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1 **Effects of plant functional traits on soil stability: intraspecific variability matters**

2

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19 **Abstract**

20 *Background and Aims:* Soil stability is a key ecosystem function provided by agricultural
21 landscapes. A multitude of influential factors such as soil texture and plant community
22 structure have been suggested, but few studies compare the relative importance of these
23 factors for soil stability in the field. In addition, studies on effects of plant traits on soil
24 stability have ignored intraspecific trait variability (ITV) despite growing evidence of its
25 importance for ecosystem functioning.

26 *Methods:* Using path model analysis, we quantified the effect of plant functional traits (PFTs),
27 abiotic soil characteristics (soil texture) and vegetation characteristics on three soil stability
28 measures in 30 field margins of an agriculture landscape of Korea, comparing models with
29 and without ITV.

30 *Results:* Variance in soil stability was explained to varying degrees (from 81% for soil
31 aggregate stability to 35% for soil shear vane strength). The three soil stability measures were
32 mainly affected directly by root density, while PFTs and soil texture exerted indirect effects
33 through root density and vegetation parameters, respectively. Including ITV improved model
34 explained variance and goodness-of-fit in all cases.

35 *Conclusion:* The current study demonstrates that considering ITV is essential for uncovering
36 the substantial effect of plant functional community composition on a key ecosystem
37 function, soil stability.

38

39 **Keywords:** agricultural landscapes, community-weighted mean traits, intraspecific trait
40 variability, plant functional traits, response and effect traits, root density, soil stability.

41 **Introduction**

42 Understanding the processes that drive the degradation of ecosystem functions in agricultural
43 landscapes is of pivotal interest given ongoing land-use and climate change (Cardinale et al.
44 2012). Although ecosystem functions are strongly affected by the direct impact of these
45 abiotic drivers, it is also modulated by biotic factors (Loreau et al. 2001). A number of studies
46 has aimed at identifying the most important biotic drivers and it has been suggested that often
47 the functional composition of ecological communities is more important for the maintenance
48 of ecosystem functioning than species richness *per se* (Diaz et al. 2006; Laughlin 2014).

49 Different metrics of functional community composition can be measured in different ways.
50 Recent studies suggest that community weighted means of functional traits (CWM), obtained
51 by taking the mean trait value of a species weighted by its relative abundance in the focal
52 community and then summed over all species (Garnier et al. 2004), relate better to ecosystem
53 functioning than functional diversity metrics (Fortunel et al. 2009; Laughlin 2011). Even
54 though commonly applied (Díaz et al. 2007; Garnier et al. 2004) this metric has the problem
55 that it ignores intraspecific trait variability. However, intraspecific variability can be large and
56 is often not random but a result of adaptation or phenotypic plasticity of traits either along
57 environmental gradients (Sandquist and Ehleringer 1997), or a response to biotic interactions
58 (Albert et al. 2011; Gross et al. 2009). Intraspecific trait variability, thus, can strongly
59 influence the estimates of community trait composition (Jung et al. 2014). Consequently, it
60 has been strongly advocated to account for intraspecific variability when calculating CWMs
61 (Albert et al. 2010).

62 Here, we suggest studying community weighted means accounting for intraspecific trait
63 variability, in order to better understand how different abiotic variables, vegetation
64 characteristics and plant functional traits interact to influence an important ecosystem
65 function: soil stability. Soil stability refers to the ecosystem function of resistance to
66 disintegration when disturbed. Soil stability is critical for infiltration, root growth, and
67 resistance to water and wind erosion (Bronick and Lal 2005; Gyssels et al. 2005) and thus is a
68 crucial soil property affecting soil sustainability and crop production (Letey 1985). Soil
69 stability can be measured in the field by several methods. The most common are: (1) Soil
70 aggregate stability, which reflects how the soil aggregates react to precipitation, as the
71 unstable aggregates tend to produce a slaked soil layer when it gets wet, which causes
72 limitation in the infiltration rate, increasing the surface runoff and limiting the plant growth
73 (Tisdall and Oades 1982). (2) Soil penetration resistance, a composite soil property that is

74 governed by more basic properties, including soil cohesion, soil compressibility and
75 soil/metal friction (Dexter et al. 2007). Penetration resistance correlates with several other
76 important variables, such as root elongation rate (Taylor and Ratliff 1969). (3) Soil shear vane
77 strength, which measures the soil cohesiveness and resistance to shearing forces exerted by
78 gravity, moving fluids and mechanical loads (Morgan 2009). It reflects how the soil-root
79 matrix produces a type of reinforced earth, which is much stronger than the soil or the roots
80 separately and how this matrix can resist the environmental factors and human activities
81 (Simon and Collison 2001).

82 There are many factors that control soil stability via direct and indirect pathways. Particularly
83 important are abiotic soil characteristics such as soil texture and clay content (Chenu et al.
84 2011; Deneff and Six 2005), biotic vegetation characteristics such as species richness,
85 vegetation cover and plant diversity (Pérès et al. 2013; Pohl et al. 2009), and biotic functional
86 characteristics such as plant roots, soil fauna, and microorganisms (Gyssels et al. 2005). In the
87 following, we will shortly review the available literature on the interdependencies of these
88 different factors and will summarize them in a conceptual path model reflecting a hypothesis
89 on how abiotic and biotic factors interact and affect soil stability directly or indirectly (Fig. 1):
90 Abiotic soil characteristics (e.g. soil texture with clay and silt percentages) influence soil
91 stability directly. For example, fine soil particles (clay and silt) tend to increase, while coarse
92 particles (sand and gravel) decrease soil stability (Nearing et al. 1991; Tisdall and Oades
93 1982). They also influence vegetation characteristics (e.g. vegetation cover, species richness
94 and root density) and functional characteristics of plant communities, i.e. plant functional
95 traits (PFTs) such as root/shoot ratio, root length and root horizontal width (Lane et al. 1998).
96 Biotic vegetation characteristics also directly influence soil stability: Both above ground
97 vegetation characteristics such as higher species richness, plant cover, and species diversity
98 (Pérès et al. 2013; Pohl et al. 2012), as well as below ground vegetation characteristics, such
99 as higher root length, root density, and root length density (Hu et al. 2013; Pohl et al. 2009)
100 increase soil stability. The effect of vegetation characteristics on soil stability is due to
101 multiple processes. First, plant roots forming a dense root network bind soil particles via root
102 excretions (Gyssels et al. 2005; Traore et al. 2000). Secondly, a dense above ground
103 vegetation protects the soil surface from wind and rain drops (Gray and Sortir 1996). Thirdly,
104 a dense vegetation and root network enhances infiltration rates and reduces runoff (Tisdall
105 and Oades 1982). Plant cover and species diversity impact not only soil stability but also
106 species assembly in communities and thus the functional composition of communities
107 (Petchey and Gaston 2002). In return, it has been shown that vegetation characteristics and

108 root density depend strongly on the functional composition of communities (Reich et al.
109 2012). Finally, as argued before, species functional traits do not only respond to local abiotic
110 and biotic characteristics but they also play an important role in ecosystem functions. For soil
111 stability it has been shown that root length, root diameter and root horizontal width are
112 important determinants (Gyssels et al. 2005; Pohl et al. 2012).

