



The legacy of deer overabundance: long-term delays in herbaceous understory recovery

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1 **Title:** The legacy of deer overabundance: long-term delays in herbaceous understory recovery

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55 **Abstract**

56 Decades of white-tailed deer overpopulation have dramatically homogenized forests across much
57 of the eastern United States, creating depauperate forest understory communities. It remains an
58 open question the rate at which these communities recover once deer browsing has been reduced.
59 We evaluate overbrowsing legacy effects by examining how forest herbaceous layers respond in
60 terms of biodiversity, density, and community composition over 11 years using exclosures and
61 control plots within a mature beech-maple forest. Although little recovery occurred in the first 5
62 years, total density and preferred-browse density rebounded substantially during the final years
63 of the study. Although community composition began to diverge between exclosure and control
64 plots after 5 years, diversity failed to recover even after 11 years of excluding browsers. Our
65 findings show that vulnerable species can increase after excluding browsers but only if those
66 species were initially present. Biodiversity recovery may be extremely slow because preferred
67 browse species have been nearly extirpated from many forests and thus unable to recruit into
68 refugia. We empirically demonstrate the extent of the ghost of herbivory past or legacy effect of
69 browsing: the substantial time delay between herbivore abatement and community response after
70 decades of high deer densities.

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75 **Keywords:** white-tailed deer, *Odocoileus virginianus*, herbivory, understory, forest recovery

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88 Introduction

89 In many areas of the United States, the population density of white-tailed deer
90 (*Odocoileus virginianus*) has dramatically increased over the past century to levels significantly
91 greater than pre-settlement estimates (Horsley et al. 2003; McCabe and McCabe 1997; Porter et
92 al. 1994). Deer display browse preferences among forest plant species, largely based on plant
93 chemical defenses and nutrient content (Augustine and McNaughton 1998; Berteaux et al. 1998;
94 Dostaler et al. 2011; Whitney 1984). Prolonged and selective overbrowsing by deer has strong
95 impacts on population and community level processes, including reducing recruitment,
96 diminishing sizes, and shifting communities towards dominance by a small subset species that
97 are browse-tolerant, browse resistant or both (Coté et al. 2004; Goetsch et al. 2011; Horsley et al.
98 2003; Rooney and Waller 2003; Waller 2014). In addition, in some cases, decades of
99 overbrowsing can cause dramatic increases in browse tolerant species that can spread to form
100 dense and recalcitrant understory layers (Royo and Carson 2006; Young and Peffer 2010).
101 These recalcitrant layers are often inimical to the recovery of vulnerable species even when
102 browsing intensity is reduced or eliminated entirely (Royo and Carson 2006; Royo and Carson
103 2008). Consequently, under heavy browsing pressure, tolerant or resistant species will spread
104 while palatable or preferred species will become uncommon and sparsely distributed across the
105 landscape (for reviews, see Carson et al. 2014; Waller 2014)

106 Forest herbaceous species are especially sensitive to over-browsing by deer because they
107 cannot reach a size refuge from browsers, as trees can. Thus they are often subjected to repeated
108 bouts of browsing throughout their lifespans, which can severely reduce plant fecundity (Russell
109 et al. 2001). Furthermore, strong herbivore pressures can severely limit sexual reproduction of
110 perennial herbs by clipping flowers, fruit, or early reproductive tissue. For example, Comisky et

111 al. (2005) found that reproductive individuals of several species of wildflowers were two orders
112 of magnitude more abundant on large boulders that served as refugia from deer versus adjacent
113 sites at the soil surface. If herbivore browsing levels remain consistently high, reproduction will
114 be limited or non-existent, and populations of perennial herbs are predicted to dwindle over time
115 (McGraw and Furedi 2005). Although patterns of low-diversity wildflower populations and
116 diminished reproduction are well documented, it remains an open question if plant communities
117 can rebound from chronic overbrowsing if herbivore populations are reduced or eliminated.
118 Long lag times in recovery are especially likely for many of these now low-density herbs due to
119 short dispersal distances, slow rates of growth and reproduction, as well as low genetic diversity,
120 Allee effects, and increased susceptibility to stochasticity (particularly physical disturbances,
121 e.g., Chips et al. 2014). Moreover, their former habitats may now be occupied by a dense and
122 recalcitrant layer of browse tolerant species.

123 Overall, the legacy of deer overabundance or ghost of herbivory past (Banta et al.
124 2005) is likely to delay biodiversity recovery for decades or prevent recovery at all because
125 browsing may have created an alternative stable state (Banta et al. 2005; Carson et al. 2014;
126 Frerker et al. 2014; Royo et al. 2010b; Stromayer and Warren 1997; Tanentzap et al. 2009). In
127 fact, the few studies to date of sufficient duration to evaluate the length of legacy effects strongly
128 suggest that recovery will take decades, particularly for herbs and shrubs (Royo et al. 2010b;
129 Tanentzap et al. 2009). Here, we ask to what degree does excluding deer via exclosures lead to
130 understory recovery within a mature beech-maple forest over 11 years, in terms of plant density,
131 species richness, species diversity, and plant species composition. We predict that long-term
132 deer exclosures will act as refugia for preferred browse wildflower species, increasing the
133 frequency of browse-susceptible understory species and overall diversity over time, relative to

134 areas that experience continual deer browse. However, we predict considerable lag times before
135 communities can recover from decades of intense herbivory.

