

## Omitted variable bias in studies of plant interactions

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Abstract. Models of plant-plant interactions underpin our understanding of species coexistence, invasive plant impacts, and plant community responses to climate change. In recent studies, models of competitive interactions failed predictive tests, thereby casting doubt on results of many past studies. We believe these model failures owe at least partly to heterogeneity in unmodeled factors (e.g., nutrients, soil pathogens) that affect both target plants and neighboring competitors. Such heterogeneity is ubiquitous, and models that do not account for it will suffer omitted variable bias. We used instrumental variables analysis to test for and correct omitted variable bias in studies that followed common protocols for measuring plant competition. In an observational study, omitted variables caused competition to seem like mutualism. In a quasi-experiment that partially controlled competitor abundances with seeding, omitted variables caused competition to seem about 35% weaker than it really was, even though the experiment occurred in an abandoned agricultural field where environmental heterogeneity was expected to be relatively low. Despite decades of research, consistently accurate estimates of competitive interactions remain elusive. The most foolproof way around this pr)oblem is true experiments that avoid omitted variable bias by completely controlling competitor abundances, but such experiments are rare.

Key words: coexistence; competition; density dependence; instrumental variables analysis; intraspecific and interspecific interactions; model; plant interactions; population and community dynamics.

## Introduction

Estimates of plant-plant interactions underpin our understanding of species coexistence (e.g., Hart et al. 2018), invasive species impacts (Parker et al. 1999), and plant community responses to climate change (e.g., Adler et al. 2012). There are longstanding concerns about methods used to estimate plant interactions (Antonovics and Levin 1980, Damgaard and Weiner 2017), and these concerns have been magnified by the discovery that empirically based competition models can generate grossly inaccurate predictions, and estimates of competitive interactions depend heavily on methods used to estimate them (Adler et al. 2018a, Tuck et al. 2018). These discoveries cast doubt on results of many past studies and show plant interaction research is not immune to the increasingly recognized "reproducibility crisis," or failure of research results in ecology and other fields to hold up across studies (Baker 2016, Fidler et al. 2017). Detto et al. (2019) helped explain failings of plant competition models by showing estimates of competitive interactions are biased when competitor abundances are measured

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[Correction added on May 29, 2020, after first online publication: an error was introduced where part of an equation was omitted and has since been fixed. We apologize to the author and our readers for this error.]

with error. Our paper resembles Detto et al. (2019) in that we explore bias in competition models, though the bias we consider stems from a different mechanism.

Plant interactions are analyzed with models in which response variables describe target plants (e.g., density, biomass, survival, growth), predictor variables describe neighbor plants (e.g., density, cover) and model parameters quantify interaction strength. The parameters are estimated from true experiments, quasi-experiments, and observational studies, study types differing in how treatment (i.e., neighbor) variables are controlled. True experiments precisely control neighbor values. For example, in greenhouse experiments, preplanned neighbor densities can be achieved by transplanting seedlings into pots (e.g., Thompson et al. 2015). Quasi-experiments differ from true experiments because neighbor values are only partly controlled using treatments (e.g., seeding, herbicide). For example, two plots sown with identical neighbor seed densities generally achieve different neighbor plant densities (e.g., Rinella et al. 2007, Godoy and Levine 2014, Petry et al. 2018). Finally, in observational studies, neighbors are naturally occurring and uncontrolled (e.g., Freckleton and Watkinson 2001, Adler et al. 2012). Quasi-experiments and observational studies are far more common than true experiments and are less reliable because of an additional assumption needed to estimate causal relationships. The assumption is that no variables (e.g., nutrient or soil microorganism concentrations) that influence both neighbor and target variables are omitted as model predictors (Fig. 1A). If this assumption is violated, estimated effects of neighbors on targets will suffer omitted variable bias (Rencher 2000, Gelman and Hill 2007). To see how omitted variable bias works, one can imagine an unmeasured variable such as topsoil depth or nitrogen concentration causing some quadrats to support low neighbor and target abundances and other quadrats to support high neighbor and target abundances, in which case graphs of neighbor versus target values will indicate beneficial relationships even when relationships are in fact competitive (Fig. 1C).

