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1 **Ecological intensification and arbuscular mycorrhizas: a meta-analysis of tillage and cover**
2 **crop effects**

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12 **Abstract**

13 1. Reliance on ecosystem services instead of synthetic, non-renewable inputs is increasingly seen
14 as key to achieving food security in an environmentally sustainable way. This process, known as
15 ecological intensification, will depend in large part on enhancing belowground biological
16 interactions that facilitate resource use efficiency. Arbuscular mycorrhizas (AM), associations
17 formed between the roots of most terrestrial plant species and a specialized group of soil fungi,
18 provide valuable ecosystem services, but the full magnitude of these services may not be fully
19 realized under conventional intensively-managed annual agricultural systems.

20 2. Here we use meta-analysis to assess how reducing soil disturbance and periods without roots
21 in agricultural systems affects the formation of AM and the diversity and community
22 composition of arbuscular mycorrhizal fungi (AMF). We compiled data from 54 field studies
23 across five continents that measured effects of tillage and/or cover cropping on AMF
24 colonization and/or communities and assessed effects of management and environmental factors
25 on these responses.

26 3. Less intensive tillage and winter cover cropping similarly increased AMF colonization of
27 summer annual cash crop roots by ~30%. The key variables influencing the change in AMF
28 colonization were the type of cover crop or the type of alternative tillage, suggesting that farmers
29 can optimize combinations of tillage and cover crops that most enhance AM formation,
30 particularly with no-till systems and legume cover crops.

31 4. Richness of AMF taxa increased by 11% in low-intensity vs. conventional tillage regimes.
32 Several studies showed changes in diversity and community composition of AMF with cover
33 cropping, but these responses were not consistent.

34 *Synthesis and applications.* This meta-analysis indicates that less intensive tillage and cover
35 cropping are both viable strategies for enhancing root colonization from the indigenous AMF
36 community across a wide range of soil types and cash crop species, and possibly also shifting
37 AMF community structure, which could in turn increase biologically-based resource use in
38 agricultural systems.

39

40 **Introduction**

41 Steady increases in crop yields since the Green Revolution have come at substantial
42 environmental cost (Pingali 2012). Any further increases in yields must not further erode the
43 natural capital upon which agriculture relies, especially in times of environmental change, and
44 must minimize negative effects on ecosystem sustainability. Increasing reliance on supporting
45 and regulating ecosystem services instead of synthetic inputs, i.e. ecological intensification, is
46 increasingly seen as one way of achieving food security in an environmentally sustainable way
47 (Jackson *et al.* 2012; Bommarco, Kleijn & Potts 2013). Ultimately, this will depend in large part
48 on enhancing below-ground biological interactions that facilitate resource use efficiency
49 (Jackson *et al.* 2012; Bender, Wagg & van der Heijden 2016).

50 Crops take up approximately only half of the nutrients in applied inorganic fertilizers, with the
51 remainder at risk of being lost from agroecosystems (Robertson & Vitousek 2009). These losses
52 have widespread and serious consequences for climate change, biodiversity, and human health
53 (Erisman *et al.* 2014). Plants have evolved many traits for optimizing nutrient acquisition and
54 utilization (Hodge 2004; York, Nord & Lynch 2013; Lambers, Martinoia & Renton 2015),
55 including the formation of arbuscular mycorrhizas (AM), associations between the roots of most
56 terrestrial plant species and a specialized group of soil fungi (Smith & Read 2008). Arbuscular
57 mycorrhizas also provide valuable ecosystem services beyond nutrient acquisition, such as
58 increasing nutrient retention (Cavagnaro *et al.* 2015), plant drought resistance (Augé, Toler &
59 Saxton 2015), and soil structure formation (Rillig & Mummey 2006). But the full magnitude of
60 these services are often not fully realized in intensively-managed, annual agricultural systems
61 (Gosling *et al.* 2006). High rates of soil disturbance and long periods when roots are not present

62 limit the formation of AMs, due to life history characteristics of these obligate biotrophs (Smith
63 & Read 2008), which depend on carbon (C) from roots to grow and reproduce. A prior meta-
64 analysis (Lekberg & Koide 2005), including both field and greenhouse studies, showed that
65 reducing soil disturbance and shortening fallow periods does increase AMF colonization. But
66 inconsistent results from field studies included in that analysis and many more recent ones (e.g.
67 Duan et al., 2010; Gavito and Miller, 1998; Higo et al., 2014; White and Weil, 2010) point to a
68 need to assess how the wide variety of conditions (e.g. soil type, crop species, soil P status)
69 across these studies influence AM responses.

70 The composition and diversity of arbuscular mycorrhizal fungal (AMF) communities is
71 increasingly recognized as an important factor in how plants respond to colonization and
72 potential benefits they receive (Verbruggen & Kiers 2010). Similar to plants, AMF species have
73 different traits that make them functionally distinct (Aguilar-Trigueros *et al.* 2015). For instance,
74 some taxa provide better disease or drought stress resistance while others better enhance nutrient
75 uptake and reduce leaching (Marulanda, Azcón & Ruiz-Lozano 2003; Maherali & Klironomos
76 2007; Köhl, Lukasiewicz & van der Heijden 2016). Ideally, agricultural management would
77 support a functionally-diverse AMF species mixture to increase the multi-functionality of the
78 symbiosis. But intensively-managed agricultural systems impose strong filters that limit the
79 community assemblage of AMF fungal species to those that can persist in the face of high rates
80 of disturbance, long fallow periods, and often monocultures of plant hosts (Verbruggen & Kiers
81 2010). Often this selects for ruderal species that invest heavily in reproduction and less in
82 nutrient scavenging or transfer to hosts (Oehl *et al.* 2003; Verbruggen & Kiers 2010; Chagnon *et*
83 *al.* 2013). By changing disturbance regimes and temporal resource availability, low-intensity
84 tillage and cover cropping would be expected to change AMF community composition and

85 potentially enhance diversity if more niche space is created, e.g. for slower-growing species
86 (Oehl *et al.* 2009). Conversely, since AMF sometimes prefer specific plant hosts (Johnson *et al.*
87 2004), AMF communities measured on the same cash crop may not differ to a great extent in
88 spite of differences in agronomic management.

89 A number of field studies have examined changes in AMF communities in response to less
90 intensive management, so that meta-analysis is now possible for assessing how less intensive
91 agricultural management could optimize this belowground interaction considered central to
92 ecological intensification. The focus here is on the impacts of two management interventions that
93 reduce soil disturbance and periods without roots – the use of low-intensity tillage regimes and
94 cover crops – and their impacts on AM colonization and the AMF community. We evaluated 278
95 comparisons from 54 field studies published between 1990–2015 (see methods), spanning five
96 continents. Studies on cover cropping encompassed a range of cover crop groups, cash crops,
97 and sampling times, and studies on tillage included different tillage types, cash crops, and soil
98 texture.

