andreetta, A.,
722 Pulettie, N., Barth. S., Cervellini, M., Campetella, G., 2020. Climate is the main driver of
723 clonal and bud bank traits in Italian forest understories. *Perspect. Plant Ecol. Evol. Syst.*
724 40, 125478. [https://https://doi:10.1016/j.ppees.2019.125478](https://doi:10.1016/j.ppees.2019.125478).

725 Chen, D., Ali, A., Yong, X.H., Lin, C.G., Niu, X.H., Cai, A.M., Dong, B.C., Zhou, Z.X., Wang,
726 Y.J., Yu, F.H., 2019. A multi-species comparison of selective placement patterns of
727 ramets in invasive alien and native clonal plants to light, soil nutrient and water
728 heterogeneity. *Sci. Total Environ.* 657, 1568-1577.

729 Chesson, P., Huntly, N. 1997. The roles of harsh and fluctuating conditions in the dynamics of
730 ecological communities. *Am. Nat.* 150, 519-553.

731 Clarke, P.J., Bell D.M., Lawes M.J., 2015. Testing the shifting persistence niche concept: plant
732 resprouting along gradients of disturbance. *Am. Nat.* 185:
733 [https://https://doi.org/10.1086/681160](https://doi.org/10.1086/681160)

734 Coelho, F.F., Deboni, L., Santos Lopes, F., 2005. Density-dependent reproductive and vegetative
735 allocation in the aquatic plant *Pistia stratiotes* (Araceae). *Rev. Biol. Trop.* 53, 369-376.

736 Craine, J.M., Froehle, J., Tilman, G.D., Wedin, D.A., Chapin, F.S., 2001. The relationships
737 among root and leaf traits of 76 grassland species and relative abundance along fertility
738 and disturbance gradients. *Oikos* 93: 274–285.

739 Czarnecka, B., 2008. Spatiotemporal patterns of genets and ramets in a population of clonal
740 perennial *Senecio rivularis*: plant features and habitat effects. *Ann. Bot. Fennici* 45, 19-
741 32.

742 de Bello, F., Doležal, J., Ricotta, C., Klimešová, J., 2011. Plant clonal traits, coexistence and
743 turnover in East Ladakh, Trans-Himalaya. *Preslia* 83, 315-327.

744 Denham, T., Barton, H., Castillo, C., Crowther, A., Dotte-Sarout, E., Florin, S.A., Pritchard, J.,
745 Barron, A., Zhang, Y.K., Fuller, D.Q., 2020. The domestication syndrome in vegetatively
746 propagated field crops. *Ann. Bot.* 125, 581-597.

747 de Kroon, H., van Groenendael, J. (Eds.), 1995. *The Ecology and Physiology of Clonal Plants*.
748 Backhuys Publishers, Leiden, The Netherlands.

749 de Witte, L.C., Scherrer, D., Stöcklin, J., 2011. Genet longevity and population age structure of
750 the clonal pioneer species *Geum reptans* based on demographic field data and projection
751 matrix modelling. *Preslia* 83, 371-386.

752 de Witte, L.C., Stöcklin, J., 2010. Longevity of clonal plants: why it matters and how to measure
753 it. *Ann. Bot.* 106, 859-870.

754 Dickson, T.L., Mittelbach, G.G., Reynolds, H.L., Gross, K.L., 2014. Height and clonality traits
755 determine plant community responses to fertilization. *Ecology* 95, 2443-2452.

756 *Dong, B-C., Alpert, P., Yu, F.-H., 2019a. Transgenerational effects of herbivory and soil
757 nutrients transmitted via vegetative reproduction in the clonal plant *Alternanthera*
758 *philoxeroides*. *Perspect. Plant Ecol. Evol. Syst.* 41, 125498.
759 [https://https://doi.org/10.1016/j.ppees.2019.125498](https://doi.org/10.1016/j.ppees.2019.125498).

760 Dong, B-C., Yu, F-H., Roiloa, S.R. 2019b. Editorial: Ecoepigenetics in clonal and inbreeding
761 plants: Transgenerational adaptation and environmental variation. *Front. Plant Sci.*
762 10:622. [https://https://doi: 10.3389/fpls.2019.00622](https://doi.org/10.3389/fpls.2019.00622).

763 Dong, M., Yu, F.-H., Alpert, P. 2014. Ecological consequences of plant clonality. *Annals of*
764 *Botany* 114:367.

765 Douhovnikoff, V., Dodd, R.S., 2015. Epigenetics: a potential mechanism for clonal plant
766 success. *Plant Ecol.* 216, 227–233. [https://https://doi: 10.1007/s11258-014-0430-z](https://doi.org/10.1007/s11258-014-0430-z).

767 Douhovnikoff, V., Hazelton, E.L.G., 2014. Clonal growth, invasion or stability? A comparative
768 study of clonal architecture and diversity in native and introduced lineages of *Phragmites*
769 *australis* (Poaceae). *Am. J. Bot.* 101, 1577-1584.

770 Douhovnikoff, V., Leventhal, M., 2016. The use of Hardy Weinberg Equilibrium in clonal plant
771 systems. *Ecol. Evol.* 30, 1-8. [https://https://doi:10.1002/ece3.1946](https://doi.org/10.1002/ece3.1946).

772 *Duchoslavová, J., Herben, T., 2020. Effect of clonal growth form on the relative performance
773 of species in experimental communities over time. *Perspect. Plant Ecol. Evol. Syst.* 44,
774 125532. [https://https://doi: 10.1016/j.ppees.2020.125532](https://doi.org/10.1016/j.ppees.2020.125532).

