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The dominant plant species *Solidago canadensis* structures multiple trophic levels in an old-field ecosystem

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Abstract

Dominant plant species are locally abundant and have large impacts on ecological communities via a variety of mechanisms. However, few studies have evaluated the influence of a dominant plant species both within and among trophic levels and on key ecosystem functions such as productivity. In this study, we evaluated the effect of the dominant plant species *Solidago canadensis* on plant and arthropod communities in an old-field ecosystem in southeastern Michigan. We found that *S. canadensis* negatively correlated with the richness and combined biomass of all other plant species in the community, likely by reducing light availability. In turn, less biomass of all other plant species led to lower arthropod abundance. Specifically, detritivore and predator arthropod abundance was lower with less biomass of all plant species excluding *S. canadensis*, but herbivore and omnivore abundance was unaffected. Our results highlight the significant role of dominant plants in determining plant diversity and ecosystem function, and further suggest that the effect of a dominant plant species on a community is observed at higher trophic levels.

Introduction

One of the fundamental patterns in ecology is that communities are composed of many rare but few common species (Preston 1948; Tokeshi 1993). Of the common species, dominant species are both highly abundant and influence community structure and ecosystem function (Smith and Knapp 2003; Gilbert et al. 2009; Avolio et al. 2019). Dominant plant species can, for example, stabilize communities over time, alter plant community diversity, and mediate ecosystem productivity (Wilsey and Potvin 2000; Smith and Knapp 2003; Emery 2007; Sasaki and Lauenroth 2011; Doherty and Zedler 2014; Avolio et al. 2019). Especially well-documented is the role that dominant plant species play in regulating plant community composition and productivity. The removal or loss of dominant species often leads to increases in the diversity and biomass of the rest of the community (McCain et al. 2010; Souza et al. 2011; Lepš 2014; Li et al. 2015). Increases in plant biomass and diversity following dominant species removal suggest that dominant species suppress the productivity and diversity of subdominant plant species.

Dominant plant species can affect community structure and subsequently shape ecosystem function via a variety of mechanisms (Zehnder et al. 2020; Hernández et al. 2022). Fundamentally, dominant plant species directly affect ecosystem function because their high biomass determines the rate of ecosystem-level processes, as described by the Mass-Ratio Hypothesis (Grime 1998). Additionally, dominant plant species may affect soil nutrient cycling by changing plant species diversity (Jiang et al. 2021) or the quality and quantity of senesced material (Koukoura et al. 2003; Hernández et al. 2022). Finally, the removal or loss of a dominant plant species increases light availability and subsequently changes plant community structure (Emery and Gross 2007; Hernández et al. 2022). Understanding the mechanisms by which dominant species affect community composition can reveal the processes underlying community assembly and may highlight the consequences of losing particular species from ecosystems (Koukoura et al. 2003; Souza et al. 2011).

The majority of previous work on dominant plants has focused on whether dominant plants affect species of the same trophic level - other plant species - but less is known about how or even whether dominant plants affect other trophic levels. This is a critical knowledge gap because communities are composed of a diverse assemblage of interacting species, and those species interact across trophic levels. However, it is well established that arthropod diversity and abundance often tracks plant diversity (Haddad et al. 2009; Kostenko et al 2012; Corcos et al. 2021). Because previous research highlights that the diversity of primary producers affects diversity in associated arthropod communities, it should follow that if dominant plant species affect plant diversity, they might ultimately influence the diversity of associated arthropod communities. Furthermore, arthropod abundance and diversity track productivity (Siemann 1998). So if dominant plant species affect productivity (Smith and Knapp 2003; McCain et al. 2010; Souza et al. 2011; Li et al. 2015), dominant plants may subsequently shape arthropod abundance and diversity by altering ecosystem productivity.

In this study, we examine the effect of *Solidago canadensis* (Canada goldenrod) on the structure of both plant and arthropod communities in an old-field ecosystem in southeastern Michigan. *Solidag*o spp. dominate roadsides and old fields across much of Eastern North America (Abrahamson & Weis 1997), and many *Solidago* spp. are invasive in Europe and Asia (Jakobs et al. 2004; Benelli et al. 2019; Zhu et al. 2022). The genus *Solidago* is a popular study system in community ecology to understand the three-way interaction among plants, their herbivores, and the predators of those herbivores (Abrahamson and Weis 1997; Crutsinger et al.