136

137 **Materials and methods**

138 Site and deer densities: We conducted this experiment in Tryon-Weber Woods in
139 Crawford County, northwestern Pennsylvania, USA (latitude 41°36'N and longitude 80°21'W).
140 This site is within a mesic temperate zone, with yearly rainfall averaging 103 cm and total
141 snowfall averages 165 cm (Linesville, PA weather station). This mature 10-ha beech-maple
142 forest is at least 100 years old and is stewarded by the University of Pittsburgh's Pymatuning
143 Laboratory of Ecology (please see Long et al. 2007 for forest structure details). This forest is
144 partially surrounded by younger secondary forest and exists within a landscape of forest
145 fragments, old-fields, and agriculture (Chips et al. 2014; Long et al. 2007). Although white-tailed
146 deer were nearly extirpated in western Pennsylvania in the late 1800s, deer were reintroduced
147 and grew to large population densities by 1940 and have remained high (Heckel et al. 2010;
148 Smith 1989; Whitney 1984). Deer densities in Crawford County from 1996-1999 averaged ~14
149 deer/km² but summer densities were likely much higher (e.g., 29 deer/km², Wallingford 2000).
150 In this region, densities greater than 8 deer/km² cause woody and herbaceous species declines
151 (Horsley et al. 2003).

152 Herbivore exclusion and plant sampling: Within Tryon-Weber Woods, twelve paired
153 plots, measuring 20m x 20m, were marked out in haphazard locations in March of 1996 (see
154 Chips et al. 2014; Long et al. 2007). Three meters separated paired plots, and treatment
155 (herbivore enclosure or control) was assigned randomly between plot pairs. Enclosure plots had
156 2.4m tall fences with 5cm x 10cm mesh constructed along their perimeter to exclude large

157 herbivores. Within each plot, we established a 15m x 15m inner plot, subdivided into 9 subplots,
158 leaving a 2.5m buffer around each inner plot. No major canopy gaps occurred across these plots
159 for the duration of the study. In late May or early June of 1997, 1998, 1999, 2001, and 2007, we
160 visually estimated the cover of each forb species using area templates of known size (e.g., 1%,
161 5%, etc.) in either 6 (randomly selected) or all 9 subplots within each large plot. Because visual
162 cover estimates can vary among observers among years, we also quantified stem densities in
163 2001 and 2007. We used these data to calculate relative abundance (species cover/total cover),
164 plant density, species richness, Shannon diversity index (as measured by cover and density) and
165 community dissimilarity. We also grouped for analysis four species known to be preferred by
166 deer, specifically *Maianthemum canadense*, *M. racemosa*, *Polygonatum pubescens* and *Trillium*
167 *grandiflorum* (Comisky et al. 2005; Korschgen et al. 1980; Kraft et al. 2004; Mosbacher and
168 Williams 2009). Finally, we also evaluated the impact of exclosures on *Podophyllum peltatum*, a
169 dominant understory species that is unpalatable and never browsed (Cassidy et al. 1982).

170 Statistical analyses: We evaluated whether excluding browsers would alter density,
171 species richness, and diversity over time using Proc Mixed (SAS ver. 9.2, SAS Institute 2008)
172 and performed repeated measures ANOVAs with autoregressive covariance structure. For 2001
173 and 2007 data, we also performed an ANOVA on total density. Analyses were conducted at the
174 subplot level, with a random statement nesting subplot within plot. We used a Satterwaite
175 unequal variance mixed model with a repeated statement (Proc Mixed) to test the effect of deer
176 herbivory on preferred browse density over time (Ruxton 2006). We used identical methodology
177 to test the effect of deer removal on the density of *Podophyllum peltatum*.

178 To test if exclosures created contrasting communities over time, we used a semi-metric
179 Bray-Curtis dissimilarity index and nonparametric MANOVA, conducted in R (R Development

180 Core Team 2011), using the vegan package and Adonis procedure (Oksanen et al. 2007). The
181 Bray-Curtis method and nonparametric MANOVA allow for binary and zero-inflated data sets as
182 well as situations where rare species lead to violations of assumptions of normality required for
183 parametric MANOVA (McArdle and Anderson 2001). The Bray-Curtis dissimilarity index (BC)
184 is

$$185 \quad BC = \frac{\sum_i |X_{ij} - X_{ik}|}{\sum_i (X_{ij} + X_{ik})} \quad [1]$$

186
187 where X_{ij} is the abundance of the i th species in treatment j and X_{ik} is the abundance of
188 the i th species in treatment k (Krebs 1989). Additionally, we repeated the analysis with the Horn
189 and Jaccard dissimilarity index to account for any abundance or sample size bias (Krebs 1989).

191

192 **Results**

193 Species richness. Across the six surveys over an 11-year period, we identified 54 species
194 of herbaceous vines and forbs. In the final census in 2007, we found a total of 38 plant species,
195 24 in control plots and 32 in fenced plots. Excluding deer caused a modest (< 2 species) but
196 significant increase ($p = 0.042$) in mean species richness by 2007 but richness did not increase
197 relative to control plots until after 2001, at least seven years after the fences were built (Figure
198 1A, Table 1). Species richness also increased over time both inside the exclosures and in control
199 plots (Figure 1A, Table 1).

200 Shannon diversity. Excluding browsers did not cause a significant increase in Shannon
201 diversity (Figure 1B, Table 1) but it did increase over time when using both cover and stem
202 densities as abundance metrics ($p=0.0233$, $p < 0.0001$, respectively Figure 1B, Table 1). It is
203 important to point out that there was no significant enclosure by time interaction, thus even after

204 11 years there was no significant increase in Shannon diversity inside the exclosures (Figure 1B,
205 Table 1).

206 Plant cover and density. Because absolute cover data exhibited substantial year-to-year
207 variability, we used our cover data only to look at patterns of relative abundance and community
208 composition using dissimilarity indices (see below). Cover estimates likely varied because of
209 observer bias among years or timing of sampling relative to the onset of warming during each
210 spring among years.