775 Duncan, J.P., Rozum, R.N., Powell, J.A., Kettenring, K.M., 2017. Multi-scale methods predict
776 invasion speeds in variable landscapes. Case study: *Phragmites australis*. *Theor. Ecol.*

777 10, 287-303.

778 Eilts, J.A., Mittelbach, G.G., Reynolds, H.L., Gross, K.L., 2011. Resource heterogeneity, soil
779 fertility, and species diversity: effects of clonal species on plant communities. *Am. Nat.*
780 177, 574–588.

781 Eriksson, O., 1988. Ramet behaviour and population growth in the clonal herb *Potentilla*
782 *anserina*. *J. Ecol.* 76, 522-536.

783 Eriksson, O., 1993. Dynamics of genets in clonal plants. *Trends Ecol. Evol.* 8, 313-317.

784 Eriksson, O., Bremer, B., 1993. Genet dynamics of the clonal plant *Rubus saxatilis*. *J. Ecol.* 81,
785 533-542.

786 *Escandón, A.B., Paula, S., Saldaña, A., 2020. Root suckering promotes recruitment in two
787 temperate rainforest trees with contrasting shade tolerance. *Perspect. Plant Ecol. Evol.*
788 *Syst.* 44, 125531. [https://doi: 10.1016/j.ppees.2020.125531](https://doi.org/10.1016/j.ppees.2020.125531).

789 Fair, J., Lauenroth, W.K., Coffin, D.P., 1999. Demography of *Bouteloua gracilis* in a mixed
790 prairie: analysis of genets and individuals. *J. Ecol.* 87, 233-243.

791 Ferrero, V., Navarro, L., Castro, S., Loureiro, J., Sanchez, J.M., Carvallo, G.O., Barrett, S.C.H.,
792 2020. Global patterns of reproductive and cytotype diversity in an invasive clonal plant.
793 *Biol. Invasions* 22, 1691-1703.

794 Fiala, K., 1978. Underground organs of *Typha angustifolia* and *Typha latifolia*, their growth,
795 propagation and production. *Acta. Sci. Nat, Brno* 12/8: 1-43.

796 Figueiredo, L., Krauss, J., Steffan-Dewenter, I., Cabral, J.S., 2019. Understanding extinction
797 debts: spatio-temporal scales, mechanisms and a roadmap for future research. *Ecography*
798 42: 1973-1990. [https://doi: 10.1111/ecog.04740](https://doi.org/10.1111/ecog.04740).

799 Fischer, B., Dieckmann, U., Taborsky, B., 2011. When to store energy in a stochastic

800 environment. *Evolution* 65, 1221–1232.

801 *Franklin, S.B., Olejniczak, P., Samulak, E., Šibíková, M., Bacigál, T., Nechaj, J., Šibík, J.,
802 2020. Clonal plants in disturbed mountain forests: Heterogeneity enhances ramet
803 integration. *Perspect. Plant Ecol. Evol. Syst.* 44, 125533. [https://doi:](https://doi:10.1016/j.ppees.2020.125533)
804 [10.1016/j.ppees.2020.125533](https://doi:10.1016/j.ppees.2020.125533).

805 Gaskin, J.F., Littlefield, J.L., 2017. Invasive Russian knapweed *Acroptilon repens* creates large
806 patches almost entirely by rhizomic growth. *Invasive Plant Sci. Manag.* 10, 119-124.

807 Gassó, N., Sol, D., Pino, J., Dana, E. D., Lloret, F., Sanz-Elorza, M., Sobrino, E., Vilà, M., 2009.
808 Exploring species attributes and site characteristics to assess plant invasions in Spain.
809 *Diversity Distrib.* 15, 50-58.

810 Gibson, A.K., Delph, L.F., Lively, C.M., 2017. The two-fold cost of sex: Experimental evidence
811 from a natural system. *Evol. Lett.* 1, 6–15, <https://doi:10.1002/evl3.1>.

812 Gigon, A., Leutert, A., 1996. The dynamic keyhole-key model of coexistence to explain diversity
813 of plants in limestone and other grasslands. *J. Veg. Sci.* 7, 29–40.

814 *Goldberg, D.E., Batzer, E., Elgersma, K., Martina, J., Klimešová, J., 2020. Allocation to clonal
815 growth: critical questions and protocols to answer them. *Perspect. Plant Ecol. Evol. Syst.*
816 43, 125511. [https://doi: 10.1016/j.ppees.2020.125511](https://doi:10.1016/j.ppees.2020.125511).

817 González, A.P.R., Preite, V., Verhoeven, K.J.F., Latzel, V., 2018. Transgenerational effects and
818 epigenetic memory in the clonal plant *Trifolium repens*. *Front. Plant Sci.* 9, 1677.

819 Gough, L., Gross, K.L., Cleland, E., Clark, C.M., Collins, S.L., Fargione, J.E., Pennings, S.C.,
820 Suding, K.N., 2012. Incorporating clonal growth form clarifies the role of plant height in
821 response to nitrogen addition. *Oecologia* 169, 1053–1062.

822 Grime, J.P., 1977. Evidence for the existence of three primary strategies in plants and its

823 relevance to ecological and evolutionary theory. *Am. Nat.* 111, 1169-1194.

