

1 **Grazing-induced changes in plant-soil feedback alter plant biomass allocation**

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21 **Running head:** Vertebrate herbivores and plant-soil feedback

1 **Abstract (248 words)**

2 Large vertebrate herbivores, as well as plant-soil feedback interactions are important
3 drivers of plant performance, plant community composition and vegetation dynamics
4 in terrestrial ecosystems. However, it is poorly understood whether and how large
5 vertebrate herbivores and plant-soil feedback effects interact. Here, we study the
6 response of grassland plant species to grazing-induced legacy effects in the soil and
7 we explore whether these plant responses can help us to understand long-term
8 vegetation dynamics in the field.

9 In a greenhouse experiment we tested the response of four grassland plant
10 species, *Agrostis capillaris* (L.), *Festuca rubra* (L.), *Holcus lanatus* (L.), and *Rumex*
11 *acetosa* (L.), to field-conditioned soils from grazed and ungrazed grassland. We relate
12 these responses to long-term vegetation data from a grassland enclosure experiment in
13 the field.

14 In the greenhouse experiment, we found that total biomass production and
15 biomass allocation to roots was higher in soils from grazed than from ungrazed plots.
16 There were only few relationships between plant production in the greenhouse and the
17 abundance of conspecifics in the field. Spatiotemporal patterns in plant community
18 composition were more stable in grazed than ungrazed grassland plots, but were not
19 related to plant-soil feedbacks effects and biomass allocation patterns.

20 We conclude that grazing-induced soil legacy effects mainly influenced plant
21 biomass allocation patterns, but could not explain altered vegetation dynamics in
22 grazed grasslands. Consequently, the direct effects of grazing on plant community
23 composition (e.g. through modifying light competition or differences in grazing
24 tolerance) appear to overrule indirect effects through changes in plant-soil feedback.

25

1 **Keywords**

2 Aboveground-belowground interactions, grassland, grazing, herbivores, plant-
3 herbivore interactions, plant-soil interactions, vegetation dynamics

4

5 **Introduction**

6 In grasslands worldwide, aboveground vertebrate herbivores are key drivers of
7 vegetation composition and dynamics (e.g. Hobbs 1996; Olf and Ritchie 1998;
8 Bakker et al. 2006). At the same time feedback effects between plants and their biotic
9 and abiotic soil environment influence plant performance and structure plant
10 communities (e.g. Bever et al. 1997; van der Putten and Peters 1997; Ehrenfeld et al.
11 2005), and aboveground herbivory and plant-soil feedback interact with each other
12 (Wardle et al. 2004). However, little is known on how grazing and plant-soil feedback
13 may interact. Here, we study plant-soil feedback effects in grazed grassland in
14 comparison with experimental plots within the grassland where grazers had been
15 excluded.

16 It has long been recognized that large herbivores speed up or slow down soil
17 nutrient cycling (Bardgett and Wardle 2003), which results in positive or negative
18 feedback effects on plant performance (McNaughton et al. 1997; Ritchie et al. 1998;
19 Hamilton and Frank 2001; Mikola et al. 2009; Medina-Roldan et al. 2012). Moreover,
20 long-lasting changes in soil conditions by grazing and defoliation can modify plant
21 competitive interactions (Medina-Roldan et al. 2012) and nutrient allocation and
22 acquisition (Mikola et al. 2005; Sørensen et al. 2008; Mikola et al. 2009). These
23 studies indicate that plants perform differently in soils from grazed and ungrazed
24 grasslands. However, it is not well understood how grazing modifies the response of
25 plant species to soils where conspecifics have been growing and how this affects long-

1 term vegetation dynamics. Many grassland plant species perform worse in soils
2 conditioned by conspecific plants than in soils where heterospecific species have been
3 dominant (Olf et al. 2000; Kulmatiski et al. 2008), due to the buildup of species-
4 specific root herbivores and pathogens (van der Putten et al. 1993; Bever 2003).

5 The aim of our study was to investigate (1) whether plant-soil feedback effects
6 differ between soils from grazed and ungrazed grasslands, (2) whether plant-soil
7 feedback effects determined under controlled conditions are related to the abundance
8 of conspecific plant species in the field in soils from grazed and ungrazed grasslands,
9 and (3) whether spatiotemporal vegetation patterns of plant species in grazed and
10 ungrazed grasslands may be explained by grazing-induced changes in plant-soil
11 feedback.

