Meta-analytic evidence that allelopathy may increase the success and impact of invasive grasses

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Background. In the grass family, a disproportionate number of species have been designated as being invasive. Various growth traits have been proposed to explain the invasiveness of grasses, however the possibility that allelopathy gives invasive grasses a competitive advantage has attracted relatively little attention. Recent research has isolated plant allelochemicals that are mostly specific to the grass family that can breakdown into relatively stable, toxic byproducts.

Methods. We conducted a meta-analysis of studies on grass allelopathy to test three prominent hypotheses from invasion biology and competition theory: 1) on native recipients, non-native grasses will have a significantly more negative effect compared to native grasses (novel weapons hypothesis); 2) among native grasses, their effect on non-native recipients will be significantly more negative compared to their effect on native recipients (biotic resistance hypothesis), and 3) allelopathic impacts will increase with phylogenetic distance (phylogenetic distance hypothesis). From 23 studies, we gathered a dataset of 524 observed effect sizes (delta log response ratios) measuring the allelopathic impact of grasses on growth and germination of recipient species, and we used non-linear mixed-effects Bayesian modeling to test the hypotheses.

Results. We found support for the novel weapons hypothesis: on native recipients, non-native grasses were twice as suppressive as native grasses (22% versus 11%, respectively). The phylogenetic distance hypothesis was supported by our finding of a significant correlation between phylogenetic distance and allelopathic impact. The biotic resistance hypothesis was not supported. Overall, this meta-analysis adds to the evidence that allelochemicals may commonly contribute to successful or high impact invasions in the grass family. Increased awareness of the role of allelopathy in soil legacy effects associated with grass invasions may improve restoration outcomes through implementation of allelopathy-informed restoration practices. Examples of allelopathy-informed practices, and the knowledge needed to utilize them effectively, are discussed, including the use of activated carbon to neutralize allelochemicals and modify the soil

microbial community.

1 **Meta-analytic Evidence that Allelopathy May Increase the Success and Impact of Invasive**
2 **Grasses**
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16 **Abstract**

17 **Background.** In the grass family, a disproportionate number of species have been designated as
18 being invasive. Various growth traits have been proposed to explain the invasiveness of grasses,
19 however the possibility that allelopathy gives invasive grasses a competitive advantage has
20 attracted relatively little attention. Recent research has isolated plant allelochemicals that are
21 mostly specific to the grass family that can breakdown into relatively stable, toxic byproducts.
22 **Methods.** We conducted a meta-analysis of studies on grass allelopathy to test three prominent
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31 **Results.** We found support for the novel weapons hypothesis: on native recipients, non-native
32 grasses were twice as suppressive as native grasses (22% versus 11%, respectively). The
33 phylogenetic distance hypothesis was supported by our finding of a significant correlation
34 between phylogenetic distance and allelopathic impact. The biotic resistance hypothesis was not
35 supported. Overall, this meta-analysis adds to the evidence that allelochemicals may commonly
36 contribute to successful or high impact invasions in the grass family. Increased awareness of the
37 role of allelopathy in soil legacy effects associated with grass invasions may improve restoration
38 outcomes through implementation of allelopathy-informed restoration practices. Examples of
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41 microbial community.
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Introduction

43
44   As a prime example of anthropogenic change, grasses have been deliberately moved by
45   human civilizations, often to feed livestock (D'Antonio & Vitousek, 1992; Fusco et al., 2021),
46   and their invasive spread has devastated many ecosystems (Marshall et al., 2011; Wied et al.,
47   2020; Kerns et al., 2020; Rhodes et al., 2021; Rayment, French & Bedward, 2022). The spread
48   of non-native grasses can diminish native biodiversity by forming monocultures and modifying
49   soil characteristics and nutrient cycling (Perkins, Johnson & Nowak, 2011; Gibbons et al.,
50   2017; Wied et al., 2020; Musso et al., 2021; Nagy et al., 2021; Soti & Thomas, 2021). Non-
51   native grasses may benefit from aspects of global change, including wildfire (Davies et al.,
52   2022), drought (Leal et al., 2021; Sommers, Davis & Chesson, 2022), and nitrogen deposition
53   (Cione, Padgett & Allen, 2002; Sigüenza, Corkidi & Allen, 2006). Non-native grass
54   establishment can lead to increased wildfire frequency and/or intensity (D'Antonio & Vitousek,
55   1992; Fusco et al., 2019; Tomat-Kelly, Dillon & Flory, 2021; Walker & Morgan, 2022), and
56   shortened fire cycles can push an ecosystem past the threshold of passive recovery (D'Antonio,
57   Hughes & Tunison, 2011), which substantially increases costs of restoration and adds urgency
58   to restoration planning in areas recently invaded by grasses.
59   Native (Hierro & Callaway, 2021), invasive (Kalisz, Kivlin & Bialic-Murphy, 2021)
60   and domesticated/crop grasses (Niculaes et al., 2018) are reported to have allelopathic abilities.
61   Across plant groups, allelochemicals differ in chemical structure and impart impacts through
62   different mechanisms (Cheng & Cheng, 2015), but researchers have identified benzoxazinoids
63   as allelochemicals that have been phylogenetically conserved within the Poaceae family (Frey
64   et al., 2009; Dutartre, Hilliou & Feyereisen, 2012; Niculaes et al., 2018), with evidence
65   supporting independent or convergent evolution of benzoxazinoids in some dicots (Schullehner
66   et al., 2008; Dick et al., 2012). When considered together, the evidence of shared
67   allelochemicals, disproportionate invasion success and impacts (Linder et al., 2018) and the
68   large number of grass species, the grass allelopathy literature provides a unique opportunity to
69   test important hypotheses in invasion biology and draw conclusions that can inform real world
70   practices used to reduce the impacts of invasive grasses.
71   The aim of this meta-analysis was to test whether three key invasion biology theories
72   are supported by studies investigating potential allelopathic abilities in grasses. First, we tested
73   if the Novel Weapons Hypothesis (Callaway, 2000; Hierro & Callaway, 2003; Callaway &
74   Ridenour, 2004) was supported (on native recipient species, effect size of non-native grass <
75   native grass). Second, we tested if the Biotic Resistance Hypothesis (D'Antonio & Thomsen,
76   2004; Cummings, Parker & Gilbert, 2012) was supported (for native grasses, effect size
77   associated with non-native recipients < native recipients, assuming the native grass is an
78   important contributor to native community resistance). Finally, we tested the hypothesis that
79   increased phylogenetic distance is associated with increased allelopathic impact due to
80   expected greater similarities in secondary chemicals among closer relatives and presumed
81   resistance to self-produced allelochemicals (Phylogenetic Distance Hypothesis, co-efficient of
82   smoothed phylogenetic distance < 0) (Wink, 2003; Zhang et al., 2020b).
83