99 **Methods**

100 *Literature search and data collection*

101 We searched the literature in 2015 using ISI Web of Knowledge (available online). Two separate
102 searches were conducted for assessing effects of cover cropping or alternative tillage on AMF
103 colonization rates on cash crop roots or on the AM community. Although AMF colonization of
104 roots is not necessarily indicative of AM functionality, e.g. benefits for plant nutrient uptake or
105 productivity, it is the most widely measured attribute of AM and the best indicator available. For
106 cover cropping, the search terms were “mycorr*” AND “cover crop*”, which resulted in 108

107 articles in March 2015. For alternative tillage, the search terms were mycorr* AND
108 ("conservation till*" OR "no-till*" OR "reduced till*"), which resulted in 239 articles in October
109 2015. We screened these articles to meet our selection criteria: i) a field trial comparing a) bare
110 winter fallow (i.e. unplanted) vs. cover crop(s), *or* b) multiple types of tillage, including a
111 comparison between a “conventional” type (usually a moldboard plow, i.e. soil inversion) and an
112 alternative (e.g. no-till, chisel till); and ii) data on AMF colonization rates (i.e. percent root
113 length colonized) on roots of the subsequent annual cash crop. We also examined studies that
114 analyzed AMF community composition from soil or root samples (by spore morphological
115 identification or genetic analysis) following incorporation of the cover crop and/or tillage. Only
116 studies with imposed, replicated treatments at one or more sites were included. We expanded our
117 search by checking the reference lists of studies that met our selection criteria.

118 Multiple comparisons within a single study (e.g. comparing different cover crop species vs. a
119 single winter fallow control) were considered distinct within-study observations to assess the
120 effect of moderator variables. In total , there were 17 papers comprising 93 comparisons for
121 cover cropping and 30 papers comprising 131 comparisons for alternative tillage (Supporting
122 Information). For effects on the AMF community, there were 15 papers comparing alternative
123 vs. conventional tillage comprising 25 comparisons for AMF abundance, 15 for AMF richness,
124 and 13 for AMF diversity (Supporting Information). The focus was on species richness (i.e. the
125 total number of species or taxa present) and the Shannon Index as a metric of diversity. Since
126 only five papers reported on AM community composition in studies comparing cover crops,
127 these papers were evaluated qualitatively in the discussion. Data were extracted from tables and
128 figures (using WebPlotDigitizer; Rohatgi, 2015) in publications meeting the selection criteria.

129 We examined several factors commonly reported across the studies as moderators: the type of
130 cash crop, the sampling stage for roots, and soil available phosphorus (P). Categories for type of
131 cash crop were based on which cash crops were commonly included in the selected studies.
132 Maize (*Zea mays* L.) was the most common crop in both cover cropping and tillage meta-
133 analyses. Other cash crop categories for cover cropping included the next most common crop,
134 soybean (*Glycine max* [L.] Merr.), and all other crops. For alternative tillage, other cash crop
135 categories included small grains (e.g. wheat, *Triticum aestivum* L., and oats, *Avena sativa* L.),
136 legumes (e.g. soybean and common bean, *Phaseolus vulgaris* L.), and all other crops. Sampling
137 stage for roots was based on the phenological stage of the cash crop, including *vegetative*,
138 *flowering*, and *maturity*. Where not stated in the journal articles, we estimated these stages by
139 determining the days after planting for each sampling time and matching with crop development
140 timelines from extension resources available close to the study area or in a similar climate. Soil
141 available P ($\mu\text{g P g}^{-1}$ soil) was a continuous variable measured in several ways across the studies,
142 most commonly as Olsen, Mehlich III, and Bray, or the measurement method was not reported.

143 Other explanatory variables were specific to either cover cropping or alternative tillage. For
144 cover cropping, non-AM hosts included species in the *Brassicaceae* family (e.g. rapeseed,
145 *Brassica napus* L., and radish, *Raphanus sativus* L.) and buckwheat (*Fagopyrum esculentum*
146 Moench), which is considered non-mycorrhizal (Wang & Qiu 2006). Functional groups of cover
147 crops included *graminoids*, *legumes*, and *non-legume dicots*. The latter were mostly non-AM
148 hosts but also included AM hosts sunflower (*Helianthus annuus* L.) and dandelion (*Taraxacum*
149 *officinale* F.H.Wigg.). Categories of weed control included whether or not weeds were controlled
150 (by herbicides or mechanical control) in the winter fallow treatment and whether or not cover

151 crops were terminated with any form of tillage or not (e.g. by herbicides or mowing and
152 mulching).

153 Alternative tillage categories were based on the level of disturbance, including *no-till*, *non-*
154 *inversion* (e.g. chisel), *shallow inversion* (e.g. shallow disking), or *ridge tillage*. The type of
155 conventional tillage was either *deep inversion* (moldboard plow, representing the majority of
156 conventional tillage treatments) or *shallow inversion* (same as above). Soil texture was divided
157 into *light* (i.e. high silt and sand content) *loam*, and *heavy* (i.e. high clay content) (NRCS 1993).
158 We also noted whether or not a cover crop was present prior to tillage.

159 *Data analysis*

160 In our meta-analysis, the log response ratio (*lnRR*) represents the influence of either cover
161 cropping or alternative tillage on mycorrhizal colonization of subsequent cash crop roots:

$$162 \quad \ln RR = \ln \bar{X}_t - \ln \bar{X}_c = \ln \frac{\bar{X}_t}{\bar{X}_c}$$

163 where \bar{X}_t and \bar{X}_c are, respectively, the treatment (cover crop or alternative tillage) and control
164 (winter fallow or conventional tillage) mean calculated for that observation. On the log scale, an
165 effect size of 0 means no difference and a positive value means that cover cropping or alternative
166 tillage has a positive effect on mycorrhizal colonization of cash crop roots. The variance of
167 response ratios was calculated according to Hedges et al. (1999) using the standard error and
168 number of replicates reported for each individual study. Where standard errors were not
169 presented or could not be calculated, the authors were contacted to request the missing data.
170 When no information was obtained, standard deviations were imputed based on the ratio of
171 standard deviations and means (of either control or treatment groups) from studies that reported

172 both (Lajeunesse 2013; Ellington *et al.* 2015). The median value of this ratio was used to impute
173 standard deviations for trials that reported only means. A sensitivity analysis assessed the effects
174 of these assumptions and found that almost all results were robust (Supporting Information). We
175 note where particular results were sensitive to the imputed standard deviations.