824 Grime, J.P., 1979. *Plant Strategies and Vegetation Processes*. John Wiley and Sons, Chichester.

825 Gross, K.L., Herben, T., Klimešová, J., 2017. Introduction to special issue on the ecology of
826 clonal plants. *Folia Geobot.* 52, 265-267.

827 Guarino, F., Ciccattelli, A., Brundu, G., Improta, G., Triassi, M., Castiglione, S., 2019. The use of
828 MSAP reveals epigenetic diversity of the invasive clonal populations of *Arundo donax* L.
829 *PLoS One* 14.

830 Guerrero-Campo, J., Palacio, S., Montserrat-Martí, G., 2008. Plant traits enabling survival in
831 Mediterranean badlands in northeastern Spain suffering from soil erosion. *J. Veg. Sci.* 19,
832 457-464. [https://doi: 10.3170/2008-8-18382](https://doi.org/10.3170/2008-8-18382).

833 Harada, Y., Kawano, S., Iwasa, Y., 1997. Probability of clonal identity: inferring the relative
834 success of sexual versus clonal reproduction from spatial genetic patterns. *J. Ecol.* 85,
835 591-600.

836 Harper, J.L. and Bell, A.D., 1979 The population dynamics of growth form in organisms with
837 modular construction. In: Anderson, R.M., Turner, B.D., Taylor, L.R. (Eds.), *Population*
838 *Dynamics*. Blackwell Scientific Publications, Oxford, pp. 29-52.

839 Harder, L.D., Barrett, S.C.H., 1995. Mating cost of large floral displays in hermaphrodite plants.
840 *Nature* 373, 512-515.

841 Herben, T., Chytrý, M., Klimešová, J., 2016. A quest for species-level indicator values for
842 disturbance. *J. Veg. Sci.* 27, 628–636. <https://doi.org/10.1111/jvs.12384>.

843 Herben, T., Klimešová, J., 2020. Evolution of clonal growth forms in angiosperms. *New Phytol.*
844 225: 999-1010.

845 Herben, T., Klimešová, J., Chytrý, M., 2018. Effects of disturbance frequency and severity on

846 plant traits: An assessment across a temperate flora. *Funct. Ecol.* 32, 799-808.

847 Herben, T., Nováková, Z., Klimešová, J., Hrouda, L., 2012. Species traits and plant performance:
848 functional trade-offs in a large set of species in a botanical garden. *J. Ecol.* 100, 1522-
849 1533.

850 Herben, T., Šerá, B., Klimešová, J., 2015. Clonal growth and sexual reproduction: tradeoffs and
851 environmental constraints. *Oikos* 124, 469–476.

852 Herben, T., Hadincová, V., Krahulec, F., Pecháčková, S., Skálová, H., 2019. Two dimensions of
853 demographic differentiation of species in a mountain grassland community: an
854 experimental test. *Funct. Ecol.* 33, 1514–1523.

855 Heidebüchel, P., Sachs, M., Stanik, N., Hussner, A., 2019. Species-specific fragmentation rate and
856 colonization potential partly explain the successful spread of aquatic plants in lowland
857 streams. *Hydrobiologia* 843, 107-123.

858 Herron, P.M., Martine, C.T., Latimer, A.M., Leicht-Young, S.A., 2007. Invasive plants and their
859 ecological strategies: prediction and explanation of woody plant invasion in New
860 England. *Diversity Distrib.* 13, 633-644.

861 Holmes, M.A., Matlack, G.R., 2019. Non-native plant species show a legacy of agricultural
862 history in second-growth forests of southeastern Ohio. *Biol. Invasions* 21, 3063-3076.

863 Honnay, O., Jacquemyn, H., 2008. A meta-analysis of the relation between mating system,
864 growth form and genotypic diversity in clonal plant species. *Evol. Ecol.* 22, 299-312.

865 Hu, Y., Barrett, S.C.H., Zhang, D.Y., Liao, W.J., 2015. Experimental analysis of mating patterns
866 in a clonal plant reveals contrasting modes of self-pollination. *Ecol. Evol.* 5, 5423-5431.

867 *Huebner, D.C., Douhovnikoff, V., Wolf, D.E., Bret-Harte, M.S., 2019. Recruitment dynamics
868 and population structure of willows in tundra disturbed by retrogressive thaw slump

869 thermokarst on Alaska's North slope. *Perspect. Plant Ecol.* 41, 125494. <https://doi:>
870 10.1016/j.ppees.2019.125494.

871 Iwasa, Y., Kubo, T., 1997. Optimal size of storage for recovery after unpredictable disturbance.
872 *Evol. Ecol.* 11, 78-105.

873 Jaafry, W.H., Li, D.Z., Fatima, S.A. . Hassan, M., (2016) Role of clonal integration among
874 different environmental conditions (a review). *Nat. Sci.* 8, 475-486.
875 <https://doi.org/10.4236/ns.2016.811049>.

876 Jakobs, G., Weber, E., Edwards, P.J., 2004. Introduced plants of the invasive *Solidago gigantea*
877 (Asteraceae) are larger and grow denser than conspecifics in the native range. *Diversity*
878 *Distrib.* 10, 11-19.

879 *Janovský, Z., Herben, T., 2020. Reaching similar goals by different means – Differences in life-
880 history strategies of clonal and non-clonal plants. *Perspect. Plant Ecol.* 44, 125534.
881 <https://doi:10.1016/j.ppees.2020.125534>.

882 Janovský, Z., Herben, T., Klimešová, J., 2017. Accounting for clonality in comparative plant
883 demography - growth or reproduction? *Folia Geobot.* 52, 433-442.