The assumption that no sources of abiotic and biotic variation jointly influence targets and neighbors typically goes unstated, even though such variation is ubiquitous across a range of spatial and temporal scales. In natural systems, nutrients (Jackson and Caldwell 1993,

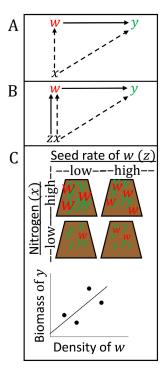


Fig. 1. Following Pearl (1995), causal diagrams (A, B) showing relationship between a neighbor plant variable w, a target plant variable y, an unmeasured variable x, and a measured variable z. Arrows originate from variables that are unmeasured and therefore excluded (dashed) or measured and therefore included (solid) in plant interaction models. In A, the unmeasured variable x will cause omitted variable bias. In B, the instrumental variable z allows omitted variable bias resulting from x to be corrected using instrumental variable analysis. C depicts a hypothetical competition experiment involving variables in A and B. Brown boxes represent field plots and different size w and y represent plants of different sizes. Species w is seeded at low and high rates, and species y is seeded at one rate. Because both the density of w and the biomass per plot of y increase with the unmeasured variable x (nitrogen concentration), a naïve plot or regression of y on w indicates w benefits y even though w competes with y. Because z (seeding rate of w) affects w but not y, z allows the biased regression estimate to be corrected using instrumental variable analysis.

Gallardo and Paramá 2007), soil organisms (e.g., Ping et al. 2017, Wang et al. 2017) and other factors that affect plant performance can vary widely among sampling locations spaced a few meters and less apart, so there is no assurance these factors are consistent across experimental units (i.e., plots, plant neighborhoods). Even within seemingly homogenous agricultural fields where competition experiments sometimes occur (e.g., Rees et al. 1996, Rinella and Sheley 2005), temporal and spatial growing condition variation is pervasive (e.g., Jaynes and Colvin 1997, Bakhsh et al. 2000), and there is evidence this variation is extensive enough to affect estimates of vital rates and competitive interactions (Table 2 of Pacala and Silander 1990). Moreover, nutrients and soil organisms vary spatiotemporally (e.g., Edwards 1984, Cain et al. 1999, Goldmann et al. 2019), which erodes confidence that spatial (e.g., plot effects) and temporal (year effects) parameters can be included in models to control for unmeasured abiotic and biotic variables (e.g., Lin et al. 2012). The tenuous, near universal assumption that variation in growing conditions has negligible effects on estimates of plant interactions has never been tested, and testing this assumption is the primary goal of this paper.

Next, we mathematically outline how omitted variables cause bias. Omitted variables bias estimates from all traditional competition models fit to observational and quasi-experimental data. For simplicity, and because linear and generalized linear models are widely used in plant interaction research, we begin by considering a linear model fit to data from an observational study where targets and neighbors are measured once within quadrats randomly distributed about a site. These studies remain common (e.g., Fraterrigo et al. 2014, Soliveres et al. 2015, Pearson et al. 2016) despite decades-old concerns about unmeasured variables causing bias (Fig. 1A; Antonovics and Levin 1980). We assume target performance (e.g., growth, biomass) y is related to an omitted variable x, neighbor abundance w, and random error u by

