

# Reports

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## Intraspecific diversity buffers the inhibitory effects of soil biota

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**Abstract.** Plant community productivity can increase with increasing intraspecific genotypic diversity. Previous studies have attributed the genetic diversity–productivity pattern to differential resource use among genotypes, as many studies have found for species. But here we ask whether suppression of productivity at low intraspecific diversity by soil biota might also drive a positive diversity–productivity relationship. In a previous study, we manipulated genetic diversity by varying the number of *Pseudoroegneria* accessions growing together in common garden plots, and used soil from that experiment to evaluate soil feedbacks. The total biomass of *P. spicata* plants grown in unsterilized soil increased with accession richness, specifically when comparing soil that had contained plants from 3 accessions to soil that had contained plants from either 8 or 12 population accessions. Furthermore, soil from high-richness (8 or 12-accession) plots drove neutral feedbacks, whereas soil in the 3-accession plots (3) drove negative feedbacks. However, within each level of richness, there was no relationship between relative yield and feedback. Our results suggest that soil biota might play an integral role in the emerging understanding of the relationship between intraspecific diversity and ecosystem productivity.

**Key words:** diversity–productivity; ecotypic diversity; negative feedback; plant productivity; soil biota.

### INTRODUCTION

Species diversity commonly increases ecosystem productivity at small spatial scales (Tilman et al. 2001, Hooper et al. 2005, Balvanera et al. 2006, Cardinale et al. 2006, Maron et al. 2011). The primary focus of most diversity–ecosystem function studies has been at the taxonomic level of species or trait-based functional groups, but a few studies have shown that genetic diversity within species can also affect some ecosystem functions. For example, Crawford and Rudgers (2012) found that plant species diversity and genetic diversity within a dominant species were related to increased productivity in experimental plots. Similar experiments have found that intraspecific or ecotypic diversity can increase pollination rates, NPP, and arthropod diversity, and decrease colonization by other species (Crutsinger et al. 2006, Fridley and Grime 2010, Genung et al. 2010). Booth and Grime (2003) found that intraspecific genetic diversity reduced the rate at which species diversity declined over time in experimental plots. Atwater and Callaway (2015) found that high population/

accession diversity of *Pseudoroegneria spicata* increased productivity to a degree similar to that generally reported in the literature for high species diversity. This “over-yielding” was due primarily to complementary interactions among individuals from different populations.

Although there is substantial evidence that intraspecific diversity can positively affect ecosystem functions, unlike species diversity, we know little about the potential mechanisms that drive these effects. For species, three mechanistic processes are generally thought to drive this relationship: “niche complementarity” (Loreau and Hector 2001, Schnitzer et al. 2011), “sampling effects” (Huston 1997, Loreau and Hector 2001), and the accumulation of leaf (Knops et al. 1999) or soil pathogens in monocultures (Maron et al. 2011, Schnitzer et al. 2011, De Kroon et al. 2012, Kulmatiski et al. 2012, Latz et al. 2012, Yang et al. 2015b). Traits can vary substantially among individuals within species, and this may lead to high functional diversity within a single plant population (Garnier et al. 2004, Albert et al. 2011), which can then influence ecological processes (Hughes et al. 2008). Some evidence indicates that genotypes can exhibit complementary resource use (Smithson and Lenne 1996, Reusch et al. 2005, Crutsinger et al. 2006, Fridley and Grime

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2010). Thus complementarity and sampling effects have the potential to affect ecotypic diversity–ecosystem function relationships. Individuals of a species also vary a great deal in resistance to consumers, including pathogens (Maron et al. 2015); however, to our knowledge no studies have tackled the potential role of soil biota in the effects of intraspecific diversity on ecosystem function (Fridley and Grime 2010, Atwater and Callaway 2015).

Soil biota have profound positive and negative effects on plants. Positive feedbacks between plants and soil biota are thought to lead to a loss of local community diversity (Bever et al. 1997, Bever 2002), whereas negative feedbacks are thought to enhance community diversity by reducing the performance of any species that becomes strongly dominant (Bever et al. 1997, Kardol et al. 2006). Furthermore, soil pathogens have been shown to have strong effects on the species diversity–ecosystem function relationship (Maron et al. 2011, Schnitzer et al. 2011, De Kroon et al. 2012, Kulmatiski et al. 2012, Latz et al. 2012).