113 The aim of this paper is to integrate vegetation characteristics and functional traits into a
114 model of abiotic soil characteristic effects on soil stability, towards an improved
115 understanding of ecosystem functioning. For this purpose we measure soil stability via soil
116 aggregate stability, soil penetration resistance and soil shear vane strength. First, we test how
117 well our conceptual model (outlined above and visualized in Fig. 1) fits data from field
118 margins in an agriculture landscape in Korea and how important intraspecific variability is for
119 this fit. Second, we investigate the importance of PFTs in comparison to the influence of
120 abiotic soil characteristics and biotic vegetation characteristics for soil stability. Finally, we
121 ask whether the identified functional effect traits are at the same time important functional
122 response traits. In other words, are the traits that determine the effect on ecosystem
123 functioning the same as those that determine the response of organisms to abiotic conditions
124 (Lavorel and Garnier 2002)?

125 **Materials and methods:**

126 Study site and experimental design:

127 The study was conducted in the Haean-myun catchment in South Korea, which is located in
128 the watershed of Soyang Lake close to the Demilitarized Zone (DMZ; 128°05' to 128°11' E,
129 38°13' to 38°20' N; Fig. 2). Elevation in the study site varies from 500 to 750 m a.s.l. The
130 mean annual air temperature is 10.5 °C, mean monthly temperature varies between -10 °C in
131 January and 27 °C in August (1999 - 2012). The average precipitation is 1,500 mm, with 70%
132 of the rain falling during the summer monsoon from June to August (Berger et al. 2013). The
133 area is subjected to very heavy rains during the monsoon season, which causes severe
134 damages to the soil, and thus soil stability is a very important ecosystem function.

135 Over the whole catchment, 30 plots of 1 m² were randomly chosen. In each plot, we estimated
136 (1) vegetation characteristics, (2) plant functional traits of in total 10 selected species, (3) soil
137 characteristics (excluding soil stability) and (4) measures of soil stability.

138

139 (1) Vegetation characteristics

140 In each plot, we estimated three different variables describing the vegetation characteristics:
141 vegetation cover (i.e. the percentage of ground covered by vegetation), species richness (i.e.
142 the number of observed species) and root density (estimated as percentage using a 30 cm x 30
143 cm metallic frame placed on the soil profile, following (Eckelmann 2006).

144

145 (2) Plant functional trait measurement and analyses

146 We measured above- and belowground plant functional traits (PFTs) for 15 individuals of the
147 10 most representative species in the study site (Table 1). The 10 most representative species
148 were chosen based on their abundance in an earlier intensive botanical survey we conducted
149 at the study site. To account for the community-level intraspecific variability of traits, we
150 collected individuals in the plots, with a maximum of 3 individuals per species per plot.

151 Depending on the distribution of the species, between 0 and 3 individuals of each species
152 were collected in each plot. Following this sampling design we finally had trait information
153 for an average of 51 % of the vegetation cover in the plots (min = 30% and max = 75%).

154 We collected the above- and belowground biomass of the 150 studied individuals. We
155 measured plant height (Cornelissen et al. 2003) and leaf size (Cornelissen et al. 2003) for the
156 aboveground compartment of each individual. We washed, dried, weighted and scanned the
157 roots of each individual in order to measure root horizontal width (Cornelissen et al. 2003;
158 Lobet et al. 2011), root length and diameter (Lobet et al. 2011), root dry mass (Cornelissen et
159 al. 2003), specific root length (SRL), which is the root length divided by the root dry weight
160 (Cornelissen et al. 2003), and root/shoot ratio (Monk 1966).

161 We then up-scaled functional properties to the community level using community weighted
162 means for each of the PFTs (Garnier et al. 2007; Lavorel et al. 2008; Violle et al. 2007). In
163 order to investigate the importance of intraspecific trait variability we used two different
164 CWM estimates, one that neglects intraspecific variability (CWM_{species}) and one that
165 integrates it at the level of each local community (CWM_j). To account for intraspecific
166 variability, we calculated the CWM_j within each plot based on the locally observed mean
167 species trait value and the species' relative cover:

168

$$170 \quad CWM_j = \sum_{i=1}^n p_{ij} * \text{trait}_{ij}$$

169

171 Where p_{ij} is the relative cover % of species (i) in the community plot (j) and trait_{ij} is the mean
172 trait value of species (i) in the community plot (j). To calculate CWM_{species} we used the
173 overall species mean trait value instead of the locally observed mean species trait value.

174

175 (3) Soil characteristic measurements and analyses (excluding stability):

176 In each plot, we estimated five different soil variables: Bulk density, water content,
177 wettability, clay % (i.e. percentage of clay), and silt % (i.e. percentage of silt). We randomly
178 sampled 30 cm deep soil profiles (from 0 to 30 cm) at each plot. For the bulk density, we took
179 three samples from the soil profile using soil rings with 2.8 cm diameter and 1 cm height. Soil
180 rings were weighted, oven-dried for 24 hours at 105°C and finally weighed again
181 (Avnimelech et al. 2001). Bulk density was calculated using the following equation:

$$182 \quad \text{Bulk density (g/cm}^3\text{)} = \text{dry sample weight} / \text{total sample volume}$$

183

184 The soil water content was calculated as the difference between the ring weight before and
185 after drying.

186 Soil wettability was assessed via the “water drop penetration time” (WDPT) (Letey 1969).
187 Droplets of distilled water were placed onto the surface of the soil sample and the time for
188 their complete infiltration was recorded. Measurements were replicated 10 times for each
189 sample, and then the mean value was used for our analysis.

190 Soil texture was expressed as clay % and silt %, following the standard sieve-pipette method
191 procedures as described by Gee and Bauder (1986); soil samples were first dispersed into
192 individual primary particles using hydrogen peroxide (H₂O₂) and sodium hexametaphosphate
193 4%, then the soil slurry was sieved through 0.63 mm, 0.2 mm and 0.063 mm sieves to
194 separate coarse, medium and fine sand fractions. The remaining suspension, containing
195 coarse, medium and fine silt and clay, was then transferred to a 1 liter cylinder and after
196 stirring a sample was taken using a 50 ml pipet at different time intervals depending on the
197 temperature, to sample the fine, medium and coarse silt and clay. After drying and weighting
198 the samples, % pipetted fraction was calculated as:

199

200 % pipetted fraction = (weight of the oven dry fraction / weight of the original sample) x 100

201

202 In addition, we used the soil profiles to estimate root density (a variable describing vegetation
203 characteristics, see above).

204

205 (4) Soil stability measurements

206 The plot specific soil cores were also used to estimate variables of soil stability. We
207 considered three different and commonly used variables: soil aggregate stability, penetration
208 resistance and soil shear vane strength. We used the modified wet sieving method by (Haynes
209 1993) to measure soil aggregate stability, based on one surface soil sample per plot. In this
210 method 100g of the air-dried 24mm soil aggregates were transferred to the uppermost of a set
211 of five sieves with apertures ranging from 0.05 to 2 mm. Then the sieves’ set were transferred
212 to a water-path where the oscillation rate was 2.5 cycles per minute and the amplitude of the
213 sieving action was 3.5 cm for 15 min. Then the sieves were oven dried at 105°C for 24 hours
214 and the remaining aggregates at each sieve were weighted and the mean weight diameter
215 (MWD) was calculated as follows:

216

$$\text{MWD} = \sum w_i * x_i$$

217

218 Where i corresponds to each fraction collected, w_i is the dry weight of the fraction collected
219 relative to the total soil used and x_i is the mean diameter of the fraction collected.

