

1 *Title: Chronosequence and direct observation approaches reveal complementary*
2 **community dynamics in a novel ecosystem**

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4 *Short title: Persistent weedy communities*

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18

19 **Abstract**

20 Non-native, early-successional plants have been observed to maintain dominance for decades,

21 particularly in semi-arid systems. Here, two approaches were used to detect potentially slow

22 successional patterns in an invaded semi-arid system: chronosequence and direct observation.

23 Plant communities in 25 shrub-steppe sites that represented a 50-year chronosequence of

24 agricultural abandonment were monitored for 13 years. Each site contained a field abandoned
25 from agriculture (ex-arable) and an adjacent never-tilled field. Ex-arable fields were dominated
26 by short-lived, non-native plants. These ‘weedy’ communities had lower species richness,
27 diversity and ground cover, and greater annual and forb cover than communities in never-tilled
28 fields. Never-tilled fields were dominated by long-lived native plants. Across the chronosequence,
29 plant community composition remained unchanged in both ex-arable and never-tilled fields. In
30 contrast, 13 years of direct observation detected directional changes in plant community
31 composition in both field types. Despite changes in community composition in both field types
32 during direct observation, there was little evidence that native plants were invading ex-arable
33 fields or that non-native plants were invading never-tilled fields. The more-controlled, direct
34 observation approach was more sensitive to changes in community composition, but the
35 chronosequence approach suggested that these changes are unlikely to manifest over longer time
36 periods, at least in part because of disturbances in the system. Results highlight the long-term
37 consequences of soil disturbance and the difficulty of restoring native perennials in disturbed
38 semi-arid systems.

39

40 *Key words:* alternate state; biocontrol; community dynamics; exotic; facilitation; fire; invasive;
41 native restoration; non-native; ex-arable; shrub-steppe; succession.

42

43 *Nomenclature:* Hitchcock and Cronquist (1973) for plants.

44

45

46 **Introduction**

47 Over the past century, early-successional, non-native plants have invaded disturbed areas around
48 the world (Richardson 2011; Jauni et al. 2015). Traditional ecological theory suggests that
49 without continued disturbances late-successional species will gradually replace these invaders
50 (Elton 1958; MacDougall & Turkington 2005; Myers & Harms 2009). Yet, in some, particularly
51 semi-arid areas, early-successional, non-native species persist for decades or longer (Stylinski &
52 Allen 1999; Courtois et al. 2004; Tognetti et al. 2010; Kachergis et al. 2014; Gill et al. 2018).
53 Distinguishing whether early-successional, non-natives follow successional patterns or if they
54 create alternate-state plant communities has important theoretical and management implications
55 (Briske et al. 2005; Cramer et al. 2008; Murcia et al. 2014; Alsted et al. 2016). Where native
56 perennial species re-establish in years or decades, management efforts may delay restoration
57 (Rinella et al. 2009). Where alternate-state communities develop or where succession occurs at
58 very slow rates (*i.e.*, centuries), intensive management approaches are likely needed (Cramer et
59 al. 2008).

60 Assessments of long-term patterns of plant community composition are important for
61 understanding how plant communities respond to disturbance and determining appropriate
62 management approaches (Strayer 2012; Flory & D'Antonio 2015). The data needed to assess
63 long-term community dynamics in semi-arid systems, however, is often lacking (Tognetti et al.
64 2010; Yelenik & D'Antonio 2013; Kachergis et al. 2014; Morris et al. 2014). Space-for-time
65 substitutions (or chronosequences) can be used to infer species replacements over long periods.
66 Chronosequence data, however, are susceptible to hidden temporal or spatial variations in factors
67 such as climate, grazing, priority effects, and soil type (Foster & Tilman 2000; Bonet & Pausas
68 2004; Walker et al. 2010; Gill et al. 2018). Direct long-term observations of plant community

69 dynamics can control for these extrinsic factors and provide a better test of community resistance
70 and resilience to changes in species composition but are more difficult to collect (Blossey 1999).

71 Kulmatiski (2006) used a chronosequence approach to describe plant community
72 dynamics in a sage-steppe ecosystem in Washington, USA. Results suggested that non-native
73 and native plants established alternate-state communities in ex-arable fields and never-tilled
74 fields, respectively. It was suggested that disturbance associated with agriculture allowed early-
75 successional, non-native plants to establish, but that once established, these species changed soil
76 conditions in ways that allowed their own persistence (*i.e.*, positive plant-soil feedbacks;
77 Kulmatiski 2006). To provide a more controlled test of how vegetation dynamics change over
78 time, in the present study the same fields in that chronosequence were monitored for an
79 additional 10 years to produce 13-year dataset of direct observation (Fukami & Wardle 2005).
80 Direct observation allows an assessment of how the community in each individual field changes
81 over time. Direct observation also allows an assessment of the effects of several extrinsic factors
82 that were not possible to address during the previous study. During the course of this study,
83 roughly half of the ex-arable fields were managed (*i.e.*, tilled, herbicided and seeded) to increase
84 native plant growth, most of the fields were burned in a wildfire in the penultimate year of
85 surveying, and across all sites a biocontrol agent nearly eliminated the dominant non-native
86 plant, *Centaurea diffusa* Lam.

87 We had three objectives in this study. First, we describe community differences in ex-
88 arable and never-tilled fields using 13 years of direct observation data. Second, we use direct
89 observation and chronosequence approaches to determine how the communities in the two fields
90 are changing over time, and if they are changing, at what rate. Differences in the results between

91 the two approaches are discussed. Third, we determine whether management and natural
92 treatments change the trajectories of these communities.

93

94 **Methods**

95

96 *Study area*

97 Research was conducted in the Methow Valley, Washington (WA), USA (48° 37' N, 120° 10'
98 W). Precipitation is seasonal with 250 of 360 mm of annual precipitation falling mostly as snow
99 between October and March (<http://www.ncdc.noaa.gov>). The growing season begins with
100 snowmelt in April and continues until snowfall in November though most native grasses and
101 forbs become dormant by July. Native shrub-steppe communities dominated by *Purshia*
102 *tridentata*, *Pseudoroegneria spicata*, *Lupinus sericeus*, *Artemesia tridentata*, and *Balsamorhizae*
103 *sagittata* occupy most of the hilly landscape, whereas valley bottoms and benches are largely
104 used for agriculture and, once abandoned, are occupied by various non-native species including
105 *Centaurea diffusa* Lam, *Medicago sativa*, *Bromus tectorum*, *Poa bulbosa*, and *Cardaria draba*.
106 Unless otherwise noted species naming follows that of Hitchcock and Cronquist (1973).

107 Aerial photographs were used to identify 25 study sites with fields that had been
108 abandoned from low-input, dryland agriculture (*Triticum aestivum* and *Medicago sativa*)
109 between 1950 and 1999 and that had adjacent undisturbed fields with similar slope, aspect and
110 soils (S1 Table). Henceforth, these field types are referred to as 'ex-arable' and 'never-tilled',
111 respectively. At least 200 m but not more than 25 km separated the 25 sites (elevation range: 630
112 to 1000 m). All sites were located on the Newbon-Concunully association (coarse-loamy, mixed
113 mesic Typic Haploxerolls; Lenfesty 1980).