Materials & Methods

In our comprehensive search, three terms were used in database searches to identify studies to be included in the invasive grass allelopathy metanalysis: "invas*", "allelo*" and "grass", where "*" indicated a wildcard character. Thus, agriculture-focused research was considered only if it was presented in the context of invasion. In May 2021, multiple search engines were used to identify relevant studies for use in the meta-analysis: Web of Science, SpringerLink, EBSCO, PubMed, Google Scholar and JSTOR (Figure 1). Specific journals were also searched: *Journal of Chemical Ecology* and *Plant and Soil* to allow searching a longer timeframe in these journals which have been historically popular for allelopathy research. Additionally, studies used in the Zhang et al. (2020b) meta-analysis (which included all volumes of *Allelopathy Journal*) that used grasses as the allelopathy species (species being tested for allelopathic potential) were included, but data from these studies was procured independently from each article to ensure that the methodology of extracting data remained consistent across all studies. Manya Singh performed the search strategy, and any disagreements were discussed between Manya Singh and Curt Daehler until a consensus was reached. This initial screening resulted in 477 studies, and after filtering for studies that included methodology that met criteria for inferring allelopathy (as described by Zhang et al. 2020b), grass species as the source of potential allelopathic abilities (referred to here as the 'allelopathy species'), ecological context of invasion, and separate reporting of control and test condition data with standard deviations or standard errors, 23 studies were left (Rasmussen & Rice, 1971; Rice, 1972; Orr, Rudgers & Clay, 2005; Blank & Sforza, 2007; Barbosa, Pivello & Meirelles, 2008; Navarro-Cano, 2008; Rudgers & Orr, 2009; Hussain, Ahmad & Ilahi, 2010; Meksawat & Pornprom, 2010; Harnden, Macdougall & Sikes, 2011; Bennett, Thomsen & Strauss, 2011; Corbett & Morrison, 2012; Ghebrehiwot, Aremu & van Staden, 2014; Greer et al., 2014; Abu-Romman & Ammari, 2015; Ismail, Tan & Chuah, 2015; Perkins, Hatfield & Espeland, 2016; Oliveira et al., 2016; Jose et al., 2016; Uddin et al., 2017; Chen et al., 2018; Możdżeń et al., 2020; Guido et al., 2020).

From each study, we collected the following information: author, year published, table/figure where data are located, name of the allelopathy species (potentially allelopathic species), name of recipient species (species impacted by the allelopathy species), mean, standard error/deviation and sample size for both control and test conditions, lifespan of each species (annual or perennial), origin of each species, experimental method (as categorized by Zhang et al. 2020b), trait measured (germination or growth, for growth, aboveground preferred, then belowground, then total), duration in days, experimental environment (controlled or otherwise), condition of plant material allelochemicals were sourced from (fresh or dry), plant part used to source allelochemicals (aboveground, belowground or mixed source), dose, dose unit type, solvent and solvent polarity. Our use of 'recipient species' instead of 'test species,' which is used in other articles (including Zhang et al. 2020b) to refer to the species receiving the allelopathic ability, is a change made to improve clarity around the species pairs, as across ecology, 'test species' is often used to refer to the species that is of main importance (i.e. not