220 In each of the 30 plots, we measured soil penetration resistance (kg/cm^2) using a EW-99039-
221 00 pocket penetrometer (Cole-Parmer Cole-Parmer Instrument Company, Vernon Hills, IL.,
222 USA). Measurements of penetration resistance were replicated three times for each plot and
223 the average value of them was included in the models.

224 For measuring soil shear vane strength (kPa), we used a shear vane with a height of 80 mm
225 and a diameter of 40 mm with three measures per plot. Shear strength was calculated using
226 the following equation:

227

$$\tau_f = \frac{T}{2\pi r_v^2 \left(\left(\frac{2}{3} \right) r_v + h \right)}$$

228

229 Where τ_f is the shear strength of the soil, T is the maximum torque at failure, h is the height of
230 the vane and r_v is the diameter of the vane (Richards 1988). Three replicate measurements
231 were made at each plot and the average value was used in the models.

232

233 Statistical Analyses:

234 The aim of our study was to evaluate our conceptual path model on the influence of
235 vegetation characteristics, soil characteristics and PFTs on soil stability that we developed in
236 the introduction (Fig. 1) with our data. Towards this aim path analyses were performed
237 independently for the three measures of soil stability.

238 In a first step, owing to the demanding field protocol of measuring intraspecific trait
239 variability, which resulted in a limited sample size, we reduced the number of variables
240 measured to describe vegetation characteristics, soil characteristics and PFTs. As suggested
241 by Wilson and Nussey (2010), variable selection was based on a redundancy analysis (RDA),
242 which allowed us to choose those variables and traits that showed a significant relation to soil
243 stability. We performed this independent pre-variable selection in order to obtain a common
244 set of variables for all three soil stability measures and thus for all three independent path
245 analyses.

246 In a second step, we fitted the conceptual path model with all remaining variables based on a
247 Partial Least Squares Path Modeling (PLS-PM) approach. Model evaluation of PLS-PMs was
248 based on the R^2 coefficient for the soil stability measure and the overall model goodness-of-fit

249 (GoF) index. All statistical analyses were done using R, version 3.1.0 (R Development Core
250 Team 2013), with package *PLSPM* (Sanchez et al. 2013) for the path analysis, the RDA was
251 done using R package *vegan* (Oksanen et al. 2013).

252 **Results**

253 We found large intraspecific trait variability within the measured traits (Fig. S1). Species
254 mean values ranged from 0.06 to 0.47 for root/shoot ratio (Fig. S1a), from 13.00 to 28.55 cm
255 for root length (Fig. S1b), and from 3.44 to 18.25 cm for root horizontal width (Fig. S1c).

256 According to the RDA (Table 2), the vegetation variables that best describe soil stability were
257 “vegetation cover percentage, species richness and root density”. For the soil characteristics,
258 the soil texture variables “silt and clay percentages” were most important and for the PFTs
259 “root/shoot ratio, root horizontal width and root length”. We kept these variables in the
260 following PLS-PM approaches, which we describe independently for the three variables of
261 soil stability.

262 We fitted of our conceptual path model to data either by ignoring intraspecific trait variability
263 (using $CWM_{species}$ as metrics for the PFTs) or by accounting for it at the scale of the
264 communities (using CWM_j as metrics for the PFTs).

265 Ignoring intraspecific trait variability resulted in lower quality performance of our path
266 models; the explained variance was 79%, 49% and 35% for aggregate stability, penetration
267 resistance and shear vane strength, respectively, and goodness-of-fit was 0.45, 0.41 and 0.38
268 (see Table S1; Figs. S2, S3). Direct and indirect effects of PFTs on soil stability were
269 negligible (with standardized path coefficients, spc , 0.16, 0.09 and -.03 for the three stability
270 measures). We therefore decided only to present the results of the models accounting for
271 intraspecific variability in more detail.

272

273 Soil aggregate stability (models accounting for intraspecific variability):

274 Our conceptual path model explained 81% of the variance of soil aggregate stability with a
275 goodness-of-fit index of 0.58 (Fig. 3a). Root density and vegetation cover were the most
276 important factors that directly affected soil aggregate stability (with standardized path
277 coefficients, spc , of 0.55 and 0.26 respectively), while the indirect effects of soil texture and
278 the PFTs on soil aggregate stability resulted in the highest total effects (with spc equal to 0.66
279 and 0.50 respectively, Table S2; Fig. 4a). The high total effects of soil texture resulted from
280 the strong direct effects of soil texture on PFTs and vegetation cover (and partly on species
281 richness, which had a moderate effect on soil aggregate stability), while the high total effects
282 of PFTs resulted from their strong link to root density which itself had a strong influence on

283 soil aggregate stability. Moreover, PFTs were significantly affected by soil texture and
284 species richness.

285 The crossloading effects that allow differentiating between the different PFTs (i.e. root/shoot
286 ratio, root length and root horizontal width) (Fig. 5a) showed that the root/shoot ratio has the
287 strongest effect on soil aggregated stability ($spc = 0.72$) followed by root length ($spc = 0.54$)
288 and root horizontal width ($spc=0.52$, Fig. 5a). The silt and clay percentages had similar effects
289 on soil aggregated stability (with spc equal to 0.65 and 0.60 respectively).

290

291 Penetration resistance (models accounting for intraspecific variability):

292 For the soil penetration resistance, our conceptual path model explained 50% of the variance
293 with a goodness-of-fit index of 0.54 (Fig. 3b). Root density and soil texture were the most
294 important factors that directly affected soil aggregate stability (with standardized path
295 coefficients, spc , of 0.58 and 0.44 respectively), while PFTs showed the strongest indirect
296 effect on penetration resistance (with spc equal to 0.30, Table S2; Fig. 4b). These strong
297 indirect effects of PFTs resulted from their strong link to root density which itself had a strong
298 influence on soil penetration resistance. As in the soil aggregate stability model, PFTs were
299 significantly affected by soil texture and species richness.

300 The crossloading effects showed a slightly different order of relative importance of the
301 different PFTs (Fig. 5b) than in the soil aggregate stability model: For soil penetration
302 resistance, root length (and not root/shoot ration) was most important ($spc = 0.51$) followed
303 by root/shoot ration ($spc = 0.48$) and root horizontal width ($spc = 0.20$, Fig. 5b). The silt and
304 clay percentages showed the same trends as in the soil aggregate stability model ($spc = 0.54$
305 and 0.53 respectively).

306

307 Soil shear vane strength (models accounting for intraspecific variability):

308 In the soil shear vane strength model, 35% of the variance was explained, with a goodness-of-
309 fit index of 0.52 (Fig. 3c). Root density was the most important factor that directly affected
310 soil aggregate stability ($spc = 0.54$), while the indirect effects of soil texture and PFTs on
311 shear vane strength had the highest total indirect effects ($spc = 0.52$ and $spc = 0.22$,
312 respectively, Table S2; Fig. 4c). Soil texture had a strong direct effect on PFTs and species
313 richness. PFTs showed a strong relation to root density which itself had a strong influence on

314 shear vane strength. As before, PFTs were significantly affected by soil texture and species
315 richness.