114

115 *Vegetation sampling*

116 From 5 to 25 June from 2002 to 2015, plant cover by species was determined in 1 m x 1 m
117 quadrats in each of 25 sites. Each of the 25 sites contained an ex-arable field and a paired never-
118 tilled field. In each field, two transects were established. These transects were parallel to and 5 m
119 or 50 m from the historical tillage boundary. Depending on field length, 15 quadrats were placed
120 at an interval of one every 5 to 10 m in each transect. This sampling design (15 quadrats x 2
121 transect distances x 2 field types x 25 sites) produced 1,500 quadrats per year. Data was not
122 available for the 2010 season, so 13 years of data are reported. The total dataset contains species
123 compositions for 18,692 quadrats.

124 Plant cover was measured as percent ground cover using visual estimation by the same
125 observer over the 13 years to the nearest 1% of cover. A 5 x 5 grid in the quadrat helped guide
126 estimation. Due to the number of plots (1,500 each year) and the request of land managers,
127 transects and plots were not permanently marked so that while fields and transects were
128 resampled each year, specific plots were not resampled each year. Visual estimates of percent
129 cover were well correlated with point-intercept-derived estimates of plant cover by species (i.e.,
130 $R^2 = 0.95$ to 0.98 ; Kulmatiski 2006).

131

132 *Management and wildfire history*

133 In 2003 and 2004, the biocontrol agent *Larinus minutus* (Gyllenahal) was released to control the
134 dominant non-native, *Centaurea diffusa* Lam. Between 2005 and 2013, 12 of the ex-arable fields
135 were managed to increase native plant abundance (Appendix Table 1). Management included
136 broad-spectrum herbicide application in the spring followed by two to three passes with a disk

137 harrow at two to four different times over two growing seasons (*e.g.*, spring and fall) prior to a
138 native plant seeding, typically in the fall. In the penultimate year of the study (August 2014),
139 most (15 of the 25) of the sites burned in a wildfire (Appendix Table 1).

140

141 *Statistical analyses*

142 To address our first objective, to test for differences between the two field types, we used non-
143 metric multidimensional scaling analyses (NMS). NMS analyses were conducted on functional
144 group (native annual, non-native annual, native forb, non-native forb, native grass, non-native
145 grass, native perennial, non-native perennial, native shrub) and species matrices using Bray-
146 Curtis dissimilarity matrices. Analysis of similarities (ANOSIM) was used to test for differences
147 in NMS scores between treatments (*i.e.*, ex-arable or never-tilled field; Clarke 1993; Sturrock &
148 Rocha 2000).

149 To further address the first objective, we provide a more detailed analysis of differences
150 in community composition between ex-arable fields and never-tilled fields, and between distance
151 transects (5 and 50 m), using generalized linear mixed models (GLIMM) with a two-way
152 factorial (field type by distance) in a split-plot design with whole plots (fields) in blocks (sites)
153 and the following response variables: native, non-native, grass, forb, annual and perennial.

154 To address the second objective, to assess community composition change over time
155 using both direct observation and chronosequence data, linear trend in the NMS1 scores over
156 years-since-abandonment and comparison of trends were assessed using a linear mixed model. In
157 addition to NMS1 scores, this analysis was done on functional groups and species (five dominant
158 in each field type). Fixed effects factors were (1) field type (ex-arable or never-tilled); (2) years-
159 since-abandonment; (3) mean number of years-since-abandonment; (4) interaction of field type

160 with years-since-abandonment, which allowed the estimate of the within-field slope of the
161 regression of NMS1 scores on number of years-since-abandonment to differ for ex-arable and
162 never-tilled fields; and (5) interaction of field type with mean number of years-since-
163 abandonment, which allowed the estimate of the between-field slope of the regression to differ
164 for ex-arable and never-tilled fields (van de Pol and Wright 2009). Random effects factors were
165 study site and field-within-study-site, which allowed for random intercepts for fields in the
166 regressions of NMS1 scores on the number of years-since-abandonment. Covariance among the
167 13 annual repeated measures on a field was modeled using a first-order autoregressive structure.
168 We also fitted a model that allowed for random slopes among field regressions; there was no
169 statistical support for random slopes so we present results for the model with only random
170 intercepts. Number of years-since-abandonment was within-field centered prior to analysis. For
171 simplicity, only data from 50 m transects were analyzed.

172 To test for management effects in ex-arable fields, the third objective, regressions of
173 NMS scores were conducted for managed and unmanaged fields separately. To test for
174 biocontrol effects on the target non-native plant, *C. diffusa*, a one-way GLIMM with year as the
175 factor and field as the random variable was used to test for differences in cover in each
176 community. To test for the effects of wildfire, differences in NMS values in 2015 were compared
177 to average NMS values from 2002 to 2014, using a t-test for each field type separately.

178 All multivariate analyses were performed in R using the LabDSV library (Roberts 2016;
179 Team 2004; Appendix). Regressions and GLIMMs were conducted using the Reg and
180 GLIMMIX procedures in SAS v.9.4 TS1M4 for Windows (SAS Institute, Cary, North Carolina,
181 USA; Appendix).

182

183 **Results**

184

185 *Community composition in ex-arable and never-tilled fields*

186 NMS of the direct observation data revealed differences in functional group and species
187 composition between ex-arable fields and never-tilled fields (ANOSIM statistic = 0.486, 0.444, P
188 < 0.001 , $P < 0.001$ for functional group and species matrices, respectively, Fig 1). NMS axis 1
189 scores distinguished differences in plant community composition between ex-arable fields and
190 never-tilled fields, while NMS axis 2 scores distinguished differences in plant community
191 composition among fields and the 13 years of observation (Fig 1).

192 Differences in plant functional group composition between ex-arable and never-tilled
193 fields helped explain community-level differences indicated by NMS (Fig 2; Table 1). Non-
194 natives, annuals and forbs were more abundant in ex-arable than never-tilled fields (Fig 2; Table
195 1). There was no difference in grass abundance between ex-arable and never-tilled fields.

196

197 *Community composition across time*

198 There was evidence for an effect of field type ($F_{1,22} = 44.44$, $P < 0.001$) and effect of time during
199 direct observation on plant community composition ($F_{1,78} = 4.88$, $P = 0.030$; Fig 3). The effect of
200 time during direct observation was significant for ex-arable fields ($F_{1,78} = 2.21$, $P = 0.030$, slope
201 $= 0.007$), but not for never-tilled fields ($F_{1,78} = 0.00$, $P = 1.00$). There was no effect of time for
202 the chronosequence data (*i.e.*, between-plot slope) for ex-arable ($F_{1,22} = -1.28$, $P = 0.213$) or
203 never-tilled fields ($F_{1,22} = -0.65$, $P = 0.520$; Fig 3).

