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

Manya Singh [Corresp., 1] , **Curtis Daehler** [1]

[1] Botany Program, School of Life Sciences, University of Hawaii at Manoa, Honolulu, Hawaii, United States

Corresponding Author: Manya Singh
Email address: msingh@hawaii.edu

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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6 Manya Singh[1], Curtis C Daehler[1]
7
8 [1]Botany Graduate Program, School of Life Sciences, University of Hawai'i at Mānoa, Honolulu,
9 HI, USA
10
11 Corresponding Author:
12 Manya Singh[1]
13 2538 McCarthy Mall Edmondson 216, Honolulu, HI, 96822, USA
14 Email address: msingh@hawaii.edu
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Introduction

As a prime example of anthropogenic change, grasses have been deliberately moved by human civilizations, often to feed livestock (D'Antonio & Vitousek, 1992; Fusco et al., 2021), and their invasive spread has devastated many ecosystems (Marshall et al., 2011; Wied et al., 2020; Kerns et al., 2020; Rhodes et al., 2021; Rayment, French & Bedward, 2022). The spread of non-native grasses can diminish native biodiversity by forming monocultures and modifying soil characteristics and nutrient cycling (Perkins, Johnson & Nowak, 2011; Gibbons et al., 2017; Wied et al., 2020; Musso et al., 2021; Nagy et al., 2021; Soti & Thomas, 2021). Non-native grasses may benefit from aspects of global change, including wildfire (Davies et al., 2022), drought (Leal et al., 2021; Sommers, Davis & Chesson, 2022), and nitrogen deposition (Cione, Padgett & Allen, 2002; Sigüenza, Corkidi & Allen, 2006). Non-native grass establishment can lead to increased wildfire frequency and/or intensity (D'Antonio & Vitousek, 1992; Fusco et al., 2019; Tomat-Kelly, Dillon & Flory, 2021; Walker & Morgan, 2022), and shortened fire cycles can push an ecosystem past the threshold of passive recovery (D'Antonio, Hughes & Tunison, 2011), which substantially increases costs of restoration and adds urgency to restoration planning in areas recently invaded by grasses.

Native (Hierro & Callaway, 2021), invasive (Kalisz, Kivlin & Bialic-Murphy, 2021) and domesticated/crop grasses (Niculaes et al., 2018) are reported to have allelopathic abilities. Across plant groups, allelochemicals differ in chemical structure and impart impacts through different mechanisms (Cheng & Cheng, 2015), but researchers have identified benzoxazinoids as allelochemicals that have been phylogenetically conserved within the Poaceae family (Frey et al., 2009; Dutartre, Hilliou & Feyereisen, 2012; Niculaes et al., 2018), with evidence supporting independent or convergent evolution of benzoxazinoids in some dicots (Schullehner et al., 2008; Dick et al., 2012). When considered together, the evidence of shared allelochemicals, disproportionate invasion success and impacts (Linder et al., 2018) and the large number of grass species, the grass allelopathy literature provides a unique opportunity to test important hypotheses in invasion biology and draw conclusions that can inform real world practices used to reduce the impacts of invasive grasses.

The aim of this meta-analysis was to test whether three key invasion biology theories are supported by studies investigating potential allelopathic abilities in grasses. First, we tested if the Novel Weapons Hypothesis (Callaway, 2000; Hierro & Callaway, 2003; Callaway & Ridenour, 2004) was supported (on native recipient species, effect size of non-native grass < native grass). Second, we tested if the Biotic Resistance Hypothesis (D'Antonio & Thomsen, 2004; Cummings, Parker & Gilbert, 2012) was supported (for native grasses, effect size associated with non-native recipients < native recipients, assuming the native grass is an important contributor to native community resistance). Finally, we tested the hypothesis that increased phylogenetic distance is associated with increased allelopathic impact due to expected greater similarities in secondary chemicals among closer relatives and presumed resistance to self-produced allelochemicals (Phylogenetic Distance Hypothesis, co-efficient of smoothed phylogenetic distance < 0) (Wink, 2003; Zhang et al., 2020b).