2008a). Numerous researchers have investigated the myriad interactions between *Solidago* and arthropods (Crutsinger et al. 2006; Crutsinger et al. 2008a; Chen et al. 2012; Lenda et al. 2013; Sterzyńska et al. 2017; Wang et al. 2018a; Ustinova et al. 2020) and other plants in the community (De Groot et al. 2007; Souza et al. 2011; Fenesi et al. 2015a; Szymura and Szymura 2016; Wang et al. 2018b; Cheng et al. 2020). However, less attention has been given to how *Solidago* affects plant diversity, productivity, and arthropod community structure. To address this research gap, we investigated a series of interrelated questions: (1) Is *S. canadensis* a dominant species, and does it affect community structure and biomass of the rest of the plant community? (2) What is the mechanism by which *S. canadensis* affects the plant community? (3) Does *S. canadensis* shape arthropod community and trophic structure?

Methods

Site description

We conducted this study in August 2021 in an old field at Matthaei Botanical Garden in Ann Arbor, Michigan (42.30° N, 83.66° W). Local average monthly temperature ranges from -4.6 ℃ in January to 22.6 ℃in July (ClimateData 2021). Average annual precipitation is 954 mm (U.S. Climate Data 2021). The old field we worked in is typically mowed annually and burned semi-annually, maintaining it in an early-successional state. The most abundant plant species at the site is *S. canadensis*, a perennial, clonal herbaceous species common in the northeastern and midwestern United States. At this site, *S. canadensis* constitutes, on average, ~ 50% of above-ground plant biomass (Eckberg, unpublished data). Other than *S. canadensis*, the four most abundant plant species include *Monarda fistulosa, Vitus riparia, Vicia tetrasperma*, and *Toxicodendron rydbergii* (Appendix S1: Table S1).

Solidago canadensis impact on plant community

At the site, we placed 24 1-m^2 quadrats in a grid. Quadrats were at least six meters apart, and we mowed paths among quadrats approximately monthly. To evaluate the effect of *S. canadensis* on light availability, we estimated light intensity above the tallest plants in each quadrat and 50 cm above the ground prior to removing all *S. canadensis* stems from each quadrat. We made five light intensity measurements above the canopy created by *S. canadensis* and five below using the iOS app Lux Light Meter Pro version 2.1.1 (Polyanskaya 2021). Then, for each quadrat, we calculated the average light intensity above and below the canopy. We calculated light availability as the proportion of light above the canopy that penetrated to 50 cm above the soil.

To evaluate the effect of *S. canadensis* on the plant community, we first estimated biomass of *S. canadensis* in each quadrat by clipping all of the *S. canadensis* stems at ground level. We then dried the *S. canadensis* stems in each 1-m^2 quadrat for 72 hours at 60℃ and weighed them. After the *S. canadensis* stems were removed from each quadrat we estimated plant species richness in each 1-m^2 quadrat. We then clipped, dried, and weighed those other plant species from each 1-m^2 quadrat as described above.

Solidago canadensis impact on other trophic groups

To evaluate the effect of *S. canadensis* on the ground-foraging arthropod community, we buried one 50mL centrifuge tube pitfall trap flush with the soil surface in the center of each quadrat after *S. canadensis* was removed, but before we removed other plants. We partially filled each pitfall trap with a mixture of water and unscented dish soap. We left traps in place for 72 hours and immediately counted and stored arthropods in ethanol upon removing pitfall traps. Using a dissecting microscope in the lab, we identified arthropods to the lowest possible taxonomic level and categorized them by trophic level (herbivore, predator, detritivore, omnivore, parasite, or pollinator) using published sources and online guides. The most common arthropod families identified were the Formicidae (ants) and Armadillidiidae (pillbugs). We collected arthropods once to limit damage to the plant community caused by arthropod sampling. Additionally, sampling arthropods multiple times may have negatively affected arthropod populations and impeded our ability to study how arthropods affect, and are affected by, the plant community in this and future studies.

To evaluate the effect of *S. canadensis* on arthropod community trophic structure, we calculated arthropod community trophic mean (CTM) using the following equation from Welti et al. 2020:

$$\mathrm{CTM} = \frac{1}{\mathrm{P}} \sum_{\mathrm{i}}^{\mathrm{N}} \mathrm{p_i} \times \mathrm{t} \qquad \text{(Equation 1)}$$

where P represents the total number of arthropod individuals, N the number of trophic levels, p_i the number of arthropods of trophic level i, and t the trophic level value. We assigned each trophic level a numerical value (herbivores, detritivores, pollinators = 2, omnivores = 2.5, predators = 3, parasites = 4) to quantify variation in the number of trophic levels within the trophic pyramid framework (Welti et al. 2020). We weighted each trophic level value by the number of individuals of that trophic level, summed across all trophic levels present, and divided by the total number of arthropod individuals to calculate CTM (Welti et al. 2020). Communities with a top-heavy trophic pyramid (ie. higher abundance of individuals of higher trophic levels) have a high CTM, while communities with at bottom heavy trophic pyramid (ie. higher abundance of individuals of lower trophic levels) have a low CTM.