124   the recipient species, but the species being tested for having or being involved in some key
125   phenomena). Additional details about data collection and the *a priori* power calculator used
126   prior to running the analyses are in the extended methods section (Supplemental File 1).
127   To account for small sample bias, the delta log response-ratio (delta LRR) formula was
128   used to calculate one "observed" effect size from each pair of control and treatment means (+
129   standard error, sample size) (Lajeunesse, 2015). Two observed effect sizes were dropped
130   because both the control and treatment mean failed the Geary check (Lajuennese 2015,
131   standard formula), indicating that these points violated the assumption of normality. After
132   dropping those points, we were left with a total of 524 observed effect sizes. Of the whole
133   dataset, 23% of pairs lacked a reported dose (or information that could be used to calculate a
134   dose), so the "mice" package was used to impute missing values based on delta LRR, standard
135   error, and all remaining predictors in the model (van Buuren & Groothuis-Oudshoorn, 2011).
136   From the "mice" function, 25 imputations were run, and for each observation missing a dose
137   value, the median of the 25 imputed dose values was extracted for use in the modeling.
138   Imputation via "mice" was done in place of the "missing values" feature included in the brms
139   package, because dose had to be rounded and converted to a categorical variable to be used as a
140   random effect, which is not supported by that feature. Plant species names were standardized
141   using NCBI (Schoch et al., 2020). The article text and/or external sources were used to
142   determine if each species was native (considered locally indigenous) or non-native. Other
143   predictors collected from each study are listed in Table S1.
144   In R (R Development Core Team, 2022), analyses utilized the 'brms' package for non-
145   linear, mixed-effect, multi-variate Bayesian modeling (Bürkner, 2017, 2018), using the
146   Student's t-distribution for the error components due to the presence of outliers. Predictors
147   were chosen based on past evidence of significance (Zhang et al., 2020b) and the hypotheses to
148   be tested. The "tree-linked" random variables refer to effects of species constrained by the
149   phylogenetic covariance matrix, as a nested model ('phyr' package in R)(Li et al., 2020). The
150   "phytools" package was used to generate the phylogenetic tree used in models (Revell, 2012),
151   and the "aptg" package was used to generate a distance matrix for the full set of plant species
152   (Benjamin, 2017), and the values from the distance matrix were included as a measure of
153   phylogenetic distance in models. Phylogenetic distance was a log-scaled, smoothed term to
154   allow for the model to inherently account for a non-linear relationship with effect size.
155   The non-linear model separated predictors into a "study" spline, with random effects
156   associated with study design (study ID, nested sub-study, nested trait measured; method
157   category, nested study duration; dose used), and a "species" spline, with random effects that
158   capture species effects (grass and recipient species, and grass and recipient species linked to
159   phylogenetic tree) and fixed effects for our hypotheses (origin status of grass, origin status of
160   recipient species, phylogenetic distance). Past reviews and meta-analyses were referenced to
161   determine which predictors were known to have correlations with allelopathic effect sizes,
162   which we then included as random effects to account for variance (Zhang et al., 2020b).

163   To deal with the lack of independence among delta LRRs that came from the same
164   study, the "study" spline consisted of random effects study ID (and nested variables sub study,
165   and measured trait), dose (as a categorical variable) and experimental method (based on Zhang
166   et al. (2020b) classification) (and nested variable study duration, as a categorical variable). The
167   "species" spline consisted of random effects grass species (allelopathy species), recipient
168   species and both species tree-linked. The fixed effects on the "species" spline were origin status
169   of grass (hereafter, grass origin), origin status of recipient species (hereafter, recipient origin),
170   and smoothed, log-scaled phylogenetic distance between the grass species being tested for
171   allelopathy and the recipient species.

172   Prior to running the full model, an intercept model was run, which did not include any
173   fixed effects. After generating both models, the "loo_compare" function was used to compare
174   the fit of both models, based on both leave-one-out cross validation (LOO) and widely
175   applicable information criteria (WAIC) values (Vehtari, Gelman & Gabry, 2017). The
176   "hypothesis" function was used to test hypotheses at the 95% confidence level. Explained
177   variance was calculated from the posterior sigma estimate (regression noise scale) and standard
178   deviation estimates of each random effect in the intercept model. To check for publication bias,
179   we ran a modified intercept model with log-scaled year published as a smoothed fixed effect in
180   the "study" spline, and an Egger's regression model based on the meta-analytic residuals from
181   the original intercept model.

182   Results
183   Power analysis determined that there was sufficient power to find a difference in average
184   allelopathic effect size, based on the number of studies and using Zhang et al (2020b) as the
185   baseline for the difference (86%, Figure S1) (Steidl, Hayes & Schauber, 1997). In the intercept
186   model, the study spline intercept was not significant (0.02, 95% CI [-0.21, 0.25]), but the
187   species spline intercept was significantly negative, with grasses suppressing the growth or
188   germination of the recipient species by approximately 24% (-0.28, 95% CI [-0.52, -0.04]).
189   Around 35% of the variance was explained by study ID and nested variables sub-study and trait
190   measured (15%, 8% and 11%, respectively). One-quarter of the variance was explained by
191   method and nested variable duration (10% and 15% respectively). Another quarter of the
192   variance was explained by grass species and recipient species (9% and 15% respectively). Dose
193   explained 9% of the variance, meaning that only 7% of the variance in the dataset was
194   unexplained at the observation (individual effect size) level. Phylogenetic signal from the tree-
195   linked random effects for either the allelopathy species or the recipient species explained < 1%
196   of the variance. The Egger's test and associated contoured funnel plot of the meta-analytic
197   residuals did not indicate significant publication bias at the p=0.05 level (Figure S2, y-intercept
198   95% CI [-0.03, 0.04]). Allelopathic impacts were not significantly related to publication year
199   (Figure S3, y-intercept 95% CI [-0.32, 0.14], slope 95% [-0.29, 0.28]). The full model was
200   better than the intercept model by LOO and WAIC criteria (Table S1).