12 Our first hypothesis was that herbivores alter plant performance via legacy
13 effects in the soil. Herbivores may increase or reduce plant growth via changes in
14 nutrient cycling (McNaughton et al. 1997; Hamilton and Frank 2001; Bardgett and
15 Wardle 2003) and direct interactions between roots and soil organisms (Todd et al.
16 1992; Allsopp 1998; Mikola et al. 2009). Our second hypothesis was that plants build
17 up species-specific negative plant-soil feedback (van der Putten et al. 1993; Bever et
18 al. 1997; Bever 2003; Kulmatiski et al. 2008). As a result, plants will perform worse
19 in soils where conspecific plants were abundant in the field (Mangan et al. 2010).
20 Finally, we hypothesized that spatiotemporal vegetation patterns become more
21 dynamic if herbivores promote negative plant-soil feedback, because negative plant-
22 soil feedback reduces the competitive ability of plants leading to increased species
23 turnover (van der Putten and Peters 1997; Olf et al. 2000; Bever 2003; Revilla et al.
24 2013).

1 We tested the hypotheses by analyzing the responses of four grassland species
2 in field-conditioned soils from grazed and ungrazed grassland plots under controlled
3 greenhouse conditions. We then related this greenhouse response of plants to the past
4 and present abundance of conspecifics in the field experiment. Finally, we explored
5 whether these plant-soil feedback patterns could help in explaining spatiotemporal
6 dynamics of plant species in a long-term grazing experiment in the field. In the
7 discussion we propose mechanisms through which grazing may alter plant-soil
8 feedback effects.

9

10 **Methods**

11 *Study site*

12 We performed our study in Junner Koeland, a 100-ha nature reserve along the river
13 Overijsselse Vecht in the north-east of the Netherlands (52°32'N, 6°36'E). Our
14 experiment was situated on a 50-ha floodplain, which used to be flooded regularly
15 until canalization of the river Vecht (around 1910) and regulation of the water level.
16 The Junner Koeland was common grazing land, used by farmers from the village
17 Junne, and has been grazed extensively by livestock for centuries. Nowadays, it is
18 managed as a nature reserve by the National Forestry Service (Staatsbosbeheer), and
19 is grazed by cattle (*Bos taurus* (Bojanus, 1827)) from April till November at stocking
20 rates of about 0.3 animals ha⁻¹. The most abundant wild larger vertebrate herbivores in
21 the area are European rabbits (*Oryctolagus caniculus* (Linnaeus, 1758)) (Bakker et al.
22 2009). Dominant plant species in the grasslands are the graminoids *Agrostis*
23 *capillaris*, *Festuca rubra*, *Holcus lanatus*, and *Luzula campestris* (L.). Frequently
24 occurring dicots are *Rumex acetosa* and *Trifolium repens* (L.) (nomenclature follows
25 van der Meijden 2005).

1

2 *Field experiment*

3 In 1994, we established a long-term enclosure experiment to study the plant
4 community response to vertebrate grazing. We created 5 randomly established blocks,
5 with 2 different grazing treatments per block. Each block contained a 12 m x 12 m
6 chicken-wire fenced enclosure plot from which cattle and rabbits were excluded
7 (“ungrazed”), and a plot of 12 m x 12 m to which all larger herbivores had free access
8 (“grazed”). Within each plot 4 permanent subplots of 2 m x 2 m were established to
9 record long-term vegetation responses to combined grazing by cattle and rabbits. All
10 subplots were positioned at least 1 m from the fences to avoid edge effects. In each of
11 the 2 m x 2 m subplots, we recorded plant species composition from 1995-2001 and
12 from 2005-2008 at peak standing biomass (in July-August). We estimated cover of
13 each plant species visually according to the decimal Londo scale (Londo 1976).

14

15 *Greenhouse experiment*

16 We grew four dominant plant species in undiluted field soil from the permanent
17 subplots of the field experiment to determine their growth potential in field soil. We
18 defined dominant plant species as species that across all years and plots had an
19 average cover of >10% in at least one of the grazing treatments. We selected the
20 grasses *Agrostis capillaris*, *Festuca rubra*, *Holcus lanatus* and the forb *Rumex*
21 *acetosa*. *Agrostis* and *Festuca* are abundant in grazed plots, while *Holcus* and *Rumex*
22 are abundant in ungrazed plots. Seeds of *Holcus* and *Rumex* were collected in the
23 Junner Koeland area. Seeds of *Agrostis* and *Festuca* were purchased from the Cruydt-
24 hoeck (Assen, The Netherlands). Seeds were germinated on sterile glass beads in
25 plastic containers in the greenhouse three weeks prior to the start of the experiment.

1 In the fall of 2006 we collected approximately 6 kg of soil of the top 15 cm
2 from each of the grazed and ungrazed 2 m x 2 m subplots from the Junner Koeland
3 exclosure experiment using a soil core. In total we used 40 subplots (5 blocks x 2
4 grazing treatments x 4 subplots). We gently homogenized the 6 kg of soil per subplot,
5 removed large roots and divided it over four 1500 ml pots, resulting in a total of 160
6 pots in the greenhouse experiment (40 subplots x 4 plant species). In each of these
7 pots we planted four seedlings of each of the plant species in monoculture.