211 Five years after the exclosures were built, excluding browsers had not caused an increase
212 in total plant density or the density of preferred species (Figure 2A,B, Table 1). However, during
213 the next 6 years, excluding browsers caused substantial increases in plant density and nearly all
214 of this (83%) was accounted for by an increase in the density of preferred species (Figure 2A,B
215 Table 1). It is important to note that total density and in particular preferred density also
216 increased significantly over time in control plots but increased most dramatically inside
217 exclosures (exclosure x time interaction for preferred species, Figure 2A,B Table 1).

218 *Podophyllum peltatum*, a species that deer never consume, was 2.5 times more dense in control
219 plots ($p = 0.0291$, Figure 2C, Table 1).

220 Plant community composition. Excluding browsers caused community composition to
221 diverge for all three community dissimilarity indices but only beginning in 2001, five years after
222 erecting the fences (Figure 3, Table 2). This was largely caused by the dominance of *P. peltatum*
223 in the control plots and the increase of preferred species, such as *Mitchella repens* inside the
224 exclosures (Figure 3). *Mitchella repens* was by far the most abundant species (by cover) inside
225 the exclosures by 2007.

226

227 Discussion

228 Within large parts of the Eastern Deciduous Forest Biome, decades of overbrowsing has created
229 depauperate herbaceous communities dominated by browse-tolerant or resistant species (Frerker
230 et al. 2014; Nuttle et al. 2013; Rooney and Dress 1997). In some cases, some of these browse-
231 tolerant or browse-resistant species can spread to form dense and recalcitrant understory layers
232 that are inimical to biodiversity recovery (Royo and Carson 2006). What is far less clear is the
233 amount of time required for herbaceous understory communities to recover their lost diversity.
234 Here, we demonstrate that excluding deer for 11 years did not lead to a significant recovery of
235 biodiversity in terms of species richness or species diversity (Figure 1, Table 2). While species
236 richness did increase significantly inside the exclosures, this increase was modest. We did,
237 however, see a 4-fold increase in the combined density of four preferred species, which were
238 present in the understory at the start of the experiment (Figure 2B). Our results demonstrate that
239 preferred species, *if they are present*, will increase following the exclusion of deer but even these
240 preferred species showed no increase in density during the first five years of deer exclusion.
241 Overall, substantial diversity recovery will likely take much longer than the 11-year duration of
242 this experiment, especially under low light regimes of mature forest (Anderson et al. 1969). Our
243 data, coupled with a few other studies (Royo et al. 2010b; Tanentzap et al. 2011; Tanentzap et al.
244 2009) suggest that even if deer are reduced to zero (excluded) or near zero, lag times in
245 biodiversity recovery will last at least a decade and likely much longer. One bright spot is that
246 species composition inside the fences began to diverge from control plots after 5 years (Table 2)
247 suggesting that some recovery had begun.

248 We were only able to classify 4 species of over 50 as being preferred by deer (*c.f.* Vankat
249 and Snyder 1991). This is not surprising since deer have been over-abundant in the region for

250 well over 50 years (Horsley et al. 2003) and depauperate understories are common throughout
251 the eastern deciduous forest (reviewed by Waller 2014) and, in particular, in Pennsylvania
252 (Carson et al. 2014). Thus, it was no surprise that *Podophyllum peltatum*, which is defended by
253 potent lignans and glycosides (Cassidy et al. 1982) was the dominant understory species in
254 control plots (Figure 3), and it increased in total density during the study (Figure 2C). It is now
255 well known that overbrowsing can lead to an increase in the abundance of resistant or tolerant
256 species and in some cases the formation of dense recalcitrant understory layers that are inimical
257 to biodiversity recovery (Carson et al. 2014; Royo and Carson 2006; Waller 2014; Young and
258 Peffer 2010). Indeed, Carson et al. (2014) demonstrated that even a stand replacement
259 disturbance or canopy gaps will cause few changes in understory diversity or abundance because
260 these disturbances occur over a depauperate understory created by nearly a century of
261 overbrowsing. In contrast, when deer are closer to historical levels, they can promote
262 herbaceous diversity following disturbance by acting as keystone species via reducing the
263 abundance of fast growing woody pioneers (Royo et al. 2010a).

264 One curious feature of our results is that plant species richness, diversity, and density
265 increased over time after 2000 *in the control plots* as well as inside exclosures (Figures 1 and 2).
266 Understory populations can certainly fluctuate with climate, pathogen outbreaks and non-
267 ungulate herbivory (and their interactions, McDowell et al. 2011) and control plots also had low
268 tree seedling densities that continued to decline over time (0.24 and 0.04 stems/m² in 1996 and
269 2005, Long et al. 2007), thus lack of competition may have aided herbaceous response.
270 However, seedling densities in enclosed plots increased but plateaued at ~0.4 stems/m² by 1999
271 (Long et al. 2007), a level that clearly did not significantly hinder population growth of
272 herbaceous species (Figure 2). The substantial herbaceous increase in control plots coincided

273 with a statewide initiative by the Pennsylvania Game Commission designed to bring deer more
274 into balance with their habitat (Frye 2006). This initiative increased antlerless harvests statewide
275 by 55% and total deer harvests by 31% relative to rates in the 1990's (Appendix A, compiled
276 from www.pgc.state.pa.us). This may provide a possible explanation for the observed increases
277 in richness and density outside of the exclosures after 2000. Unfortunately, this conservation-
278 oriented deer management program quickly floundered (Carson et al. 2014; Frye 2006) and deer
279 densities again began to rise in the latter part of the decade (Rosenberry et al. 2011). We should
280 note, however, that Tryon Webber Woods and other forests in the region remain depauperate
281 (Carson et al. 2014; Waller 2014) relative to forests without chronic deer overpopulation. For
282 example, Vankat and Snyder (1991) found 2 to 3 times the number of herbaceous species in
283 similar glacial moraine mature beech-maple forests in Ohio, where deer densities were
284 consistently under 1 deer/km² for decades (ODNR 1996). This was true even though our
285 vegetation surveys cover ~13 times the area sampled by Vankat and Snyder (1991).