59 **Materials & Methods**
60 In our comprehensive search, three terms were used in database searches to identify
61 studies to be included in the invasive grass allelopathy metanalysis: "invas*", "allelo*" and
62 "grass", where "*" indicated a wildcard character. Thus, agriculture-focused research was
63 considered only if it was presented in the context of invasion. In May 2021, multiple search
64 engines were used to identify relevant studies for use in the meta-analysis: Web of Science,
65 SpringerLink, EBSCO, PubMed, Google Scholar and JSTOR (Figure 1). Specific journals were
66 also searched: *Journal of Chemical Ecology* and *Plant and Soil* to allow searching a longer
67 timeframe in these journals which have been historically popular for allelopathy research.
68 Additionally, studies used in the Zhang et al. (2020b) meta-analysis (which included all
69 volumes of *Allelopathy Journal*) that used grasses as the allelopathy species (species being
70 tested for allelopathic potential) were included, but data from these studies was procured
71 independently from each article to ensure that the methodology of extracting data remained
72 consistent across all studies. This initial screening resulted in 477 studies, and after filtering for
73 studies that included methodology that met criteria for inferring allelopathy (as described by
74 Zhang et al. 2020b), grass species as the source of potential allelopathic abilities (referred to
75 here as the 'allelopathy species'), ecological context of invasion, and separate reporting of
76 control and test condition data with standard deviations or standard errors, 23 studies were left
77 (Rasmussen & Rice, 1971; Rice, 1972; Orr, Rudgers & Clay, 2005; Blank & Sforza, 2007;
78 Barbosa, Pivello & Meirelles, 2008; Navarro-Cano, 2008; Rudgers & Orr, 2009; Hussain,
79 Ahmad & Ilahi, 2010; Meksawat & Pornprom, 2010; Harnden, Macdougall & Sikes, 2011;
80 Bennett, Thomsen & Strauss, 2011; Corbett & Morrison, 2012; Ghebrehiwot, Aremu & van
81 Staden, 2014; Greer et al., 2014; Abu-Romman & Ammari, 2015; Ismail, Tan & Chuah, 2015;
82 Perkins, Hatfield & Espeland, 2016; Oliveira et al., 2016; Jose et al., 2016; Uddin et al., 2017;
83 Chen et al., 2018; Możdżeń et al., 2020; Guido et al., 2020).
84 From each study, we collected the following information: author, year published,
85 table/figure where data are located, name of the allelopathy species (potentially allelopathic
86 species), name of recipient species (species impacted by the allelopathy species), mean,
87 standard error/deviation and sample size for both control and test conditions, lifespan of each
88 species (annual or perennial), origin of each species, experimental method (as categorized by
89 Zhang et al. 2020b), trait measured (germination or growth, for growth, aboveground preferred,
90 then belowground, then total), duration in days, experimental environment (controlled or
91 otherwise), condition of plant material allelochemicals were sourced from (fresh or dry), plant
92 part used to source allelochemicals (aboveground, belowground or mixed source), dose, dose
93 unit type, solvent and solvent polarity. Our use of 'recipient species' instead of 'test species,'
94 which is used in other articles (including Zhang et al. 2020b) to refer to the species receiving
95 the allelopathic ability, is a change made to improve clarity around the species pairs, as across
96 ecology, 'test species' is often used to refer to the species that is of main importance (i.e. not
97 the recipient species, but the species being tested for having or being involved in some key
98 phenomena). Additional details about data collection and the *a priori* power calculator used
99 prior to running the analyses are in the extended methods section (Supplemental File 1).

100   To account for small sample bias, the delta log response-ratio (delta LRR) formula was
101   used to calculate one "observed" effect size from each pair of control and treatment means (+
102   standard error, sample size) (Lajeunesse, 2015). Two observed effect sizes were dropped
103   because both the control and treatment mean failed the Geary check (Lajuennese 2015,
104   standard formula), indicating that these points violated the assumption of normality. After
105   dropping those points, we were left with a total of 524 observed effect sizes. Of the whole
106   dataset, 23% of pairs lacked a reported dose (or information that could be used to calculate a
107   dose), so the "mice" package was used to impute missing values based on delta LRR, standard
108   error, and all remaining predictors in the model (van Buuren & Groothuis-Oudshoorn, 2011).
109   From the "mice" function, 25 imputations were run, and for each observation missing a dose
110   value, the median of the 25 imputed dose values was extracted for use in the modeling.
111   Imputation via "mice" was done in place of the "missing values" feature included in the brms
112   package, because dose had to be rounded and converted to a categorical variable to be used as a
113   random effect, which is not supported by that feature. Plant species names were standardized
114   using NCBI (Schoch et al., 2020). The article text and/or external sources were used to
115   determine if each species was native (considered locally indigenous) or non-native. Other
116   predictors collected from each study are listed in Table S1.
117   In R (R Development Core Team, 2022), analyses utilized the 'brms' package for non-
118   linear, mixed-effect, multi-variate Bayesian modeling (Bürkner, 2017, 2018), using the
119   Student's t-distribution for the error components due to the presence of outliers. Predictors
120   were chosen based on past evidence of significance (Zhang et al., 2020b) and the hypotheses to
121   be tested. The "tree-linked" random variables refer to effects of species constrained by the
122   phylogenetic covariance matrix, as a nested model ('phyr' package in R)(Li et al., 2020). The
123   "phytools" package was used to generate the phylogenetic tree used in models (Revell, 2012),
124   and the "aptg" package was used to generate a distance matrix for the full set of plant species
125   (Benjamin, 2017), and the values from the distance matrix were included as a measure of
126   phylogenetic distance in models. Phylogenetic distance was a log-scaled, smoothed term to
127   allow for the model to inherently account for a non-linear relationship with effect size.
128   The non-linear model separated predictors into a "study" spline, with random effects
129   associated with study design (study ID, nested sub-study, nested trait measured; method
130   category, nested study duration; dose used), and a "species" spline, with random effects that
131   capture species effects (grass and recipient species, and grass and recipient species linked to
132   phylogenetic tree) and fixed effects for our hypotheses (origin status of grass, origin status of
133   recipient species, phylogenetic distance). Past reviews and meta-analyses were referenced to
134   determine which predictors were known to have correlations with allelopathic effect sizes,
135   which we then included as random effects to account for variance (Zhang et al., 2020b).
136   To deal with the lack of independence among delta LRRs that came from the same
137   study, the "study" spline consisted of random effects study ID (and nested variables sub study,
138   and measured trait), dose (as a categorical variable) and experimental method (based on Zhang
139   et al. (2020b) classification) (and nested variable study duration, as a categorical variable). The