8 Pots were placed in the greenhouse at a day/night rhythm of 15/9h at
9 temperatures of 21/15°C respectively. Soil moisture content in all pots was kept
10 constant at 25% w/w by watering 2-3 times per week using demineralized water. To
11 account for possible light and temperature differences within the greenhouse the
12 position of the pots was randomized once a week. Pots in the greenhouse were
13 arranged in a randomized block design so that pots containing soil from the same
14 subplot and block in the field were kept in one block in the greenhouse. The plants did
15 not receive nutrients during the experiment, because this could modify the response of
16 the plants to pure field soil.

17 After 12 weeks we harvested shoot biomass and used half of the soil from
18 each pot to measure root biomass. Roots were washed with tap water. Shoot and root
19 biomass were dried at 70°C for 48 hours and weighed. Total root biomass per pot was
20 calculated by multiplying by 2.

21

22 *Data analysis*

23 We determined the growth of each plant species in the greenhouse as total biomass
24 (root + shoot biomass), shoot biomass and root biomass per pot. In addition, we

1 calculated the ratio shoot biomass/total biomass (shoot weight ratio; SWR), to
2 determine what proportion of the biomass was allocated aboveground.

3 For each of the four dominant plant species we calculated temporal stability in
4 the field as the average cover of a plant species over different years in an individual
5 plot divided by the standard deviation (Bezemer and van der Putten 2007). Spatial
6 stability in the field was calculated as the average cover of a plant species over the
7 four subplots within one grazing treatment within a block divided by the standard
8 deviation. This resulted in 5 replicate spatial stability measures per grazing treatment
9 for each year.

10 To test the influence of grazing treatment and plant species on biomass
11 production, SWR, and vegetation stability, we used general linear mixed models with
12 each of the respective measures as response variables. We used plant species and
13 grazing treatment as fixed factors and subplot and block as random factors. When
14 testing spatial stability we used block and year as a random factor.

15 For each of the plant species, we used a Pearson's correlation analyses to
16 determine the relationship between greenhouse biomass production and field
17 abundance in the year previous to (2005) and the year of (2006) the greenhouse
18 experiment. A negative correlation between greenhouse biomass and field abundance
19 indicates a negative plant-soil feedback. When plants in the field build up species-
20 specific soil pathogens, plant performance in the greenhouse experiment will be
21 reduced. In contrast, a positive correlation indicates that species-specific soil
22 conditions favor plant growth. If plants in the field grow in spots where species-
23 specific biotic and abiotic conditions stimulate plant performance, conspecifics in the
24 greenhouse may also perform well. We test the year previous to the experiment to
25 account for legacy effects of plant species on soil conditions. *P*-values were corrected

1 using a sequential Bonferroni correction for multiple testing. P -values were ranked
2 from largest to smallest and regarded significant when $P < \alpha/k$, where α is 0.05, and k
3 the rank of the P -value.

4 All data were analyzed using R, version 2.14. We implemented the lme4
5 package (Bates and Maechler 2009) for general linear mixed models. We used
6 maximum likelihood estimation and determined effects of our fixed factors by
7 comparing models with and without the variable of interest with a chi-square test
8 statistic (Crawley 2007).

9

10 **Results**

11 *Plant biomass and root-shoot allocation*

12 Total plant biomass was higher in soils from grazed plots than in soils from ungrazed
13 plots (Table 1). Shoot and root biomass responses to soils from grazed and ungrazed
14 plots differed among plant species (Table 1). Shoot biomass was lower in soils from
15 grazed plots for *Holcus* and *Rumex*, but not for *Agrostis* and *Festuca* (Fig 1 a). Root
16 biomass was higher in soils from grazed plots than from ungrazed plots for *Agrostis*,
17 *Festuca* and *Holcus*, but not for *Rumex* (Fig 1b). Plant species allocated more biomass
18 aboveground in soils from ungrazed plots than from grazed plots, indicated by a
19 significantly higher SWR for all species (Table 1, Fig 1c). Total-, root- and shoot
20 biomass, as well as the SWR, were different among plant species (Table 1, Fig 1).

21

22 *Relationship between plant biomass and field abundance*

23 Biomass production of *Holcus* in the greenhouse was positively related to the
24 abundance in the field in 2005 in soils from grazed plots. It tended to be positively
25 related to abundance in the field in 2006, while it tended to be negatively related to

1 field cover in ungrazed plots, but both relationships were not significant. Biomass of
2 *Rumex* tended to be positively related to 2005-field cover in grazed plots only (Table
3 2).