316 The crossloading effects were comparable to those in the penetration resistance path model
317 (Fig. 5c), as both the root/shoot ratio and root length were most important (spc = 0.43 and
318 0.40 respectively), while the root horizontal was much less important (spc = 0.10). As before,
319 silt and clay percentages were equally important (spc = 0.47 and 0.40 respectively).

320 Overall, we found that ignoring intraspecific trait variability resulted in lower fit for our
321 conceptual model to the data. Accounting for intraspecific variability, the three components of
322 soil stability were either moderately (soil shear vane strength, soil penetration resistance) or
323 well (soil penetration resistance) explained by our conceptual path model. In all three
324 analyses, root density had the strongest direct effect on soil stability. Accounting in addition
325 for indirect effects, we could show that PFTs had a similarly strong influence, which was
326 mostly mediated by root density. The most important PFTs were root length and the
327 root/shoot ratio. PFTs themselves were strongly affected by species richness and soil texture.

328 **Discussion:**

329 Our study is one of the few to investigate the combined influence of plant functional traits
330 (PFTs), vegetation characteristics and abiotic soil characteristics on ecosystem functioning in
331 the field. We built a conceptual path model to disentangle the different abiotic and biotic
332 drivers of soil stability as one of the important ecosystem functions impacting erosion control
333 and nutrient supply in agriculture landscapes. We confronted this model with data collected in
334 field margins in South Korea. Results highlight the important effect of the functional
335 composition of communities on soil stability. Notably, this effect could only be seen when
336 considering intraspecific variability in PFTs.

337

338 Explained variation in soil stability

339 Our conceptual model hypothesizes that soil stability is not only strongly influenced by
340 abiotic variables (e.g. soil structure) and vegetation structure (e.g. cover, species richness) but
341 also by the functional composition of plant communities. Overall, our data from South
342 Korean field margins support this hypothesis.

343 When intraspecific trait variability was considered, the conceptual model explained moderate
344 to large parts of the variation in the three considered measures of soil stability. Aggregated
345 stability was best explained (81%) followed by penetration (50%) and shear strength (35%).
346 In comparison, goodness-of-fit values were not very high (0.52-0.58), a result that is due to
347 the relative low sample size resulting from the considerable practical challenge posed by the
348 indispensability of accounting for intraspecific variability in trait compositions.

349 The three measures of soil stability quantify different facets of soil stability: Aggregate
350 stability has a strong influence on infiltration rate and surface runoff (Gyssels et al. 2005);
351 penetration resistance strongly influences root elongation rates (Dexter et al. 2007), and is
352 further related to retention, erosion, crusting and nutrient cycling (Bronick and Lal 2005;
353 Chapman et al. 2012); finally, soil shear strength influences the resistance of the soil-root
354 matrix to disturbances (Simon and Collison 2001), erosion (Morgan 1996), and crushing
355 (Gyssels et al. 2005). While the amount of variation explained by our models differed across
356 these three facets of soil stability, the models were largely congruent in the attribution of
357 relative importance to soil texture, root density, and, notably, the role of intraspecific
358 variability in PFTs, emphasizing the robustness of our results.

359 Importance of plant functional traits and intraspecific variability

360 One of our most striking results is that fitting the conceptual model with average trait data
361 (i.e. ignoring intraspecific trait variability) led to poor model performance. Especially, the
362 effect of functional plant community composition on the different components of soil stability
363 was strongly underestimated when ignoring intraspecific variability. In addition we found that
364 even though species significantly differ in their mean trait values, intraspecific trait variation
365 is large and trait distributions of different species overlap (see supplementary material, Fig.
366 S1). Together these results imply that soil stability is significantly influenced by functional
367 plasticity of plants.

368 The abiotic variable soil texture was the most important variable in our model. The fine
369 particles of the soil texture (clay and silt) improve soil stability (Chenu et al. 2011; Nearing et
370 al. 1991; Tisdall and Oades 1982). It has been currently suggested that this positive effect is
371 rather due to the electrostatic bonds or physical forces (Arvidsson and Keller 2011; Deneff and
372 Six 2005), than due to organic cementing agents (Six et al. 2000). Functional community
373 composition and root density had very strong impacts as well. Root/shoot ratio, root length
374 and root horizontal width influenced all components of soil stability strongly and mostly via
375 their impacts on root density. The effect of root/shoot ratio, root length or root horizontal
376 width is mediated via root density due to its role in (1) microbial community compositions in
377 the rhizosphere which in turn supports soil stability (Gyssels and Poesen 2003), (2) in
378 reducing soil porosity (Graf and Frei 2013; Pérès et al. 2013; Pohl et al. 2009), and (3)
379 binding soil particles together via root exudates and mucilage (Eisenhauer et al. 2010; Pojasok
380 and Kay 1990; Traore et al. 2000).

381 Interestingly, the effect of PFTs on soil stability via root density is much more important than
382 the effects of species richness and partly vegetation cover, a result that is in concordance with
383 recent literature (Graf and Frei 2013; Pérès et al. 2013). Species richness did not directly
384 affect soil stability at all but affected root density and PFTs. The impact of vegetation cover
385 was overall small. Our results highlight, the importance of not only abiotic but also biotic
386 variables for soil stability. The most important biotic variables are strongly related to
387 ecosystem functioning.

388 To our knowledge, this is the first field study to demonstrate the key role of plant functional
389 traits in soil stability, while accounting for intraspecific trait variability. Soil stability of field
390 margins is of particular relevance for agricultural landscapes subjected to extreme heavy rains
391 during the monsoon season, as it contributes to the control of soil erosion and nutrient

392 cycling. Our results further corroborate the notion that ecosystem functions (e.g. soil stability)
393 are related to the functional composition of the community rather than species diversity *per se*
394 (Díaz and Cabido 2001).

395

396 Effect vs. response traits

397 In our analyses we first selected effect traits that related well to soil stability. The integration
398 of these effect traits into our conceptual model allowed us then to evaluate if the same traits
399 well described responses to abiotic conditions. Results showed a strong influence of soil
400 texture on PFTs. Consequently we can conclude that root/shoot ratio, root length and root
401 horizontal width, are at the same time important response and effect traits.

402 Our results suggest that understanding the response of plant communities to abiotic conditions
403 benefits from accounting for plant phenotypic plasticity. High plant phenotypic plasticity in
404 response and effect traits renders the challenge of managing field margins more difficult and
405 simpler; more difficult, because management is difficult to optimize when targeting species
406 based on their mean traits is not likely to work, and simpler, because management will be
407 robust when several target species can provide the same required effect traits.

408

409 Conclusion

410 Our study demonstrates the important role of intraspecific trait variability not only in
411 responses of plant communities to changing conditions but also in their effect on key
412 ecosystem functions. Results corroborate for an important specific example (soil stability in
413 agricultural landscapes) earlier findings suggesting that the functional trait composition of
414 communities can be much more important for ecosystem functioning than vegetation cover or
415 species richness. These findings have important implications for managing field margins in
416 order to improve soil stability as communities should not only be enriched by species with
417 favorable root traits but it should also be considered that species show important plasticity in
418 their root traits.