140 "species" spline consisted of random effects grass species (allelopathy species), recipient
141 species and both species tree-linked. The fixed effects on the "species" spline were origin status
142 of grass (hereafter, grass origin), origin status of recipient species (hereafter, recipient origin),
143 and smoothed, log-scaled phylogenetic distance between the grass species being tested for
144 allelopathy and the recipient species.
145   Prior to running the full model, an intercept model was run, which did not include any
146 fixed effects. After generating both models, the "loo_compare" function was used to compare
147 the fit of both models, based on both leave-one-out cross validation (LOO) and widely
148 applicable information criteria (WAIC) values (Vehtari, Gelman & Gabry, 2017). The
149 "hypothesis" function was used to test hypotheses at the 95% confidence level. Explained
150 variance was calculated from the posterior sigma estimate (regression noise scale) and standard
151 deviation estimates of each random effect in the intercept model. To check for publication bias,
152 we ran a modified intercept model with log-scaled year published as a smoothed fixed effect in
153 the "study" spline, and an Egger's regression model based on the meta-analytic residuals from
154 the original intercept model.
155 **Results**
156   Power analysis determined that there was sufficient power to find a difference in average
157 allelopathic effect size, based on the number of studies and using Zhang et al (2020b) as the
158 baseline for the difference (86%, Figure S1) (Steidl, Hayes & Schauber, 1997). In the intercept
159 model, the study spline intercept was not significant (0.02, 95% CI [-0.21, 0.25]), but the
160 species spline intercept was significantly negative, with grasses suppressing the growth or
161 germination of the recipient species by approximately 24% (-0.28, 95% CI [-0.52, -0.04]).
162 Around 35% of the variance was explained by study ID and nested variables sub-study and trait
163 measured (15%, 8% and 11%, respectively). One-quarter of the variance was explained by
164 method and nested variable duration (10% and 15% respectively). Another quarter of the
165 variance was explained by grass species and recipient species (9% and 15% respectively). Dose
166 explained 9% of the variance, meaning that only 7% of the variance in the dataset was
167 unexplained at the observation (individual effect size) level. Phylogenetic signal from the tree-
168 linked random effects for either the allelopathy species or the recipient species explained < 1%
169 of the variance. The Egger's test and associated contoured funnel plot of the meta-analytic
170 residuals did not indicate significant publication bias at the p=0.05 level (Figure S2, y-intercept
171 95% CI [-0.03, 0.04]). Allelopathic impacts were not significantly related to publication year
172 (Figure S3, y-intercept 95% CI [-0.32, 0.14], slope 95% [-0.29, 0.28]). The full model was
173 better than the intercept model by LOO and WAIC criteria (Table S1).
174   Novel Weapons Hypothesis was supported by the full model (Table 1). For native
175 recipients, non-native grasses on average were almost twice as suppressive (24%) as native
176 grasses (13%). The predicted average effect size of native grasses on native recipients, was
177 weakly significantly different from zero (-0.14, 95% CI [-0.29, 0.02], 90% CI [-0.26, -0.01],
178 Figure 2). The predicted average effect size of non-native grasses on native recipients was
179 significantly negative (-0.27, 95% CI [-0.44, -0.09], Figure 2).