4

5 *Temporal and spatial plant community stability*

6 In the field, the cover of the four dominant plant species changed over time (Fig 2).
7 Both spatial and temporal stability were higher for *Agrostis* and *Festuca* than for
8 *Holcus* and *Rumex* (Figs 3, 4). Grazing treatment affected the stability of these species
9 differently (Table 4, Figs 3, 4). *Agrostis*, *Festuca* and *Rumex* were more stable over
10 time under grazing by large herbivores, while the stability of *Holcus* was not different
11 between grazed and ungrazed plant communities (Fig 3). Spatial stability of *Agrostis*
12 and *Festuca* was higher in grazed than in ungrazed plots, while for *Holcus* and *Rumex*
13 there was no difference between grazing treatments (Fig 4).

14

15 **Discussion**

16 *Plant biomass and root-shoot allocation*

17 In accordance with our first hypothesis we found that grazing-induced soil legacy
18 effects altered plant growth. Plant biomass increased on soils with a grazing history,
19 which is in line with many previous studies (McNaughton et al. 1997; Hamilton and
20 Frank 2001; Mikola et al. 2009; Medina-Roldan et al. 2012). However, in our study
21 this effect appeared very small for most of the plant species (Fig 1a, b) and hence may
22 not be ecologically relevant for driving vegetation dynamics. The influence of grazing
23 on plant biomass allocation patterns was more pronounced (Fig 1c). Previous work
24 already showed that plants can allocate resources differently as a direct response to
25 grazing (Holland et al. 1996) and that grazing-induced legacy effects in the soil can

1 increase nitrogen allocation (Mikola et al. 2005) and biomass allocation to shoots
2 (Medina-Roldan et al. 2012). We now show that grazing-induced changes in soil
3 properties can also feedback to increase biomass allocation to roots (Fig 1c).

4 We did not test how grazing altered plant-soil feedback effects on plant
5 biomass allocation, but there are two potential mechanisms that may explain this
6 effect. First, plant-soil feedback effects on biomass allocation can optimize the ability
7 of plants to compete for limiting resources (te Beest et al. 2009). Indeed, we found
8 increased biomass allocation to roots, which may enhance the competitive ability of
9 plants for nutrients (Wilson 1988; Aerts et al. 1991; Casper and Jackson 1997) in soils
10 from grazed plots where nitrogen mineralization has been shown to be slower (Bakker
11 et al. 2004; Veen et al. 2010). At the same time, increased biomass allocation to
12 shoots in soils from ungrazed plots increases the competitive abilities of plants for
13 light, which may be a limiting factor under ungrazed conditions (Bakker and Olff
14 2003). Alternatively, reduced biomass allocation to roots may occur when
15 belowground grazing and pathogen pressure is lower (Holah and Alexander 1999).
16 We did not find evidence for reduced belowground grazing pressure in our study
17 system, as the abundance of plant-feeding nematodes was not different between
18 grazed and ungrazed plots (Veen et al. 2010). Therefore, it appears that altered
19 biomass allocation in response to grazing-induced soil legacy effects was mainly
20 mediated via abiotic pathways. However, in order to fully understand what drives the
21 altered biomass allocation in response to grazing-induced changes in soil conditions it
22 will be necessary to quantify the contribution of soil biotic and abiotic factors to
23 plant-soil feedback in more detail in future experiments.

24 Our greenhouse experiment lasted for 12 weeks, but we do not believe that
25 this limited the potential of plant species to respond to grazing-induced soil legacy

1 effects (Fig 1 a, b). Most plant-soil feedback experiments that used field-conditioned
2 soils had growing periods between 6 and 15 weeks and are able to detect strong plant-
3 soil feedback effects (e.g. van der Putten et al. 1993; Bezemer et al. 2006; Mikola et
4 al. 2009).

5

6 *Relationship between plant biomass and field abundance*

7 Although we expected to find negative plant-soil feedback effects for most of our
8 species (Kulmatiski et al. 2008), we only found a tendency for a negative relation
9 between greenhouse biomass and field abundance for *Holcus* in soils from ungrazed
10 plots. In soils from grazed plots, *Holcus*, as well as *Rumex*, actually experienced a
11 positive plant-soil feedback. These results show that grazing can alter the direction of
12 plant-soil feedback. The negative plant-soil feedback effects on *Holcus* may play a
13 role in ungrazed sites, because this species can become very abundant in the absence
14 of grazing. Under such conditions species-specific root herbivores and pathogens may
15 strongly increase and limit plant performance (van der Putten et al. 1993; Bever
16 2003). In contrast, positive feedback in grazed plots, where *Holcus* is not very
17 abundant, may be explained by favorable biotic and abiotic soil conditions.