176 Response ratios were calculated and analyzed using the “metafor” package (Viechtbauer 2010)
177 in R (R Development Core Team 2015) using a mixed effects approach. A publication-level
178 random effect allowed us to account for non-independence of multiple within-study observations
179 (Mengersen, Gurevitch & Koricheva 2013). A model was first run without any moderator
180 variables to assess the overall heterogeneity, and each moderator was subsequently tested one by
181 one as a sole covariate. A categorical moderator variable was considered to have a significant
182 effect on the change in AMF colonization of cash crop roots when the omnibus test of all model
183 coefficients (i.e. including all levels of a categorical variable) was significant ($p < 0.05$)
184 (Viechtbauer 2010). We used funnel plots to confirm there was no evidence of publication bias
185 (Philibert, Loyce & Makowski 2012). All models were fit using restricted maximum likelihood
186 estimation. To facilitate ease of interpretation, mean log response ratios and upper and lower
187 bounds of 95% confidence intervals around the mean were back-transformed ($e^{\ln R}$) and
188 expressed as a percent change relative to the control.

189 **Results**

190 Field studies spanning five continents (all but Africa and Antarctica; Fig. S1) showed strong
191 positive effects of cover cropping and alternative tillage on AMF colonization of cash crop roots.
192 Cover crops increased colonization of summer cash crop roots by 28.5% (95% CI: 12.1–47.4%;
193 Fig. 1) relative to winter fallows. Median colonization rates across all observations were 47 and

194 37% for cover cropping vs. fallow, respectively (Fig. S2). The change in colonization was
195 greater when the cover crop was an AM host (30.5 vs. 17.4%), but even non-AM host cover
196 crops (e.g. radish or rape) significantly increased root colonization (95% CI: 2.2–34.8% for non-
197 AM hosts and 14.1–49.3% for AM hosts). Legume cover crops had a greater effect on root
198 colonization than graminoids or non-legume dicots (Fig. 1). Roots of maize and soybeans, the
199 two most common cash crops in the studies, had similarly higher AMF colonization following a
200 cover crop (95% CI: 16.2–62.8% for maize and 16.5–80.5% for soybeans), but this was not
201 apparent for other cash crops, which encompassed a number of different crop species. The
202 sampling stage of cash crop roots, fallow weed control, or prior tillage did not affect the change
203 in colonization of cash crop roots following a cover crop (Fig. 1). Soil available P had a
204 marginally significant ($p=0.08$) negative, but weak, effect on the magnitude of the effect size
205 (Fig. 2).

206 Across all observations, alternative tillage increased colonization of cash crop roots by 27.0%
207 (95% CI: 14.4–41.0) relative to conventional tillage (Fig. 3). Median colonization rates across all
208 observations were 38 and 29% for low-intensity vs. conventional tillage, respectively (Fig. S2).
209 The strongest influence on the magnitude of change was the type of alternative tillage. No-tillage
210 increased colonization by 30.3% (95% CI: 17.3–44.8%), which was similar to shallow-inversion
211 and ridge tillage but higher than the 11.2% (95% CI: -1.5–25.6%) change for non-inversion
212 tillage. Maize and small grain cash crops had less of a change in root colonization than legumes
213 or other cash crops (e.g. sorghum, flax, or cotton). The presence of a prior cover crop affected
214 how AMF colonization responded to alternative tillage, increasing colonization by 41.5% (95%
215 CI: 24.0–61.5%) compared to 23.8% (95% CI: 11.7–37.2%) when no cover crop was present. All
216 cover crops grown in field studies comparing tillage treatments were AM legumes (e.g. hairy

217 vetch, *Vicia villosa* Roth). The sampling stage of roots did not affect the change in colonization.
218 Whereas the overall effect of soil texture was not significant, colonization in heavy (i.e. clayey)
219 soils showed no change from alternative tillage, whereas changes occurred in colonization in
220 light and loam textured soils (Fig. 3). The type of conventional tillage did not affect the change
221 in colonization, although only a small number of trials were shallow-inversion (Fig. 3).

222 Richness of AMF taxa increased by 11.3% (95% CI: 1.0–22.6%) in alternative tillage regimes
223 compared to conventional tillage (Table 1). A metric of diversity, the Shannon Index, was not
224 significantly different for AMF taxa in alternative vs. conventional tillage regimes. Within the
225 set of studies reporting effects on AMF community composition or diversity, alternative tillage
226 increased AMF abundance by 60.5%, as measured primarily by spore counts in soil, although the
227 response was highly heterogeneous (95% CI: 15.5–123.0%).

228 **Discussion**

229 Although it is often stated that reducing soil disturbance and bare fallows increases AM
230 formation (Gosling *et al.* 2006; de Vries & Bardgett 2012; Schipanski *et al.* 2014), a lack of a
231 systematic analysis of results across field studies have precluded decisive conclusions about the
232 relative efficacy of these interventions, and the key management and soil factors that moderate
233 their effect. The results of this meta-analysis show that across replicated field studies from five
234 continents, less intensive tillage and winter cover cropping similarly increased AM formation in
235 summer annual cash crop roots by ~30%. These results suggest that farmers could optimize
236 combinations of tillage and cover crops that most enhance AM formation, particularly with no-
237 till systems and legume cover crops. But importantly, cover crops increased AM formation
238 similarly whether tillage was used or not, suggesting that the continuity of root associations with

239 cover crops is at least as important for AM formation as decreasing disturbance. This is a
240 significant finding, especially for agricultural systems that may rely more heavily on services
241 provided by AM, for instance organic management (Gosling et al., 2006) or low-input systems
242 used by most of the world's farmers (Cardoso & Kuyper 2006). In such systems, tillage is often
243 required for weed control and incorporation of organic matter into the soil (Smukler *et al.* 2008).
244 When a cover crop, especially a legume, is used in these systems, then AM formation in the cash
245 crop apparently can withstand some tillage. Although AMF colonization rates are widely
246 measured, their relationship with actual functions remains unclear (Lekberg & Koide 2005), so
247 future work that uses innovative approaches like non-AM plant mutants (Watts-Williams &
248 Cavagnaro 2015) will be needed to determine decisively how and when these changes are linked
249 to enhancements in ecosystem services like crop productivity.

250 The 11% increase in richness of AMF taxa in response to alternative tillage suggests that lower-
251 intensity soil disturbance creates more niche space in the rhizosphere and root zone that
252 accommodates tillage-sensitive taxa, e.g. those that rely more on intact root fragments or
253 extraradical mycelia vs. spores for AM formation. Other studies showing that changes in
254 diversity and community composition of AMF are possible (e.g. Ramos-Zapata *et al.* 2012; Higo
255 *et al.* 2013; Säle *et al.* 2015), but not consistent (e.g. Njeru *et al.* 2015; Hu *et al.* 2015), with
256 alternative tillage or cover cropping suggest that determining how to manage AMF community
257 composition will be somewhat site-specific, and tailored to farming goals for productivity and
258 environmental quality.