884 Jongejans, E., de Kroon, H., 2005. Space versus time variation in the population dynamics of
885 three co-occurring perennial herbs. *J. Ecol.* 93, 681-692.

886 Keneni, G., Bekele, E., Imtiaz, M., Dagne, K., 2012. Genetic vulnerability of modern crop
887 cultivars: causes, mechanism and remedies. *Internat. J. Plant Res.* 2, 69-79.
888 <https://doi10.5923/j.plant.20120203.05>.

889 Klimeš, L., Klimešová, J., Hendriks, R., van Groenendael, J., 1997. Clonal plant architecture: a
890 comparative analysis of form and function. In: de Kroon, H., van Groenendael, J., (Eds.).
891 *The Ecology and Evolution of Clonal Plants*. Backhuys Publishers, Leiden, The

892 Netherlands, pp. 1-29.

893 Klimešová J. 2018. Temperate Herbs: An Architectural Analysis. Academia, Praha.

894 Klimešová J. 2011. Vegetative propagation. In: Simberloff, D., Rejmánek, M. (Eds.),
895 Encyclopedia of Invasive Introduced Species. University of California Press, Berkeley,
896 pp. 678-679.

897 Klimešová, J., Herben, T., Martínková, J., 2017. Disturbance is an important factor in the
898 evolution and distribution of root-sprouting species. *Evol. Ecol.* 31, 387-399.

899 Klimešová, J., Martínková, J., Ottaviani, G., 2018. Belowground plant functional ecology:
900 Towards an integrated perspective. *Funct. Ecol.* 32, 2115–2126.

901 Klimešová, J., Nobis, M.P., Herben, T., 2015. Senescence, ageing and death of the whole plant:
902 morphological prerequisites and constraints of plant immortality. *New Phytol.* 206: 14–
903 18.

904 Klimešová, J., Martínková, J., Pausas, J.G., de Moraes, M.G., Herben, T., Yu, F.H., Puntieri, J.,
905 Vesk, P.A., de Bello, F., Janeček, Š., Altman, J., Appezzato-da-Glória, B., Bartušková,
906 A., Crivellaro, A., Doležal, J., Ott, J.P., Paula, S., Schnablová, R., Schweingruber, F.H.,
907 Ottaviani, G., 2019. Handbook of standardized protocols for collecting plant modularity
908 traits. *Perspect. Ecol. Evol. Syst.* 40, 125485.

909 Klimešová, J., Tackenberg, O., Herben, T., 2016. Herbs are different: clonal and bud bank traits
910 can matter more than leaf–height–seed traits. *New Phytol.* 210, 13-17.

911 Kraft, N.J.B., Adler, P.B., Godoy, O., James, E.C., Fuller, S., Levine, J.M., 2015. Community
912 assembly, coexistence and the environmental filtering metaphor. *Funct. Ecol.* 29, 592-
913 599.

914 Küster, E.C., Kühn, I., Bruelheide, H., Klotz, S., 2008. Trait interactions help explain plant

915 invasion success in the German flora. *J. Ecol.* 96, 860-868.

916 Lanfear, R., 2013. Taller plants have lower rates of molecular evolution. *Nat. Commun.* 4, 1879.

917 Larson, J.E., Funk, J.L., 2016. Regeneration: An overlooked aspect of trait-based plant
918 community assembly models. *J. Ecol.* 104, 1284–1298.

919 Lenssen, J.M.P., Hershock, C., Speek, T., During, H.J., De Kroon, H., 2005. Experimental ramet
920 aggregation in the clonal plant *Agrostis stolonifera* reduces its competitive ability.
921 *Ecology* 86, 1358–1365.

922 Liang, J.F., Yuan, W.Y., Gao, J.Q., Roiloa, S.R., Song, M.H., Zhang, X.Y., Yu, F.H., 2020. Soil
923 resource heterogeneity competitively favors an invasive clonal plant over a native one.
924 *Oecologia* 193, 155-165.

925 Liu, J., Dong, M., Miao, S.L., Li, Z.Y., Song, M.H., Wang, R.Q., 2006. Invasive alien plants in
926 China, role of clonality and geographical origin. *Biol. Invasions* 8, 1461-1470.

927 Liu, F.H., Liu, J., Dong, M., 2016. Ecological consequences of clonal integration in plants.
928 *Front. Plant Sci.* 7, 770. [https://doi: 10.3389/fpls.2016.00770](https://doi.org/10.3389/fpls.2016.00770).

929 Liu, Y.Y., Sun, Y., Müller-Scharer, H., Yan, R., Zhou, Z.X., Wang, Y.J., Yu, F.H., 2019. Do
930 invasive alien plants differ from non-invasives in dominance and nitrogen uptake in
931 response to variation of abiotic and biotic environments under global anthropogenic
932 change? *Sci. Total Environ.* 672, 634-642.

933 Lloret, F., Médail, F., Brundu, G., Camarda, I., Moragues, E.V.A., Rita, J., Lambdon, P., Hulme,
934 P.E., 2005. Species attributes and invasion success by alien plants on Mediterranean
935 islands. *J. Ecol.* 93, 512-520.

936 Lovett-Doust, L., 1981. Population dynamics and local specialization in a clonal perennial
937 (*Ranunculus repens*). *J. Ecol.* 69: 743–755.