18 For most species we did not find a relationship between greenhouse biomass
19 and field abundance. It is possible that these plant species were not inhibited or
20 stimulated by species-specific soil biota. However, this was unexpected as many
21 grassland species experience negative plant-soil feedback (Kulmatiski et al. 2008).
22 The use of pure field soils in our greenhouse experiment may partly explain why
23 relationships were not as strong as hypothesized. In such soils many factors, such as
24 variation in abiotic soil properties (Bezemer et al. 2006; Manning et al. 2008;
25 Harrison and Bardgett 2010; Schrama et al. 2013) and competitive interactions

1 between plant species (Casper and Castelli 2007; Kardol et al. 2007; Medina-Roldan
2 et al. 2012), have been proposed to interfere with the response of plant species to soil
3 legacy effects (Brinkman et al. 2010). Moreover, we collected soils at the plot-scale,
4 which may not concur with the landscape-scale of operation of large herbivores and
5 with the individual plant scale at which plant-soil feedback effects operate. Finally,
6 for *Festuca* and *Agrostis* we did not use seeds originating from the field site. The
7 response of plant species to grazing-induced soil legacy effects might have been
8 stronger when using seeds from the field plots, or when using transplants from grazed
9 and ungrazed plots, as plants may genetically adapt to local environmental conditions
10 (Linhart and Grant 1996). Indeed, previous studies found that genetically different
11 populations of the same plant species respond differently to biotic legacy effects in the
12 soil (Felker-Quinn et al. 2011).

13

14 *Temporal and spatial plant community stability*

15 We found that plant-soil feedbacks were not related to plant community stability. This
16 is in contrast to our final hypothesis that negative plant-soil feedbacks increase
17 vegetation dynamics, while positive plant-soil feedback increases vegetation stability
18 (van der Putten and Peters 1997; Bever 2003; Revilla et al. 2013). Plant communities
19 were more stable in grazed than in ungrazed grassland plots, whereas plant-soil
20 feedback effects were generally not different between grazing treatments (Fig 1, Table
21 2). Only for *Holcus*, plant-soil feedback effects appeared to be more positive in soils
22 from grazed plots (Table 2), but the stability of this species was not different between
23 grazed and ungrazed plots (Fig 3, 4). Therefore, our results indicate that plant-soil
24 feedback effects on plant community stability in grazed grasslands are being
25 overridden by grazing of large herbivores (Veen and Olff 2011; Veen et al. 2012). For

1 moderate to high grazing intensity, foraging decisions of large herbivores result in a
2 homogeneous grazing pressure over large spatial scales (Ritchie and Olff 1999;
3 Haskell et al. 2002; Laca et al. 2010). Also, other factors, such as gap creation and
4 changes in soil abiotic properties through trampling may be important grazing-
5 induced drivers of vegetation dynamics (Medina-Roldan et al. 2012; Schrama et al.
6 2013).

7

8 We conclude that grazing-induced legacy effects in the soil enhanced plant biomass
9 allocation to roots, but had only minor impact on the strength and direction of plant-
10 soil feedback effects for most of the plant species. Moreover, plant-soil feedback
11 effects did not explain vegetation dynamics in grazed grassland. Therefore, the direct
12 effect of grazing on vegetation dynamics appeared more important than indirect
13 effects through changes in plant-soil feedback.

14

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22

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15

1 **Table 1**

2 Overview of general linear models testing the influence of grazing and plant species
 3 on total biomass, shoot biomass, root biomass and shoot weight ratio (SWR) for the
 4 four different plant species in the greenhouse experiment. Values in boldface
 5 represent significant effects at $P < 0.05$. Degrees of freedom are 1 for all the analyses
 6 of main factors and 3 for the analyses of two-way interaction effects.

	Grazing		Species		Two-way interaction	
	χ^2	P	χ^2	P	χ^2	P
Total biomass	4.04	0.045	42.93	<0.001	7.04	0.134
Shoot biomass	3.18	0.075	57.56	<0.001	13.82	0.008
Root biomass	18.68	<0.001	21.80	<0.001	12.27	0.015
SWR	35.19	<0.001	24.37	<0.001	12.11	0.017

7

1 **Table 2**

2 Relationships between biomass production in the greenhouse and abundance of plant
 3 species in the field for all four plant species in the year before (2005) and the year of
 4 (2006) the experiment. r = Pearson's correlation coefficient, P = P -value, df = degrees
 5 of freedom. Values in boldface represent significant correlations at $P < 0.05/k$, where
 6 k is the rank of the P -value (sequential Bonferroni correction). Correlations with $P <$
 7 $0.10/k$ are displayed in italic.

8

	Ungrazed			Grazed		
	r	P	df	r	P	df
2005						
<i>Agrostis</i>	0.47	0.035	18	-0.49	0.034	17
<i>Festuca</i>	-0.22	0.366	17	-0.29	0.208	18
<i>Holcus</i>	-0.62	0.003	18	0.73	<0.001	17
<i>Rumex</i>	0.11	0.666	17	0.62	0.003	18
2006						
<i>Agrostis</i>	0.10	0.666	18	-0.24	0.325	1,17
<i>Festuca</i>	-0.01	0.965	17	-0.19	0.430	1,18
<i>Holcus</i>	-0.61	0.004	18	0.59	0.007	1,17
<i>Rumex</i>	0.33	0.164	17	0.11	0.649	1,18

9

1 **Table 3**

2 Overview of general linear models testing the influence of grazing and plant species
3 on temporal and spatial stability for the four different plant species in the field. Values
4 in boldface represent significant differences between grazed and ungrazed treatments
5 at $P < 0.05$. Degrees of freedom are 1 for all the analyses of main factors and 3 for the
6 analyses of two-way interaction effects.