259 *Impacts of cover cropping and alternative tillage on AM colonization*

260 The 28.5% increase in AMF colonization of cash crop roots following a winter cover crop may
261 be a result of increased AMF spore abundance in soil (Lehman *et al.* 2012; Njeru *et al.* 2015).
262 Since AMF are obligate biotrophs, they require C resources from roots to grow and reproduce
263 (Smith & Read 2008), which are not available during a fallow period. Reduced AMF
264 colonization in crops grown after long plant-free periods has been associated with poor crop
265 growth and P and zinc deficiencies (Thompson, Clewett & Fiske 2013). The larger effect of
266 cover cropping on colonization rates reported in a previous meta-analysis (90% increase;
267 Lekberg & Koide 2005) may be due to the inclusion of greenhouse experiments in that meta-
268 analysis, which showed a greater positive response than field experiments (Lekberg & Koide
269 2005). The stronger response of AMF colonization to legume cover crops compared to
270 graminoids or non-legume dicots likely reflects the high mycorrhizal dependency of typical
271 legume cover crops (e.g. *Vicia villosa*. and *Trifolium* spp.), which could lead to greater spore
272 production and higher levels of colonization in the cash crop (Galvez *et al.* 1995; Njeru *et al.*
273 2014).

274 Whereas reductions in AM formation could be expected following a non-AMF host cover crop
275 species, either as a result of a reduction in AM populations (similar to a bare fallow) or
276 production of fungal inhibitory compounds like isothiocyanates by *Brassicaceae*, experimental
277 results have been inconsistent (Gavito & Miller 1998; Pellerin *et al.* 2007; White & Weil 2010;
278 Koide & Peoples 2012). In this study, the change in AM colonization in cash crop roots was
279 indeed greater following cover crops that were AMF hosts compared to non-AMF hosts, but
280 there was still a significant increase in colonization following a non-AMF host cover crop. This
281 may in part be related to the presence of weeds that are AMF hosts in the non-AM cover crop
282 treatment (Njeru *et al.* 2014) or differences in soil moisture and temperature patterns in cover

283 cropped vs. fallow soils that impact spore viability, for instance. It is also possible that additional
284 organic matter from non-AM cover crops make soil physical properties more conducive to
285 hyphal growth and colonization of subsequent crops (Drew, Murray & Smith 2006).

286 The 27.0% increase in AM colonization in alternative tillage regimes compared to conventional
287 tillage reflects the detrimental effects of soil disturbance on AM hyphal networks (Evans &
288 Miller 1990) and resulting reductions in root colonization (Lekberg & Koide 2005). The stronger
289 response of no-till compared to other forms of alternative tillage was expected since it eliminates
290 belowground disturbance and thus leaves mycelial networks intact, which form an important
291 component of inoculum potential (Evans & Miller 1990; Kabir 2005). In this meta-analysis, the
292 positive interaction between tillage and cover cropping may have been accentuated because all
293 cover crops included in trials evaluating alternative tillage were legumes.

294 Soil P availability did not strongly affect the response of AMF colonization of cash crop roots to
295 cover cropping or alternative tillage. Using just the most commonly reported test for available P
296 (Olsen; 34 % of studies) also showed no relationship with the change in colonization. Nor was a
297 relationship found between available soil P levels in control treatments and the level of AMF
298 colonization, which may be more affected by soil available P than the response ratio (Bolan,
299 Robson & Barrow 1984). High soil P may reduce the plant growth response from AM more than
300 the rate of colonization (Sorensen et al., 2005), but not necessarily (Köhl, Lukasiewicz & van der
301 Heijden 2016).

302 *Impacts of cover cropping and alternative tillage on AMF communities*

303 The slight (11%) increase in AMF species richness (based on spore taxonomy or genetics) in
304 response to alternative tillage, but lack of changes in a diversity index (measured by the Shannon

305 Index), suggests that alternative tillage has relatively small effects on AMF habitats, or arrival of
306 additional taxa is slow after a change in soil disturbance. Taxonomic changes can occur in the
307 absence of changes in AMF diversity or richness (e.g. Jansa et al., 2003, 2002) in response to
308 types of tillage. For instance, Jansa et al. (2003) observed that *Scutellospora* sp. were absent in
309 maize roots from plowed or chisel tilled plots but present in no-till plots, while several species in
310 the genus formerly known as *Glomus* (Krüger et al., 2012) were more prevalent in tilled soils,
311 and *Gigaspora* sp. were present in all treatments, suggesting differing dependences of these
312 genera on an intact hyphal network for survival and root colonization.

313 The few field-based studies that examined the effect of fall/winter cover cropping on AMF
314 communities show limited changes in response to cover cropping (Table 2). For instance,
315 Ramos-Zapata et al. (2012) showed on average approximately four more AMF taxa (identified
316 from spores in trap cultures) following a velvetbean (*Mucuna deeringiana* [Bort] Merr.) cover
317 crop compared to a non-weeded fallow (10.7 vs. 6.3 species) at the end of a 13-year experiment.
318 Specifically, spores from *Acaulospora* and *Rhizophagus* sp. were found only in cover cropped
319 soils. But several other studies (Higo et al. 2014, 2015; Njeru et al. 2015) did not show any
320 changes in AMF richness or diversity in soil or roots following cover crops in multi-year trials.
321 Fallow treatments tended towards AMF genera with larger spores, perhaps indicating greater
322 viability during long fallows, whereas cover crops tended to support greater abundance of some
323 species in the former genus *Glomus* (Higo et al. 2013, Ramos-Zapata et al. 2012). While cover
324 crops and associated weeds offer a different host environment and more resources compared to
325 fallows, other management practices (e.g. continued tillage) may constrain changes in AMF
326 community composition.

327 *Management implications and conclusions*

328 This meta-analysis shows that cover cropping and reducing soil disturbance are strategies that
329 farmers can use to increase AM formation and potentially alter the AMF community across a
330 wide range of soil types and cash crops. Specifically, combining no-till and legume cover
331 cropping would best increase AMF colonization of cash crop roots, highlighting positive
332 interactions across management practices. But cover cropping even appears to counteract some
333 of the negative impacts of soil disturbance on AM formation. Systems approaches that combine
334 cover cropping and reduced tillage with other AM-promoting practices like crop diversification
335 and organic management (Oehl *et al.* 2004; Verbruggen *et al.* 2010) may offer the most promise
336 for enhancing AM communities, while also increasing soil C storage and nutrient cycling, and
337 reducing nutrient losses and soil erosion (Quemada *et al.* 2013; McDaniel, Tiemann & Grandy
338 2014; Schipanski *et al.* 2014). Fostering indigenous AMF communities through plant choices
339 and soil management could become an essential component of ecological intensification, which
340 relies on such “service providing organisms” to support crop productivity while reducing
341 environmental impacts and external inputs (Bender, Wagg & van der Heijden 2016). Future
342 work that links changes in AMF root colonization and functional diversity with specific
343 ecosystem functions would help optimize agricultural systems for both food production and
344 environmental quality.