$$y_i = \beta_0 + \beta_x x_i + \beta_w w_i + u_i. \tag{1}$$

We assume w is competitive ( $\beta_w < 0$ ) and think of x as a variable that positively affects both y and w (Fig. 1A), such as topsoil depth under target plant, quadrat, or plot i. Because x is unknown,  $y_i = \beta_0^* + \beta_w^* w_i + u_i^*$  is fit instead of Eq. 1. Consequently, instead of the true  $\beta_w$ , the estimate tends toward  $\beta_w^* = \beta_w + \gamma$  where  $\gamma = \beta_x \cos(w,x)/\sin(w)$ . Recall that x positively affects y and w, so  $\beta_x$ ,  $\cos(w,x)$  and  $\gamma$  are positive, and  $\beta_w$  is overestimated by  $\gamma$ . Notice that if x negatively affects y and y remains positive, and  $\beta_w$  is still be overestimated by  $\gamma$ . Notice also that if x does not affect targets, then  $\cos(w,x) = 0$ ,  $\gamma = 0$ , and  $\beta_w$  is unbiased. The expression for  $\gamma$  reveals consequences of other possibilities, such as x positively effecting the target ( $\beta_x > 0$ ) and negatively affecting the neighbor ( $\cos(w,x) < 0$ ).

In moving from linear to nonlinear models, and from static data to time series data, consequences of omitted variables remain similar, as we demonstrate in Appendix S1 for a widely used competition model (e.g., Rees et al. 1996, Tuck et al. 2018). However, with some nonlinear models, such as logistic regressions used for modeling survival and colonization (e.g., Rees et al. 1996, Martorell and Freckleton 2014, Adler et al. 2018a), omitted variables that affect targets but not neighbors will cause neighbor competition to be underestimated. This feature of logistic regression is generally unknown among ecologists but is well described in other fields (Wooldridge 2002, Mood 2010).

In this paper, we use instrumental variables analysis to test for and correct omitted variable bias. We apply instrumental variables analysis to three competition studies. One study resembles controversial observational studies described above (e.g., Fraterrigo et al. 2014, Soliveres et al. 2015, Pearson et al. 2016), so detecting omitted variable bias would reinforce past warnings about these studies (Antonovics and Levin 1980, Damgaard and Weiner 2017). The other studies are quasi-experimental and occurred in former agricultural fields (Wilson and Tilman 1993, Rinella and Sheley 2005), so neighbors were partly controlled and environmental conditions were presumably relatively homogenous. Detecting even modest bias in these studies would encourage caution about other study types more prone to omitted variable bias, such as observational studies and quasi-experiments in natural systems (e.g., Rees et al. 1996, Godoy and Levine 2014, Martorell and Freckleton 2014). As explained in relation to Eq. 1 and in Appendix S1, omitted variables that positively or negatively affect both targets and neighbors cause competition to seem weaker than it truly is. Since plants typically respond positively (e.g., nutrients) and negatively (e.g., generalist pathogens) to the same factors, we hypothesized omitted variables would cause competition to seem weaker than it is. We do not formally test for omitted variable bias in recently developed models that failed predictive tests (Adler et al. 2018a, Tuck et al. 2018), though we will show omitted variable bias is a likely cause of these model failures. The observational data of Adler et al. (2018a) lacks instruments to allow testing, but omitted variable bias will prove problematic in similar data we analyze that does contain an instrument. With the quasi-experiment of Tuck et al. (2018), we use simulation to show prediction failures were likely caused by omitted variables.

## MATERIALS AND METHODS

## Instrumental variables analysis

Explaining our research necessitates defining instrumental variables and briefly explaining instrumental variable models. For those interested in the details, Appendix S2 is a primer on instrumental variable analysis, Appendix S3 fully explains our models, and Appendix S4 explains our model fitting algorithm. Instrumental variables analysis is not used in plant ecology but is routine in the social sciences and medical research (Angrist and Krueger 2001). Instrumental variables analysis allows omitted variable bias to be tested for and corrected without knowing what the omitted variables even are (Angrist and Krueger 2001). The analysis requires data on special variables called instruments (Fig. 1B). The variable z is an instrument if it directly affects the neighbor w but affects the target y only indirectly by affecting w (Fig. 1B). The assumption that z does not affect y except by affecting w is not statistically testable (Angrist and Krueger 2001), so it must be justified via theory or subject matter knowledge. For example, in an analysis of observational data, we will argue that fall precipitation is a valid instrument for studying effects of exotic winter annual grass neighbors on native plant targets. Specifically, we will argue fall precipitation regulates winter annual neighbor germination but is too low to affect target plants. With quasi-experiments, treatment variables are often valid instruments. For example, the instrument in one of our analyses is a variable equaling 0 or 1 if neighbors were or were not removed with herbicide. This randomly assigned treatment variable can affect the target only by affecting the neighbor, so it is a valid instrument (Fig. 1B).