201   Novel Weapons Hypothesis was supported by the full model (Table 1). For native
202   recipients, non-native grasses on average were almost twice as suppressive (24%) as native

203 grasses (13%). The predicted average effect size of native grasses on native recipients, was
204 weakly significantly different from zero (-0.14, 95% CI [-0.29, 0.02], 90% CI [-0.26, -0.01],
205 Figure 2). The predicted average effect size of non-native grasses on native recipients was
206 significantly negative (-0.27, 95% CI [-0.44, -0.09], Figure 2).
207   The Biotic Resistance Hypothesis was rejected by the full model, with weakly
208 significant support for the alternative hypothesis, that native grasses have more negative effects
209 on native recipients compared to non-native recipients, instead of vice versa (0.09, 90% CI
210 [0.02, 0.16], Table 1). On average, native grasses suppressed native recipients 9% more
211 compared to non-native recipients, opposite to expectations for the biotic resistance hypothesis
212 (positive model coefficient, Table 1). The predicted average effect size of native grasses on
213 non-native recipients was not significantly different from zero (-0.05, 95% CI [-0.22, 0.14],
214 with the model finding a 66% predicted probability that the average would be negative (Figure
215 3).
216   The Phylogenetic Distance Hypothesis was supported by the full model (Table 1).
217 There was a significant negative correlation between smoothed, log-scaled phylogenetic
218 distance and effect size. The co-efficient of a smoothed variable cannot be interpreted directly
219 as magnitude of change between intervals, but from model posteriors, the average allelopathic
220 effect size for conspecific species pairs is closer to zero, compared to other species pairs with
221 increasing phylogenetic distance (Figure 4).
222 **Discussion**
223 Support for the novel weapons hypothesis and phylogenetic distance hypothesis
224   The novel weapons hypothesis (Callaway et al., 2008)(NWH) suggests that a lack of
225 shared evolutionary history between non-native plants and native plants can result in
226 allelochemical production by non-natives that has unusually large impacts on natives. We
227 found that on a native recipient, non-native grasses are twice as suppressive as native grasses,
228 which supports NWH. Although non-native grasses may directly release allelochemicals that
229 have large impacts on native plants, support for NWH can also be explained by novel microbial
230 communities associated with non-native plants, producing novel allelochemicals that the
231 existing soil microbial community (recruited by native plants), has not evolved the ability to
232 degrade (Inderjit et al., 2011; Cipollini, Rigsby & Barto, 2012). The establishment of invasive
233 plants is generally associated with modifications to the soil bacterial community (Torres et al.,
234 2021), which plays a key role in degrading allelochemicals. The identity of the microbe
235 degrading allelochemicals may be significant if different microbes result in different by-
236 products, and stable by-products of allelochemical degradation can be toxic (Macías et al.,
237 2006, 2007; Jilani et al., 2008; Hickman et al., 2021).
238   In some allelopathy studies, species are studied in a reciprocal design, where each
239 species is examined as both a potential allelopathic and recipient species. The native grasses
240 being studied may have been chosen based on their suspected susceptibility to the soil legacy of
241 non-native grasses, thus resulting in an over-estimation of the impact of non-native grasses. In a
242 reciprocal design, native grasses are tested as both an allelopathic and a recipient species. Only

243   three studies used a native grass as both an allelopathy species and the recipient species of a
244   non-native grass (*Andropogon gerardi* in Greer et al. 2014 and Harnden et al. 2011; *Nassella*
245   *pulchra* in Chen et al. 2018), and these points comprise just over 7% of the dataset. In a post-
246   hoc analysis, we examined the predicted average allelopathic effect of native grasses
247   *Andropogon gerardi* and *Nasella pulchra* on a native recipient species and found that the
248   average for these grasses was more negative than the overall average (Figure 2), suggesting that
249   these grasses do not bias the NWH result by being less allelopathic than other grasses.
250   Alternatively, native grasses used in studies of allelopathy may have been selected as closely
251   related analogs of invasive species (congeneric approach, Inderjit et al. 2008). This type of
252   species selection may bias allelopathic impacts downward. Less than 1% of the data consisted
253   of a species pair where two species had the same genus (*Eragrostis,* Figure S4), but at the
254   family level, 39% of the data consisted of *Poaceae* pairs. Like other analyses of the allelopathy
255   literature (Zhang et al., 2020b), we found support for an increasing magnitude of allelopathic
256   impact with increasing phylogenetic distance, but the predicted average effect size on the grass
257   recipient species ranged from positive (ex. *Agropyron cristatum)* to negative (ex. *Eragrostis*
258   *bahiensis)* (Figure S4), indicating a high degree of variation in the overall statistical pattern of
259   increasing allelopathic impacts with increasing phylogenetic distance. Finally, it is possible that
260   native grasses used in allelopathic studies were chosen based on evidence of their own
261   allelopathic abilities, against native or non-native species, seen in the field, which could result
262   in under-estimation of the difference in impact compared to non-native grasses. Without
263   knowing the intention of each author, it is not possible to determine how common this
264   explanation may be, which highlights how unstated aspects of experimental design can
265   influence our meta-analytic interpretation and understanding of important phenomena.
266   Biotic resistance hypothesis
267   The biotic resistance hypothesis (D'Antonio & Thomsen, 2004) suggests that native
268   plants may have stronger impacts on growth and establishment of non-native plants than they
269   do on other native plants. Although biotic resistance is generally discussed in the context of an
270   entire native community, in native plant communities that are locally characterized by one or
271   just a few dominant species (as is often observed in modern native grasslands), a single plant
272   species may be the most important contributors of biotic resistance (Prober & Lunt, 2009;
273   Bennett et al., 2014). The weapons of a native grass would be naïve to a non-native recipient
274   species, so the lack of support for the Biotic Resistance Hypothesis suggests that a difference in
275   mechanism or magnitude of impact of weapons may be a separating feature between grasses
276   that have seen significant range expansion (invasive grasses), and native grasses that have been
277   studied for allelopathy in their native range. Observations of biotic resistance associated with
278   some native grasses may result from other aspects of competition, such as being more resilient
279   to stressors like drought (Conti et al., 2018). Additionally, it is possible that biotic resistance is
280   reliant on soil characteristics, or the degree to which the native soil microbial community has
281   avoided disturbance (disturbance hypothesis, Enders et al., 2020), which may be challenging to
282   replicate in controlled experiments, and, potentially helping to explain the lack of evidence for