286 The next step in understanding legacy effects is to further quantify the severity of these
287 effects in regions both within the Eastern Deciduous Forest biome and biomes elsewhere (e.g.,
288 Wright et al. 2012). Perhaps, however, it is more important to parse out the myriad of potential
289 causes that underlie long lag times in biodiversity and community recovery. Understory species
290 face sparse distributions, slow growth rates, low fecundity, limited dispersal, and Allee effects
291 (Bierzychudek 1982; Handel et al. 1981; Matlack 1994). However, there may be an array of
292 additional hurdles including dense recalcitrant understory layers, low light levels, disruption of
293 mutualisms (e.g., arthropod seed dispersers, pollinators, and mycorrhizal fungi), invasive plant
294 species (e.g., garlic mustard) and exotic earthworms. Many of these factors may be operating
295 simultaneously. Though speculative, all of these factors together may be creating the perfect

296 storm of events that contribute to the development of alternative stable states that may create
297 fundamentally different and depauperate forest herbaceous communities across broad regions
298 (Stromayer and Warren 1997). These communities are already forming for woody species
299 throughout the east (e.g., Nuttle et al. 2013) and in other temperate forests around the world
300 (Askins 2014; Wright et al. 2012).

301 **Conclusions**

302 The chronic high deer densities throughout many regions of the eastern United States have
303 critical implications for the current and future understory diversity. Our results strongly support
304 forest management techniques that decrease deer populations to promote viable understory
305 communities. Additionally, we must expect time lags on the scale of decades before herbaceous
306 populations can recover following a decrease in top-down pressure. Although refugia may
307 provide local seed sources to reestablish palatable species following herbivory abatement,
308 alternative successional pathways may result in lower diversity recalcitrant understories, with
309 herbivore sensitive species functionally extirpated.

310

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455 **Table 1.** Response of species richness, herbaceous cover, and Shannon Diversity Index (1997,
 456 1998, 1999, 2001, 2007) and total wildflower, preferred browse, and *Podophyllum peltatum*
 457 density (2001 and 2007) to deer exclosures, analyzed using a repeated measures ANOVA in SAS
 458 Proc Mixed. Boldface P-values indicate significance.

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Source of Variation	F	DF (N, D)	P
Species Richness			
Exclosure	4.24	1,106	0.0421
Year	13.52	4,266	<0.0001
Exclosure x Year	1.04	4,266	0.3868

Shannon Diversity Index (by Cover)			
Exclosure	3.59	1,86.5	0.0615
Year	5.29	1,109	<0.0233
Exclosure x Year	0.42	1,109	0.5177

Shannon Diversity Index (by Density)			
Exclosure	2.08	1,106	0.1518
Year	7.5	4,266	<0.0001
Exclosure x Year	1.75	4,266	0.1389

Total Density			
Exclosure	12.19	1,176	0.0006
Year	39.16	1,176	<0.0001
Exclosure x Year	8.72	1,176	0.0036

Preferred Browse Density			
Exclosure	9.7	1,108	0.0024
Year	30.46	1,143	<0.0001
Exclosure x Year	9.43	1,108	0.0027

<i>Podophyllum peltatum</i> Density			
Exclosure	4.87	1,127	0.0291
Year	14.74	1,154	0.0002
Exclosure x Year	3.15	1,127	0.0784

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466 **Table 2.** Bray-Curtis, Jaccard, and Horn Indices of Community Dissimilarity. Boldface P-
467 values indicate that fenced and unfenced herbaceous communities are significantly different.

Year	Bray Curtis		Jaccard		Horn	
	F Model	P-value	F Model	P-value	F Model	P-value
1997	1.5976	0.1268	1.4106	0.0899	1.3872	0.2368
1998	1.5551	0.1179	1.5017	0.9191	1.9215	0.1349
1999	1.5576	0.1044	1.4640	0.0869	1.3921	0.2198
2001	3.1071	0.0090	2.2542	0.0070	3.7531	0.0042
2007	2.5795	0.0040	2.0240	0.0010	2.5723	0.0350

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486 **Figure Captions**

487 **Figure 1.** Species richness and Shannon diversity indices of herbaceous understory species in
488 fenced and unfenced plots established in 1996, monitored from 1997 through 2007. The vertical
489 gray dashed line indicates when antlerless deer harvest was increased. **(A)** Species richness at
490 5x5 m subplot level. Species richness increased if protected from deer ($p=0.0421$) and over time
491 ($p < 0.0001$). **(B)** Shannon Diversity Indices did not differ in the first 5 years, but enclosure plots
492 showed only a trend of increased diversity by 2007 ($p=0.0615$), and increased over time
493 ($p=0.0233$). Relevant statistics presented in Table 1.

494

495 **Figure 2.** Subplot stem densities of all herbaceous understory species and preferred browse
496 species in fenced and unfenced plots established in 1996, monitored from 2001 through 2007.
497 **(A)** Stem density was significantly higher in the enclosure treatment in 2007 ($p = 0.006$), but also
498 increased over time ($p < 0.0001$). **(B)** Preferred browse density increased with deer enclosure and
499 over time, but increased most dramatically in protected plots (Fence x Year: $p = 0.0027$). **(C)**
500 The herbivore resistant *Podophyllum peltatum* density increased over time ($p = 0.0002$) but ore
501 substantially in control plots ($p = 0.0291$). Relevant statistics presented in Table 1.

502

503 **Figure 3.** Relative abundance (by total cover) of herbaceous species in control and enclosure
504 plots from 1997 to 2007. We have identified by genus the 10 most abundant species in the 2007
505 control plots in the legend; all other abundance data can be found in Appendix B. These two
506 wildflower communities are significantly disparate (Bray-Curtis Community Dissimilarity Index,
507 $p=0.001$).