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351 **Data accessibility**

352 Data will be made available via the Dryad Digital Repository and location details provided at
 353 acceptance.

354 **Supporting Information**

355 Additional supporting information may be found in the online version of this article.

356 Appendix S1: Papers included in meta-analysis, map of study locations, and sensitivity analysis.

357 **References**

- 358 Aguilar-Trigueros, C.A., Hempel, S., Powell, J.R., Anderson, I.C., Antonovics, J., Bergmann, J.,
 359 Cavagnaro, T.R., Chen, B., Hart, M.M., Klironomos, J., Petermann, J.S., Verbruggen, E.,
 360 Veresoglou, S.D. & Rillig, M.C. (2015) Branching out: Towards a trait-based understanding
 361 of fungal ecology. *Fungal Biology Reviews*, **29**, 1–8.
- 362 Augé, R.M., Toler, H.D. & Saxton, A.M. (2015) Arbuscular mycorrhizal symbiosis alters
 363 stomatal conductance of host plants more under drought than under amply watered
 364 conditions: A meta-analysis. *Mycorrhiza*, **25**, 13–24.
- 365 Bender, S.F., Wagg, C. & van der Heijden, M.G.A. (2016) An underground revolution:
 366 Biodiversity and soil ecological engineering for agricultural sustainability. *Trends in*
 367 *Ecology & Evolution*, **31**, 1–13.
- 368 Bolan, N., Robson, A. & Barrow, N. (1984) Increasing phosphorus supply can increase the
 369 infection of plant roots by vesicular-arbuscular mycorrhizal fungi. *Soil Biology and*
 370 *Biochemistry*, **16**, 419–420.
- 371 Bommarco, R., Kleijn, D. & Potts, S.G. (2013) Ecological intensification: Harnessing ecosystem
 372 services for food security. *Trends in Ecology & Evolution*, **28**, 230–8.
- 373 Cardoso, I.M. & Kuyper, T.W. (2006) Mycorrhizas and tropical soil fertility. *Agriculture,*
 374 *Ecosystems and Environment*, **116**, 72–84.
- 375 Cavagnaro, T.R., Bender, S.F., Asghari, H.R. & van der Heijden, M.G.A. (2015) The role of
 376 arbuscular mycorrhizas in reducing soil nutrient loss. *Trends in Plant Science*, **20**, 283–290.

- 377 Chagnon, P.L., Bradley, R.L., Maherali, H. & Klironomos, J.N. (2013) A trait-based framework
378 to understand life history of mycorrhizal fungi. *Trends in Plant Science*, **18**, 484–491.
- 379 Drew, E.A., Murray, R.S. & Smith, S.E. (2006) Functional diversity of external hyphae of AM
380 fungi: Ability to colonise new hosts is influenced by fungal species, distance and soil
381 conditions. *Applied Soil Ecology*, **32**, 350–365.
- 382 Duan, T., Shen, Y., Facelli, E., Smith, S.E., Nan, Z., Plant, S. & June, N. (2010) New
383 agricultural practices in the Loess Plateau of China do not reduce colonisation by arbuscular
384 mycorrhizal or root invading fungi and do not carry a yield penalty. *Plant and Soil*, **331**,
385 265–275.
- 386 Ellington, E.H., Bastille-Rousseau, G., Austin, C., Landolt, K.N., Pond, B.A., Rees, E.E., Robar,
387 N. & Murray, D.L. (2015) Using multiple imputation to estimate missing data in meta-
388 regression. *Methods in Ecology and Evolution*, **6**, 153–163.
- 389 Erisman, J.W., Galloway, J.N., Seitzinger, S., Vbleeker, A., Dise, N., Petrescu, R., Leach, A. &
390 Vries, W. (2014) Consequences of human modification of the global nitrogen cycle. *Phil*
391 *Trans R Soc B*, **368**, 1–9.
- 392 Evans, B.Y.D.G. & Miller, M.H. (1990) The role of the external mycelial network in the effect
393 of soil disturbance upon vesicular-arbuscular mycorrhizal colonization of maize. *New*
394 *Phytologist*, **114**, 65–71.
- 395 Galvez, L., Douds, D.D., Wagoner, P., Longnecker, L.R., Drinkwater, L.E. & Janke, R.R. (1995)
396 An overwintering cover crop increases inoculum of VAM fungi in agricultural soil.
397 *American Journal of Alternative Agriculture*, **10**, 152–156.
- 398 Gavito, M.E. & Miller, M.H. (1998) Early phosphorus nutrition, mycorrhizae development, dry
399 matter partitioning and yield of maize. *Plant and Soil*, **199**.
- 400 Gosling, P., Hodge, a, Goodlass, G. & Bending, G. (2006) Arbuscular mycorrhizal fungi and
401 organic farming. *Agriculture, Ecosystems and Environment*, **113**, 17–35.
- 402 Hedges, L. V., Gurevitch, J. & Curtis, P.S. (1999) The meta-analysis of response ratios in
403 experimental ecology. *Ecology*, **80**, 1150–1156.
- 404 Higo, M., Isobe, K., Drijber, R.A., Kondo, T., Yamaguchi, M., Takeyama, S., Suzuki, Y.,
405 Niiijima, D., Matsuda, Y., Ishii, R. & Torigoe, Y. (2014) Impact of a 5-year winter cover
406 crop rotational system on the molecular diversity of arbuscular mycorrhizal fungi
407 colonizing roots of subsequent soybean. *Biology and Fertility of Soils*, **50**, 913–926.
- 408 Higo, M., Isobe, K., Kondo, T., Yamaguchi, M., Takeyama, S., Drijber, R. a. & Torigoe, Y.
409 (2015) Temporal variation of the molecular diversity of arbuscular mycorrhizal
410 communities in three different winter cover crop rotational systems. *Biology and Fertility of*
411 *Soils*, **51**, 21–32.
- 412 Higo, M., Isobe, K., Yamaguchi, M., Drijber, R.A., Jeske, E.S. & Ishii, R. (2013) Diversity and
413 vertical distribution of indigenous arbuscular mycorrhizal fungi under two soybean
414 rotational systems. *Biology and Fertility of Soils*, **49**, 1085–1096.
- 415 Hodge, A. (2004) The plastic plant: Root responses to heterogeneous supplies of nutrients. *New*