283   the biotic resistance hypothesis in our study. Finally, the greatest chance of finding evidence for
284   the biotic resistance hypothesis would be if the native species are dominants in their native
285   communities. In general, we were not able to assess this, and therefore our study provides only
286   a weak test of the biotic resistance hypothesis.
287   Variance explained by experimental design
288   The experimental design variables that were included as random effects in the intercept model
289   (study/sub-study/trait, method/duration, dose, species, and tree-linked species, Figure S4 – S9)
290   accounted for over 90% of variance in delta LRR. We included more variables as random
291   effects compared to other meta-analyses of the allelopathy literature (Zhang et al., 2020b). The
292   high level of explained variance may also be attributable to the choice of a Student's t-
293   distribution over a Gaussian distribution for error terms, or to use of non-linear over linear
294   formulation. One source of potential bias for the intercept model could be the imputed values
295   for dose, as dose explained 10% of the variance in delta LRR. The magnitude of explained
296   variance highlights the strength of Bayesian meta-analyses for mixed-effect modeling of
297   complex, non-linear ecological phenomenon that are highly context dependent.
298   Allelopathy-informed restoration practices
299   Based on our finding of support for NWH, in non-native grass-invaded areas, practices
300   that account for the impact of allelochemicals may contribute to improved restoration success.
301   Because the impact of allelopathy is dose-dependent, and the concentration of an
302   allelochemical is influenced by soil characteristics and processes (Kobayashi, 2004),
303   amendments and practices that alter these processes may result in an indirect effect on the
304   overall allelopathic effect. For many years, activated carbon was used as a way of neutralizing
305   or ameliorating allelochemical impacts in the field (Callaway, 2000), but recent research
306   suggests that in addition to a direct impact on allelochemicals, activated carbon has a broader
307   impact on plant-soil feedback via modifying soil characteristics (Lau et al., 2008) and shifting
308   the microbial community (Shan et al., 2015; Nolan et al., 2015). This suggests that activated
309   carbon amendments may be useful in disrupting any dis-advantage to native plants created by
310   soil legacy effects caused by allelopathy and altered soil feedback more generally; however it
311   should be noted that carbon amendments do not universally benefit native plants (Zhang et al.,
312   2020a), and that benefit from carbon amendments is better predicted by plant functional traits
313   than native/invasive status (Knauf et al., 2021; Cole et al., 2021). Other options for field
314   amendments to disrupt allelochemicals include re-conditioning the soil by growing another
315   plant less susceptible to the allelochemicals (Li et al., 2017; Schütz et al., 2019); conducting a
316   soil transplant from an area with a healthy native ecosystem or trying to reduce the
317   concentration of allelochemicals with the addition of specific microbes via an inoculum
318   approach (Gong et al., 2018; He et al., 2020; Kheirabadi et al., 2020). Four allelopathy-
319   informed restoration practices are summarized in Figure 5.
320   Some restoration projects in grass invaded areas have included native grasses based on
321   their potential for resisting invasion through their functional traits (Funk et al., 2008) and/or
322   limiting similarity (Hess et al., 2020), but we did not find support for the biotic resistance

323   hypothesis in our analysis. Support for the phylogenetic distance hypothesis does contribute to
324   evidence supporting the limiting similarity hypothesis, assuming that more closely related
325   species will also share traits that have been evolutionarily conserved. There are, however,
326   concerns about the utility and practicality of basing restoration efforts on the hypothesis that
327   limiting similarity may lead to biotic resistance, due to the challenge of determining the
328   necessary degree of similarity, and due to the specific conditions or amount of time needed for
329   effects of limiting similarity to act (Hess et al., 2020).
330   Research Needs for Improved Allelopathy-informed Restoration Practices
331   For some of the allelopathy informed restoration practices, background knowledge is
332   needed for the practice to be implemented successfully (Figure 5). These "knowledge needs"
333   point to areas where there is an urgent need for additional research. Research on the ability of
334   specific microbes to degrade allelochemicals can contribute to the use of microbial inoculum in
335   restoration practices. There are commercial soil amendments that include specific microbes for
336   improving plant growth, so research into these microbes may contribute to similar commercial
337   products that can be specifically targeted towards grass-invaded areas. Research testing the
338   ability of different plant species to "re-culture" grass-invaded soil is also needed, and
339   researchers may want to prioritize testing common resilient native plants or domesticated crop
340   species, as these species may be more accessible for use in the field. Finally, the continued use
341   of activated carbon in a variety of contexts can contribute to an improved understanding of
342   what contexts are appropriate for activated carbon amendments. The consideration and
343   simulation of climate change on the efficacy of allelopathy-informed restoration practices is
344   critical, as there is evidence that some climate events like drought can increase the potency of
345   allelochemicals (Borbély & Dávid, 2008). In addition, innovative communication strategies are
346   needed for research to have meaningful impact on restoration practices outside of academia.
347   Platforms like the Restor Foundation's RESTOR (restor.eco) have been developed during the
348   UN's Decade of Restoration (United Nations, 2020) with the aim of collecting relevant data,
349   but practitioners may still need to invest substantial time and effort to determine the most
350   appropriate, financially feasible practice for their context.
351
352   **Conclusions**
353   The rise and fall of allelopathy as a trending research topic has left research gaps, but our
354   findings supporting allelopathy as a potential mechanism that can help explain strong dominance
355   and impact (including legacy effects) by invasive grasses. By highlighting evidence that invasive
356   grasses may often produce allelochemicals, we hope to stimulate further research and promote
357   consideration of allelochemical amelioration strategies after invasive grass removal, as a strategy
358   for producing tangible improvements in conservation and restoration outcomes. It's clear that in
359   the UN Decade of Restoration, the stakes for restoration success are high, and when it comes to
360   the broad impacts of invasive grasses worldwide, allelopathy research presents an important
361   opportunity to make major headway.
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653