As is typically the case with instrumental variables models, our models have two stages. The first stage predicts neighbors from instruments z and any other measured variables r

$$w_i = \sum_j \alpha_{z,j} z_{i,j} + \sum_k \alpha_{r,k} r_{i,k} + \nu_i.$$
 (2)

Subscripts i, j, and k reference experimental units, instrumental variables, and other measured variables, respectively. The second stage predicts targets from r and the neighbor

$$y_i = \sum_k \beta_{r,k} r_{i,k} + \beta_w w_i + u_i.$$
 (3)

Errors,  $v_i$ , and  $u_i$ , are bivariate normal

$$\begin{pmatrix} v_i \\ u_i \end{pmatrix} \sim N \left( \begin{pmatrix} 0 \\ 0 \end{pmatrix}, \begin{pmatrix} \sigma_1^2 & \sigma_{12} \\ \sigma_{12} & \sigma_2^2 \end{pmatrix} \right). \tag{4}$$

If  $\sigma_{12} \neq 0$ , omitted variables affect both targets and neighbors. Setting  $\sigma_{12} = 0$  instead of estimating it is equivalent to adopting a typical one-stage competition model that assume no omitted variables. More specifically, setting  $\sigma_{12} = 0$  and fitting Eqs. 2–4 results in the same estimate for  $\beta_w$  as fitting Eq. 3 with  $u_i \sim N(0, \sigma_2^2)$ .

## Observational study methods

Two similar exotic winter annual grasses, Bromus arvensis L. and Bromus tectorum L., have invaded many

western U.S. grasslands (Duncan et al. 2004). We estimated competition of bromes with non-bromes at ungrazed sites (Sites 1 and 2) with silty soils separated by 8.6 km on the Fort Keogh Livestock and Range Research Laboratory in Montana (46°22'52.60" N, 105°53′03.29" W). The dominant non-brome was the perennial grass Pascopyrum smithii (Rydb.) A. Löve, and other non-bromes included perennial grasses (Bouteloua gracilis (Willd. ex Kunth.) Lag. ex Griffiths and Hesperostipa comata (Trin. & Rupr.) Barkworth) and forbs (Logfia arvensis (L.) Holub and Vicia americana Muhl. ex Willd.). From 1994 to 2008 and in 2010, 2012, 2014, 2016, and 2018, all biomass produced in the March through June growing season was clipped in early July from 20 randomly placed 0.25-m<sup>2</sup> circular quadrats per site. Different quadrats were clipped different years, and biomass was sorted by species, dried (72 h, 60°C) and weighed.

Target and neighbor variables were (natural log) total biomass per square meter of non-bromes and bromes, respectively. Growing season (March through June) precipitation was a predictor in first and second stage models (Appendix S3: Eqs. S1, S2). Our one instrument was precipitation the fall (September and October) preceding the growing season. Bromes germinate in fall, so fall precipitation regulates brome seedling emergence and drives brome biomass the next growing season (Haferkamp et al. 1998). There are sound reasons to believe fall precipitation (z) meets the instrumental variable criteria of affecting non-bromes (y) only by affecting bromes (w) (Fig. 1B). Bromes partly or fully utilize fall precipitation before entering winter dormancy, which leaves this precipitation unavailable to non-bromes the following growing season. Also, fall precipitation comprised just  $17\% \pm 8\%$  (mean  $\pm$  SD) of annual precipitation, whereas growing season precipitation comprised 61% ± 11% (NOAA station ≤15 km from sites). For non-bromes, effects of high growing season precipitation should override effects of low precipitation from several months earlier.