To examine the effects of soil biota on ecotypic diversity–ecosystem function, we utilized a common garden with experimentally created, intraspecific plant assemblages that varied in the numbers of *Pseudoroegneria spicata* population accessions in plots, and in which high accession richness increased productivity (see Atwater and Callaway 2015). As for most other studies of intraspecific diversity on ecosystem function, the mechanism for complementary “overyielding” reported by Atwater and Callaway (2015) was not clear. Working in this same system, Yang et al. (2015a) found evidence that some form of detection and avoidance mechanism among more closely related *Pseudoroegneria* plants had the potential to contribute to the population diversity–productivity relationship. Regardless, Atwater and Callaway (2015) found no evidence that overyielding was related to resource depletion, nor was the diversity–productivity relationship affected by fungicide. Here we further explored soil biota as a potential mechanism contributing to intraspecific diversity–ecosystem function by collecting soil from plots with low to high intraspecific diversity and then comparing the effects of sterilizing these soils on the growth of *Pseudoroegneria*.

#### METHODS

We collected soil from the rhizospheres of individual plants within experimental assemblages that varied in intraspecific, or population accession, diversity. We obtained seeds of the widespread and often dominant North American native *Pseudoroegneria spicata* (Pursh) Å. Löve (bluebunch wheatgrass) from 12 sites throughout western North America. With one exception, seeds were field collected in Montana or acquired from true-bred lines managed by the USDA Plant Germplasm Introduction and Testing Research Station in Pullman, Washington, USA. The one exception was a high-yielding wild-selected cultivar from southeastern Washington, “Goldar,” which we purchased because of problems with

seed viability of some of the naturally collected accessions. These assemblages were established in 2010 (see Atwater and Callaway 2015). Plants from different *Pseudoroegneria* accessions were grown at four levels of richness (1-, 3-, 8-, and 12-population accessions) in a common garden in a fallow field at Fort Missoula (Missoula, Montana, USA) in the spring of 2010. We used six of these accessions, which occurred in all species richness treatments, in a soil feedback experiment. These accessions were from Colorado, Idaho, Montana, and Washington, and included “Goldar.” All accessions were equally represented in both the field plots and the feedback study. Soil from each polyculture (3-, 8-, and 12-accessions) was either sterilized or not. Soils from monocultures were not used, as not all accessions were grown in monoculture, meaning the monoculture/polyculture treatments are not directly comparable.

In July 2013, we collected soil from each of 34 plots. There were 10 3-accession plots, 12 8-accession plots, and 12 12-accession plots. For each plot, soil was collected from 20 to 30 haphazardly chosen locations throughout the plot and combined into one 3–4 L sample per plot. Soil was sieved to remove stones, roots, and organic debris >8 mm diameter, and refrigerated at 0–4°C until use 10–15 d later. Half of the combined sample was sterilized by autoclaving three times, with an overnight period between each autoclaving, and half was not sterilized. A major challenge for plant–soil biota feedback studies is to separate the effects of killing soil biota from other effects of sterilization on soil, such as the release of nutrients from organic matter or an increase in toxins. One solution has been to sterilize most soil in both “sterile” and non-sterile” treatments and then to add small amounts of live or sterile soil to this sterile background. This risks applying insufficient amounts of soil biota for effective inoculation, but reduces the more important confounding direct and indirect effects of sterilizing soils (Reinhart et al. 2005). We placed 25 g of silica sand (20/30 grit) at the bottom of 125 mL pots to promote drainage. We then added a 75 mL layer of sterilized soil that had been collected from one of the field plots. For the live-soil treatment, we added a 25 mL plug of unsterilized soil, from the same plot as the 75 mL layer, to each pot, whereas for the sterilized treatment, we added a 25 mL plug of sterilized soil, again from the same plot from which the 75 mL layer was collected.