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Figure 1

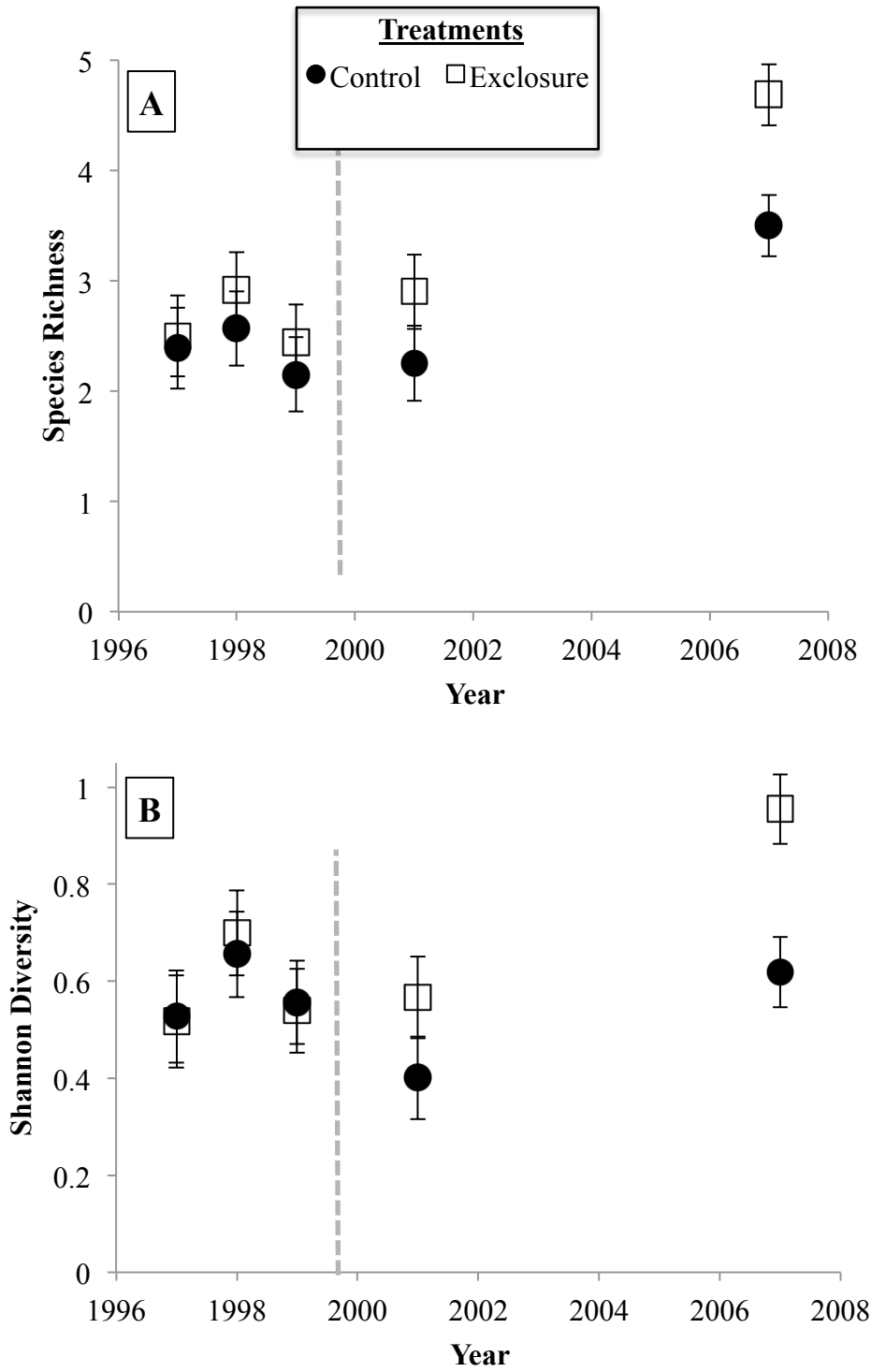