204 Non-native plant abundance did not change across the chronosequence in ex-arable or
205 never-tilled fields ($F_{1,23} = 0.00$, $P = 0.974$; S1 Fig), but non-native abundance did decrease in ex-

206 arable fields during direct observation ($F_{1,48} = 6.49$, $P = 0.014$) at a rate of -0.84% cover per year
207 (S1 Fig). Native plant abundance did not change across the chronosequence ($F_{1,46} = 0.75$, $P =$
208 0.391), but native abundance decreased in never-tilled fields during direct observation ($F_{1,46} =$
209 7.2, $P = 0.010$) at a rate of -0.67% cover per year (S1 Fig).

210 Among native plant species, *A. tridentata* cover did not change during direct observation
211 ($F_{1,106} = 0.02$, $P = 0.895$; Appendix Fig 2) or the chronosequence ($F_{1,11} = 4.07$, $P = 0.069$; data
212 not shown). *B. sagittata* cover did not change during direct observation ($F_{1,86} = 1.54$, $P = 0.218$)
213 or the chronosequence ($F_{1,11} = 0.67$, $P = 0.432$). *L. sericeus* cover increased in ex-arable fields
214 during direct observation ($F_{1,69} = 3.28$, $P = 0.002$, slope = 0.23% per year) but not during the
215 chronosequence ($F_{1,22} = 0.00$, $P = 0.99$). *P. spicata* cover decreased in never-tilled fields during
216 direct observation ($F_{1,108} = 7.59$, $P = 0.001$, slope = -0.35% per year) but increased across the
217 chronosequence ($F_{1,21} = 2.66$, $P = 0.015$, slope = 0.174). *P. tridentata* cover decreased during
218 direct observation in never-tilled fields ($F_{1,48} = 19.21$, $P < 0.001$, slope = -0.42% per year), but
219 not across the chronosequence ($F_{1,46} = 0.17$, $P = 0.678$).

220 Among non-native plants, *B. tectorum* cover decreased during direct observation in ex-
221 arable fields ($F_{1,98} = 5.97$, $P = 0.016$; slope = -0.10; S2 Fig) and the chronosequence ($F_{1,22} = 4.30$,
222 $P = 0.050$; slope = -0.004% per year; data not shown). *C. diffusa* Lam. cover did not change
223 during direct observation ($F_{1,124} = 0.66$, $P = 0.509$), but decreased across the chronosequence in
224 ex-arable fields ($F_{2,30} = 5.16$, $P = 0.012$; slope = -0.13% per year). *C. draba* cover did not change
225 during direct observation ($F_{1,48} = 2.00$, $P = 0.164$) or the chronosequence ($F_{1,23} = 0.65$, $P = 0.43$).
226 *M. sativa* cover did not change across direct observation ($F_{1,48} = 0.35$, $P = 0.558$) or the
227 chronosequence ($F_{1,23} = 1.15$, $P = 0.295$). *P. bulbosa* cover decreased during direct observation

228 in both field types ($F_{1,48} = 5.58$, $P = 0.022$; slope = -0.277), but not across the chronosequence
229 ($F_{1,46} = 3.43$, $P = 0.070$).

230

231 *Community composition responses to management, biocontrol and wildfire*

232 When data from managed and unmanaged ex-arable fields were analyzed separately,
233 communities in unmanaged fields became more similar to never-tilled fields while communities
234 in managed fields did not show a directional change in composition [i.e., NMS axis 1 values
235 increased with time in unmanaged fields ($F_{1,11} = 18.38$, $P = 0.001$), but not in managed fields
236 ($F_{1,10} = 2.07$, $P = 0.18$; data not shown)]. In response to biocontrol treatment, cover of the target,
237 *C. diffusa* Lam., decreased to near zero in 2003 and 2004 and increased to become a dominant
238 species in 2014 and 2015 (S2 Fig). In ex-arable fields, NMS axis 1 scores did not differ before
239 and after wildfire ($T_{23} = 0.43$, $P = 0.67$, Fig 4). However, in never-tilled fields, NMS axis 1
240 values were smaller after wildfire indicating that these fields became more like ex-arable fields
241 ($T_{23} = 3.90$, $P < 0.001$, Fig 4).

242

243 **Discussion**

244 Agricultural abandonment creates two distinct plant communities in the study system. Fields that
245 have been disturbed by agriculture and abandoned are dominated by short-lived non-natives.
246 Never-tilled fields are dominated by long-lived natives. Thirteen years of direct observation
247 revealed directional changes in both field types. Non-native abundance decreased in ex-arable
248 fields while native abundance decreased in never-tilled fields. These changes made the two
249 communities more similar, but there was little evidence that the two community types would
250 eventually converge because there was little evidence of species exchange between field types.

251 Further, there was no evidence of directional changes in community composition across the
252 chronosequence. In summary, the more-controlled, direct observation approach detected changes
253 in community composition over 13 years, but the chronosequence approach suggests that these
254 changes are unlikely to be realized over longer time periods.

255 Communities in ex-arable and never-tilled fields are distinct (Fig 1). In ex-arable fields,
256 the five most abundant species are non-native, typically live a maximum of 1 to 10 years
257 (Rumbaugh 1982) and demonstrate wide fluctuations in percent cover from year to year (Fig 1
258 and S2 Fig). These ‘weedy’ communities have fewer species, less perennial cover, and more
259 annual and forb cover than communities in never-tilled fields. In contrast, the five most abundant
260 species in never-tilled fields are native, often live more than 10 years (Rumbaugh 1982), and
261 demonstrate more stable abundances over annual and decadal time scales.

262 While plant communities in ex-arable fields remained distinct from communities in
263 never-tilled fields for 65 years, there was some evidence of directional change in community
264 composition in the 13 years of direct observation. Multivariate analyses suggested that plant
265 communities in ex-arable fields were becoming more similar to plant communities in never-tilled
266 fields (i.e., NMS 1 values increased in ex-arable fields during direct observation; Fig 3). This
267 was consistent with a decline in the abundance of *B. tectorum* and *P. bulbosa*. Both species are
268 small-statured, winter-active, non-native grasses that are dominant in ex-arable fields but
269 uncommon in never-tilled fields. The only evidence that native species were becoming more
270 abundant in ex-arable fields over time was for the N-fixing *L. sericeus*; total native cover in ex-
271 arable fields did not change during direct observation or the chronosequence. Thus, while two
272 common non-natives decreased and one native species increased, there was little evidence that
273 ex-arable communities would return to native community composition over 50 to 100 year

274 timescales. In contrast to ex-arable fields, there was no directional change in whole-community
275 composition in never-tilled fields during direct observation. At the functional group and species-
276 levels, however, there were declines in native plant abundance reflecting a decline in the
277 common shrub, *Purshia tridentata*. There was no evidence that non-native plants were invading
278 never-tilled fields. Broadly, direct observation data appeared sensitive to detecting within-
279 community changes in species composition, but chronosequence data suggested that
280 communities will remain dissimilar over long (60+) time periods.