On nearby (7 km) sites like ours, Haferkamp et al. (1997, 1998) conducted brome removal experiments, which provided an opportunity to compare our estimates of brome competition to experimental benchmarks. Removal experiments were quasi-experimental, but instrumental variables estimates we derive from can be considered experimental (Appendix S3). Haferkamp et al. (1997) compared hand removal of bromes to no removal at four sites (one silty clay loam and one clay site in 1991 and 1992). Similarly, Haferkamp et al. (1998) factorially combined removal treatments with three P. smithii clipping treatments at two clay sites, one in 1993 and one in 1995. Bromes were removed periodically from early April through mid-May or early June, and brome and non-brome biomass were measured early to mid-July.

## Quasi-experimental methods of Wilson and Tilman (1993)

In a former farm field, Wilson and Tilman (1993) replicated a factorial combination of nitrogen (with or without ammonium nitrate) and disturbance (with or without tillage) treatments in  $5 \times 5$  m plots. Biomass per perennial grass (*Schizachyrium scoparium* (Michx.) Nash) transplant ( $\log_{10} y$ ) was determined after transplants grew four months in subplots where naturally occurring neighbors (grasses and forbs) were present or removed with herbicide. The neighbor variable was  $\log_{10}(\text{biomass})$  within 15 cm of the transplant. Our instrument was a variable equaling 0 if neighbors were removed, 1 otherwise (Appendix S3).

# Quasi-experimental methods of Rinella and Sheley (2005)

The exotic perennial forb Euphorbia esula L. infests millions of hectares of western U.S. grasslands (Duncan et al. 2004). To estimate competition of E. esula with grasses, Rinella and Sheley (2005) randomly factorially combined four Poa pratensis L. and six P. smithii seed rates and six E. esula transplant densities in 1.0  $\times$  1.0 m plots arranged in a grid (12 columns × 12 rows) in a former farm field. Biomass by species was measured the fourth year after planting. Neighbor and target variables were E. esula and total grass biomass ( $ln[g/m^2]$ ), respectively, and instruments were variables equaling 0 or 1 depending on whether transplant density was 0, 4, 9, 16, 49, or 64 m<sup>-2</sup> (Appendix S3: Eq. S3). The model had P. pratensis and P. smithii seed rate main effects and interactions and plot row, column, and row x column terms to help control for spatial heterogeneity (Appendix S3: Eqs. S3–S4).

## RESULTS

## Results for observational study

At Sites 1 and 2, bromes increased 370% (25%, 1,645%) and 432% (50%, 1,787%) with every 1-SD increase in the instrument (fall precipitation). Therefore, the criteria that the instrument affects the neighbor is satisfied (Fig. 1B).

For Site 1, the regression model that assumed no omitted variables by setting  $\sigma_{12}=0$  (Eq. 4) indicated a mutualistic effect of bromes on non-bromes ( $\beta_w > 0$ ), which conflicted with experimental benchmarks (Fig. 2). When we estimated  $\sigma_{12}$  instead of assuming  $\sigma_{12}=0$ ,  $\sigma_{12}$  was positive 0.58 (0.20, 0.86) (mean and (95% CI)), and this indicated omitted variables affected non-bromes and bromes at Site 1. The instrumental variable model that does not assume  $\sigma_{12}=0$  indicated  $\beta_w < 0$  for Site 1, consistent with experimental benchmarks (Fig. 2). These results support our hypothesis that omitted variables cause competition to seem weaker than it is. The

instrumental variables estimate for Site 1 is imprecise (Fig. 2). If greater precision were required, Sites 1 and 2 could be analyzed jointly (we analyzed them separately) to increase sample sizes for estimating parameters that did not vary appreciably between sites (e.g., β<sub>2</sub> of Appendix S3: Eq. S2), or an informative prior distribution could be used. Compared to the instrumental variables estimate for Site 1, experimental estimates suggest weaker competition (Fig. 2), though if experimental estimates included confidence intervals most or all of them would likely overlap the instrumental variable's confidence interval. Moreover, bromes grew awhile before being removed, so removal experiments may have somewhat underestimated brome competition. For Site 2,  $\sigma_{12}$ is nearly zero at -0.02 (-0.39, 0.35), so omitted variable effects were trivial, and it would be logical to adopt the more precise regression estimate for Site 2 (Fig. 2).