Statistical analyses

We performed all statistical analyses using R version 4.1.3 (R Core Team 2021). We fit linear regressions to test the effect of *S. canadensis* biomass (g m^{-2}) on a suite of response variables: subdominant plant biomass (i.e, all plant species except *S. canadensis*), subdominant species richness, and light availability. We fit additional linear regressions to test the effect of light availability on subdominant plant biomass, and the effect of subdominant plant biomass and species richness on arthropod abundance. We also fit linear regressions to test the effect of *S. canadensis* biomass, subdominant plant biomass and subdominant species richness on arthropod CTM, and herbivore, detritivore, omnivore, and predator abundance, respectively.

Results

Solidago canadensis impact on plant community

Subdominant plant community biomass was negatively correlated with *S. canadensis* biomass ($r^2 = 0.61$, $p < 0.001$; Figure 1a). On average, subdominant plant biomass was 78% lower in the five quadrats with the highest *S. canadensis* biomass (89.6 g $m^{-2} \pm 32.6$) relative to the five quadrats with the lowest *S. canadensis* biomass (329.1 g $m^{-2} \pm 72.0$). Similarly, plant species richness was negatively correlated with *S. canadensis* biomass ($r^2 = 0.19$, $p = 0.02$; Figure 1b): quadrats with higher *S. canadensis* biomass tended to have lower plant species richness.

Light availability was lower when *S. canadensis* biomass was higher ($r^2 = 0.48$, $p < 0.001$; Figure 2a). On average, light availability was 67% lower in the five quadrats with the highest *S. canadensis* biomass (0.47 ± 0.17) relative to the five quadrats with the lowest *S. canadensis* biomass (0.85 ± 0.14). Subdominant plant biomass was higher when light availability was higher ($r^2 = 0.18$, $p = 0.02$; Figure 2b). On average, subdominant plant biomass was 26%

higher in the five quadrats with the highest light availability (321.3 ± 108.5 g m^{-2}) relative to the five quadrats with the least light available (154.5 ± 115.5 g m^{-2}).

Solidago canadensis impact on other trophic groups

Arthropod abundance tracked subdominant plant community biomass ($r^2 = 0.28$, $p = 0.005$; Figure 3a), but was not related to subdominant plant richness ($r^2 = -0.03$, $p = 0.56$; Figure 3b). On average, arthropod abundance was 59% lower in the five quadrats with the lowest subdominant plant biomass (12.0 ± 5.7) relative to the five quadrats with the highest subdominant plant biomass (28.6 ± 17.6). More specifically, detritivore ($r^2 = 0.29$, $p = 0.004$; Table 1) and predator ($r^2 = 0.21$, $p = 0.01$; Table 1) abundance were lower with lower subdominant plant biomass, but herbivore and omnivore abundance did not vary systematically with subdominant plant biomass. There was no correlation between *S. canadensis* biomass, subdominant plant biomass or subdominant species richness and arthropod CTM (Table 1).

Discussion

Solidago canadensis impact on plant community

Our work demonstrates that *S. canadensis* is a dominant plant species that alters subdominant plant diversity and biomass in an old-field ecosystem, with indirect effects on arthropod community structure. Specifically, *S. canadensis* comprised the majority of plant biomass (50 ± 22%) in each plot and was negatively correlated with both the biomass and species richness of the rest of the plant community. These results are in line with previous studies in other systems demonstrating that dominant plant species influence community structure and ecosystem function (e.g., Avolio et al. 2019). For instance, dominant grasses can suppress the biomass of subdominant grass species (Hernández et al. 2022).