Seeds of each ecotype were planted into germinated in Petri dishes and one week after germination seedlings were transplanted into the pots (one seedling per pot). Accessions were matched to those that occurred in the field plots. For example, if Plot A contained accessions a, b, and c, then accessions a, b, and c were planted into sterile and non-sterile soil treatments. For each accession-plot-soil treatment combination, we grew three replicates per plot-soil combination, resulting in a total  $n$  of 762. During the experiment pots were randomly reorganized on the table once a week and watered every one or 2 d. Pots were not fertilized. After 10 weeks, the plants were

harvested, separated into above and belowground parts, dried to a constant weight at 60°C, and weighed.

We used the following equation to calculate the soil feedback RII: Soil feedback RII for total biomass =  $(\text{Total biomass}_{\text{live}} - \text{Total biomass}_{\text{sterile}}) / (\text{Total biomass}_{\text{live}} + \text{Total biomass}_{\text{sterile}})$  (see Maron et al. 2014). We tested the effects of soil sterilization and ecotypic diversity on plant total biomass in a generalized linear mixed model with total biomass as a response variable and richness and sterilization as factors. We also compared soil feedbacks measured in the greenhouse to relative overyielding in the same field plots from which soil was collected (Atwater and Callaway 2015). We used accession and source plot as random effects using the “lme4” package (Bates et al. 2014) in R version 3.0.1 (R Core Team 2013). For richness contrasts, we used the 3-accession plots as the reference values. Because this design is equivalent to a split-plot design with subsampled incomplete plots (not all accessions were grown in soil from all plots), test statistics and degrees of freedom for mixed models were estimated using Kenward-Roger’s approximation (Kenward and Roger 1997), with package “lmerTest” (Kuznetsova et al. 2015). This approximation is appropriate for unbalanced multilevel designs fit by restricted maximum likelihood. Subsamples were averaged to simplify model specification.

RESULTS

At the lowest level of richness (3 accessions per plot) sterilization of field soil increased the total growth of the paired plants by 38% (Fig. 1). Root allocation (measured as the ratio of root mass to total mass) depended upon sterilization ( $F_{(1,238.7)}; P = 0.0003$ ) but not richness ( $F_{(2, 238.7)}; P = 0.5490$ ). Sterilization of soil from higher levels of accessional richness (8 and 12 ecotypes per plot) had no effect on the growth of the paired plants. In unsterilized soil, *Pseudoroegneria* grown in soil from 3-population plots were 21% smaller than plants grown in soil from 8-accession plots and 20% smaller than plants grown in soil from 12-accession plots. In other words, *Pseudoroegneria* ecotypes grew larger in unsterilized soil that contained high population richness, but not when soil was not sterilized.

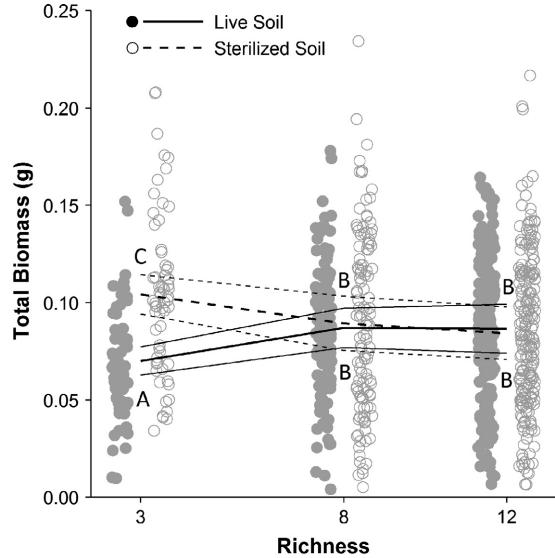


FIG. 1. Total biomass of *Pseudoroegneria spicata* in 3, 8, or 12 accessions, and either in sterilized (dotted lines, open circles) and non-sterilized soil (solid lines, closed circles). Error bars show 1 SE calculated using Kenward-Roger’s approximation. Letters show significant differences according to a post-hoc test of least-squares means, with Tukey adjustment. Actual data are shown as a cloud of points.