Estimated difference and 95% CI for each hypothesis.

Negative differences were predicted *a priori* for each hypothesis test.

	Estimate	95 LCI	95 UCI	
Novel Weapons Hypothesis	-0.14	-0.25	-0.03	*
Biotic Resistance Hypothesis	0.09	-0.01	0.19	
Phylogenetic Distance Hypothesis	-0.22	-0.36	-0.07	*

Figure 1

PRISMA flowchart.
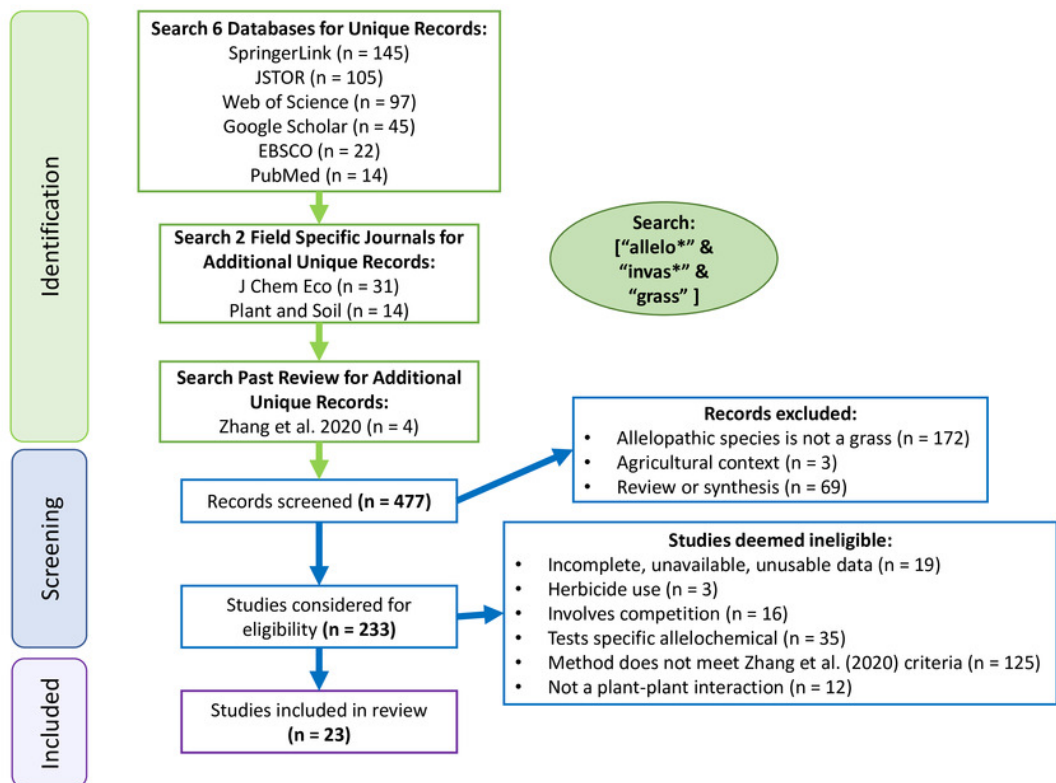
Figure 2

Test of the novel weapons hypothesis.