Additionally, related studies found that other dominant plant species reduce plant community diversity in a variety of ecosystems, ranging from old fields to tall grass prairies (Bazzaz 1975; Souza et al. 2011; Avolio et al. 2019; Hejda et al. 2019; Hernández et al. 2022). Studies of *Solidago* in both its native and invasive range show that it regulates plant diversity: typically, plots with high *Solidago* stem density have lower plant diversity (Crutsinger et al. 2008b; Ledger et al. 2015). Removal of *S. altissima* found that biomass and diversity of subdominant species were both reduced when *S. altissima* was present (De Groot et al. 2007; Simao et al. 2010; Souza et al. 2011; Avolio et al. 2019). In sum, the effect of *S. canadensis* on subdominant plant biomass and richness in this system is on par with the effect of other dominant plants in other systems (Avolio et al. 2019; Appendix S2). Our study examined the impacts of *S. canadensis* in 1-m^2 quadrats, as have other studies focused on impacts of *Solidago* species (Crutsinger et al. 2008a; Crutsinger et al. 2008b; Ledger et al. 2015). However, it would be interesting to conduct similar removal experiments at larger scales and for longer time periods.

A key mechanism by which *S. canadensis* reduces subdominant plant productivity and diversity is by reducing light availability. In plots with higher *S. canadensis* biomass, light availability near the soil and subdominant plant biomass were substantially lower. In a grassland system, removing a dominant grass species led to higher light availability and subsequently higher forb biomass, in line with our results which similarly suggest that reducing light availability is one way dominant plants regulate productivity (McCain et al. 2010). Another study found that the above ground morphology of a dominant shrub species mediated how that shrub affected light availability and soil temperature, with areas occupied by taller morphs having higher light availability and soil temperature relative to areas occupied by lower growing morphs (Crutsinger et al. 2010). The variation in light availability and soil temperature caused by dominant shrub morphology subsequently altered plant community richness, highlighting how the alteration of light availability by dominant plants affects plant community structure (Crutsinger et al. 2010). Furthermore, several studies found that competition for light is an important mechanism regulating plant diversity and productivity (Hautier et al. 2009; Borer et al. 2014; DeMalach et al. 2017). However, we note that *S. canadensis* is allelopathic and could adversely affect subdominant plants, and in turn arthropods, through the release of chemicals that inhibit subdominant plant germination or growth (Yang et al. 2007; Yuan et al. 2013; Zhu et al. 2022). *Solidago canadensis* can have stronger allelopathic effects on other plant species in its invasive range (Yuan et al. 2013) but may still reduce the growth of other plants in its native range via allelopathy.

Solidago canadensis impact on other trophic groups

Our research expands our understanding of the ecological impact of dominant species by showing how dominant plants indirectly and negatively affect associated arthropod communities via effects on subdominant plants. More productive ecosystems often support more arthropod individuals and subsequently more species at viable population sizes (Storch et al. 2018), a concept known as the More Individuals Hypothesis (Srivastava & Lawton 1998). We found a positive correlation between subdominant plant biomass and arthropod abundance but no relationship between *S. canadensis* biomass and arthropod abundance, suggesting that subdominant plants provide resources to the ground-foraging arthropod communities that *S. canadensis* does not. Though a growing number of studies have documented a positive relationship between total plant biomass and arthropod abundance in terrestrial ecosystems (Borer et al. 2012; Prather and Kaspari 2019; Prather et al. 2020), none explicitly evaluated the role of dominant species in shaping arthropod abundance. Here, we show that by reducing light availability, *S. canadensis* inhibits subdominant plant productivity and in turn, arthropod abundance. Changes in plant community structure can alter arthropod community structure (Haddad et al. 2009). Indeed, several studies found that resource availability primarily influenced herbivorous arthropod community structure relative to predation, highlighting the influence of primary producers on herbivore community structure (Gruner 2004; Borer and Gruner 2009; Haddad et al. 2009). The effect of dominant plants in particular on other trophic levels is less well-documented. Here we found that *S. canadensis* had no direct effect on the abundances of arthropod detritivores, herbivores, omnivores, or predators. There was no correlation between subdominant plant biomass and arthropod herbivore or omnivore abundance, however, we found a positive correlation between subdominant plant biomass and the abundance of both arthropod detritivores and predators. Another study similarly found that the abundance of detritivores was positively correlated with productivity, a pattern likely driven by high productivity providing more resources in the form of plant detritus (Siemann 1998). Predator abundance was also positively correlated with subdominant plant biomass, potentially driven by habitat provisioning by subdominant plants. Plant biomass is often positively correlated with habitat heterogeneity and subsequently arthropod abundance, highlighting both the role of plant biomass in creating habitat heterogeneity and habitat heterogeneity in supporting arthropod communities (Haddad et al. 2009, Prather and Kaspari 2019). The correlation between subdominant plant biomass and arthropod detritivore and predator abundance underscores that the indirect effect of dominant plants on arthropod abundance affects multiple trophic levels.