938 *Lubbe, F.C., Henry, H.A.L., 2019. Plant rhizome positioning in the soil and under litter: Trade-
939 offs of frost avoidance versus growth. *Perspect. Plant Ecol. Evol. Syst.* 41, 125500.
940 [https://doi: 10.1016/j.ppees.2019.125500](https://doi.org/10.1016/j.ppees.2019.125500).

941 *Martínková, J., Klimeš, A., Puy, J., Klimešová, J., 2020. Response of clonal versus non-clonal
942 herbs to disturbance: Different strategies revealed. *Perspect. Plant Ecol. Evol. Syst.* 44,
943 125529. [https://doi: 10.1016/j.ppees.2020.125529](https://doi.org/10.1016/j.ppees.2020.125529).

944 Midgley, J.J., 1996. Why the world's vegetation is not totally dominated by resprouting plants;
945 because resprouters are shorter than reseeders. *Ecography* 3, 92-95.

946 Martínková, J., Klimeš, A., Klimešová, J., 2018. No evidence for nutrient foraging in root-
947 sprouting clonal plants. *Basic Appl. Ecol.* 28, 27-36.

948 Matsuo, A., Tomimatsu, H., Sangetsu, Y., Suyama, Y., Makita, A., 2018. Genet dynamics of a
949 regenerating dwarf bamboo population across heterogeneous light environments in a
950 temperate forest understorey. *Ecol. Evol.* 8, 1746-1757.

951 Mayfield, M.M., Levine, J.M., 2010. Opposing effects of competitive exclusion on the
952 phylogenetic structure of communities. *Ecol. Lett.* 13, 1085-1093.

953 McKey, D., Elias, M., Pujol, B., Duputie, A., 2010. The evolutionary ecology of clonally
954 propagated domesticated plants. *New Phytol.* 186, 318-332,

955 Molofsky, J., Bever, J.D., Antonovics, J., Newman, T.J., 2002. Negative frequency dependence
956 and the importance of spatial scale. *Ecology* 83, 21–27.

957 Mortimer, A., 1983. On weed demography. In: Fletcher, W. (Ed.), *Recent advances in weed*
958 *research*. CABI Publishing, pp. 3-40.

959 Münkemüller, T., Gallien, L., Pollock, L.J., Barros, C., Carboni, M., Chalmandrier, L., Mazel,
960 F., Mokany, K., Roquet, C., Smycka, J., Talluto, M.V., Thuiller, W., 2020. Dos and

961 don'ts when inferring assembly rules from diversity patterns. *Glob. Ecol. Biogeog.* 29,
962 1212-1229.

963 Münzbergová, Z., Křivánek, M., Bucharová, A., Jukličková, V., Herben, T., 2005. Ramet
964 performance in two tussock plants - Do the tussock-level parameters matter? *Flora* 200,
965 275-284.

966 Oborny, B., 2019. The plant body as a network of semi-autonomous agents: a review. *Phil.*
967 *Trans. R. Soc. B* 374, 20180371. <https://doi.org/10.1098/rstb.2018.0371>.

968 Oborny, B., Bartha, S., 1995. Clonality in plant communities: an overview. In: Oborny, B.,
969 Podani, J. (Eds), *Clonality in Plant Communities. Special Features in Vegetation Science*
970 11. Opulus Press, Uppsala, pp. 115–127.

971 Orive, M.E., Barfield, M., Fernandez, C., Holt, R.D., 2017. Effects of clonal reproduction on
972 evolutionary lag and evolutionary rescue. *Am. Nat.* 190, 469-490.

973 Ott, J.P., Hartnett, D.C., 2015. Vegetative reproduction and bud bank dynamics of the perennial
974 grass *Andropogon gerardii* in mixedgrass and tallgrass prairie. *Am. Midland Nat.* 174, 14-
975 32.

976 Ott, J., Klimešová, J., Hartnett, D.C., 2019. The ecology and significance of below-ground bud
977 banks in plants. *Ann. Bot.* 123, 1099–1118. <https://doi: 10.1093/aob/mcz051>.

978 Ottaviani, G., Martínková, J., Herben, T., Pausas, J.G., Klimešová, J., 2017. On plant modularity
979 traits: functions and challenges. *Trends Plant Sci.* 22, 648-651.

980 Pennings, S.C., Callaway, R.M., 2000. The advantages of clonal integration under different
981 ecological conditions: A community-wide test. *Ecology* 81, 709-716

982 Portela, R., Roiloa, S.R., 2017. Effects of clonal integration in the expansion of two alien
983 *Carpobrotus* species into a coastal dune system - a field experiment. *Folia Geobot.* 52,

984 327-335.

985 Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O., Kunin, W.E., 2010.

986 Global pollinator declines: trends, impacts and drivers. *Trends Ecol. Evol.* 25, 345–353.

987 Pyšek, P., Manceur, A.M., Alba, C., McGregor, K.F., Pergl, J., Štajerová, K., Chytrý, M.,

988 Danihelka, Kartesz, J.J., Klimešová, J., Lučanová, M., Moravcová, L., Nishino, M.,

989 Sádlo, J., Suda, J., Tichý, L., Kühn, I., 2015. Naturalization of central European plants in

990 North America: species traits, habitats, propagule pressure, residence time. *Ecology* 96,

991 762–774.

992 Pyšek, P., Cuda, J., Smilauer, P., Skalova, H., Chumova, Z., Lambertini, C., Lucanova, M.,

993 Rysava, H., Travnicek, P., Semberova, K., Meyerson, L.A., 2020. Competition among

994 native and invasive *Phragmites australis* populations: An experimental test of the effects

995 of invasion status, genome size, and ploidy level. *Ecol. Evol.* 10, 1106-1118.