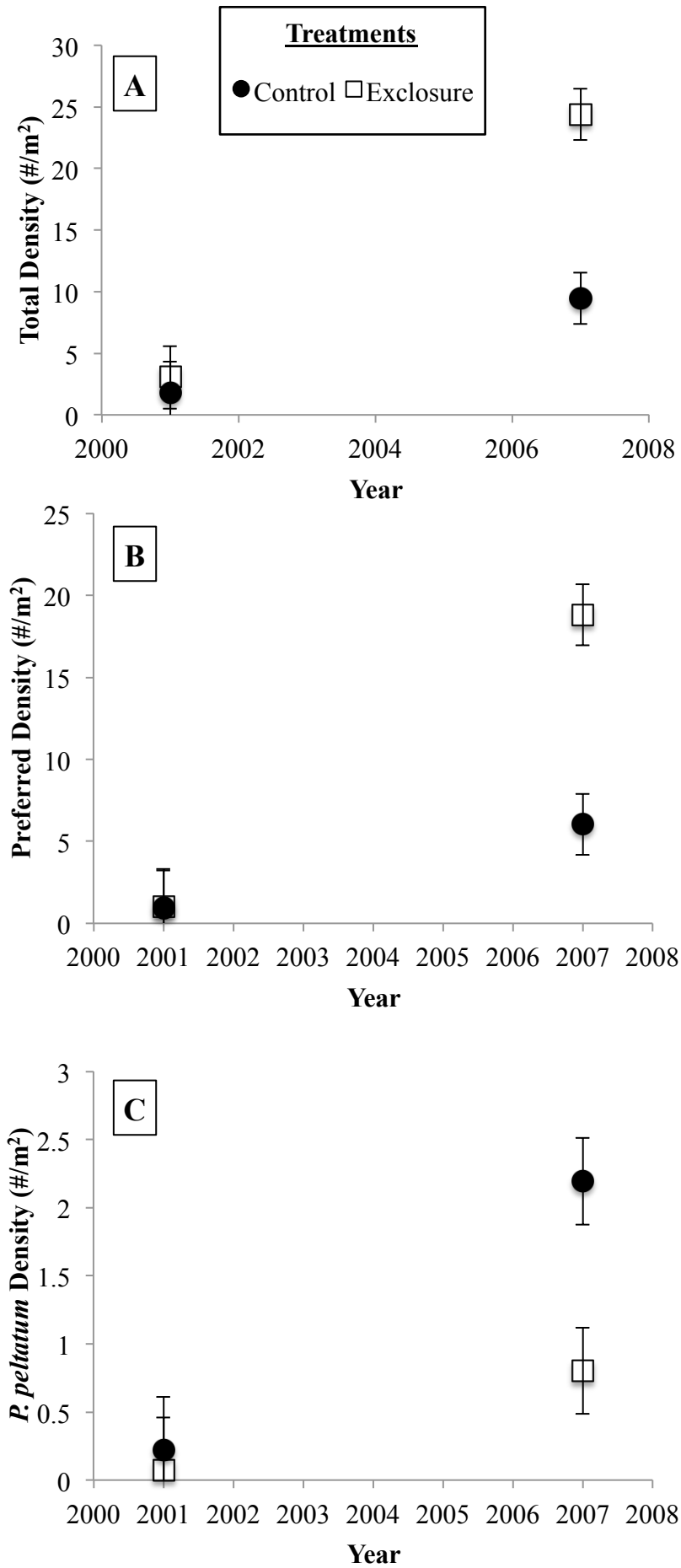
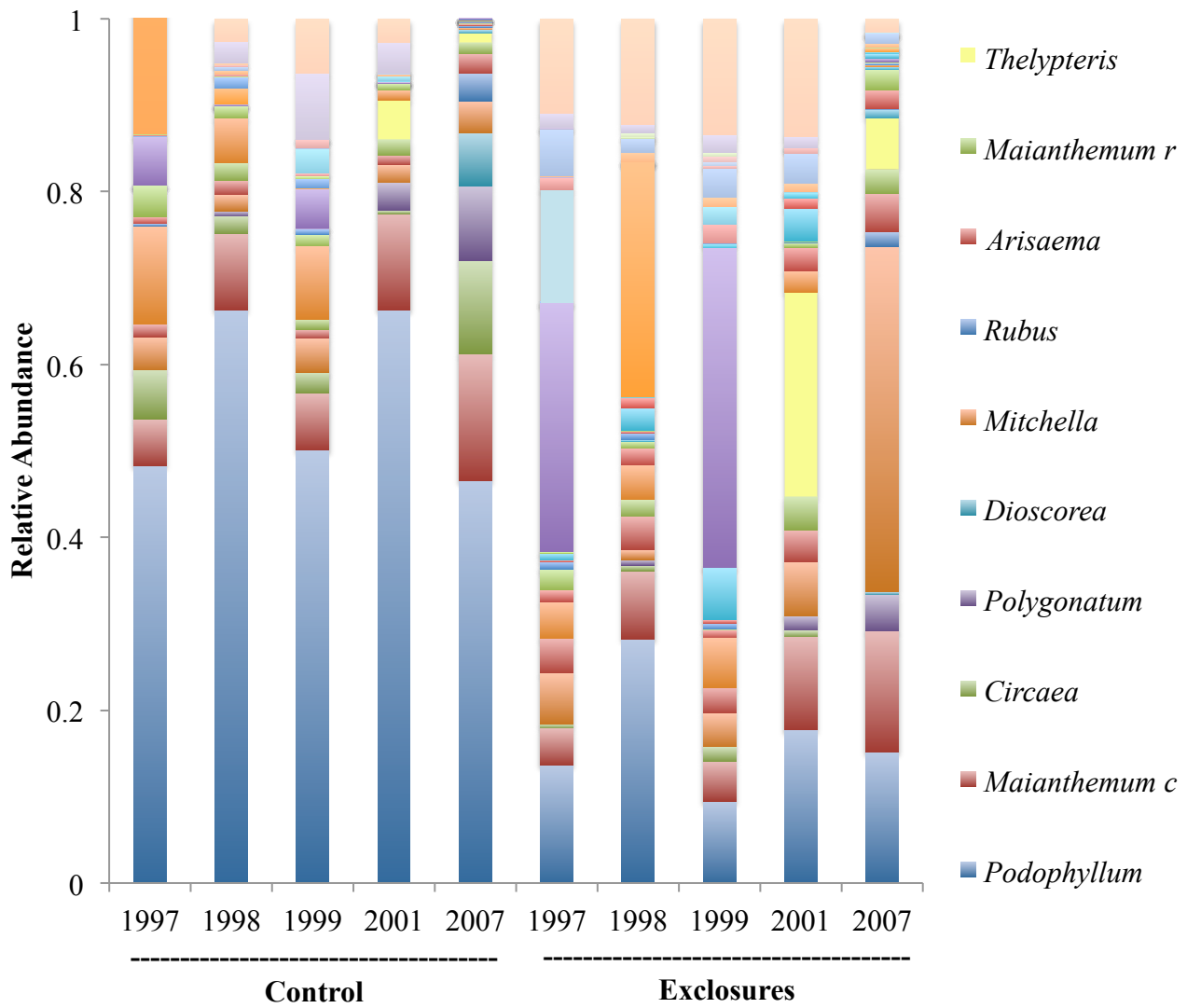
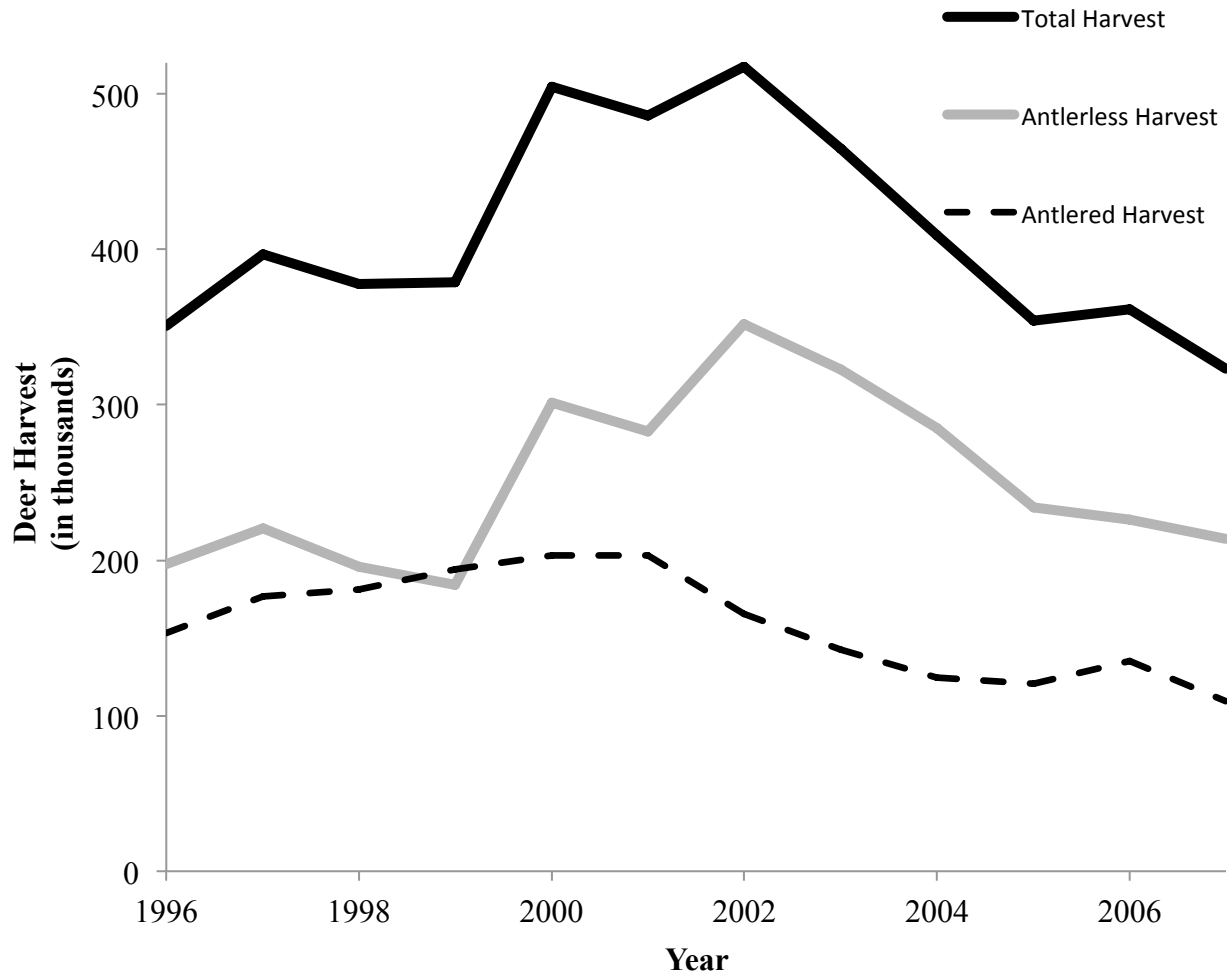
Figure 2