Why was there no direct effect of *S. canadensis* on arthropod richness and abundance when so many other studies (Maddox and Root 1990; Abrahamson and Weis 1997; Carson and

Root 2000; Crutsinger et al. 2008a; Crutsinger et al. 2009; Fenesi et al. 2015b; Dudek et al. 2016) have shown that *Solidago* species clearly do affect arthropod richness and abundance? The arthropod fauna associated with many *Solidago* species is well documented and studied. But more often than not, the arthropods studied are those that are hosted by the plant – its herbivores, pollinators, gallers, and the like (Root 1996; Abrahamson and Weis 1997; Uriarte 2000; Crawford et al. 2007; Crutsinger et al. 2009; Williams and Avakian 2015). In our study, however, we focused on the ground-foraging species that are associated with the rest of the plant community – the species that are typically not closely associated with *S. canadensis*. Nevertheless, we suggest that *S. canadensis*, at least in the old-field ecosystem we worked in, indirectly affects those arthropod species by affecting the subdominant plant community.

Solidago canadensis had no direct or indirect effect on arthropod trophic structure, though related *Solidago* species clearly do in other systems (e.g., Abrahamson and Weis 1997; Crutsinger et al. 2009). Productivity can have variable effects on arthropod trophic structure (Abrams 1993; McCauley et al. 2018; Welti et al. 2020). Ecosystems with more plant biomass should in theory support more individual arthropod herbivores and subsequently more predators and parasitoids, leading to a top-heavy trophic pyramid (McCauley et al. 2018). However, ecosystems with high plant biomass can alternatively support a bottom-heavy trophic pyramid with a greater abundance of detritivores and herbivores (Welti et al. 2020). In our study, differences in detritivore and predator abundance driven by subdominant plant biomass did not ultimately affect arthropod trophic structure, likely because concurrent systematic differences in the abundance of both low and high trophic level arthropods effectively cancel each other out when quantifying trophic structure. Furthermore, diverse plant communities support a higher abundance of arthropod predators and alter arthropod trophic structure (Haddad et al. 2009), suggesting that both plant diversity and productivity may play a role in determining arthropod trophic structure though we did not find an effect of subdominant biomass or diversity on arthropod trophic structure here.

Previous work highlights the effect of invasive plants on arthropod community structure, and despite being non-native species, invasive plants share similar characteristics with native dominant plants in that they are often abundant and affect community structure and ecosystem function (Aguilera et al. 2010; Kuebbing 2014). One study found that the density of an invasive forb was negatively correlated with the abundance of arthropod herbivores and detritivores, highlighting the effect of invasive plants on the abundance of multiple arthropods trophic levels and arthropod trophic structure (Foster et al. 2021). *Solidago* spp. negatively affect multiple trophic groups in their invasive range, including nematodes (Čerevková et al. 2020), ants (Kajzer-Bonk et al. 2016), pollinators, (Fenesi et al. 2015b), and other plant species (Fenesi et al. 2015b, Wang et al. 2018b). Despite finding no effect of *S. canadensis* on arthropod trophic structure in our study in its native range, *S. canadensis* indirectly affects the abundance of multiple arthropod trophic levels. This suggests that native dominant plants similarly determine arthropod abundance, which could in turn alter ecosystem function and resilience (Haddad et al. 2009). The importance of understanding how dominant plant species interact with other trophic levels and affect ecosystem function emphasizes the need to conduct broader research on dominant plant species, and their influence on community composition and ecosystem function.

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Data Availability Statement

Data (Eckberg et al. 2022) are available from Dryad: https://doi.org/10.5061/dryad.2ngf1vhsn.

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Table 1: Results from linear regressions predicting the effect of *S. canadensis* biomass, subdominant plant biomass and subdominant plant species richness on arthropod community trophic mean and herbivore, detritivore, omnivore and predator abundance.