281 There are several reasons why direct observation data may have revealed different
282 patterns in community composition than chronosequence data (Johnson and Miyanishi 2008).
283 First, unlike chronosequence data, direct observation data are not confounded by space-for-time
284 substitutions. For example, differences in community composition among fields can ‘mask’
285 within-community changes over time in chronosequence datasets (Foster & Tilman 2000; Bonet
286 & Pausas 2004; Walker et al. 2010; Gill et al. 2018). Second, shorter-term, direct observation
287 data are more likely to detect short-term linear patterns, even if longer-term patterns are non-
288 linear. It is likely, for example, that weedy communities shift from annual to perennial
289 dominance over five to ten year timescales, but that these communities then maintain dominance
290 by perennial non-natives indefinitely. While the direct observation approach appeared more
291 controlled and more sensitive to detecting community level changes, the inference it provides to
292 community composition in the future is not as strong as from chronosequence data. It is possible,
293 for example, that patterns observed in the direct observation dataset will be periodically ‘reset’
294 by disturbances from pocket gophers, drought, wildfire or human disturbance in ex-arable fields
295 (Kyle et al. 2006; Gill et al. 2018). In any case, the patterns observed during direct observation
296 are unlikely to be maintained over longer time periods because 1) these directional changes were

297 not observed in the chronosequence and 2) plant cover was observed to decline in both field
298 types during direct observation, but plant cover cannot be expected to decline indefinitely.

299 It is surprising that native, late-successional species did not recolonize ex-arable fields
300 (Csecserits et al. 2001; Bonet & Pausas 2004; Meiners 2007). Ex-arable fields are typically less
301 than 200 m wide allowing native propagule pressure and results were similar in transects that
302 were 5 m and 50 m from tillage boundaries. Ex-arable fields had less ground cover and more
303 variable populations, which should have provided establishment opportunities for many
304 generations of plants (Richardson & Pyšek 2006; Gill et al. 2018). Species in ex-arable fields
305 likely experienced 30 to 60 generations during the chronosequence (e.g., *C. draba* and *M.*
306 *officinale*; Rumbaugh 1982; Dietz & Schweingruber 2002; Lauenroth and Adler 2008; Chu et al.
307 2014). Even the longest-lived native shrubs in the study system, *A. tridentata* and *P. tridentata*,
308 have mean ages less than 25 years, and realize recruitment events every 2 to 3 years (Krannitz &
309 Hicks 2000; Barry et al. 2001; Maier et al. 2001; Ziegenhagen & Miller 2009; Schlaepfer et al.
310 2014). Thus, establishment, recruitment and mortality were expected in both the direct
311 observation and chronosequence data in both communities (Dalglish et al. 2011), yet these
312 communities remained distinct for 65 years.

313 Results stand in contrast to many studies demonstrating succession over similar time-
314 scales (Foster & Tilman 2000; Csecserits et al. 2001; Bonet & Pausas 2004; Keeley et al. 2006;
315 Meiners 2007; Li et al. 2016). It is not clear why succession would be rapid in some systems and
316 not in others (Didham et al. 2005), though arid and semi-arid systems seem to be more likely to
317 show very slow to no change (Stylinski & Allen 1999; Jackson & Bartolome 2002; Kulmatiski
318 2006; Kachergis et al. 2014) relative to more mesic systems (Rejmanek 1996; Bonet & Pausas
319 2004; MacDougall & Turkington 2005; Sojneková & Chytrý 2015). It is possible that slow

320 succession or alternate-state communities are more likely in more stressful environments with
321 greater facilitation (Flory & Bauer 2014; He & Bertness 2014; Michalet et al. 2014).

322 Direct observation data provided some insight into the processes through which short-
323 lived non-natives may maintain dominance. It is particularly notable that the dominant species in
324 ex-arable fields were resilient from changes in abundance. Perhaps the most dramatic example
325 was that *C. diffusa* Lam. abundance declined to almost zero following the introduction of a
326 biocontrol agent in 2003, then again become the dominant non-native species in 2014 and 2015.
327 The temporary loss of *C. diffusa* Lam. was notable, but it was not the only source of variation in
328 species abundances in ex-arable fields; most of the dominant species in ex-arable fields
329 demonstrated large year-to-year changes in abundance. In addition to being resilient from
330 changes in abundance, ex-arable communities were resistant to changes caused by management
331 and wildfire. Active and intensive management failed to shift ex-arable communities toward the
332 composition of never-tilled fields and wildfire had no effect on ‘weediness’ in ex-arable fields
333 (Fig 4). Together, these results illustrate that ex-arable plant communities were either resistant to
334 or resilient from large disturbances (*i.e.*, biocontrol addition, native plant restoration efforts or
335 wildfire; Klinger et al. 2017; Monaco et al. 2017).

336 Previous research at this and other sites suggests that facilitation among non-natives is
337 more likely than agricultural legacies in explaining non-native persistence in ex-arable fields. For
338 example, soil biological and nutrient traits were better associated with plant origin than
339 agricultural history (Kulmatiski et al. 2006; Kulmatiski & Beard 2008). Once established in
340 disturbed soils, non-native plants have been found to 1) create unique soil microbial communities
341 (Kulmatiski et al. 2006; Stark and Norton 2015), 2) create soils with low penetration resistance
342 (Kyle et al. 2007; Kyle et al. 2008), and 3) change water-use patterns in ways that inhibit the

343 germination and establishment of native plants (Warren et al. 2015). In short, non-natives appear
344 to create an environment that facilitates the growth of short-lived species and delays succession.

345

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352

353 *Data accessibility*: Upon acceptance, data will be made available at Utah State University Digital

354 Commons (https://digitalcommons.usu.edu/all_datasets/) and by contacting the author.

References

- Alsted, A.O., Damschen E.I., Givnish T.J., Harrington J.A., Leach M.K., Rogers D.A., Waller D.M. (2016). The pace of plant community change is accelerating in remnant prairies. *Science Advances*, 2 (2). DOI: 10.1126/sciadv.1500975
- Barry, L.P., Aaron, M.M., Ann, L.H. & Olson, R.A. (2001). Demographic characteristics of 3 *Artemisia tridentata* Nutt. subspecies. *Journal of Range Management*, 54: 166-170.
- Blossey, B. (1999). Before, During and after: The need for long-term monitoring in invasive plant species management. *Biological Invasions*, 1, 301-311.
- Bonet, A. & Pausas, J.G. (2004). Species richness and cover along a 60-year chronosequence in ex-arable fields of southeastern Spain. *Plant Ecology*, 174, 257-270.
- Briske, D.D., Fuhlendorf, S.D. & Smeins, F.E. (2005). State-and-transition models, thresholds, and rangeland health: A synthesis of ecological concepts and perspectives. *Rangeland Ecology & Management*, 58, 1-10.
- Chu, C., Havstad, K.M., Kaplan, N., Lauenroth, W.K., McClaran, M.P., Peters, D.P., Vermeire, L.T. & Adler, P.B. (2014). Life form influences survivorship patterns for 109 herbaceous perennials from six semi-arid ecosystems. *Journal of Vegetation Science*, 25. 947-954.
- Clarke, K.R. (1993). Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology*, 18, 117-143.
- Courtois, D.R., Perryman, B.L. & Hussein, H.S. (2004). Vegetation change after 65 years of grazing and grazing exclusion. *Journal of Range Management*, 57, 574-582.
- Cramer, V.A., Hobbs, R.J. & Standish, R.J. (2008). What's new about old fields? Land abandonment and ecosystem assembly. *Trends in Ecology & Evolution*, 23, 104-112.