996 Pyšek, P., Prach, K., Smilauer, P., 1995. Relating invasion success to plant traits, an analysis of

997 the Czech alien flora. In: Pyšek, P., Prach, K., Rejmánek, M., Wade, M. (Eds.), *Plant*

998 *Invasions - General Aspects and Special Problems*. SPB Academic Publishing,

999 Amsterdam, pp. 39-60.

1000 Qureshi, F.A., Spanner, D.C., 1971. Unidirectional movement of tracers along the stolon of

1001 *Saxifraga sarmentosa*. *Planta* 101, 133–146.

1002 Qureshi, F.A., Spanner, D.C., 1973. Movement of [¹⁴C] sucrose along the stolon of *Saxifraga*

1003 *sarmentosa*. *Planta* 110, 145–152.

1004 Reichard, S.H., Hamilton, C.W., 1997. Predicting invasions of woody plants introduced into

1005 North America. *Conserv. Biol.* 11, 195-203.

1006 Reijers, V.C., Siteur, K., Hoeks, S., van Belzen, J., Borst, A.C.W., Heusinkveld, J.H.T., Govers,

1007 L.L., Bouma, T.J., Lamers, L.P.M., van de Koppel, J., van der Heide, T., 2019. A Levy
1008 expansion strategy optimizes early dune building by beach grasses. Nat. Commun. 10.
1009 *Ricono, A., Gustafson, N.W., Eichenberger, E., Stahl, K., Call, H., Couture, J.J., Puzey, J.R.,
1010 Dagleish, H.J., 2020. Fine-scale spatial structuring of genotypes and phenotypes in
1011 natural populations of *Asclepias syriaca*. Perspect. Plant Ecol. Evol. Syst. 45, 125546.
1012 <https://doi10.1016/j.ppees.2020.125546>.
1013 *Roiloa, S.R., 2019. Clonal traits and plant invasiveness: The case of *Carpobrotus* NEBr.
1014 Aizoaceae. Perspect. Plant Ecol. Evol. Syst. 40, 125479. [https://doi:](https://doi:10.1016/j.ppees.2019.125479)
1015 [10.1016/j.ppees.2019.125479](https://doi:10.1016/j.ppees.2019.125479).
1016 Roiloa, S.R., Alpert, P., Barreiro, R., 2019. Differences in physiological integration between
1017 invasive and noninvasive introduced clonal species of *Carpobrotus*. J. Plant Ecol. 12,
1018 972-981.
1019 Roiloa, S.R., Retuerto, R., Campoy, J.G., Novoa, A., Barreiro, R., 2016. Division of labor brings
1020 greater benefits to clones of *Carpobrotus edulis* in the non-native range, evidence for
1021 rapid adaptive evolution. Frontiers Plant Sci. 7, 349.
1022 Roquet, C., 2013. Replicated radiations of the alpine genus *Androsace* (Primulaceae) driven by
1023 range expansion and convergent key innovations. J. Biog. 40, 1874-1886.
1024 Salguero-Gómez, R., 2018. Implications of clonality for ageing research. Evol. Ecol. 32, 9-28.
1025 Salguero-Gómez, R., Jones, O.R., Jongejans, E., Blomberg, S.P., Hodgson, D.J., Mbeau-Ache,
1026 C., Zuidema, P.A., de Kroon, H., Buckley, Y.M., 2016. Fast-slow continuum and
1027 reproductive strategies structure plant life-history variation worldwide. Proc. Natl. Acad.
1028 Sci. USA 113, 230–235.
1029 Serebriakova, T.I., 1977. On major architectural models of herbaceous perennials and patterns of

1030 their reconfiguration [in Russian]. Byulleten Moskovskogo Obshchestva Ispytatelei
1031 Prirody Otdel Biologicheskii 82, 112-128.

1032 Schoen, D.J., Schultz, S.T., 2019. Somatic mutation and evolution in plants. *Ann. Rev. Ecol.*
1033 *Evol. Syst.* 50, 49-73.

1034 Sebens, K.P., Thorne, B.L., 1985. Coexistence of clones, clonal diversity, and the effects of
1035 disturbance. In: Jackson, J.B.C, Buss, L.W., Cook, R.E. (Eds.), *Population Biology and*
1036 *Evolution of Clonal Organisms*. Yale University Press, New Haven, pp. 357-398.

1037 Shah, A.B., Reshi, Z.A., Shah, M.A., 2014. Clonal trait diversity in relation to invasiveness of
1038 alien macrophytes in two Himalayan Ramsar sites. *J. Veg. Sci.* 25, 839-847.

1039 Shefferson, R.P., 2009. The evolutionary ecology of vegetative dormancy in mature herbaceous
1040 perennial plants. *J. Ecol.* 97, 1000-1009

1041 Shi, W., Chen, X.J., Gao, L.X., Xu, C.Y., Ou, X.K., Bossdorf, O., Yang, J., Geng, Y.P., 2019.
1042 Transient stability of epigenetic population differentiation in a clonal invader. *Front.*
1043 *Plant Sci.* 9.

1044 Smith, S.A., Donoghue, M.J., 2008. Rates of molecular evolution are linked to life history in
1045 flowering plants. *Science* 322, 86-89.

1046 Song, Y.B., Yu, F.H., Keser, L.H., Dawson, W., Ficher, M., Dong, M., van Kleunen, M., 2013.
1047 United we stand, divided we fall, a meta-analysis of experiments on clonal integration
1048 and its relationship to invasiveness. *Oecologia* 171, 317-327.