Center, bean plot of distribution of predicted mean effect size with long line showing the average prediction, overlayed on strip-chart of distribution of predicted population. To each side, notched boxplot, overlayed with jittered points, showing distribution of observed effect sizes. Colors represent effect of native (green, right) and non-native (magenta, left) grasses on native recipients. Center-left, bean plot of predicted difference (light pink) between average effect of native grasses and average effect of non-native grasses on native recipients, with long line showing average predicted difference. Annotation "**" denotes significance at 95% CI level.
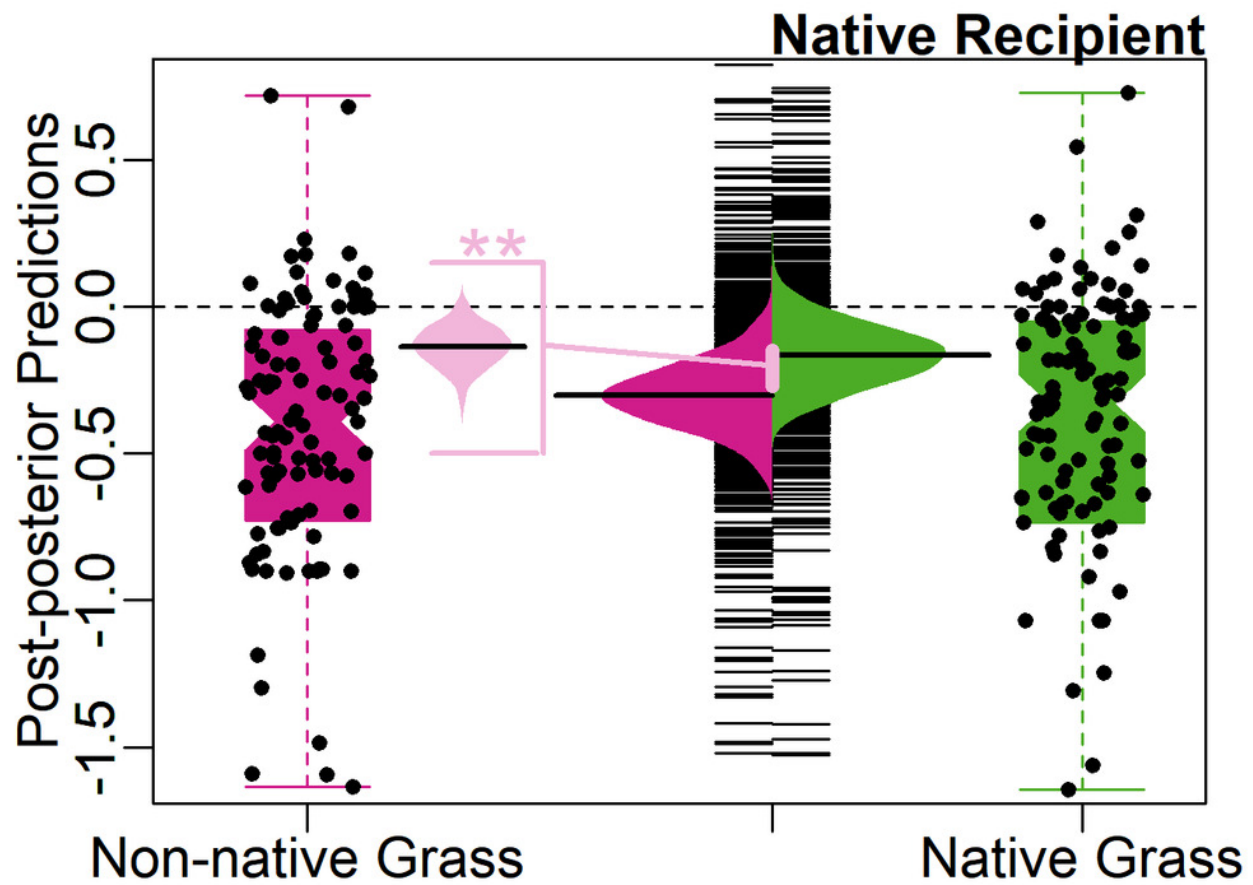
Figure 3

Test of the biotic resistance hypothesis.

Center, bean plot of distribution of predicted mean effect size with long line showing the average prediction, overlayed on strip-chart of distribution of predicted population. To each side, notched boxplot, overlayed with jittered points, showing distribution of observed effect sizes. Colors represent effect of native grasses on native (green, right) and non-native (light green, left) recipients. Center-left, bean plot of predicted difference (light pink) in average effect size of native grasses on native recipients compared to non-native recipients, with long line showing average predicted difference. Contrary to the hypotheses, natives had stronger impacts on natives than on non-natives. Annotation "**" denotes significance at 95% CI level.
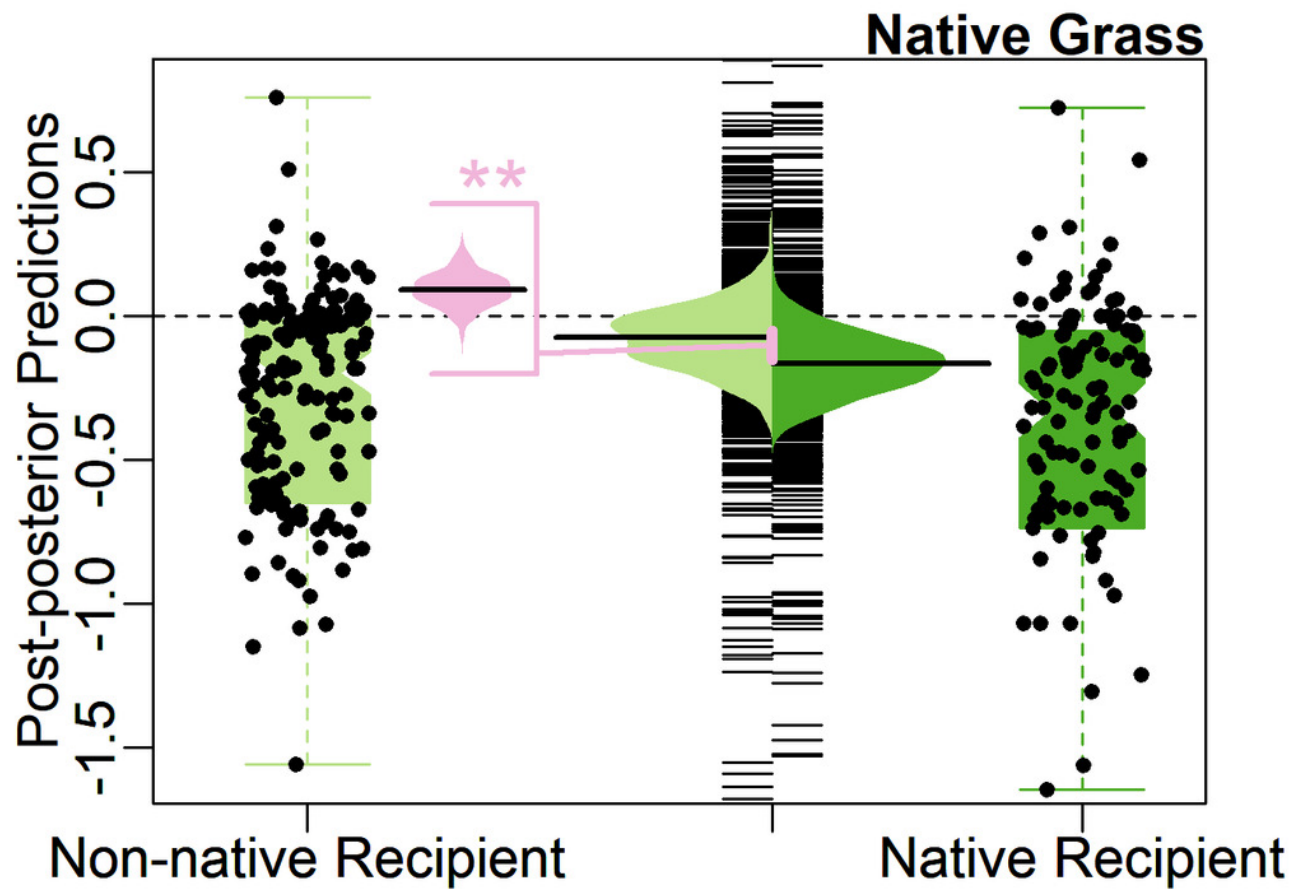
Figure 4