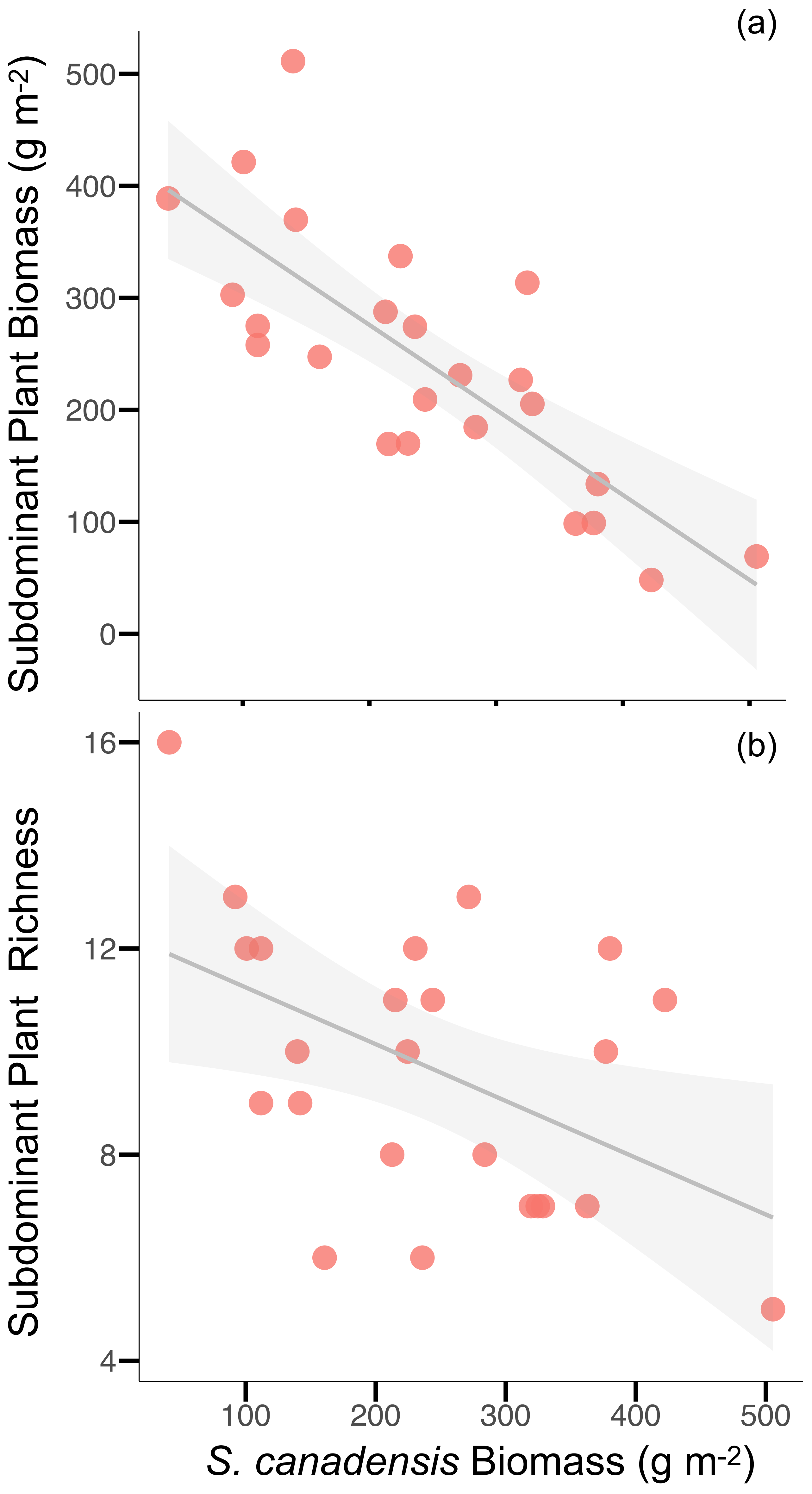
Characteristic	**Herbivore abundance**			**Detritivore abundance**			**Omnivore abundance**			**Predator abundance**			**Community trophic mean**		
	SE	R^2	P	SE	R^2	P	SE	R^2	P	SE	R^2	P	SE	R^2	P
***S. canadensis* biomass (g m^{-2})**	1.1	-0.01	0.4	10.4	0.06	0.13	4.9	-0.04	0.89	2.2	-0.02	0.48	0.2	-0.04	0.75
Subdominant plant biomass (g m^{-2})	1.1	-0.01	0.38	9.0	0.29	**0.004**	4.9	-0.01	0.38	1.9	0.21	**0.01**	0.2	-0.04	0.74
Subdominant plant richness	1.1	0.01	0.26	10.9	-0.04	0.69	4.9	-0.04	0.77	2.2	-0.02	0.49	0.2	-0.04	0.91