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424 and suggestions on our field protocol and soil analyses and John Tenhunen for his comments
425 and coordination of the TERRECO fieldwork.

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592 **Table legends**

593 Table 1. Above and below ground characteristics of the ten plant species studied in Haean-myun
594 catchment.

595

596 Table 2. RDA results between the three stability measures and the vegetation and soil parameters and
597 PFTs.

598

Name	Family	Duration	Life Form	Height (cm)	Root / shoot ratio	Root length (cm)	Root diameter (cm)	Root horizontal width (cm)	Specific root length	Leaf size (cm ²)
<i>Artemisia princeps</i> Pamp.	Asteraceae	Perennial	Phanerophytes	88.03 (11.80)	0.24 (0.07)	20.55 (5.41)	0.24 (0.03)	18.25 (1.98)	14.03 (7.70)	75.28 (28.72)
<i>Chelidonium majus</i> var. <i>asiaticum</i> (Hara) Ohwi	Papaveraceae	Annuals or biennials	Phanerophytes	83.07 (15.97)	0.12 (0.03)	19.41 (5.90)	0.23 (0.05)	10.77 (4.96)	13.38 (12.31)	99.83 (37.56)
<i>Conyza canadensis</i> (L.) Cronquist	Asteraceae	Annual	Therophyte	69.07 (11.25)	0.22 (0.05)	18.46 (3.60)	0.15 (0.03)	14.79 (5.72)	8.19 (4.99)	22.22 (4.65)
<i>Equisetum arvense</i> L.	Equisetaceae	Perennial	Geophyte	30.27 (9.45)	0.38 (0.13)	22.12 (7.33)	0.17 (0.03)	3.44 (3.39)	89.07 (61.27)	2.28 (0.69)
<i>Erigeron strigosus</i> Muhl.	Asteraceae	Annuals or biennials	Phanerophytes	82.53 (14.52)	0.26 (0.11)	15.11 (4.77)	0.04 (0.03)	13.87 (4.20)	15.73 (12.54)	24.68 (14.81)
<i>Humulus japonicus</i> Sieboid & Zucc.	Cannabaceae	Annual	Therophyte	88.00 (9.77)	0.07 (0.03)	18.57 (7.29)	0.04 (0.01)	4.19 (2.56)	120.52 (87.10)	108.40 (49.98)
<i>Oenothera biennis</i> L.	Onagraceae	Biennial	Hemicryptophyte	81.07 (17.51)	0.19 (0.0)	28.55 (9.31)	0.33 (0.11)	18.25 (8.36)	6.85 (5.60)	39.24 (11.87)
<i>Persicaria vulgaris</i> Webb & Moq.	Polygonaceae	Annual	Therophyte	38.60 (18.02)	0.14 (0.06)	13.00 (4.12)	0.14 (0.19)	7.39 (4.51)	49.33 (31.65)	27.98 (12.99)
<i>Phragmites japonica</i> Steud.	Poaceae	Perennial	Phanerophytes	77.8 (25.61)	0.48 (0.25)	24.25 (10.43)	0.11 (0.04)	13.06 (4.56)	19.12 (13.51)	52.11 (26.88)
<i>Rorippa palustris</i> (Leyss.) Besser	Brassicaceae	Annual	Therophyte	50.47 (13.8)	0.16 (0.08)	15.55 (5.32)	0.08 (0.02)	7.89 (4.29)	24.63 (13.57)	25.91 (17.12)

601 Values are means with standard deviation in parentheses.

602 **Table 2.**
603

Vegetation parameters	RDA 1 (46.2%)	RDA 2 (1.2%)
Vegetation Cover	-0.453	-0.802
Species richness	-0.680	-0.243
Root density	-0.960	0.278
Soil parameters	RDA 1 (42.9%)	RDA 2 (1.4%)
Bulk density	-0.399	-0.322
Water content	-0.225	-0.691
Wettability	-0.332	-0.595
Clay %	-0.794	0.427
Silt %	-0.857	0.295
Plant functional traits	RDA 1 (49.5%)	RDA 2 (3.9%)
Plant height	-0.540	0.180
Root/shoot ratio	-0.790	-0.463
Root length	-0.544	0.265
Root diameter	0.225	-0.598
Root horizontal width	-0.372	-0.656
Specific root length	-0.087	0.575
Leaf size	0.110	0.452

604

605

606 **Figure legends**

607 Fig. 1. A conceptual path model for effects of the abiotic soil characteristics (soil texture “silt % and
608 clay%”), vegetation characteristics (vegetation cover, species richness and root density) and PFTs (RSR =
609 root/shoot ratio, RL = root length and RW = root horizontal width) on three soil stability measures (Soil
610 aggregate stability, soil penetration resistance and soil shear vane strength). Numbers on arrows indicate
611 previous studies that support the path. 1. Lane et al. (1998), 2. Deneff and Six (2005), 3. Petchey and
612 Gaston (2002), 4. Pohl et al. (2009), 5. Reich et al. (2012), 6. Pérès et al. (2013) and 7. Gysels et al.
613 (2005).

614

615 Fig. 2. The 30 sampling plots for the plant functional traits in Haean-myun catchment.

616

617 Fig. 3. The path models outputs for the effects of the soil texture “silt % and clay%”, vegetation cover,
618 species richness, root density and PFTs “root/shoot ratio, root length and root horizontal width” with
619 accounting for the intraspecific trait variability, on three soil stability measures. (a) soil aggregate stability
620 (b) penetration resistance and (c) soil shear vane strength. Numbers on arrows are standardized path
621 coefficients. Solid arrows are positive and dashed are negative, bold arrows indicate significant
622 standardized paths ($P < 0.05$); thin arrows indicate non-significant path coefficient ($P > 0.05$). Percentages
623 close to the boxes indicate the variance explained by the model (R^2). The goodness-of-fit indices for the
624 models are 0.58 for (a), 0.54 for (b) and 0.52 for (c).