Figure 3



Appendix A



Appendix A. Between 2000 and 2004, Pennsylvania increased the number of antlerless deer tags, resulting in 55% increase in antlerless (largely doe) deer harvest. Deer densities decreased to approximately 14 deer/kilometer² in 2004 but increased to 20 deer/kilometer² by 2006 (Rosenberry et al. 2011). Deer harvest data obtained from the Pennsylvania Game Commission website (www.pgc.state.pa.us)

Appendix B. Relative abundance, by cover, of all wildflower species sampled in 1997, 1998, 1999, 2001, and 2007. For brevity and possible identification issues, we have combined data for species in the *Actaea*, *Dioscorea*, *Galium*, and *Viola* genera.

Species	Control					Exclosure				
	1997	1998	1999	2001	2007	1997	1998	1999	2001	2007
<i>Actaea</i> spp.	0	0	0	0	0	0.00818	0.02568	0.06085	0.03752	0.00489
<i>Arisaema triphyllum</i> (L.) Schott	0.01433	0.01646	0.01053	0.01095	0.02298	0.03983	0.03852	0.02993	0.03683	0.04385
<i>Asarum canadense</i> L.	0	0	0	0	0	1.6E-05	0	0	0	0
<i>Carex</i> spp.	0.03647	0.0144	0.01353	0.0076	0.00133	0.02454	0.00803	0.001	0.00546	0.02362
<i>Chimaphila maculata</i> (L.) Pursh	0	0	0	0	0	0	0	0	0	9.4E-05
<i>Circaea lutetiana</i> L.	0.05666	0.02058	0.02406	0.00395	0.10851	0.00533	0.00642	0.01696	0.00728	0
<i>Claytonia virginica</i> L. var. <i>virginica</i>	0	0	0	0	0	0	0.01124	0	0.01137	0
<i>Comandra umbellata</i> (L.) Nutt.	0	0	0	0	0	0.00164	0	0	0	0
<i>Dennistaedtia punctiloba</i> (Michx.) T. Moore	0.056	0	0.04511	0	0	0.28788	0	0.36911	0	0
<i>Dioscorea</i> spp.	0	0	0	0	0.06182	0	0	0	0	0.00339
<i>Disporum lanuginosum</i> (Michx.) G. Nicholson	0	0	0	0.00152	0	0	0.00161	0.00499	0.00682	0.00263
<i>Dryopteris carthusiana</i> (Vill.) H.P. Fuchs	0	0.01852	0.0015	0	0	0	0.27127	0	0	0.00376
<i>Epifagus americana</i> (L.) W. Bartram	0.00132	0.01235	0.01053	0	0	0.00025	0	0.001	0	0
<i>Fragaria virginia</i> Duchesne	0.0013	0	0	0	0	0	0	0	0	0
<i>Galium</i> spp.	0.114	0.05144	0.08421	0.01156	0.00252	0.04212	0.04013	0.05736	0.02478	0
<i>Geranium maculata</i> L.	0.00052	0.00206	0.00301	0	0	0	0	0	0	0
<i>Geum canadense</i> Jacq.	0	0	0	0	0	0.13086	0	0	0	0
<i>Glechoma hederaceae</i> L.	0	0	0	0	0	6.5E-05	0	0	0	0.00038
<i>Impatiens pallida</i> Nutt.	0	0	0	0	0.00015	0	0.00161	0	0.00136	0.00141