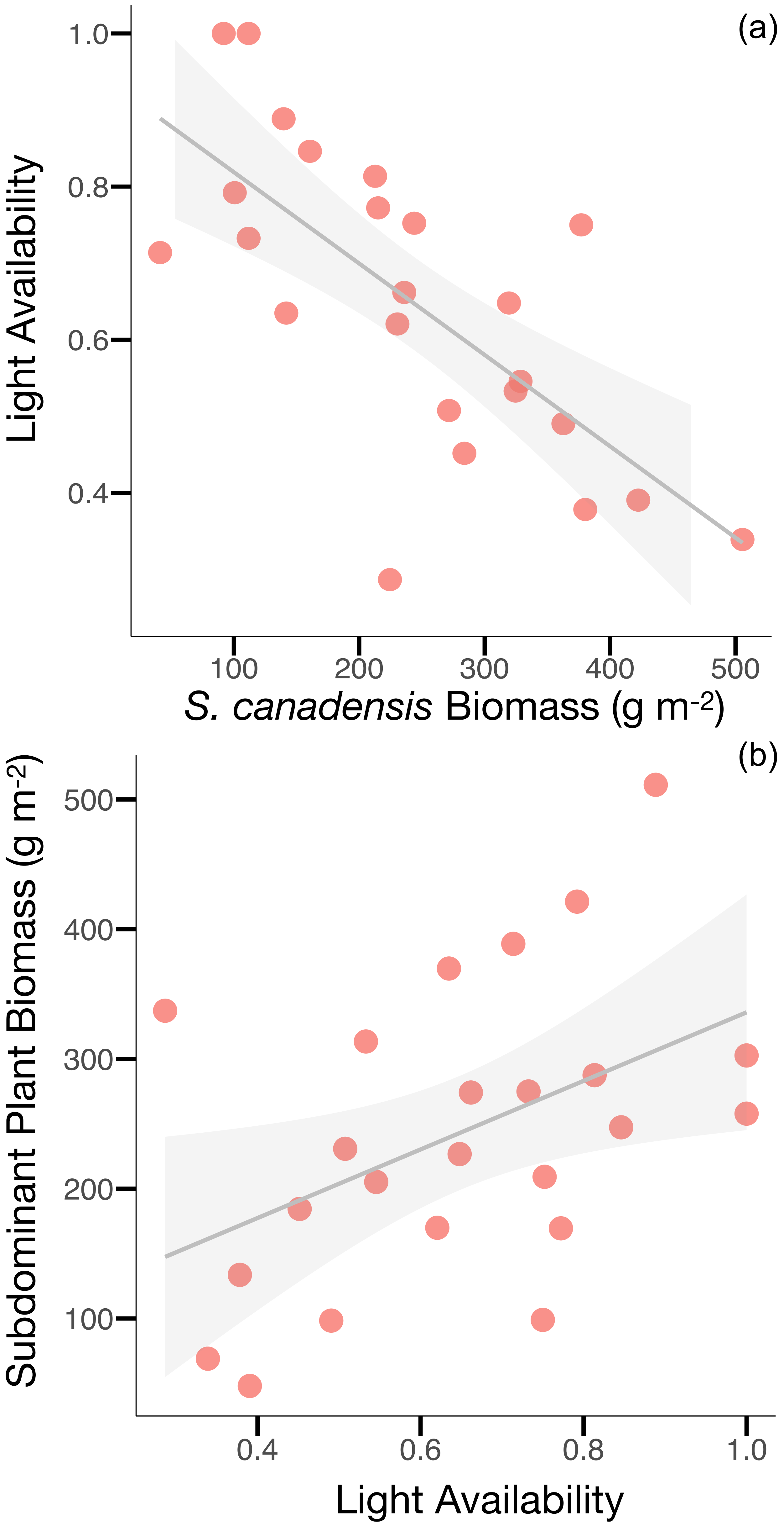
Notes: Boldface indicates significance.