	Grazing		Species		Two-way interaction	
	χ^2	P	χ^2	P	χ^2	P
Temporal	26.91	<0.001	75.85	<0.001	116.17	<0.001
Spatial	20.79	<0.001	63.01	<0.001	59.85	<0.001

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1 **Figure legends**

2 Fig 1. (a) Shoot biomass (BM) (g dry weight), (b) Root biomass (g dry weight) and
3 (c) shoot weight ratio (SWR), expressed as the shoot biomass/total biomass, for the
4 four plant species grown in the greenhouse in soils from grazed and ungrazed
5 grassland communities (n = 5). Bars show mean values (\pm SE). Different letters
6 indicate significant differences at $P < 0.05$.

7

8 Fig 2. Yearly cover (%) of four dominant plant species (three grasses *Agrostis*
9 *capillaris*, *Festuca rubra* and *Holcus lanatus* and one herb *Rumex acetosa*) in the (a)
10 ungrazed and (b) grazed treatments of the enclosure experiment in the field.

11

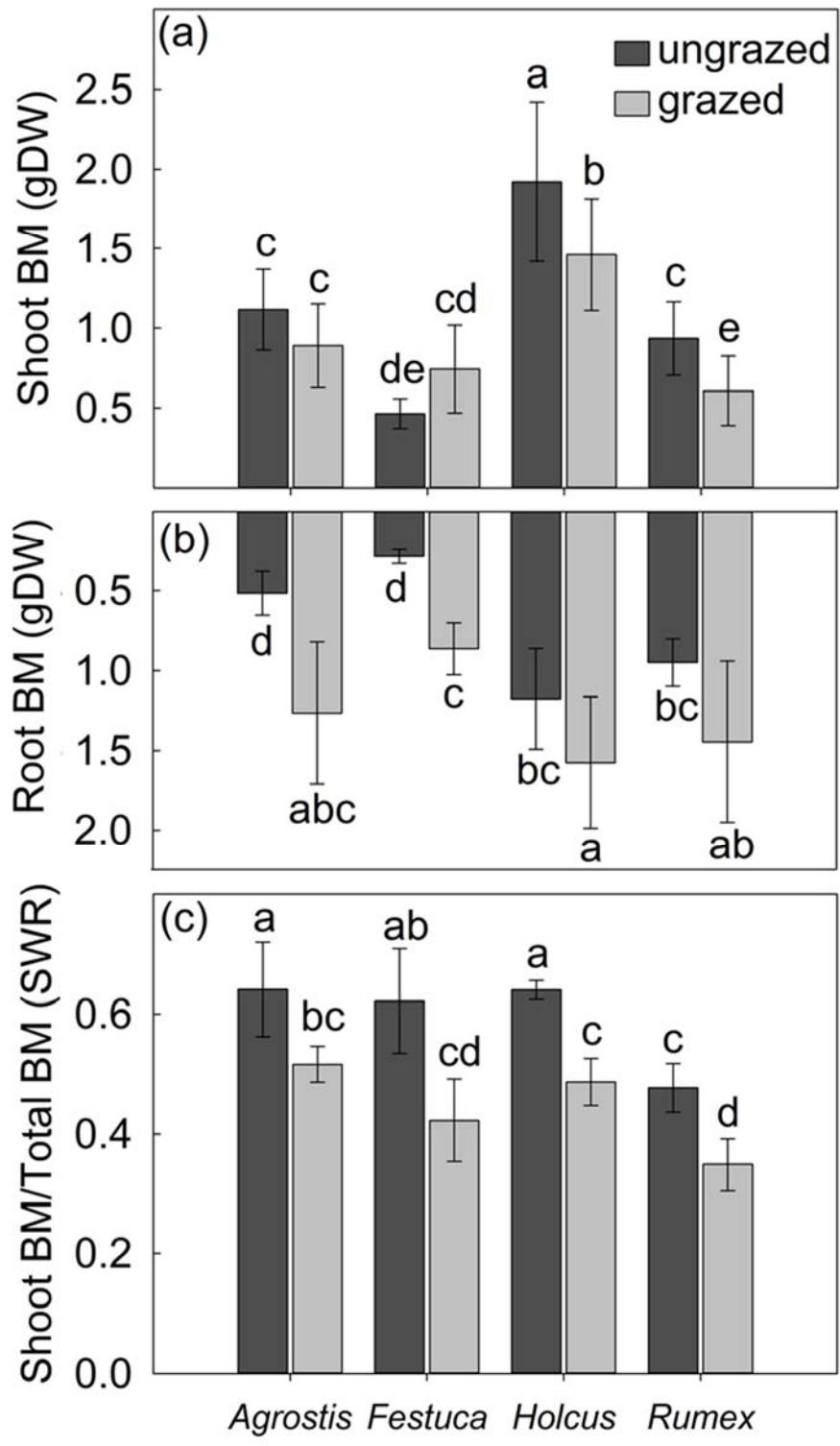
12 Fig 3. Temporal stability (average over all years/standard deviation over all years) for
13 the four dominant plant species in the different grazing treatments of the enclosure
14 experiment in the field. Bars show mean values (\pm SE). Different letters indicate
15 significant differences at $P < 0.05$.