Biomass varied significantly between richness and sterilization treatments. This was driven particularly by the 3-accession plots (Table 1), which had much lower biomass in sterilized soil than the other plots, demonstrating that sterilization of 3-accession soils consistently increased plant growth more than sterilization of 8-accession and 12-accession soils. Across all plots there was a significant relationship between intraspecific diversity and plant-soil feedbacks ( $F_{(2,20.6)} = 20.58; P < 0.0001$ ). Soil in 8-accession and 12-accession plots had neutral feedbacks; soil in 3-accession plots had stronger negative feedbacks. But within each level of richness linear mixed models with soil feedback and richness as crossed predictors, plot as a random factor, and 2011 relative overyielding as a response variable revealed no relationship between relative yield and

TABLE 1. Results from generalized linear mixed model with total biomass as a response variable and richness and sterilization as crossed factors. Test statistics and degrees of freedom were calculated using Kenward-Roger’s approximation. Results of select planned contrasts are provided. Degrees of freedom are shown in parentheses next to the appropriate test statistic.

	<i>B</i> ± SE	<i>t</i>	<i>F</i>	<i>P</i>
Sterilization			25.08 (1, 235.8)	<0.0001
Richness			4.498 (2, 79.9)	0.0141
Richness (8)	0.018 ± 0.007	2.623 (113.6)		0.0100
Richness (12)	0.018 ± 0.006	2.844 (96.1)		0.0054
Sterilization × Richness			11.72 (2, 235.8)	<0.0001
Steril. × Rich. (8)	−0.033 ± 0.008	−3.928 (235.8)		0.0001
Steril. × Rich. (12)	−0.038 ± 0.008	−4.786 (235.8)		<0.0001

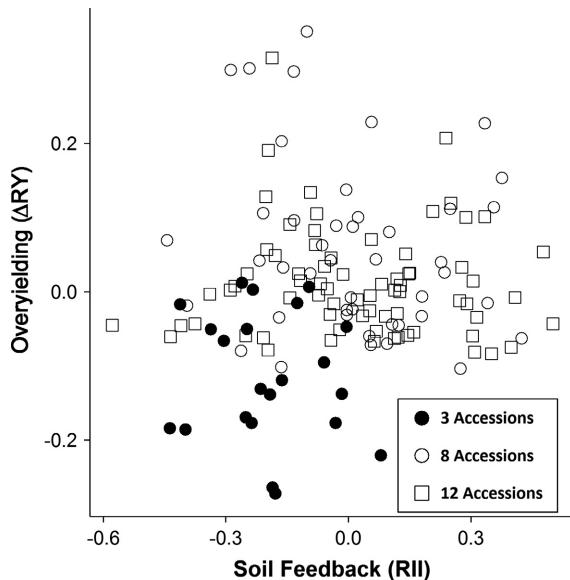


FIG. 2. Relationship between soil feedback measured in this experiment and relative overyielding ( $\Delta RY$ ) measured in 2011 in the same plots. Relationships for the 3-accession (filled circle), 8-accession (open circle), and 12-accession (open square) plots are shown.

feedback (Fig. 2; Appendix S1: Table S1). Linear discriminant analysis with one-at-a-time cross validation corroborated these results; the 3-ecotype plots were predicted with a 67% success rate and the 8- and 12-ecotype plots could not be distinguished.

#### DISCUSSION

Our results indicate that the inhibitory effects of soil biota at low population diversity has the potential to contribute to the positive relationship between intraspecific diversity and ecosystem productivity. We found that the total biomass of *Pseudoroegneria* increased with increasing population accession or ecotypic diversity in unsterilized soil conditions. A number of recent studies have shown that soil biota affects the species diversity–production relationship (Maron et al. 2011, Schnitzer et al. 2011, De Kroon et al. 2012), but to our knowledge this is the first report of such an effect of soil biota on intraspecific diversity and ecosystem function.