- 416 *Phytologist*, **162**, 9–24.
- 417 Hu, J., Yang, A., Wang, J., Zhu, A., Dai, J., Wong, M.H. & Lin, X. (2015) Arbuscular
418 mycorrhizal fungal species composition, propagule density, and soil alkaline phosphatase
419 activity in response to continuous and alternate no-tillage in Northern China. *Catena*, **133**,
420 215–220.
- 421 Jackson, L.E., Pulleman, M.M., Brussaard, L., Bawa, K.S., Brown, G.G., Cardoso, I.M., de
422 Ruyter, P.C., García-Barrios, L., Hollander, a. D., Lavelle, P., Ouédraogo, E., Pascual, U.,
423 Setty, S., Smukler, S.M., Tschardtke, T. & Van Noordwijk, M. (2012) Social-ecological and
424 regional adaptation of agrobiodiversity management across a global set of research regions.
425 *Global Environmental Change*, **22**, 623–639.
- 426 Jansa, J., Mozafar, a, Anken, T., Ruh, R., Sanders, I.R. & Frossard, E. (2002) Diversity and
427 structure of AMF communities as affected by tillage in a temperate soil. *Mycorrhiza*, **12**,
428 225–34.
- 429 Jansa, J., Mozafar, A., Kuhn, G. & Anken, T. (2003) Soil tillage affects the community structure
430 of mycorrhizal fungi in maize roots. *Ecological Applications*, **13**, 1164–1176.
- 431 Johnson, D., Vandenkoornhuyse, P.J., Leake, J.R., Gilbert, L., Booth, R.E., Grime, J.P., Young,
432 J.P.W., Read, D.J. & Booth, E. (2004) Plant communities affect arbuscular mycorrhizal
433 fungal diversity and community composition in grassland microcosms. *New Phytologist*,
434 **161**, 503–515.
- 435 Kabir, Z. (2005) Tillage or no-tillage: Impact on mycorrhizae. *Canadian Journal of Plant*
436 *Science*, **85**, 23–29.
- 437 Köhl, L., Lukasiewicz, C.E. & van der Heijden, M.G.A. (2016) Establishment and effectiveness
438 of inoculated arbuscular mycorrhizal fungi in agricultural soils. *Plant, Cell and*
439 *Environment*, 136–146.
- 440 Koide, R.T. & Peoples, M.S. (2012) On the nature of temporary yield loss in maize following
441 canola. *Plant and Soil*, **360**, 259–269.
- 442 Krüger, M., Krüger, C., Walker, C., Stockinger, H. & Schüssler, A. (2012) Phylogenetic
443 reference data for systematics and phylotaxonomy of arbuscular mycorrhizal fungi from
444 phylum to species level. *New Phytologist*, **193**, 970–984.
- 445 Lajeunesse, M.J. (2013) Recovering missing or partial data from studies: A survey of
446 conversions and imputations for meta-analysis. *Handbook of Meta-analysis in Ecology and*
447 *Evolution* (eds K. Mengersen), J. Gurevitch), & J. Koricheva), pp. 195–206. Princeton
448 University Press, Princeton.
- 449 Lambers, H., Martinoia, E. & Renton, M. (2015) Plant adaptations to severely phosphorus-
450 impoverished soils. *Current Opinion in Plant Biology*, **25**, 23–31.
- 451 Lehman, R.M., Taheri, W.I., Osborne, S.L., Buyer, J.S. & Douds, D.D. (2012) Fall cover
452 cropping can increase arbuscular mycorrhizae in soils supporting intensive agricultural
453 production. *Applied Soil Ecology*, **61**, 300–304.
- 454 Lekberg, Y. & Koide, R.T. (2005) Is plant performance limited by abundance of arbuscular

- 455 mycorrhizal fungi? A meta-analysis of studies published between 1988 and 2003. *New*
456 *Phytologist*, **168**, 189–204.
- 457 Maherali, H. & Klironomos, J.N. (2007) Influence of phylogeny on fungal community assembly
458 and ecosystem functioning. *Science*, **316**, 1746–1748.
- 459 Marulanda, A., Azcón, R. & Ruiz-Lozano, J.M. (2003) Contribution of six arbuscular
460 mycorrhizal fungal isolates to water uptake by *Lactuca sativa* plants under drought stress.
461 *Physiologia Plantarum*, **119**, 526–533.
- 462 McDaniel, M., Tiemann, L. & Grandy, A. (2014) Does agricultural crop diversity enhance soil
463 microbial biomass and organic matter dynamics? A meta-analysis. *Ecological Applications*,
464 **24**, 560–570.
- 465 Mengersen, K., Gurevitch, J. & Koricheva, J. (2013) *Handbook of Meta-Analysis in Ecology and*
466 *Evolution*. Princeton University Press, Princeton.
- 467 Njeru, E.M., Avio, L., Bocci, G., Sbrana, C., Turrini, A., Bàrberi, P., Giovannetti, M. & Oehl, F.
468 (2015) Contrasting effects of cover crops on ‘hot spot’ arbuscular mycorrhizal fungal
469 communities in organic tomato. *Biology and Fertility of Soils*, **51**, 151–166.
- 470 Njeru, E.M., Avio, L., Sbrana, C., Turrini, A., Bocci, G., Bàrberi, P. & Giovannetti, M. (2014)
471 First evidence for a major cover crop effect on arbuscular mycorrhizal fungi and organic
472 maize growth. *Agronomy for Sustainable Development*, **34**, 841–848.
- 473 NRCS. (1993) *Soil Survey Manual*. United States Department of Agriculture.
- 474 Oehl, F., Sieverding, E., Ineichen, K., Mäder, P., Boller, T., Wiemken, A. & Ma, P. (2003)
475 Impact of land use intensity on the species diversity of arbuscular mycorrhizal fungi in
476 agroecosystems of central Europe. *Applied and Environmental Microbiology*, **69**, 2816–
477 2824.
- 478 Oehl, F., Sieverding, E., Ineichen, K., Mäder, P., Wiemken, A. & Boller, T. (2009) Distinct
479 sporulation dynamics of arbuscular mycorrhizal fungal communities from different
480 agroecosystems in long-term microcosms. *Agriculture, Ecosystems and Environment*, **134**,
481 257–268.
- 482 Oehl, F., Sieverding, E., Mäder, P., Dubois, D., Ineichen, K., Boller, T. & Wiemken, A. (2004)
483 Impact of long-term conventional and organic farming on the diversity of arbuscular
484 mycorrhizal fungi. *Oecologia*, **138**, 574–83.
- 485 Pellerin, S., Mollier, A., Morel, C. & Plenchette, C. (2007) Effect of incorporation of *Brassica*
486 *napus* L. residues in soils on mycorrhizal fungus colonisation of roots and phosphorus
487 uptake by maize (*Zea mays* L.). *European Journal of Agronomy*, **26**, 113–120.
- 488 Philibert, A., Loyce, C. & Makowski, D. (2012) Assessment of the quality of meta-analysis in
489 agronomy. *Agriculture, Ecosystems and Environment*, **148**, 72–82.
- 490 Pingali, P. (2012) Green Revolution: Impacts, Limits, and the path ahead. *Proceedings of the*
491 *National Academy of Science*, **109**, 12302–12308.
- 492 Quemada, M., Baranski, M., Nobel-de Lange, M.N.J., Vallejo, A. & Cooper, J.M. (2013) Meta-
493 analysis of strategies to control nitrate leaching in irrigated agricultural systems and their