16

17 Fig 4. Spatial stability (average over plots within a year/standard deviation over plots
18 within a year) for the four dominant plant species in the different grazing treatments
19 of the enclosure experiment in the field: (a) *Agrostis capillaris*, (b) *Festuca rubra*, (c)
20 *Holcus lanatus* and (d) *Rumex acetosa*. Dots show mean values (\pm SE).

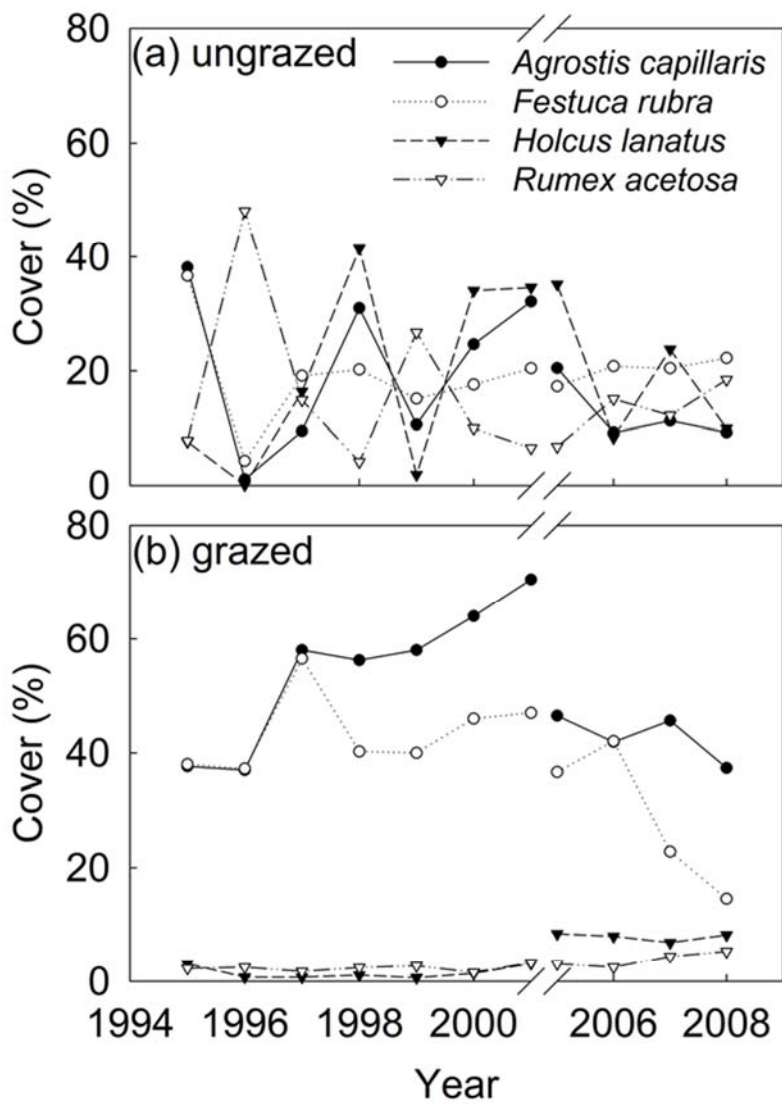
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1 Fig 1