- Csecserits, A., xf, xe & dei, T. (2001). Secondary succession on sandy ex-arable fields in Hungary. *Applied Vegetation Science*, 4, 63-74.
- Dalgleish, H.J., Koons, D.N., Hooten, M.B., Moffet, C.A. & Adler, P.B. (2011). Climate influences the demography of three dominant sagebrush steppe plants. *Ecology*, 92, 75-85.
- Didham, R.K., Watts, C.H. & Norton, D.A. (2005). Are systems with strong underlying abiotic regimes more likely to exhibit alternative stable states? *Oikos*, 110, 409-416.
- Dietz, H. & Schweingruber, F.H. (2002). Annual rings in native and introduced forbs of lower Michigan, U.S.A. *Canadian Journal of Botany*, 80, 642-649.
- Elton, C.S. (1958). *The Ecology of Invasions*. Methuen, London.
- Flory, S.L. & Bauer, J.T. (2014). Experimental evidence for indirect facilitation among invasive plants. *Journal of Ecology*, 102, 12-18.
- Flory, S.L. & D'Antonio, C.M. (2015). Taking the long view on the ecological effects of plant invasions. *American Journal of Botany*, 102, 817-818.
- Foster, B.L. & Tilman, D. (2000). Dynamic and static views of succession: Testing the descriptive power of the chronosequence approach. *Plant Ecology*, 146, 1-10.
- Fukami, T. & Wardle, D.A. (2005). Long-term ecological dynamics: reciprocal insights from natural and anthropogenic gradients *Proceedings of the Royal Society B*, 272, 2105-2115.
- Gill, R.A., O'Connor, R.C., Rhodes, A., T.B.B. Bishop, D.C. Laughlin, S.B. St. Clair. (2018). Niche opportunities for invasive annual plants in dryland ecosystems are controlled by disturbance, trophic interactions, and rainfall. *Oecologia*, 187, 755-765.
- He, Q. & Bertness, M.D. (2014). Extreme stresses, niches, and positive species interactions along stress gradients. *Ecology*, 95, 1437-1443.

- Hitchcock, C.L. & Cronquist, A. (1973). *Flora of the Pacific Northwest*. University of Washington Press, Seattle, WA.
- Jackson, R.D. & Bartolome, J.W. (2002). A state-transition approach to understanding nonequilibrium plant community dynamics in Californian grasslands. *Plant Ecology*, 162, 49-65.
- Jauni, M., Gripenberg, S. & Ramula, S. (2015). Non-native plant species benefit from disturbance: a meta-analysis. *Oikos*, 124, 122-129.
- Johnson, E.A. & Miyanishi, K. (2008). Testing the assumptions of chronosequences in succession. *Ecology Letters*, 11, 419-431.
- Kachergis, E., Rocca, M.E. & Fernández-Giménez, M.E. (2014). Long-term vegetation change provides evidence for alternate states in silver sagebrush. *Rangeland Ecology & Management*, 67, 183-194.
- Keeley, J.E., Fotheringham, C. & Baer-Keeley, M. (2006). Demographic patterns of postfire regeneration in mediterranean climate shrublands of California. *Ecological Monographs*, 76, 235-255.
- Klinger, R., Brooks, M. and D'Antonio, C. (2017). Alternative pathways to landscape transformation: invasive grasses, burn severity and fire frequency in arid ecosystems. *Journal of Ecology*, 105, 1521-1533.
- Krannitz, P.G. & Hicks, S.L. (2000). Browsing of antelope bitterbrush (*Purshia tridentata*: Rosaceae) in the south Okanagan valley, British Columbia, Age preferences and seasonal differences. *The American Midland Naturalist*, 144, 109-122.
- Kulmatiski, A. (2011). Changing soils to manage plant communities: activated carbon as a restoration tool in ex-arable fields *Restoration Ecology*, 19, 102-110.

Kulmatiski, A. (2006). Exotic plants establish persistent communities. *Plant Ecology*, 187, 261-275.

Kulmatiski, A. & Beard, K.H. (2008). Decoupling plant-growth from land-use legacies in soil microbial communities. *Soil Biology & Biochemistry*, 40, 1059-1068.

Kulmatiski, A., Beard, K.H. & Stark, J.M. (2006). Soil history as a primary control on plant invasion in abandoned agricultural fields. *Journal of Applied Ecology*, 43, 868-876.

Kyle, G.P., Beard, K.H. & Kulmatiski, A. (2007). Reduced soil compaction enhances the establishment of non-native plant species. *Plant Ecology*, 193, 223-232.

Kyle, G.P., Kulmatiski, A. & Beard, K.H. (2008). Influence of pocket gopher mounds on nonnative plant establishment in a shrub steppe ecosystem. *Western North American Naturalist*, 68, 374-381.

Lauenroth, W.K. & Adler, P.B. (2008). Demography of perennial grassland plants: survival, life expectancy and life span. *Journal of Ecology*, 96, 1023-1032.

Lenfesty, C.D. (1980). *Soil Survey of Okanogan County Area, Washington*. National Cooperative Soil Survey.

Li, S.-p., Cadotte, M.W., Meiners, S.J., Pu, Z., Fukami, T. & Jiang, L. (2016). Convergence and divergence in a long-term ex-arable succession: the importance of spatial scale and species abundance. *Ecology Letters*, 19, 1101-1109.

MacDougall, A.S. & Turkington, R. (2005). Are invasive species the drivers or passengers of change in degraded ecosystems? *Ecology*, 86, 42-55.

Maier, A.M., Perryman, B.L., Olson, R.A. & Hild, A.L. (2001). Climatic influences on recruitment of 3 subspecies of *Artemisia tridentata*. *Journal of Range Management*, 54, 699-703.

- Meiners, S.J. (2007). Native and exotic plant species exhibit similar population dynamics during succession. *Ecology*, 88, 1098-1104.
- Michalet, R., Le Bagousse-Pinguet, Y., Maalouf, J.-P. & Lortie, C.J. (2014). Two alternatives to the stress-gradient hypothesis at the edge of life, the collapse of facilitation and the switch from facilitation to competition. *Journal of Vegetation Science*, 25, 609-613.
- Monaco, T.A., J.M. Mangold, B.A. Meador, R.D. Meador & C.S. Brown. (2017). Downy brome control and impacts on perennial grass abundance: A systematic review spanning 64 years. *Rangeland Ecology & Management*, 70, 396-404.
- Morris, L.R., Monaco, T.A. & Sheley, R.L. (2014). Impact of cultivation legacies on rehabilitation seedings and native species re-establishment in Great Basin shrublands. *Rangeland Ecology & Management*, 67, 285-291.
- Murcia, C., Aronson, J., Kattan, G.H., Moreno-Mateos, D., Dixon, K. & Simberloff, D. (2014). A critique of the 'novel ecosystem' concept. *Trends in Ecology & Evolution*, 29, 548-553.
- Myers, J.A. & Harms, K.E. (2009). Seed arrival, ecological filters, and plant species richness: a meta-analysis. *Ecology Letters*, 12, 1250-1260.
- Rejmanek, M. (1996). A theory of seed plant invasiveness: The first sketch. *Biological Conservation*, 78, 171-181.
- Richardson, D.M. (2011). Fifty years of invasion ecology: The legacy of Charles Elton. In, pp. 432. Wiley-Blackwell, New Jersey.
- Richardson, D.M. & Pyšek, P. (2006). Plant invasions: merging the concepts of species invasiveness and community invasibility. *Progress in Physical Geography*, 30, 409-431.