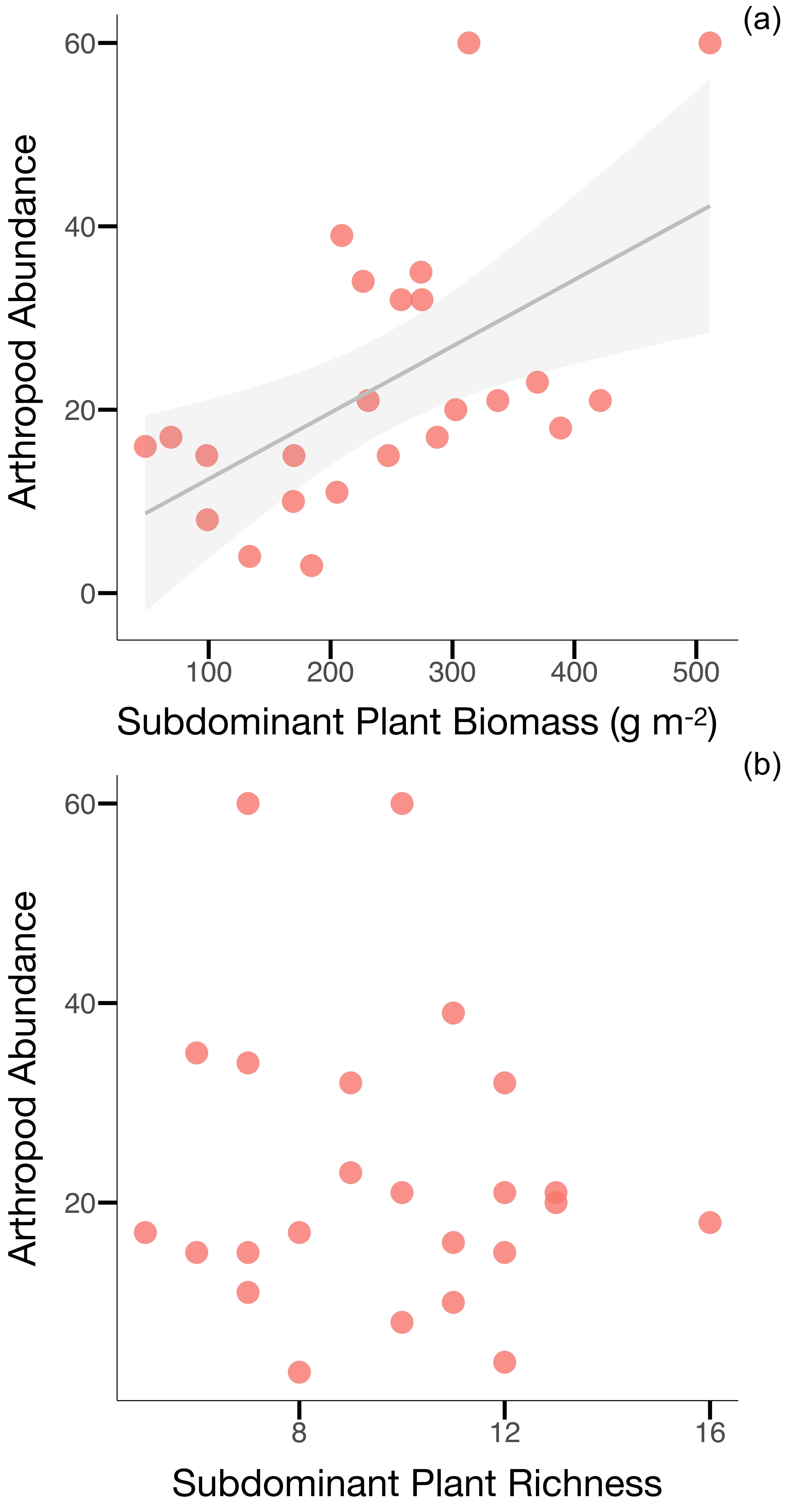
Figure 1: Effect of *S. canadensis* biomass on the biomass (a) and species richness (b) of subdominant plants. Gray line and gray area represent the linear regression line of best fit and confidence interval (a: $r^2 = 0.61$, $p < 0.001$, df = 22; b: $r^2 = 0.19$, $p = 0.02$, df = 22).

Figure 2: Effect of *S. canadensis* biomass on light availability 50 cm above the soil (a) and the effect of light availability 50 cm above the soil on subdominant plant biomass (b). Gray line and gray area represent the linear regression line of best fit and confidence interval (a: $r^2 = 0.48$, $p < 0.001$, df = 22; b: $r^2 = 0.18$, $p = 0.02$, df = 22).

Figure 3: Effect subdominant plant biomass (a) and subdominant plant species richness (b) on arthropod abundance. Gray line and gray area represent the linear regression line of best fit and confidence interval (a: $r^2 = 0.28$, $p = 0.005$, df = 22; b: $r^2 = -0.03$, $p = 0.56$, df = 22).


(a)
(b)
Subdominant Plant Biomass (g m-2)
Subdominant Plant Richness
0
100
200
300
400
500
4
8
12
16
100
200
300
400
500
S. canadensis Biomass (g m-2)


(a)
Light Availability
1.0
0.8
0.6
0.4
100
200
300
400
500
S. canadensis Biomass (g m-2)
(b)
Subdominant Plant Biomass (g m-2)
500
400
300
200
100
0.4
0.6
0.8
1.0
Light Availability


(a)
Arthropod Abundance
0
20
40
60
100
200
300
400
500
Subdominant Plant Biomass (g m-2)
(b)
Arthropod Abundance
20
40
60
8
12
16
Subdominant Plant Richness