625

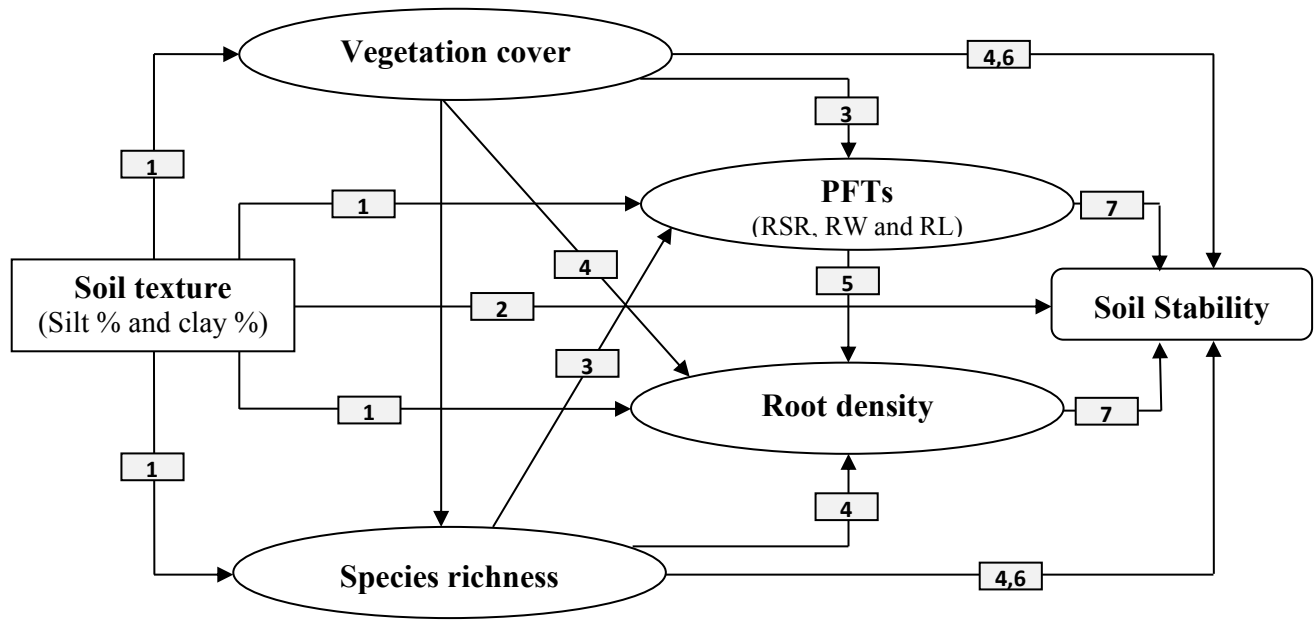
626 Fig. 4. The standardized path coefficient for direct and indirect effects of PFTs “root/shoot ratio, root
627 length and root horizontal width”, root density, soil texture “silt % and clay%”, species richness and
628 vegetation cover on (a) soil aggregate stability, (b) soil penetration resistance and (c) soil shear strength.

629

630 Fig. 5. The path model crossloadings effect of the soil texture “silt and clay contents” and PFTs
631 “root/shoot ratio, root length and root horizontal width” on (a) soil aggregate stability, (b) soil penetration
632 resistance and (c) soil shear strength.

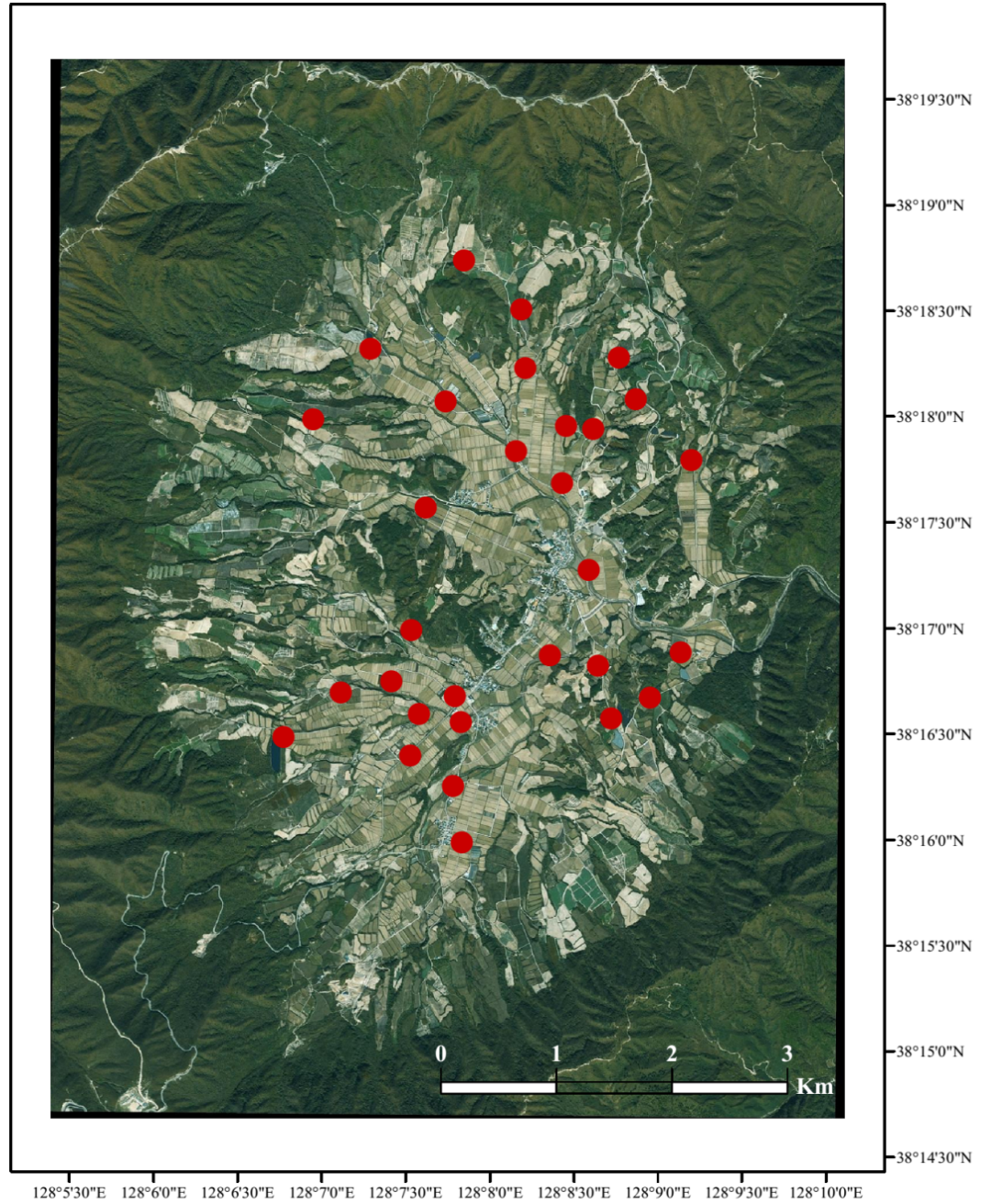
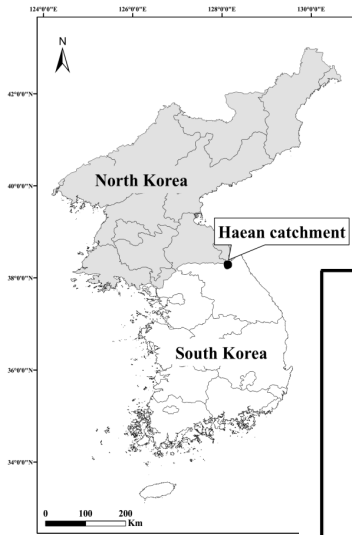
633