180   The Biotic Resistance Hypothesis was rejected by the full model, with weakly
181 significant support for the alternative hypothesis, that native grasses have more negative effects
182 on native recipients compared to non-native recipients, instead of vice versa (0.09, 90% CI
183 [0.02, 0.16], Table 1). On average, native grasses suppressed native recipients 9% more
184 compared to non-native recipients, opposite to expectations for the biotic resistance hypothesis
185 (positive model coefficient, Table 1). The predicted average effect size of native grasses on
186 non-native recipients was not significantly different from zero (-0.05, 95% CI [-0.22, 0.14],
187 with the model finding a 66% predicted probability that the average would be negative (Figure
188 3).
189   The Phylogenetic Distance Hypothesis was supported by the full model (Table 1).
190 There was a significant negative correlation between smoothed, log-scaled phylogenetic
191 distance and effect size. The co-efficient of a smoothed variable cannot be interpreted directly
192 as magnitude of change between intervals, but from model posteriors, the average allelopathic
193 effect size for conspecific species pairs is closer to zero, compared to other species pairs with
194 increasing phylogenetic distance, with the change in effect size becoming more negative as
195 phylogenetic distance between the pair of species increases (Figure 4).
196
197 **Discussion**
198 <u>Support for the novel weapons hypothesis and phylogenetic distance hypothesis</u>
199   The novel weapons hypothesis (Callaway et al., 2008)(NWH) suggests that a lack of
200 shared evolutionary history between non-native plants and native plants can result in
201 allelochemical production by non-natives that has unusually large impacts on natives. We
202 found that on a native recipient, non-native grasses are twice as suppressive as native grasses,
203 which supports NWH. Although non-native grasses may directly release allelochemicals that
204 have large impacts on native plants, support for NWH can also be explained by novel microbial
205 communities associated with non-native plants, producing novel allelochemicals that the
206 existing soil microbial community (recruited by native plants), has not evolved the ability to
207 degrade (Inderjit et al., 2011; Cipollini, Rigsby & Barto, 2012). The establishment of invasive
208 plants is generally associated with modifications to the soil bacterial community (Torres et al.,
209 2021), which plays a key role in degrading allelochemicals. The identity of the microbe
210 degrading allelochemicals may be significant if different microbes result in different by-
211 products, and stable by-products of allelochemical degradation can be toxic (Macías et al.,
212 2006, 2007; Jilani et al., 2008; Hickman et al., 2021).
213   In some allelopathy studies, species are studied in a reciprocal design, where each
214 species is examined as both a potential allelopathic and recipient species. The native grasses
215 being studied may have been chosen based on their suspected susceptibility to the soil legacy of
216 non-native grasses, thus resulting in an over-estimation of the impact of non-native grasses. In a
217 reciprocal design, native grasses are tested as both an allelopathic and a recipient species. Only
218 3 studies used a native grass as both an allelopathy species and the recipient species of a non-
219 native grass (*Andropogon gerardi* in Greer et al. 2014 and Harnden et al. 2011; *Nassella*