1049 Sosnová, M., van Diggelen, R., Klimešová, J., 2010. Distribution of clonal growth forms in
1050 wetlands. *Aquat. Bot.* 92, 33-39.

1051 Stoll, P. Prati, D., 2001. Intraspecific aggregation alters competitive interactions in experimental
1052 plant communities. *Ecology* 82, 319-327. Suehs, C.M., Affire, S., Cabido, M., Urcelay,

1053 C., 2010. Functional traits of alien plants across contrasting climatic and land-use
1054 regimes, do aliens join the locals or try harder than them? *J. Ecol.* 98, 17-27.

1055 Suzuki, J., Hara, T., 2001. Partitioning of stored resources between shoots in a clone and its
1056 effects on shoot size hierarchy. *Ann. Bot.* 87, 655-659.

1057 Svensson, B.M., Rydin H., Carlsson, B.A., 2013. Clonality in the plant community, In: van der
1058 Maarel, E., Franklin, J. (Eds.), *Vegetation Ecology*, Wiley-Blackwell, pp. 141-163.

1059 Tecco, P.A., Diaz, S., Cabido, M., Urceley, C., 2010. Functional traits of alien plants across
1060 contrasting climatic and land-use regimes: do aliens join the locals or try harder than
1061 them? *J. Ecol.* 998, 17-27.

1062 Tsujimoto, M., Araki, K.S., Honjo, M.N., Yasugi, M., Nagano, A.J., Akama, S., Hatakeyama,
1063 M., Shimizu-Inatsugi, R., Sese, J., Shimizu, K.K., Kudoh, H., 2020. Genet assignment
1064 and population structure analysis in a clonal forest-floor herb, *Cardamine leucantha*,
1065 using RAD-seq. *AoB Plants* 12.

1066 Tuomi, J., Vuorisalo, T., 1989. What are the units of selection in modular organisms. *Oikos* 54,
1067 227–233.

1068 Uya, M., Bulleri, F., Gribben, P.E., 2018. Propagules are not all equal: traits of vegetative
1069 fragments and disturbance regulate invasion success. *Ecology* 99, 957-965.

1070 Vallejo-Marín, M., Dorken, M.E., Barrett, S.C.H., 2010. The ecological and evolutionary
1071 consequences of clonality for plant mating. *Ann. Rev. Ecol. Evol. Syst.* 41, 193-213.

1072 Van Drunen, W.E, Husband, B.C. 2019. Evolutionary associations between polyploidy, clonal
1073 reproduction, and perenniality in the angiosperms. *New Phytol.* 224, 1266–1277
1074 <https://doi: 10.1111/nph.15999>.

1075 *Vesk, P.A., Yen, J.D.L., 2019. Plant resprouting: How many sprouts and how deep? Flexible
1076 modelling of multi-species experimental disturbance. *Perspect. Plant Ecol. Evol. Syst.* 41,
1077 125497. [https://doi: 10.1016/j.ppees.2019.125497](https://doi.org/10.1016/j.ppees.2019.125497).

1078 Vilà, M., Rohr, R.P., Espinar, J.L., Hulme, P.S., Pergl, J., Le Roux, J.J., Schaffner, U., Pyšek, P.,
1079 2015. Explaining the variation in impacts of non-native plants on local-scale species
1080 richness, the role of phylogenetic relatedness. *Glob. Ecol. Biogeog.* 24, 139-146.

1081 Vilas, M.P., Adams, M.P., Oldham, C.E., Marti, C.L., Hipsey, M.R., 2017. Fragment dispersal
1082 and plant-induced dieback explain irregular ring-shaped pattern formation in a clonal
1083 submerged macrophyte. *Ecol. Model.* 363, 111-121.

1084 Vojtkó, A.E., Freitag, M., Bricca, A., Martello, F., Compañ, J.M., Küttim, M., Kun, R., de Bello,
1085 F., Klimešová, J., Götzenberger, L., 2017. Clonal vs leaf-height-seed (LHS) traits: which
1086 are filtered more strongly across habitats? *Folia Geobot.* 52, 269-281.

1087 *Wang, Y.J., Chen, D., Yan R., Yu, F.H., van Kleunen, M., 2019. Invasive alien clonal plants
1088 are competitively superior over co-occurring native clonal plants. *Perspect. Plant Ecol.*
1089 *Evol. Syst.* 40, 125484. [https://doi:10.1016/j.ppees.2019.125484](https://doi.org/10.1016/j.ppees.2019.125484).

1090 Wang, P., Alpert, P., Yu, F.-H. 2021. Physiological integration can increase competitive ability
1091 in clonal plants if competition is spatially heterogeneous. *Oecologia* [published online,
1092 not yet in print]. <https://doi.org/10.1007/s00442-020-04823-5>.

1093 Wang, Y.J., Müller-Scharer, H., van Kleunen, M., Cai, A.M., Zhang, P., Yan, R., Dong, B.C.,
1094 Yu, F.H., 2017. Invasive alien plants benefit more from clonal integration in
1095 heterogeneous environments than natives. *New Phytol.* 216, 1072-1078.