## Results for Wilson and Tilman (1993)

Separately for each treatment combination, Wilson and Tilman (1993) regressed seedling biomass on neighbor biomass. Our instrumental variable estimates (data not shown) are nearly identical to the original estimates (Fig. 4 of Wilson and Tilman 1993), indicating omitted variable effects were negligible.

## Results for Rinella and Sheley (2005)

The *E. esula* transplant density variables we used as instruments were statistically significant (P < 0.001; Appendix S3). Despite including plot row and column parameters to control for spatial variation in omitted

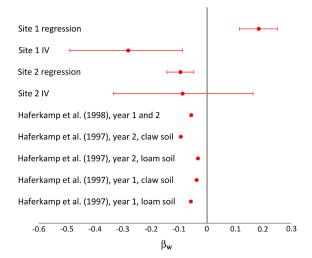


Fig. 2. Estimates of  $\beta_{\rm in}$ , a parameter describing the relationship between log(brome biomass) (measured as  $g/m^2$ ) and log (non-brome biomass). Negative values indicate bromes competed with non-bromes. Regression and instrumental variables (IV) estimates (point estimates and 95% CIs) are from observational data gathered at Sites 1 and 2, and estimates of Haferkamp et al. (1997, 1998) are from removal experiments conducted near Sites 1 and 2.

variables (Appendix S3: Eqs. S3,S4),  $\sigma_{12}$  is 53 (23, 83), indicating the presence of omitted variables. Compared to the regression estimate, the instrumental variables estimate indicates more intense competition (Fig. 3). This result further confirms our hypothesis that, when present, omitted variables cause competition to seem weaker than it is.

#### DISCUSSION

The results support our hypothesis that omitted abiotic (e.g., soil fertility) and biotic (i.e., soil biota) variables cause competition to seem weaker than it truly is. In a quasi-experiment, omitted variables caused competition to be underestimated, and in observational data, omitted variables caused competition to seem like mutualism.

Predictions from competition models are rarely evaluated against independent test data, yet we know of three studies besides ours' where traditional competition models failed predictive tests (Pacala and Silander 1990, Adler et al. 2018a, Tuck et al. 2018). In each study, omitted variables provide a compelling explanation for incorrect model predictions. Pacala and Silander (1990) convincingly attribute incorrect predictions to competition, growth rate and survival differences between plots used to parameterize models and plots used to test models, even though all their plots were within the same small  $(30 \times 60 \text{ m})$  agricultural field. It is hard to imagine these parameter differences stemmed from anything but smallscale variability in omitted environmental and/or soil biota variables, especially since all plots were sown with the same seed lots, which rules out genetic variation.

Like us, Adler et al. (2018a) developed models from observational data and tested models using removal treatments. And like our model that did not correct omitted variable bias (Site 1 regression of Fig. 2), models of Adler et al. (2018a) generally indicated weaker competition than removal treatments. This supports our hypothesis that omitted variables cause models developed from observational data to underestimate competition. One model of Adler et al. (2018a) indicated stronger competition than removal treatments, but the authors were suspicious of this model for unrelated reasons (i.e., low, episodic recruitment of the target shrub).

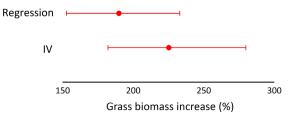


Fig. 3. Estimated percent increases (point estimates and 95% CIs) in grass biomass caused by reducing leafy spurge biomass from the mean  $(560 \text{ g/m}^2)$  to one standard deviation below the mean  $(220 \text{ g/m}^2)$  in a competition experiment. Estimates are from regression and instrumental variables (IV) models.