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

260   In general, we were not able to assess this, and therefore our study provides only a weak test of
261   the biotic resistance hypothesis.
262   Had the biotic resistance hypothesis been supported, that would have supported the
263   inclusion of native grasses in restoration projects based on their potential for resisting invasion
264   through functional trait-based assembly (Funk et al., 2008) and/or limiting similarity (Hess et
265   al., 2020) in areas at risk for grass invasion. Support for the phylogenetic distance hypothesis
266   does contribute to evidence supporting the limiting similarity hypothesis, assuming that more
267   closely related species will also share traits that have been evolutionarily conserved. There are,
268   however, concerns about the utility and practicality of basing restoration efforts on the
269   hypothesis limiting similarity may lead to biotic resistance, due to the challenge of determining
270   the necessary degree of similarity, and due to the specific conditions or amount of time needed
271   for effects of limiting similarity to act (Hess et al., 2020).
272   <u>Variance explained by experimental design</u>
273   The experimental design variables that were included as random effects in the intercept model
274   (study/sub-study/trait, method/duration, dose, species, and tree-linked species, Figure S4 – S9)
275   accounted for over 90% of variance in delta LRR. We included more variables as random
276   effects compared to other meta-analyses of the allelopathy literature (Zhang et al., 2020b). The
277   high level of explained variance may also be attributable to the choice of a Student's t-
278   distribution over a Gaussian distribution for error terms, or to use of non-linear over linear
279   formulation. One source of potential bias for the intercept model could be the imputed values
280   for dose, as dose explained 10% of the variance in delta LRR. The magnitude of explained
281   variance highlights the strength of Bayesian meta-analyses for mixed-effect modeling of
282   complex, non-linear ecological phenomenon that are highly context dependent.
283   <u>Allelopathy-informed restoration practices</u>
284   Based on our finding of support for NWH, in non-native grass-invaded areas, practices
285   that account for the impact of allelochemicals may contribute to improved restoration success.
286   Because the impact of allelopathy is dose-dependent, and the concentration of an
287   allelochemical is influenced by soil characteristics and processes (Kobayashi, 2004),
288   amendments and practices that alter these processes may result in an indirect effect on the
289   overall allelopathic effect. For many years, activated carbon was used as a way of neutralizing
290   or ameliorating allelochemical impacts in the field (Callaway, 2000), but recent research
291   suggests that in addition to a direct impact on allelochemicals, activated carbon has a broader
292   impact on plant-soil feedback via modifying soil characteristics (Lau et al., 2008) and shifting
293   the microbial community (Shan et al., 2015; Nolan et al., 2015). This suggests that activated
294   carbon amendments may be useful in disrupting any dis-advantage to native plants created by
295   soil legacy effects caused by allelopathy and altered soil feedback more generally; however it
296   should be noted that carbon amendments do not universally benefit native plants (Zhang et al.,
297   2020a), and that benefit from carbon amendments is better predicted by plant functional traits
298   than native/invasive status (Knauf et al., 2021; Cole et al., 2021). Other options for field
299   amendments to disrupt allelochemicals include re-conditioning the soil by growing another

300   plant less susceptible to the allelochemicals (Li et al., 2017; Schütz et al., 2019); conducting a
301   soil transplant from an area with a healthy native ecosystem or trying to reduce the
302   concentration of allelochemicals with the addition of specific microbes via an inoculum
303   approach (Gong et al., 2018; He et al., 2020; Kheirabadi et al., 2020). Four allelopathy-
304   informed restoration practices are summarized in Figure 5.
305   <u>Research Needs for Improved Allelopathy-informed Restoration Practices</u>
306   For some of the allelopathy informed restoration practices, background knowledge is
307   needed for the practice to be implemented successfully (Figure 5). These "knowledge needs"
308   point to areas where there is an urgent need for additional research. Research on the ability of
309   specific microbes to degrade allelochemicals can contribute to the use of microbial inoculum in
310   restoration practices. There are commercial soil amendments that include specific microbes for
311   improving plant growth, so research into these microbes may contribute to similar commercial
312   products that can be specifically targeted towards grass-invaded areas. Research testing the
313   ability of different plant species to "re-culture" grass-invaded soil is also needed, and
314   researchers may want to prioritize testing common resilient native plants or domesticated crop
315   species, as these species may be more accessible for use in the field. Finally, the continued use
316   of activated carbon in a variety of contexts can contribute to an improved understanding of
317   what contexts are appropriate for activated carbon amendments. The consideration and
318   simulation of climate change on the efficacy of allelopathy-informed restoration practices is
319   critical, as there is evidence that some climate events like drought can increase the potency of
320   allelochemicals (Borbély & Dávid, 2008). In addition, innovative communication strategies are
321   needed for research to have meaningful impact on restoration practices outside of academia.
322   Platforms like the Restor Foundation's RESTOR (restor.eco) have been developed during the
323   UN's Decade of Restoration (United Nations, 2020) with the aim of collecting relevant data,
324   but practitioners may still need to invest substantial time and effort to determine the most
325   appropriate, financially feasible practice for their context.
326
327   **Conclusions**
328   The rise and fall of allelopathy as a trending research topic has left research gaps, but our
329   findings supporting allelopathy as a potential mechanism that can help explain strong dominance
330   and impact (including legacy effects) by invasive grasses. By highlighting evidence that invasive
331   grasses may often produce allelochemicals, we hope to stimulate further research and promote
332   consideration of allelochemical amelioration strategies after invasive grass removal, as a strategy
333   for producing tangible improvements in conservation and restoration outcomes. It's clear that in
334   the UN Decade of Restoration, the stakes for restoration success are high, and when it comes to
335   the broad impacts of invasive grasses worldwide, allelopathy research presents an important
336   opportunity to make major headway.
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627

Table 1(on next page)