- 494 effects on crop yield. *Agriculture, Ecosystems and Environment*, **174**, 1–10.
- 495 R Development Core Team. (2015) R: A Language and Environment for Statistical Computing.
- 496 Ramos-Zapata, J.A., Marrufo-Zapata, D., Guadarrama, P., Carrillo-Sánchez, L., Hernández-
497 Cuevas, L. & Caamal-Maldonado, A. (2012) Impact of weed control on arbuscular
498 mycorrhizal fungi in a tropical agroecosystem: A long-term experiment. *Mycorrhiza*, **22**,
499 653–661.
- 500 Rillig, M.C. & Mummey, D.L. (2006) Mycorrhizas and soil structure. *The New phytologist*, **171**,
501 41–53.
- 502 Robertson, G.P. & Vitousek, P.M. (2009) Nitrogen in agriculture: Balancing the cost of an
503 essential resource. *Annual Review of Environment and Resources*, **34**, 97–125.
- 504 Rohatgi, A. (2015) WebPlotDigitizer, <http://arohatgi.info/WebPlotDigitizer/>
- 505 Säle, V., Aguilera, P., Laczko, E., Mäder, P., Berner, A., Zihlmann, U., van der Heijden, M.G. &
506 Oehl, F. (2015) Impact of conservation tillage and organic farming on the diversity of
507 arbuscular mycorrhizal fungi. *Soil Biology and Biochemistry*, **84**, 38–52.
- 508 Schipanski, M.E., Barbercheck, M., Douglas, M.R., Finney, D.M., Haider, K., Kaye, J.P.,
509 Kemanian, A.R., Mortensen, D. a., Ryan, M.R., Tooker, J. & White, C. (2014) A
510 framework for evaluating ecosystem services provided by cover crops in agroecosystems.
511 *Agricultural Systems*, **125**, 12–22.
- 512 Smith, S.E. & Read, D.J. (2008) *Mycorrhizal Symbiosis*, 3rd ed. Academic Press, Cambridge,
513 UK.
- 514 Smukler, S.M., Jackson, L.E., Murphree, L., Yokota, R., Koike, S.T. & Smith, R.F. (2008)
515 Transition to large-scale organic vegetable production in the Salinas Valley, California.
516 *Agriculture, Ecosystems and Environment*, **126**, 168–188.
- 517 Sorensen, J.N., Larsen, J. & Jakobsen, I. (2005) Mycorrhiza formation and nutrient concentration
518 in leeks (*Allium porrum*) in relation to previous crop and cover crop management on high P
519 soils. *Plant and Soil*, **273**, 101–114.
- 520 Thompson, J.P., Clewett, T.G. & Fiske, M.L. (2013) Field inoculation with arbuscular-
521 mycorrhizal fungi overcomes phosphorus and zinc deficiencies of linseed (*Linum*
522 *usitatissimum*) in a vertisol subject to long-fallow disorder. *Plant and Soil*, **371**, 117–137.
- 523 Verbruggen, E. & Kiers, E.T. (2010) Evolutionary ecology of mycorrhizal functional diversity in
524 agricultural systems. *Evolutionary Applications*, **3**, 547–560.
- 525 Verbruggen, E., Rölling, W.F.M., Gamper, H. a, Kowalchuk, G. a, Verhoef, H. a & van der
526 Heijden, M.G. a. (2010) Positive effects of organic farming on below-ground mutualists:
527 large-scale comparison of mycorrhizal fungal communities in agricultural soils. *The New*
528 *Phytologist*, **186**, 968–79.
- 529 Viechtbauer, W. (2010) Conducting meta-analyses in R with the metafor package. *Journal of*
530 *Statistical Software*, **36**, 1–48.
- 531 de Vries, F.T. & Bardgett, R.D. (2012) Plant–microbial linkages and ecosystem nitrogen

- 532 retention: Lessons for sustainable agriculture. *Frontiers in Ecology and the Environment*,
533 **10**, 425–432.
- 534 Wang, B. & Qiu, Y.L. (2006) Phylogenetic distribution and evolution of mycorrhizas in land
535 plants. *Mycorrhiza*, **16**, 299–363.
- 536 Watts-Williams, S.J. & Cavagnaro, T.R. (2015) Using mycorrhiza-defective mutant genotypes of
537 non-legume plant species to study the formation and functioning of arbuscular mycorrhiza:
538 A review. *Mycorrhiza*.
- 539 White, C.M. & Weil, R.R. (2010) Forage radish and cereal rye cover crop effects on mycorrhizal
540 fungus colonization of maize roots. *Plant and Soil*, **328**, 507–521.
- 541 York, L.M., Nord, E.A. & Lynch, J.P. (2013) Integration of root phenes for soil resource
542 acquisition. *Frontiers in Plant Science*, **4**, 355.
- 543
- 544

545 **Tables**

546 **Table 1.** Response ratios and 95% confidence intervals (CI) for AMF abundance, community
 547 richness, and diversity (the Shannon Index) in response to alternative tillage from field
 548 experiments. Response ratios that do not overlap zero are considered significant.

	Response ratio estimate	95% CI lower bound	95% CI upper bound	Number of observations (n)	Number of studies
Abundance	0.4730	0.1441	0.8019	25	9
Richness	0.1072	0.0103	0.2040	15	9
Diversity (Shannon)	0.0256	-0.0673	0.1186	13	7

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550

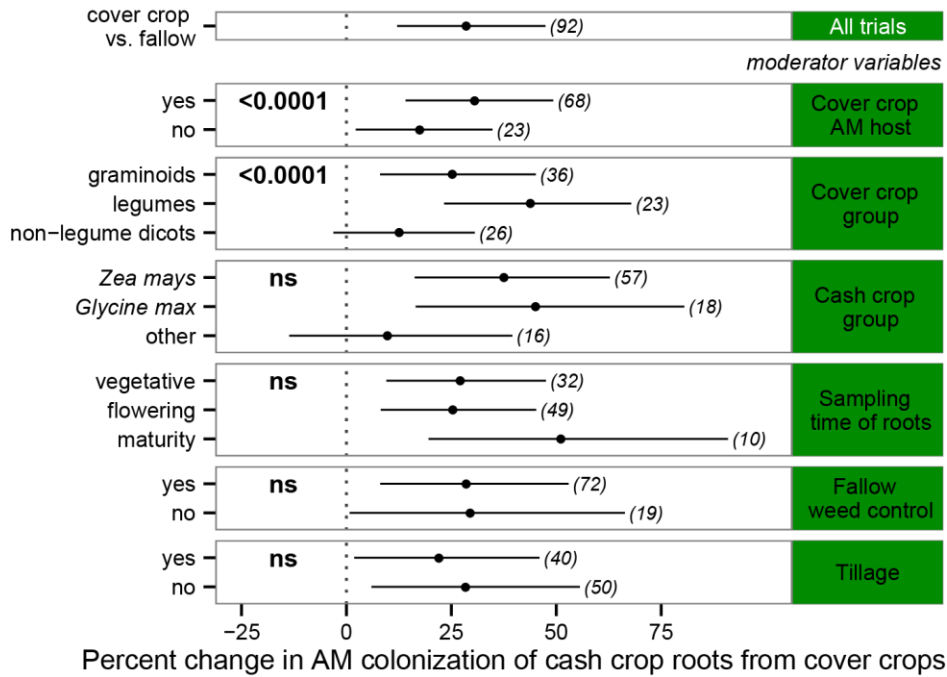
551 **Table 2.** Effects of fall/winter cover crops on AMF species richness, diversity, and community
 552 composition from field studies.