634 Fig. 1.
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636



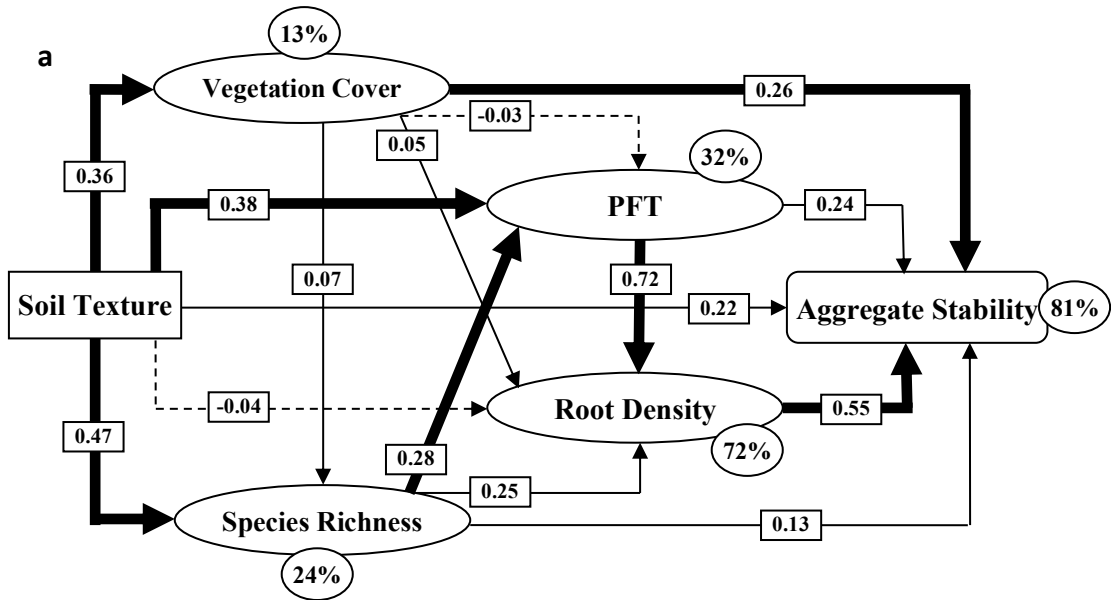
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639 Fig. 2.
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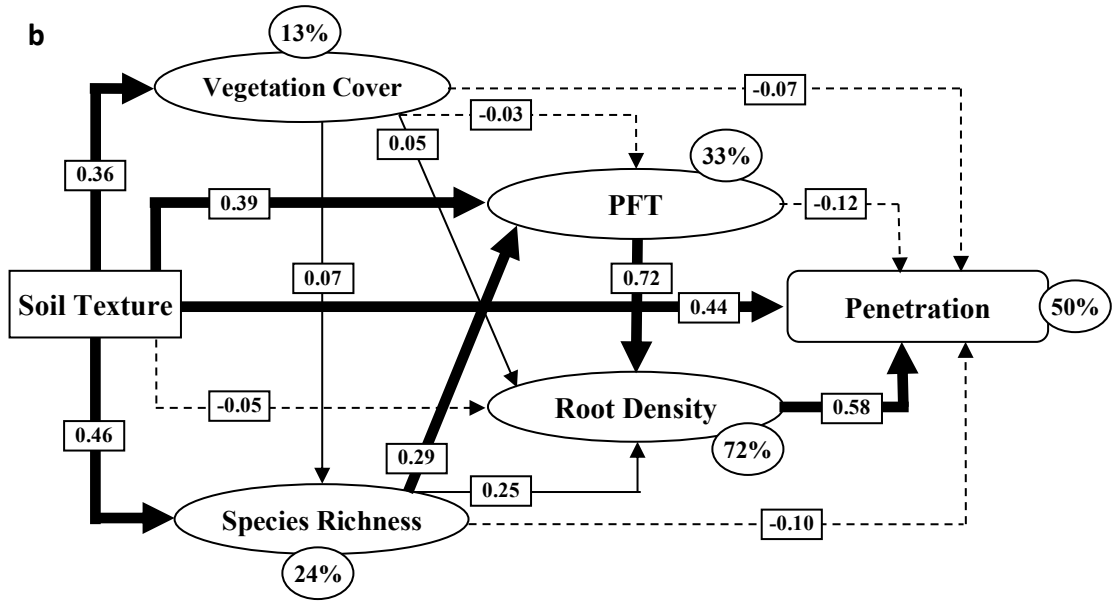
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642 Fig. 3.
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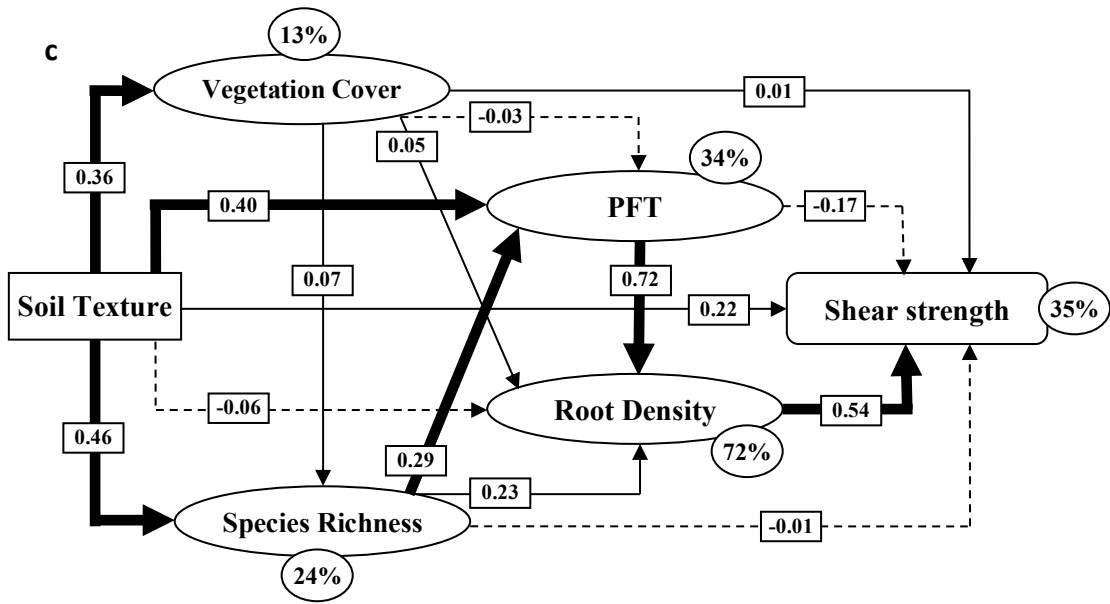