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	*

1

Figure 1

PRISMA flowchart.
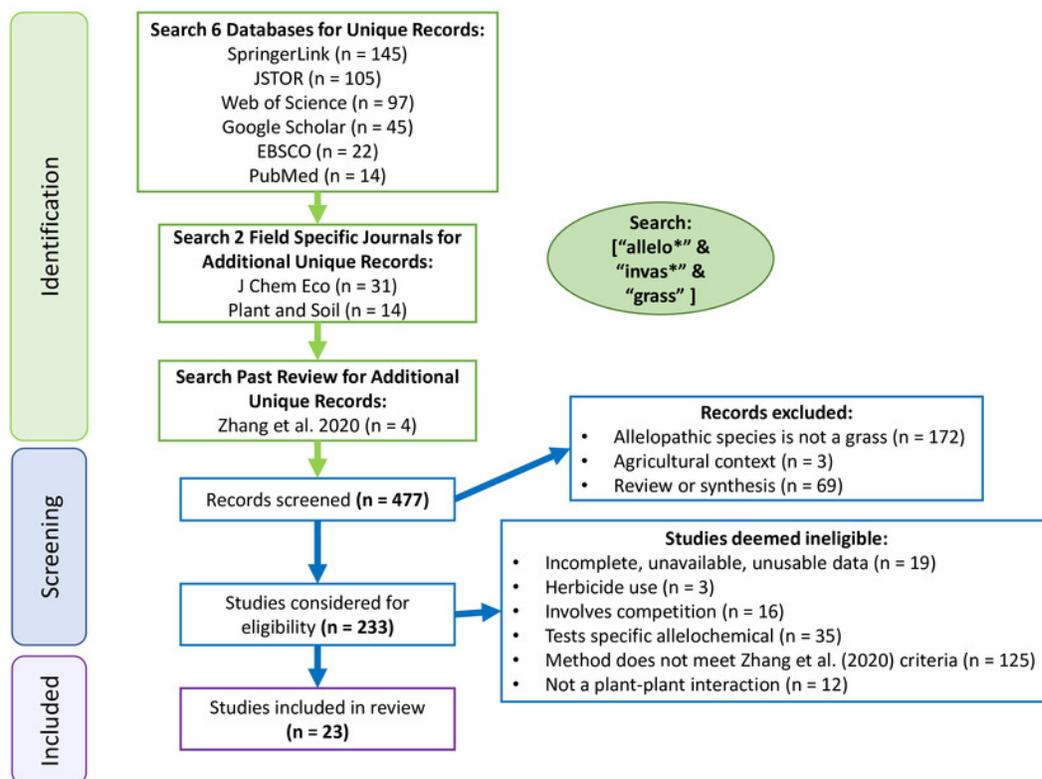
Figure 2

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 (magenta, right) and non-native (green, 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.
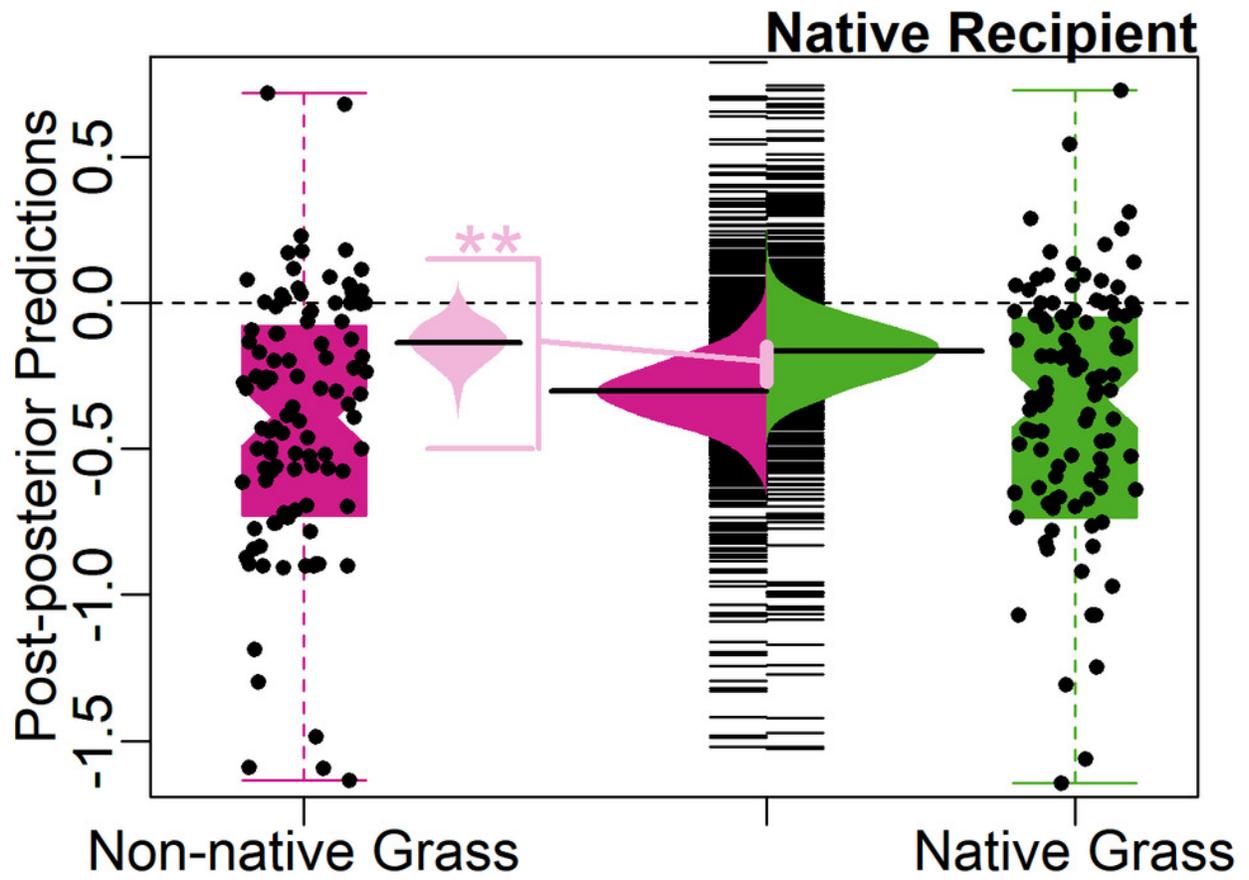
Figure 3