Cover crops	Cash crop	Effect on AMF species richness?	Effect on AMF species diversity?	Effect on AMF community composition?	Study
<i>Vicia villosa</i> Roth, <i>Brassica juncea</i> (L.) Coss, Mix	<i>Solanum lycopersicum</i> L.	no	no	no	Njeru et al. 2015
<i>Triticum aestivum</i> (L.), <i>Trifolium pretense</i> L., <i>Brassica napus</i> L.	<i>Glycine max</i> (L.) Merr	no	no	no	Higo et al. 2014
<i>T. aestivum</i>	<i>G. max</i>	yes, <i>T. aestivum</i> > fallow	yes, <i>T. aestivum</i> > fallow	yes	Higo et al. 2013
<i>T. aestivum</i> , <i>B. napus</i>	<i>G. max</i>	no	no	yes	Higo et al. 2015
<i>Mucuna deeringiana</i> (Bort) Merr.	<i>Zea mays</i> L.	yes, <i>M. deeringiana</i> > fallow	NA	yes	Ramos-Zapata et al. 2012

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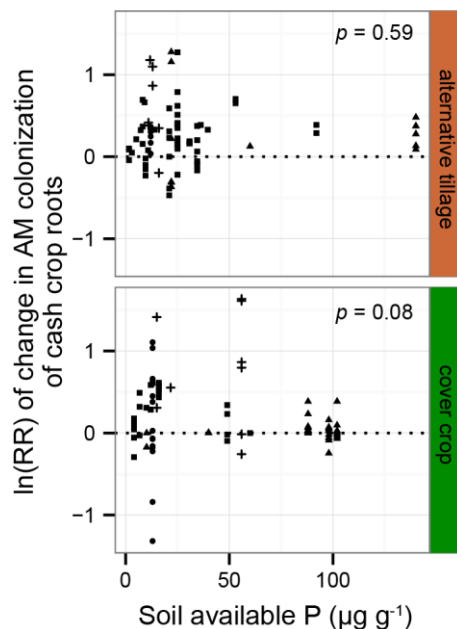
555 **Figures**



556

557 **Fig. 1. Meta-analysis results of the change in AMF colonization of cash crop roots in**
 558 **response to fall/winter cover cropping from field experiments in five continents.** Error bars
 559 represent 95% confidence intervals. Omnibus tests of significance for moderator variables are
 560 shown on the left (ns: “not significant”). The number of observations in each category are shown
 561 in parentheses.

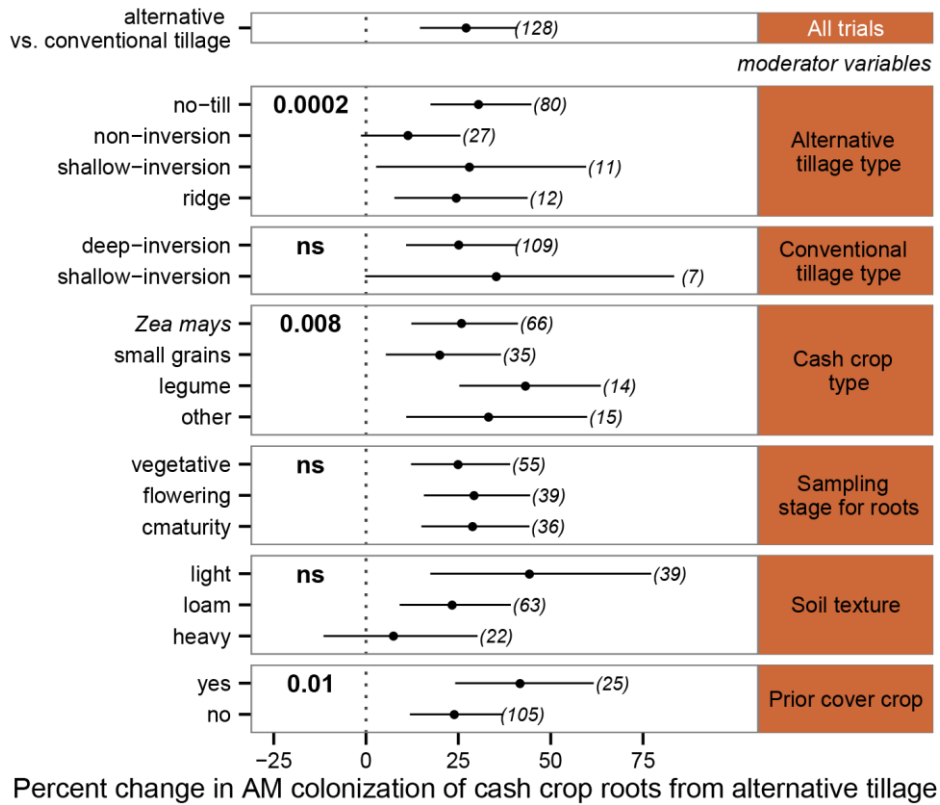
562



563

564 **Fig. 2. Meta-analysis results of the change in AMF colonization of cash crop roots as**
 565 **affected by soil available phosphorus (P) levels for field studies on alternative tillage and**
 566 **cover cropping.** Symbols are different measurement methods for soil available P. *Circles* : Bray;
 567 *Triangles*: Mehlich III; *Squares*: Olsen; *Crosses*: All other methods. ln(RR): log response ratio.
 568 The significance of the linear regressions is shown in the upper right, separately for alternative
 569 tillage and cover cropping.

570



571

572 **Fig. 3. Meta-analysis results of the change in AMF colonization of cash crop roots in**
 573 **response to alternative tillage from field experiments in five continents.** Error bars represent
 574 95% confidence intervals. Omnibus tests of significance for moderator variables are shown on
 575 the left (ns: “not significant”). The number of observations in each category is shown in
 576 parentheses.

577