- Rinella, M.J., Maxwell, B.D., Fay, P.K., Weaver, T. & Sheley, R.L. (2009). Control effort exacerbates invasive-species problem. *Ecological Applications*, 19, 155-162.
- Roberts, David W. (2016).. labdsv: Ordination and multivariate analysis for ecology. R package version 1.8-0. <https://CRAN.R-project.org/package=labdsv>
- Rumbaugh, M.D. (1982). Reseeding by eight alfalfa populations in a semiarid pasture. *Journal of Range Management*, 35, 84-86.
- Schlaepfer, D.R., Lauenroth, W.K. & Bradford, J.B. (2014). Natural regeneration processes in big sagebrush (*Artemisia tridentata*). *Rangeland Ecology & Management*, 67, 344-357.
- Sojneková, M. & Chytrý, M. (2015). From arable land to species-rich semi-natural grasslands: Succession in abandoned fields in a dry region of central Europe. *Ecological Engineering*, 77, 373-381.
- Stark, J.M. and J.M. Norton. (2015). The invasive annual cheatgrass increases nitrogen availability in 24-year-old replicated field plots. *Oecologia*, 177, 799-809.
- Strayer, D.L. (2012). Eight questions about invasions and ecosystem functioning. *Ecology Letters*, 15, 1199-1210.
- Sturrock, K. & Rocha, J. (2000). A Multidimensional scaling stress evaluation table. *Field Methods*, 12, 49-60.
- Stylinski, C.D. & Allen, E.B. (1999). Lack of native species recovery following severe exotic disturbance in southern Californian shrublands. *Journal of Applied Ecology*, 36, 544-554.
- Team, R.C.R. (2004). R: A language and environment for statistical computing. In. R Foundation for Statistical Computing, Vienna, Austria.

- Tognetti, P.M., Chaneton, E.J., Omacini, M., Trebino, H.J. & León, R.J.C. (2010). Exotic vs. native plant dominance over 20 years of ex-arable succession on set-aside farmland in Argentina. *Biological Conservation*, 143, 2494-2503.
- van de Pol, M. and Wright J. (2009). A simple method for distinguishing within- versus between-subject effects using mixed models. *Animal Behavior*, 77, 753-758
- Walker, L.R., Wardle, D.A., Bardgett, R.D. & Clarkson, B.D. (2010). The use of chronosequences in studies of ecological succession and soil development. *Journal of Ecology*, 98, 725-736.
- Warren, C.P., Kulmatiski, A. & Beard, K.H. (2015). A combined tracer/evapotranspiration model approach estimates plant water uptake in native and non-native shrub-steppe communities. *Journal of Arid Environments*, 121, 67-78.
- Yelenik, S.G. & D'Antonio, C.M. (2013). Self-reinforcing impacts of plant invasions change over time. *Nature*, 503, 517-520.
- Ziegenhagen, L.L. & Miller, R.F. (2009). Postfire recovery of two shrubs in the interiors of large burns in the intermountain west, USA. *Western North American Naturalist*, 69, 195-205.

Table 1. Mean cover of dominant plant species and functional groups and several community traits in adjacent ex-arable and never-tilled fields, Methow Valley, Washington, USA. Cover values within fields (replicate plots) and among years were averaged prior to calculations so that values represent averages and standard errors associated with the 25 fields.

Measure	Ex-arable fields	Never-tilled fields
Species richness	5.4 ± 0.3 b	6.6 ± 0.3 a
Ground Cover (%)	59.2 ± 1.2 b	68.6 ± 1.6 a
Native:	19.2 ± 1.8 b	62.4 ± 2.1 a
<i>Pseudoroegneria spicata</i>	2.8 ± 1.2 b	18.9 ± 1.3 a
<i>Balsamorhiza sagittata</i>	0.4 ± 0.1 b	15.3 ± 1.9 a
<i>Purshia tridentata</i>	0.1 ± 0.0 b	4.8 ± 0.9 a
<i>Lupinus</i> spp.	2.3 ± 0.5 b	4.3 ± 0.5 a
<i>Artemisia tridentata</i>	0.1 ± 0.0 b	2.4 ± 0.8 a
Non-native:	39.6 ± 2.1 a	6.6 ± 0.8 b
<i>Medicago sativa</i>	7.1 ± 1.7 a	0.3 ± 0.1 b
<i>Poa bulbosa</i>	5.9 ± 0.9 a	1.7 ± 0.3 b
<i>Centaurea diffusa</i>	5.1 ± 0.8 a	0.2 ± 0.1 b
<i>Bromus tectorum</i>	4.5 ± 0.7 a	1.4 ± 0.3 b
<i>Cardaria draba</i>	4.3 ± 0.1 a	0.1 ± 0.1 b
Native annual	4.4 ± 0.7 b	2.0 ± 0.2 a
Native forb	7.9 ± 1.0 a	8.2 ± 0.6 a
Native grass	9.8 ± 1.5 b	24.0 ± 0.6 a

Native perennial	14.7 ± 1.7 b	60.4 ± 2.1 a
Native shrub	1.2 ± 0.2 b	30.2 ± 2.7 a
Non-native annual	11.3 ± 1.6 a	2.6 ± 0.5 b
Non-native forb	23.8 ± 2.2 a	3.1 ± 0.4 b
Non-native grass	15.8 ± 1.6 a	3.5 ± 0.5 b
Non-native perennial	28.3 ± 2.4 a	4.0 ± 0.5 b
Non-native shrub	0.0 ± 0.0 a	0.0 ± 0.0 a
Annual	15.8 ± 1.8 a	4.6 ± 0.6 b
Forb	31.7 ± 2.3 a	11.3 ± 0.8 b
Grass	25.7 ± 1.8 a	27.4 ± 1.3 a
Perennial	42.9 ± 1.8 b	64.4 ± 1.9 a
Shrub	1.2 ± 0.2 b	30.2 ± 2.7 a

¹ Values represent the average from thirty quadrats and 13 sampling years in each plant community in 25 fields (n = 25). The SE represents the error associated with the 25 fields and not error associated with quadrats, transects, or years.

² Values in the same row followed by the same letter were not significantly different at the 0.05 level.