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.
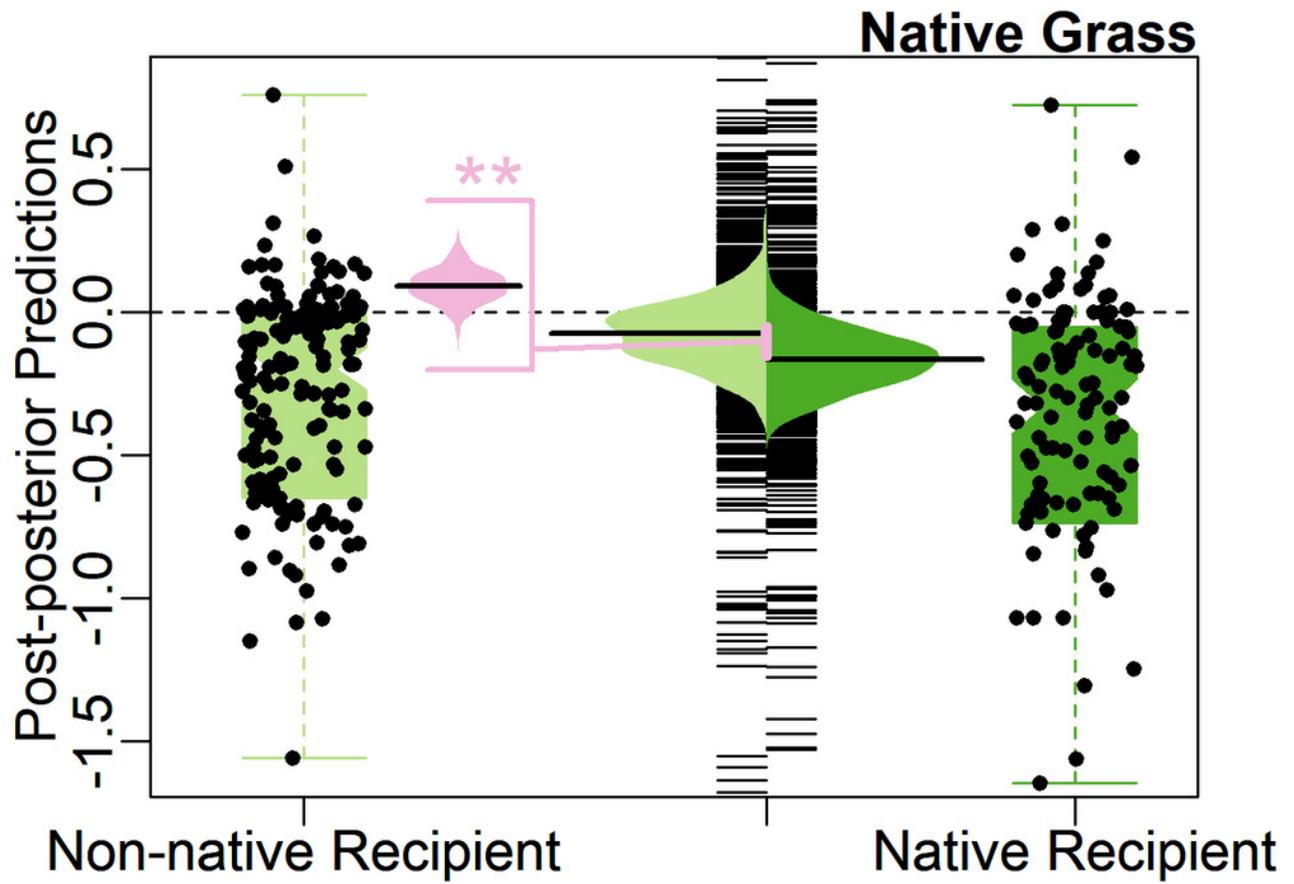
Figure 4