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646 Fig. 3 (cont.).
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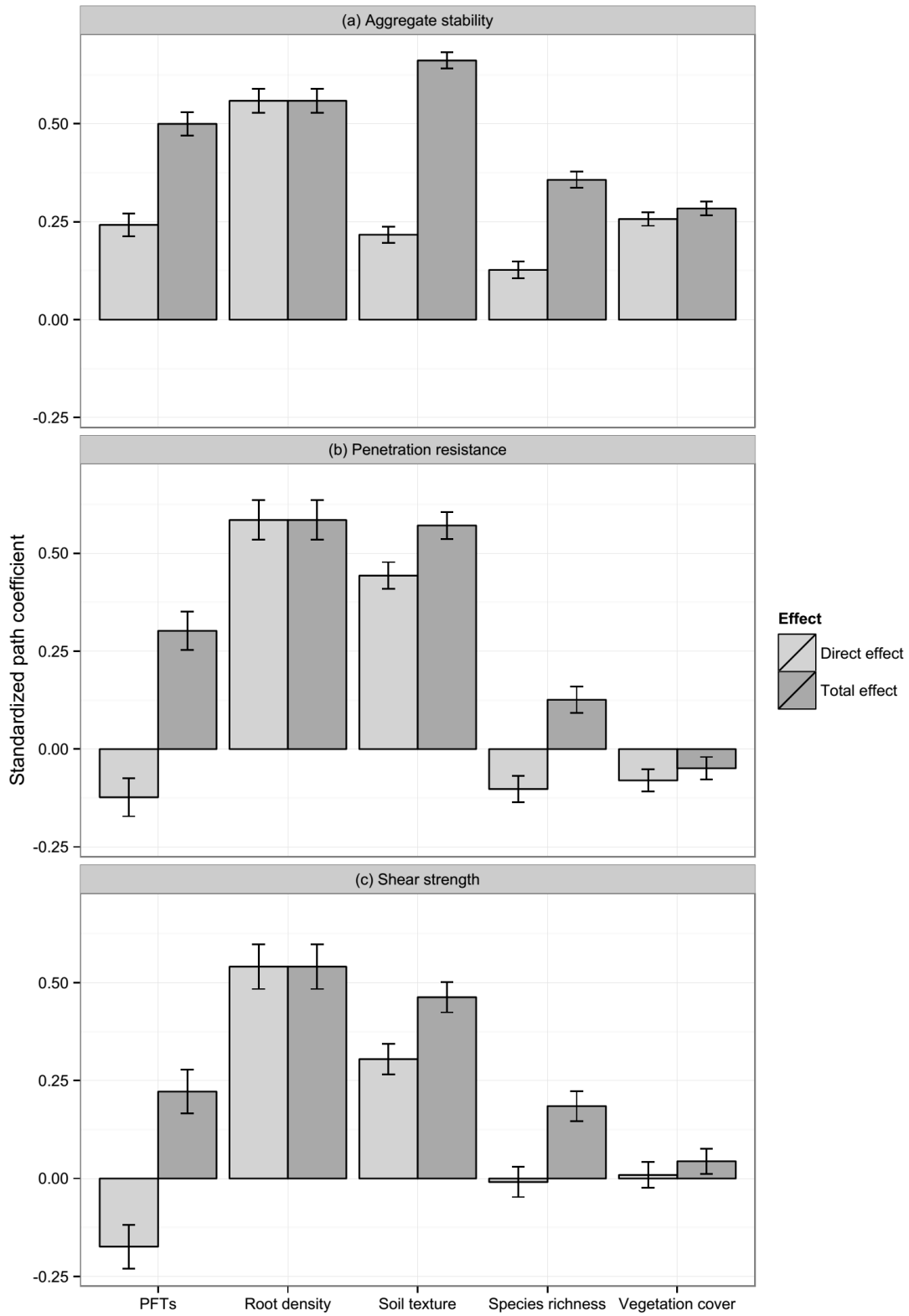


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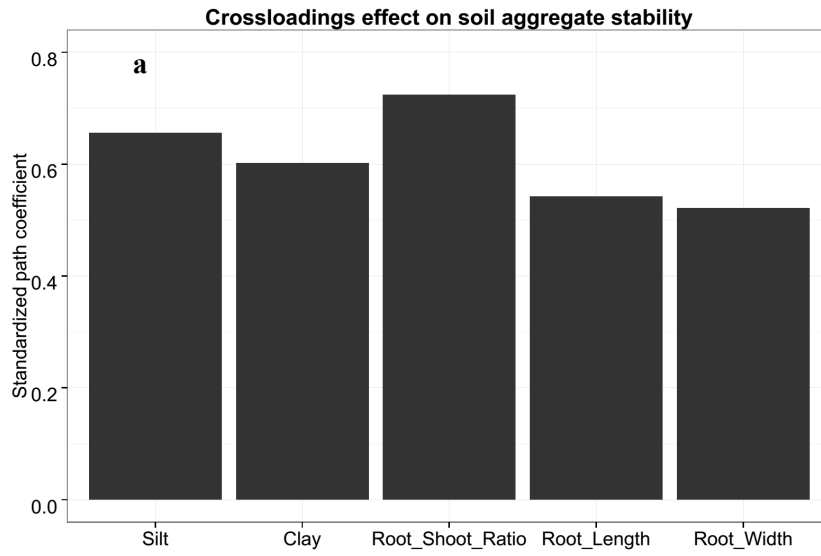
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 652

653 Fig. 4.

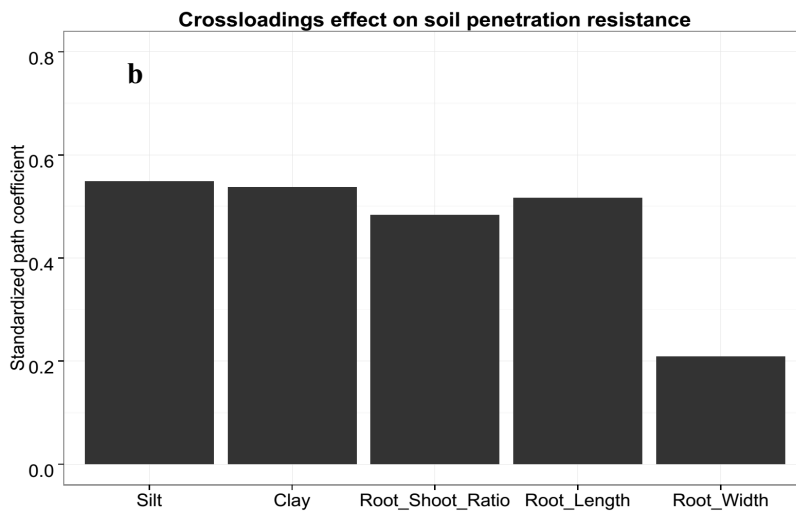


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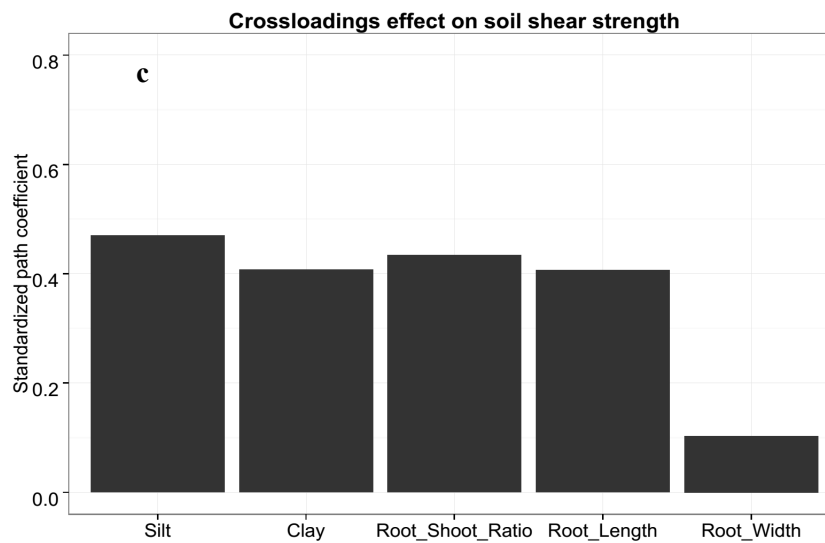
655 Fig. 5.



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