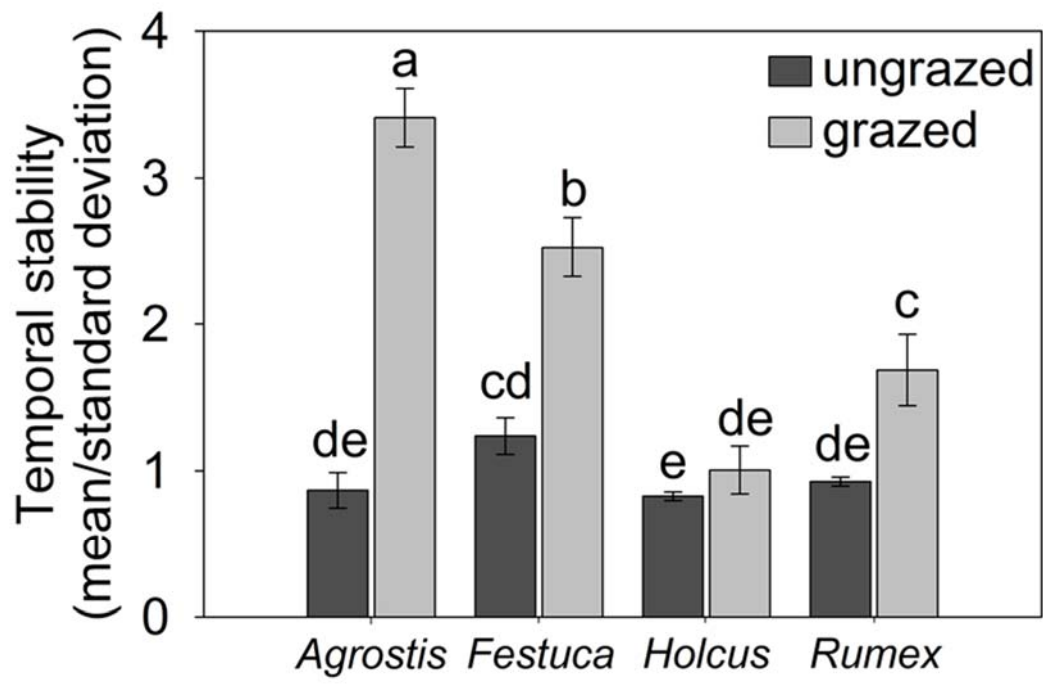
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1 Fig 2



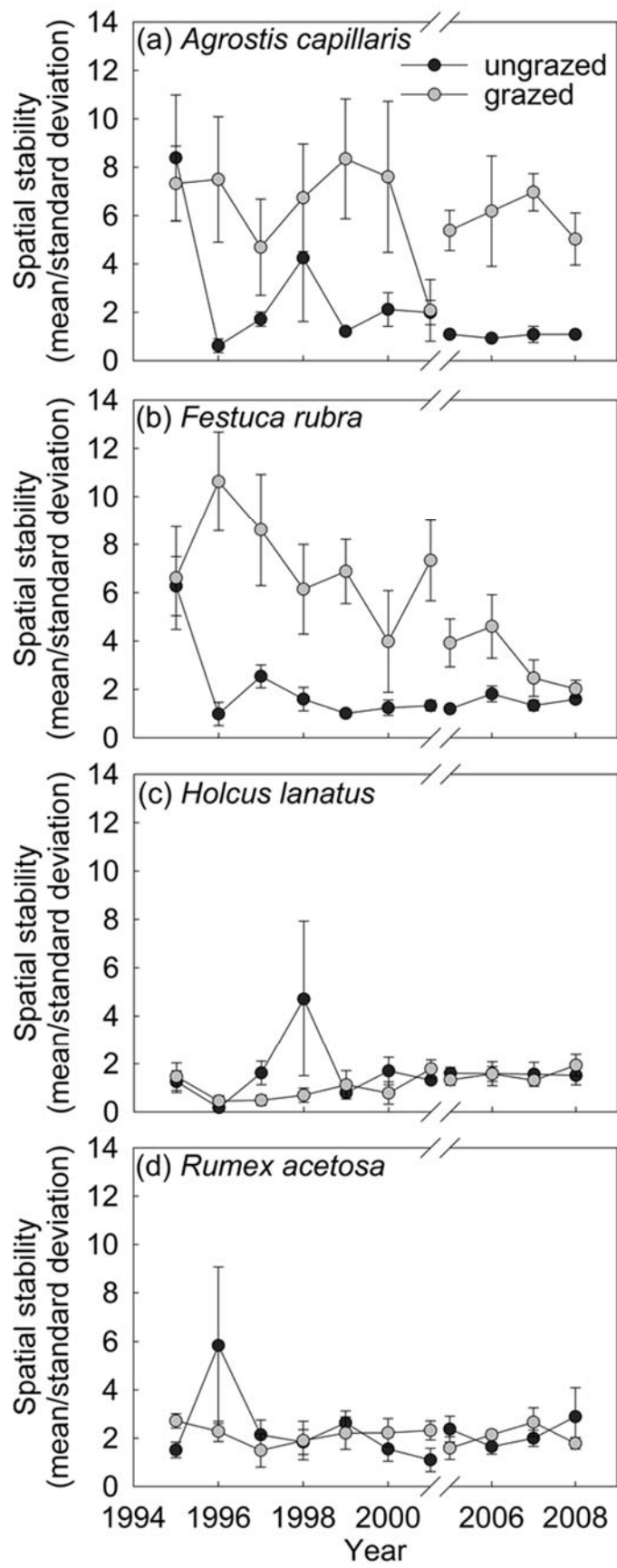
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1 Fig 3



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1 Fig 4



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