De Kroon et al. (2012) explored the hypothesis that pathogen-constrained growth in monocultures would lead to disproportionately low root production, which in turn would limit the optimal acquisition of nutrients. They indeed found that species in monocultures were “under-rooted”, which appeared to be due to pathogen-constrained growth. They suggested that elevated root production in polycultures of species might come at a cost to individual plants, but improved nutrition might eventually result in an overall increase in community performance. There is an interesting parallel in our *Pseudoroegneria* population diversity system to these

results. Yang et al. (2015a) explored the potential for identity recognition among the roots of different *Pseudoroegneria* populations to contribute to the overyielding in plots with high intraspecific richness of this species relative to monocultures, the field experiment which forms the foundation of the results reported here (Atwater and Callaway 2015). They found that when plants from different populations were planted together in pots, the total biomass yield was 30% more than in pots with two plants from the same population. Perhaps more importantly, in a root chamber experiment, the elongation rates of roots of *Pseudoroegneria* plants that contacted roots from another plant from the same population decreased more than after contact with roots from a plant from a different population. These results suggest the possibility of some form of detection and avoidance mechanism among related *Pseudoroegneria* plants. Considered with our results, much as found by De Kroon et al. (2012) for species richness, reduced root production in *Pseudoroegneria* monocultures be due “pathogen-constrained growth.”

Soil biota plays a key role in determining the growth, productivity, and reproductive success of individual plants, and plants can influence biotic and abiotic soil properties in ways that alter the soil’s ability to support or inhibit subsequently plant conspecifics (van der Putten et al. 2013). To our knowledge, our results are the first to implicate soil biota in the intraspecific diversity–productivity relationship. This is important because we know little about population variation in the effects of soil biota in general. Maron et al. (2015) compared the magnitude of plant–soil feedbacks experienced by native and exotic genotypes of the perennial forb, *Solidago gigantea* in soil collected across 14 sites sampled across the western part of *Solidago*’s native range in the United States. Both native and exotic genotypes suffered consistently negative plant–soil feedbacks when grown in North American soil. However, the magnitude of these effects varied tremendously among populations—population-level variation in feedback strength (coefficient of variation =  $-1.8$ ) was greater than site-level variation in feedback strength (coefficient of variation =  $-0.57$ ). Wagner et al. (2011) studied soil biota effects on ten populations of the steppe grass *Stipa capillata* from two distinct regions, Europe and Asia. They found consistent negative soil biota effects, no differences among regions, but substantial variation in the responses of different populations of *Stipa*. In contrast, Kardol et al. (2014) did not find variation in the responses of different ecotypes of *Bistorta vivipara* in response to soil biota.

Host-specific enemies such as soil pathogens and diseases may play important roles in explaining the stable maintenance of species diversity in many ecosystems (Klironomos 2002, Mangan et al. 2010), and these effects can be manifest through shifts in the strengths of plant–soil feedbacks. For example, soil pathogens can impair growth and kill young plants (Packer and Clay 2000, Reinhart et al. 2005, Bell et al. 2006, Van der

Heijden et al. 2008), and play an important role in determining characteristics of plant communities (Maron et al. 2011). Disease caused by host-specific soil microbes have been shown previously to lead to negative plant–soil feedbacks (Bever et al. 1997, Knops et al. 1999, Klironomos 2002, Van der Heijden et al. 2008, Mangan et al. 2010), and such feedbacks can affect the relationship between species diversity and productivity. We provide a new perspective on intraspecific diversity in that populations with high diversity may dilute negative plant–soil feedbacks effects.

It is important to note that we used accessions of *Pseudoroegneria* (potentially ecotypes) from across a very large portion of the regional distribution of the species. The seeds of each accession were pooled samples from a larger population, not single seed descent families. Thus we do not yet know if enough genetic variation exists within populations to create important effects on overyielding in natural populations. However, by using such a wide breadth of *Pseudoroegneria* accessions, we have explored the potential of intraspecific diversity–ecosystem function relationships and provided a working hypothesis for a mechanism.

Our findings suggest a mechanistic hypothesis for the intraspecific diversity–productivity relationship. Clearly this mechanism is not mutually exclusive with others (see Schnitzer et al. 2011); however, a better understanding of plant–soil biota relationships may continue to expand our understanding of the importance of intraspecific diversity in natural ecosystems.

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