Incorrect model predictions of Tuck et al. (2018) likely resulted partly or wholly because they omitted treatment variables from their models. Similar to us and Adler et al. (2018a), Tuck et al. (2018) developed models using observations on target plants grown with interspecific competitors and tested models using observations on targets grown in monoculture, although Tuck et al. (2018) sowed plants instead of studying natural communities. To create density variation necessary for model fitting, Tuck et al. (2018) used clipping to reduce seed production of their seven annual species by 12.5%, 25%, 50%, 75%, or 87.5% depending on plot, and they did not include these categorical clipping treatments in their models. (In keeping with our paper's theme, omitting clipping treatments is like omitting, say, insect or nutrient variables that influence neighbor and target densities.) They clipped once annually from 2010 to 2012, used plant densities measured before clipping in 2012 as their neighbor predictors and used densities measured in 2013 as their target response variables. By reducing target plant seed input, clipping presumably directly reduced target densities, and Tuck et al. (2018) indicate clipping directly reduced neighbor densities. Therefore, all the conditions are in place for omitted variable bias. Depending on species, models under- or over-predicted competition intensity and growth rates in monoculture plots (Fig. 2 of Tuck et al. 2018), and in Appendix S5 we show how omitted clipping variables could have caused these incorrect predictions. There may be additional reasons why models of Tuck et al. (2018) failed predictive tests, but the most likely single reason is omitted clipping variables.

An important theoretical prediction is that intraspecific competition exceeds interspecific competition, and a recent review of many studies empirically supports this prediction (Adler et al. 2018b). However, Detto et al. (2019) believe results of Adler et al. (2018b) may reflect measurement error bias. Yet, Detto et al. (2019) describe too few situations where measurement errors compromise competition estimates to account for findings from many studies following diverse methods (Adler et al. 2018b). This led us to investigate whether omitted variables can bias comparisons of intraspecific and interspecific competition (Appendix S6). According to our analysis, when the intraspecific competitor covaries most strongly with the omitted variable, its competitive ability is most underestimated, and when the interspecific competitor covaries most strongly with the omitted variable, its competitive ability is most underestimated. While our analysis considered only linear models, we suspect this finding holds for all models. Our analysis suggests omitted variables could promote the incorrect conclusion that interspecific competition exceeds intraspecific competition; bias in the opposite direction of that postulated by Detto et al. (2019). To see how this might be, recall covariation between omitted and target variables is a precondition for omitted variable bias (Fig. 1A). Where this precondition is met, omitted variables might tend to covary more strongly with intraspecific than interspecific competitors, because intraspecific competitors have the same traits as the target. This opens the possibility that Adler et al. (2018b) underestimate the extent to which intraspecific competition exceeds interspecific competition

How should plant interaction research proceed? Given the heterogeneity of natural systems, and the bias this heterogeneity causes, it is unsurprising that models built from observational data fail predictive tests. Energy devoted to gathering observational data seems better devoted to manipulative studies. One exception is when instruments are available, but observational data rarely contain instruments. The most trustworthy estimates of competitive interactions will come from true experiments that eliminate the possibility of omitted variable bias by completely controlling neighbor values. As we show, trustworthy estimates can also be derived from quasi-experiments by using treatment variables as instruments. It is sometimes viewed as disadvantageous that experimental and quasi-experimental approaches construct or manipulate the community being studied (Freckleton and Watkinson 2001). However, for plant interaction research to progress, we must accurately predict how target plants will respond when neighbor abundances are changed with everything else held constant. It has become increasingly difficult to see how to make these predictions without manipulative experiments.

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Author contributions: M. Rinella conceived the ideas; All authors designed and implemented the data collection protocols; M. Rinella analyzed the data and led writing of the manuscript; L. Vermeire, and D. Strong contributed critically to writing the manuscript and gave final approval for publication.

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