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.
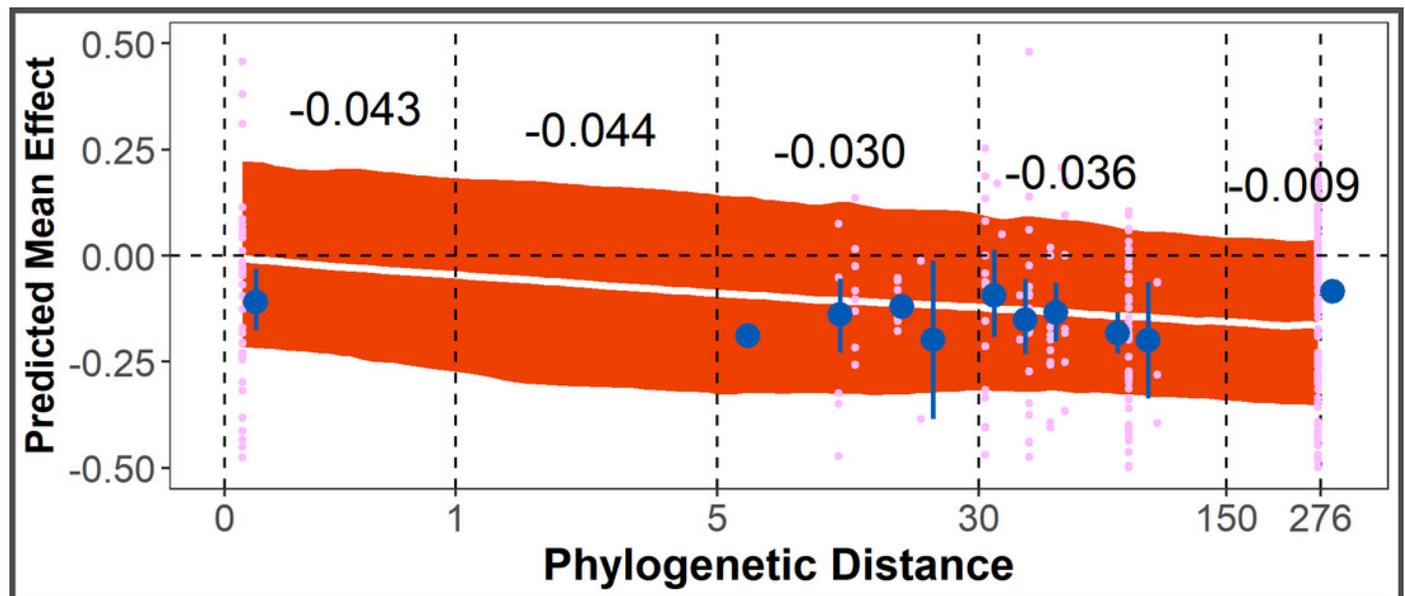
Figure 5

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.

ALLELOPATHY INFORMED RESTORATION PRACTICES

Microbial Inoculum

Add specific microbe, then microbe degrades allelochemicals
Requires:
- knowledge of **what microbe to use**
- resources and skillset to **isolate and grow microbe** to sufficient concentration for widespread use

Activated Carbon

Add carbon amendment to soil, then amendment shrinks and shifts microbial community, and modifies soil characteristics, which leads to adsorbtion of allelochemicals and mitigation of allelopathic impact
Requires:
- resources to **purchase in bulk quantities,** price depends on source material
- context where **soil modification is beneficial,** and **native species have key traits** to benefit from the amendment

Soil Transplant

Add soil and microbial community, then microbial community degrades allelochemicals
Requires:
- **access to source site, where significant soil collection can occur** (may only be realistic for mitigation projects)

Outplanting

New plant recruits microbial community, then microbial community degrades allelochemicals
Requires:
- knowledge of **what plant to use**