Test of phylogenetic distance hypothesis.

Post-posterior predicted mean effect size (+ 95% CI) across phylogenetic distance (unitless, from distance matrix calculated using aptg package), overlayed with points representing observed effect sizes (pink) and point-ranges (in blue) representing mean + SE of observed effect sizes within y-axis bounds. Black numbers are average predicted change in effect size for that interval of phylogenetic distance.
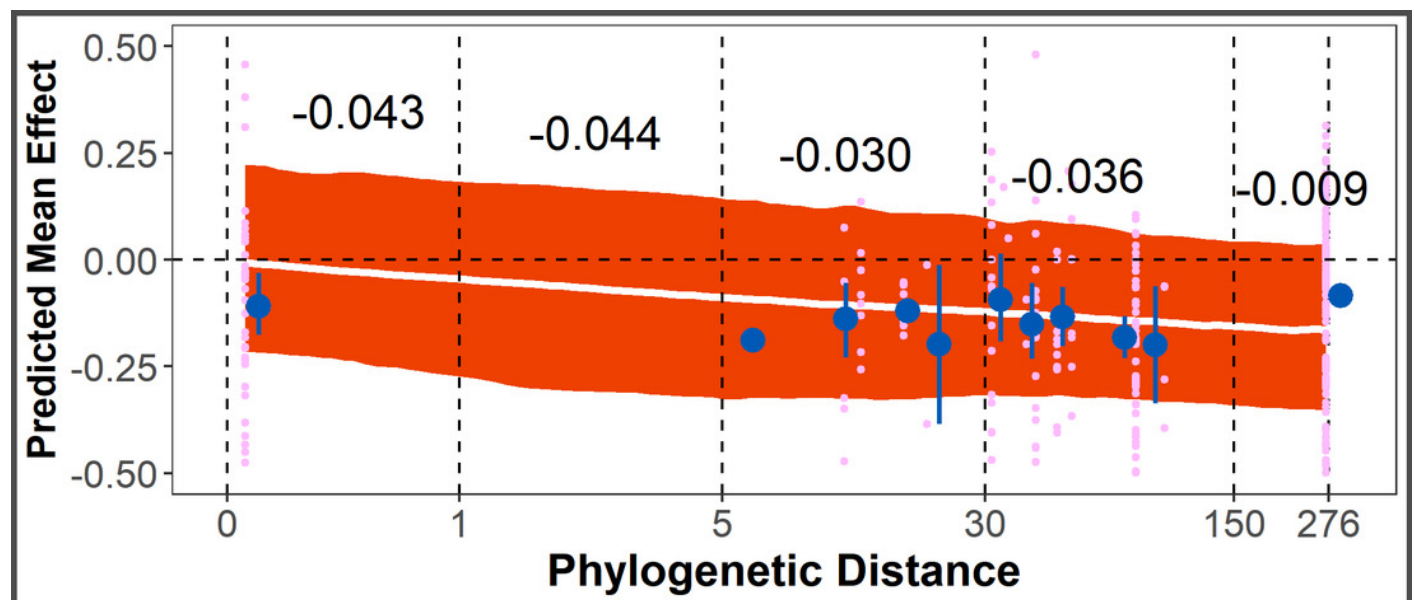
Figure 5

Four allelopathy informed restoration practices (out planting, microbial inoculum, soil transplant and activated carbon).

A summary of their underlying mechanisms and what is required to utilize the practice effectively.