<i>Ipomoea pandurata</i> (L.) G. Mey.	0	0	0	0	0	0	0	0	0	0.00019
<i>Lycopodium complanatum</i> L.	0.00781	0	0	0	0.00148	0.01349	0.01926	0.00898	0.02729	0.02174
<i>Maianthemum canadense</i> Desf.	0.05356	0.08848	0.06617	0.11131	0.14617	0.04253	0.07865	0.04589	0.10778	0.13993
<i>Maianthemum stellatum</i> (L.) Link	0.03543	0.00206	0.00301	0	0	0.01358	0	0.02195	0	0
<i>Mianthemum racemosum</i> L.	0	0.02058	0.01203	0.01825	0.01357	0	0.01926	0	0.03865	0.02785
<i>Mitchella repens</i> L.	0.03875	0.01852	0.0391	0.02099	0.0371	0.05889	0.01124	0.03891	0.06207	0.39917
<i>Monotropa uniflora</i> L.	0	0	0	0	0.00119	0	0.00161	0	0	0.00376
<i>Onoclea sensibilis</i> L.	0	0	0	0	0.00133	0	0	0	0	0
<i>Osmorhiza claytonii</i> (Michx.) C.B. Clarke	0	0	0.00602	0	0.00059	0.00867	0.00803	0.00698	0.00068	0.0016
<i>Parthenocissus quinquefolia</i> (L.) Planch.	0	0	0	0.00061	0	0	0	0	0	0.00085
<i>Phytolaca americana</i> L.	0	0.66255	0	0	0	0.00123	0.2825	0	0	0
<i>Poa</i> sp.	0.0026	0	0	0	0.00237	0	0	0	0	0.00075
<i>Podophyllum peltatum</i> L.	0.4832	0.00412	0.50075	0.66302	0.46592	0.13658	0.01124	0.09477	0.17735	0.15188
<i>Polygonatum biflorum</i> (Walter) Elliot	0	0.00617	0.02857	0.00517	0	0	0.00642	0.02045	0.00159	0
<i>Polygonatum pubescens</i> (Willd.) Pursh	0	0	0	0.03193	0.08539	0	0	0	0.01705	0.04187
<i>Polygonum</i> spp.	0.00912	0	0	0	0	0.00147	0	0.00998	0	0.00395
<i>Polygonum virginianum</i> L.	0	0	0	0.00182	0	0	0	0	0.0091	0
<i>Polystichum acrostichoides</i> (Michx.) Schott	0	0	0	0	0.00119	0	0	0	0	0.00207
<i>Potentilla simplex</i> Michx.	0.0293	0.00412	0.0015	0.00091	0	0.05398	0.01605	0.03382	0.03456	0.01214
<i>Pyrola elliptica</i> Nutt.	0	0.00206	0.00902	0	0	0	0	0.00299	0.00682	0
<i>Ranunculus</i> sp.	0	0	0	0	0	0	0.00161	0	0	0
<i>Rubus</i> sp.	0	0	0	0	0.03158	0	0	0	0	0.01731

<i>Sanicula sp.</i>	7.8E-05	0	0	0	0	0.00164	0	0	0	0
<i>Smilax spp.</i>	0	0	0	0	0.0003	0.00164	0.00161	0.00399	0	0
<i>Sphagnum platyphyllum</i> (Lindb. ex Braithw.) Sull. ex Warnst.	0.0026	0	0	0	0	0	0	0	0	0
<i>Symphyotrichum sp.</i>	0	0.00206	0	0	0	0	0	0	0	0
<i>Thelypteris noveboracensis</i> (L.) Nieuwl.	0	0	0	0.04562	0.00993	0	0	0	0.23647	0.05938
<i>Toxicodendron radicans</i> (L.) Kuntze	0	0	0	0	0.00445	0	0	0	0	0.01035
<i>Trientalis borealis</i> Raf.	0	0	0	0	0	0	0	0.00499	0	0
<i>Trillium grandiflorum</i> (Michx.) Salisb.	0	0.00206	0.0015	0.00152	0.00015	0	0	0	0	0.00452
<i>Triodanis sp.</i>	0	0	0	0	0	0	0.00161	0.00599	0	0
<i>Urtica dioica</i> L.	0	0	0	0	0	0	0.00482	0.00449	0	0
<i>Uvularia perfoliata</i> L.	0.0086	0.02469	0.07669	0.03558	0	0.01636	0.00963	0.01995	0.01296	0
<i>Veronica officinale</i> L.	0	0	0	0	0	0	0	0	0	0.00075
<i>Viola spp.</i>	0.04836	0.02675	0.06316	0.02768	0	0.10926	0.12199	0.13468	0.1362	0.0159