1096 *Watts, D.A., Douhovnikoff, V., Post, E. 2019. Sexual reproduction is more prevalent in
1097 continental landscapes in the expanding arctic shrub, *Salix glauca*. *Perspect. Plant Ecol.*

1098 Evol. Syst. 41, 125499. [https://doi: 10.1016/j.ppees.2019.125499](https://doi.org/10.1016/j.ppees.2019.125499).

1099 Weiser, M., Koubek, T., Herben, T., 2016. Root foraging performance and life-history traits.

1100 Front. Plant Sci. 7, 779.

1101 Wikberg, S., Svensson, B.M., 2006. Ramet dynamics in a centrifugally expanding clonal sedge:

1102 a matrix analysis. Plant Ecol. 183, 55-63.

1103 Winkler, E., Fischer, M., Schmid, B., 1999. Modelling the competitiveness of clonal plants by

1104 complementary analytical and simulation approaches. Oikos 85, 217-233.

1105 Ye, D., Hu, Y.K., Song, M.H., Pan, X., Xie, X.F., Liu, G.F., Ye, X.H., Dong, M., 2014.

1106 Clonality-climate relationships along latitudinal gradient across China: adaptation of

1107 clonality to environments. PLoS One 9, e94009.

1108 Zhang, Y.Y., Zhang, D.Y., Barret, S.C.H., 2010. Genetic uniformity characterizes the invasive

1109 spread of water hyacinth (*Eichhornia crassipes*), a clonal aquatic plant. Molec. Ecol. 19,

1110 1774-1786.

1111 Zheng, Z., Bai, W., Zhang, W-H., 2019. Clonality-dependent dynamic change of plant

1112 community in temperate grasslands under nitrogen enrichment. Oecologia 189, 255–266.

1113 [https://https://doi.org/10.1007/s00442-018-4317-x](https://doi.org/10.1007/s00442-018-4317-x).

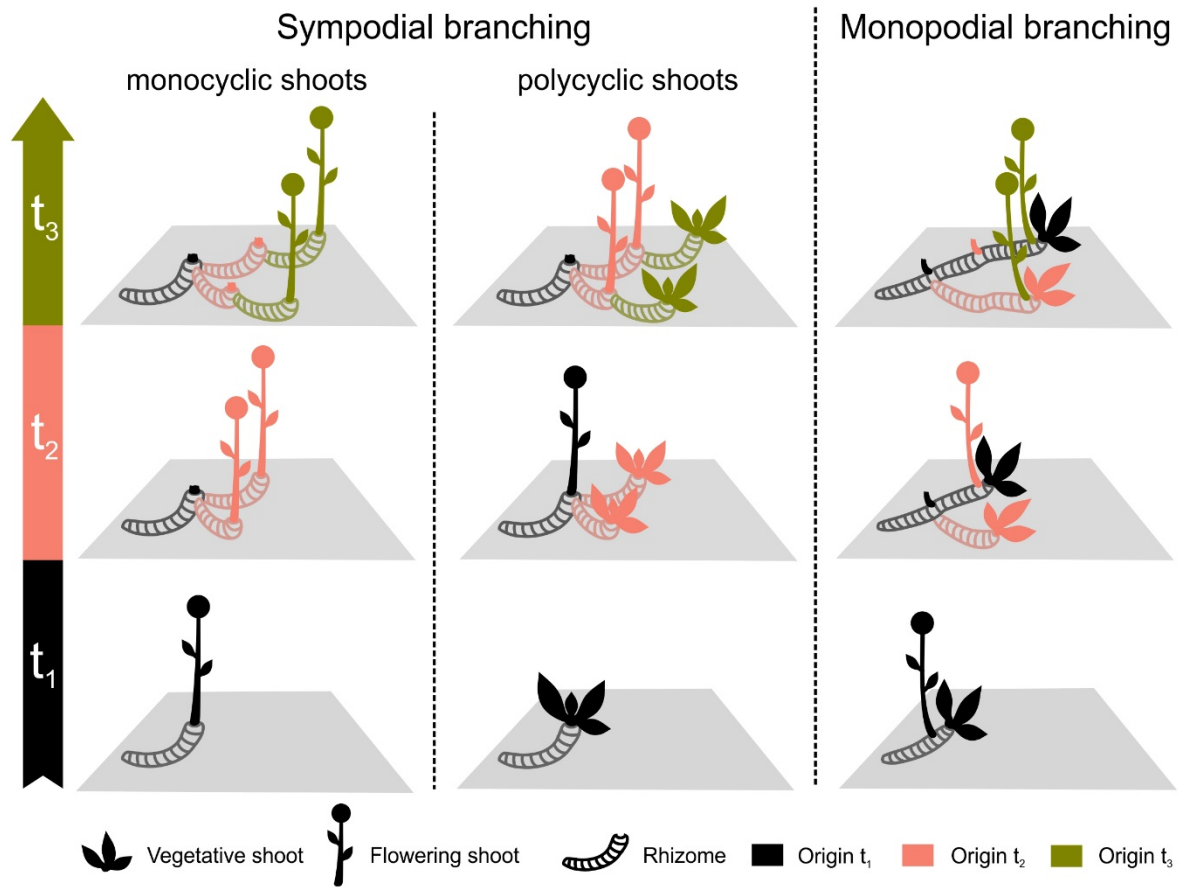
1114

1115 **Figure legends**

1116

1117 Figure 1. Architectural development of sympodial and monopodial branching over three time
1118 periods (t). Demographers frequently fail to record clonality in species with monocyclic shoots,
1119 whose ramets emerge at different positions each season. There is also a lack of studies on species
1120 with very low and very high intensities of clonal growth, especially those with extensive rhizome
1121 systems. Illustration by Alena Bartušková.

1122



1123

1124 Fig. 1