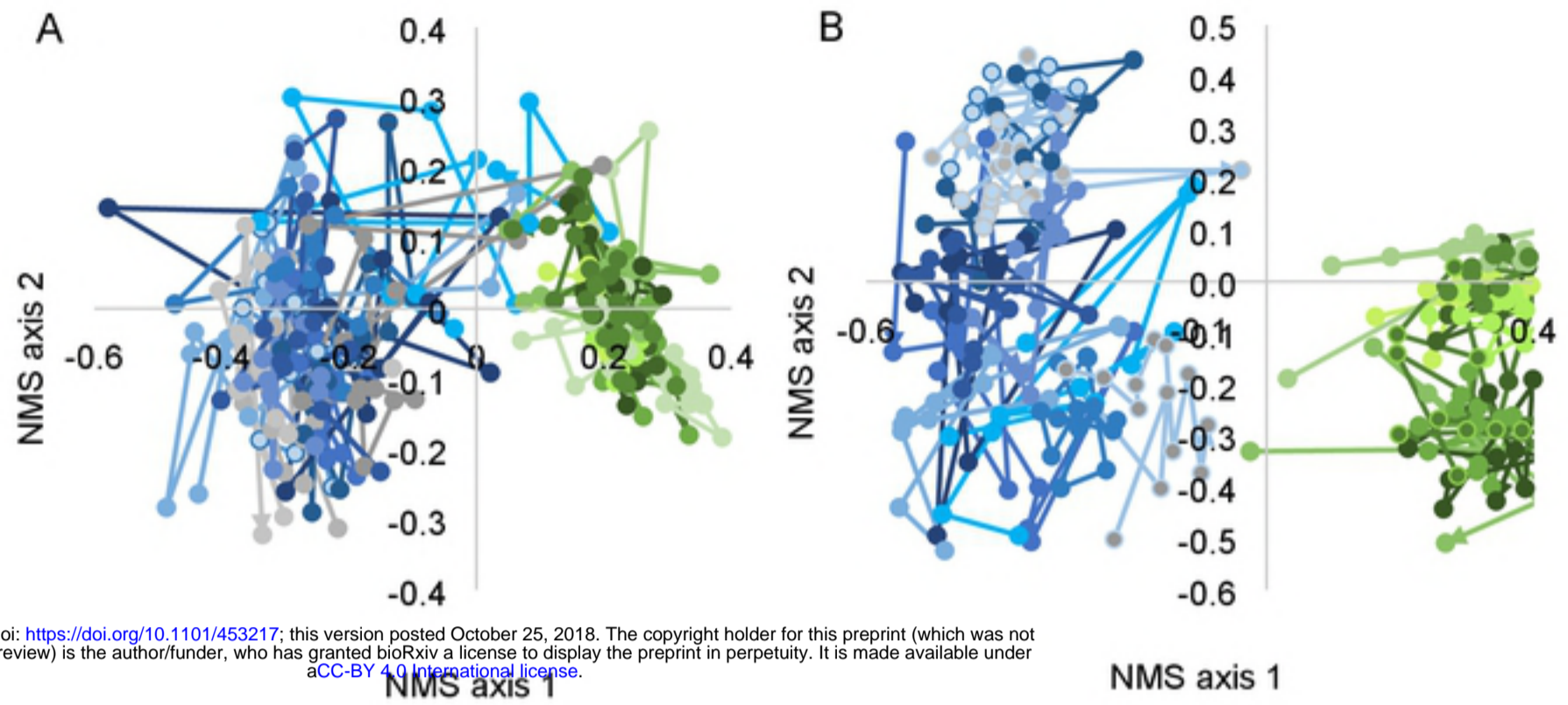


Fig. 1. Non-metric multidimensional scaling (NMS) graph by (A) functional group and (B) species of plant community composition in adjacent ex-arable fields (blue colors) and never-tilled fields (green colors) over 13 years. Each point represents the mean composition of vegetation across a transect located 50 m from a tillage boundary. Lines connect values from a field over 13 years of direct observation. For clarity, data from 12 of 25 randomly selected sites is shown.

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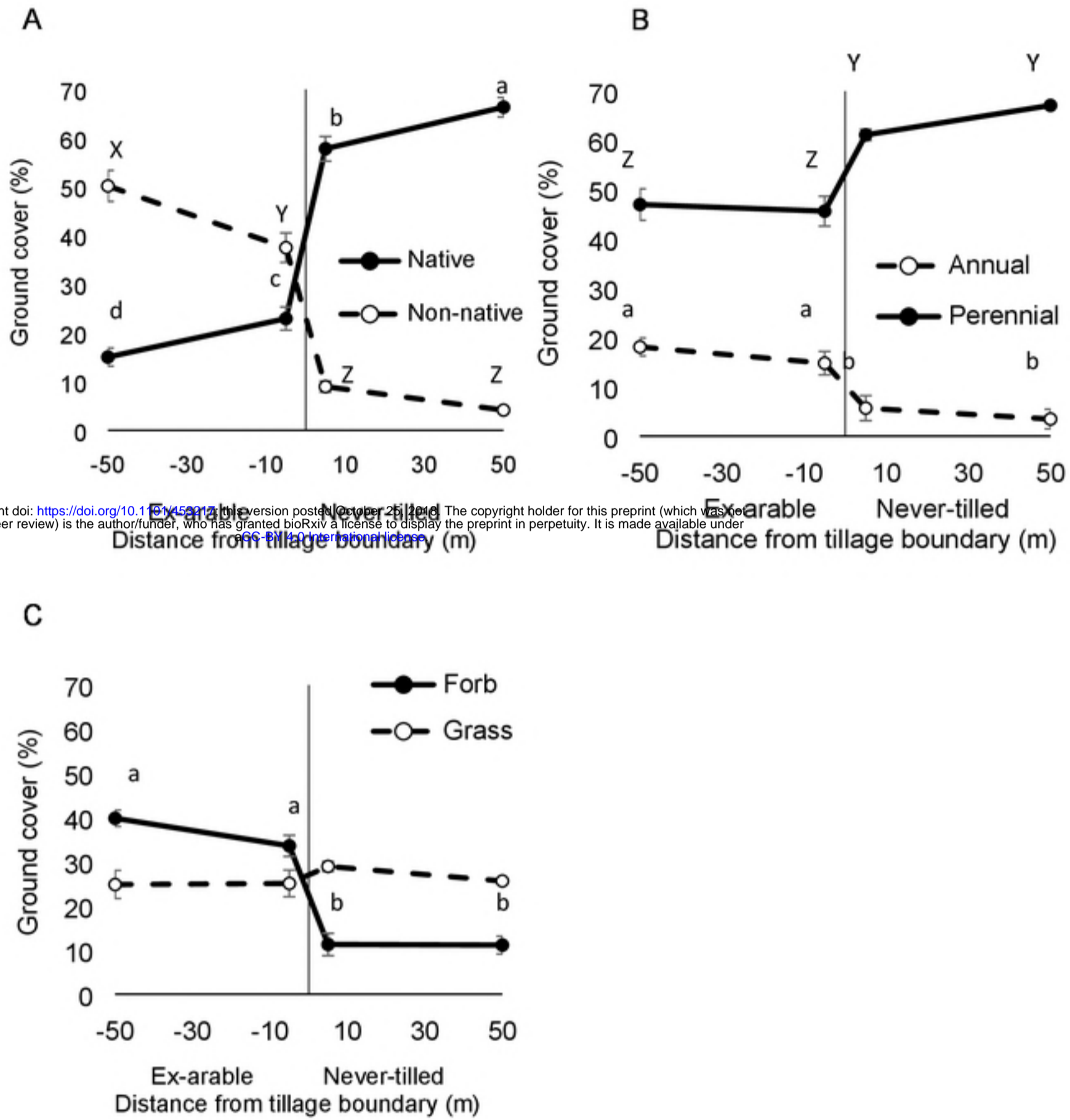


Fig. 2. Percent ground cover of (A) native and non-native plants, (B) annual and perennial plants, and (C) forbs and grasses across tillage boundaries. Negative x-axis values are in ex-arable fields. Positive x-axis values are in never-tilled fields. Values represent the mean and standard error associated with the 25 sampled fields (values from replicate plots and years were averaged prior to calculations). Different letters are different at the $\alpha = 0.05$ level.

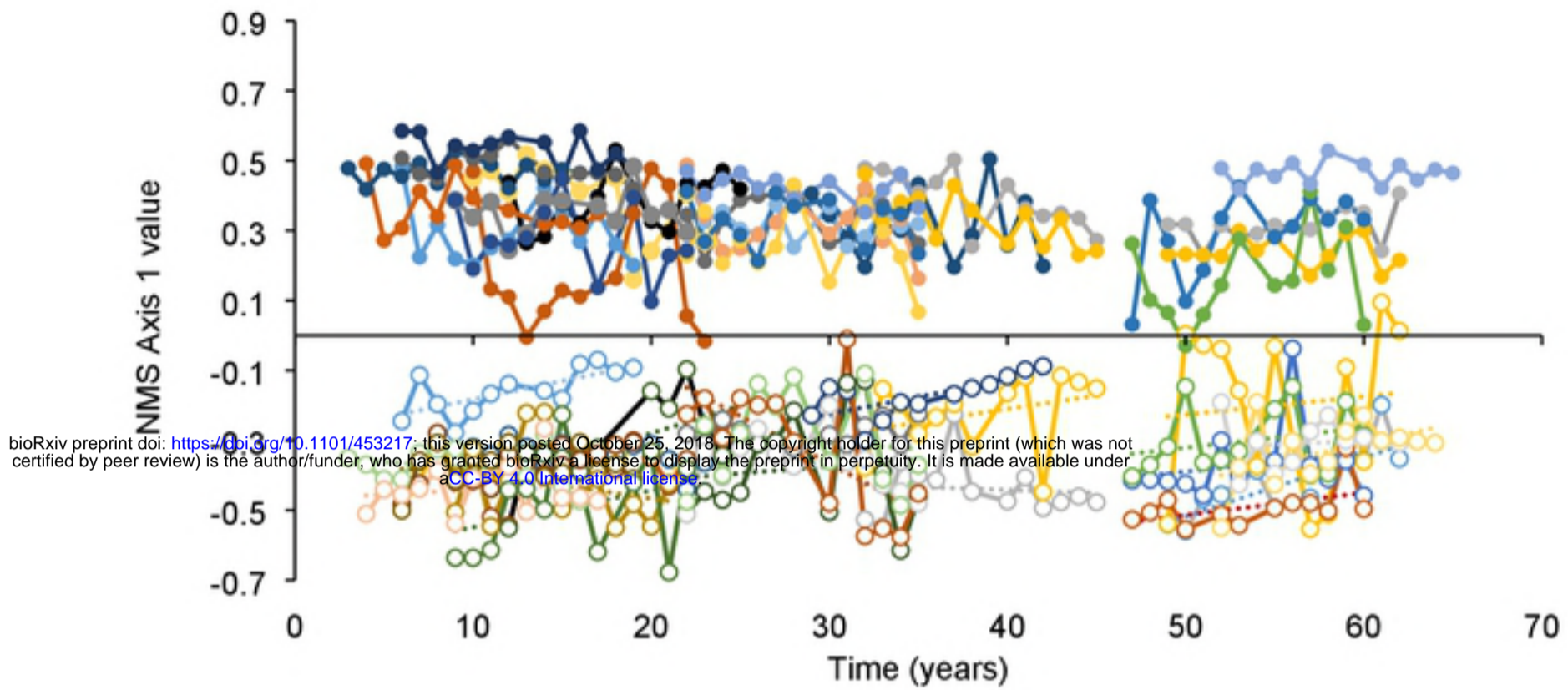
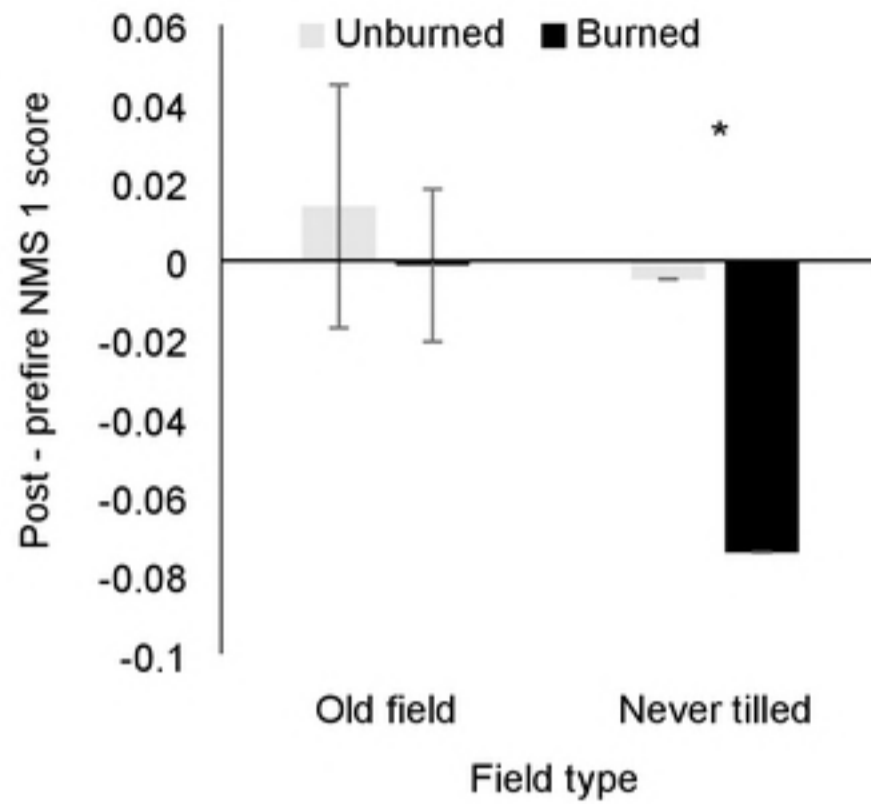


Fig. 3. NMS axis 1 scores (species matrix) over time. Data from ex-arable fields shown with open symbols and data from never-tilled fields shown with filled symbols. Data from transects located 50 m from tillage boundaries. Positive y-axis values were associated with native, long-lived perennial communities (Table 1; Fig. 1). NMS 1 values increased with time during 13 years of observation in ex-arable fields, but did not change with time in never-tilled communities or across the chronosequence in either community type.



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Fig. 4. Change in NMS axis 1 values after a wildfire in 2014. Values calculated as the difference between 2015 scores and the average of 2002 to 2014 values. Positive NMS axis 1 scores were associated with weediness (Fig. 1). An asterisk indicates a difference between Unburned and Burned values at the $\alpha = 0.05$ level.