2-1-2013

Poised to Prosper? A Cross-system Comparison of Climate Change Effects on Native and Non-native Species Performance

Cascade J. B. Sorte
University of Massachusetts Boston

Ines Ibáñez
University of Michigan - Ann Arbor

Dana M. Blumenthal
USDA Agricultural Research Service, Fort Collins, CO, USA

Nicole A. Molinari
University of California - Santa Barbara

Luke P. Miller
Stanford University, luke.miller@sjsu.edu

See next page for additional authors

Recommended Citation

Cascade J. B. Sorte, Ines Ibáñez, Dana M. Blumenthal, Nicole A. Molinari, Luke P. Miller, Edwin D. Grosholz, Jeffrey M. Diez, Carla M. D'Antonio, Julian D. Olden, Sierra J. Jones, and Jeffrey S. Dukes. "Poised to Prosper? A Cross-system Comparison of Climate Change Effects on Native and Non-native Species Performance" *Ecology Letters* (2013): 261-270.

Authors

Cascade J. B. Sorte, Ines Ibáñez, Dana M. Blumenthal, Nicole A. Molinari, Luke P. Miller, Edwin D. Grosholz, Jeffrey M. Diez, Carla M. D'Antonio, Julian D. Olden, Sierra J. Jones, and Jeffrey S. Dukes

Article type: Review and Synthesis

Running title: Will climate change favor non-native species?

Poised to prosper? A cross-system comparison of climate change effects on native and non-native species performance

Cascade J. B. Sorte[1*], Ines Ibáñez[2], Dana M. Blumenthal[3], Nicole A. Molinari[4], Luke P. Miller[5], Edwin D. Grosholz[6], Jeffrey M. Diez[7], Carla M. D'Antonio[8], Julian D. Olden[9], Sierra J. Jones[10], Jeffrey S. Dukes[11]

[1]*Department of Environmental, Earth and Ocean Sciences, University of Massachusetts, Boston, MA, USA; cjsorte@ucdavis.edu*
[2] *School of Natural Resources, University of Michigan, Ann Arbor, MI, USA; iibanez@umich.edu*
[3] *Rangeland Resources Research Unit, USDA Agricultural Research Service, Fort Collins, CO, USA; dana.blumenthal@ars.usda.gov*
[4] *Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, CA, USA; nicole.molinari@lifesci.ucsb.edu*
[5]*Hopkins Marine Station, Stanford University, Pacific Grove, CA, USA; contact@lukemiller.org*
[6] *Department of Environmental Science and Policy, University of California, Davis, CA, USA; tedgrosholz@ucdavis.edu*
[7]*Institute of Integrative Biology, ETH, Zurich, Switzerland; jeffrey.diez@env.ethz.ch*
[8] *Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, CA, USA; dantonio@es.ucsb.edu*
[9] *School of Aquatic and Fishery Sciences, University of Washington, Seattle, WA, USA; olden@uw.edu*
[10] *Department of Biological Sciences, University of South Carolina, Columbia, SC, USA; sierra.jenell@gmail.com*
[11] *Department of Forestry and Natural Resources and Department of Biological Sciences, Purdue University, West Lafayette, IN, USA; jsdukes@purdue.edu*

**Correspondence: E-mail: cjsorte@ucdavis.edu*
Cascade J. B. Sorte
Department of Environmental, Earth and Ocean Sciences
University of Massachusetts, Boston
100 Morrissey Blvd.
Boston, MA 02125-3393, USA
Tel: 978-530-8051
Fax: 617-287-7474

Statement of authorship: CJBS, II and DMB designed the study and database; all authors contributed to the database; CJBS, II, LPM and JMD performed analyses; CJBS, II, and DMB led the writing; and all authors contributed to the writing.

Keywords: climate change, CO_2, effect size, forecasting, global warming, invasive species, meta-analysis, performance, precipitation, resource utilization

Word counts: *abstract* – 198, *main text* – 5,324, *text boxes* – none
Reference count: 72
Number of: *figures* – 4, *tables* – 1, *text boxes* – 0

Abstract

Climate change and biological invasions are primary threats to global biodiversity that may interact in the future. To date, the hypothesis that climate change will favor non-native species has been examined exclusively through local comparisons of single or few species. Here, we take a meta-analytical approach to broadly evaluate whether non-native species are poised to respond more positively than native species to future climatic conditions. We compiled a database of studies in aquatic and terrestrial ecosystems that reported performance measures of non-native (157 species) and co-occurring native species (204 species) under different temperature, CO_2, and precipitation conditions. Our analyses revealed that in terrestrial (primarily plant) systems, native and non-native species responded similarly to environmental changes. By contrast, in aquatic (primarily animal) systems, increases in temperature and CO_2 largely inhibited native species. There was a general trend towards stronger responses among non-native species, including enhanced positive responses to more favorable conditions and stronger negative responses to less favorable conditions. As climate change proceeds, aquatic systems may be particularly vulnerable to invasion. Across systems, there could be a higher risk of invasion at sites becoming more climatically hospitable, while sites shifting towards harsher conditions may become more resistant to invasions.

INTRODUCTION

Future climate change may facilitate biological invasions, accentuating its effects on local and regional biodiversity (D'Antonio & Vitousek 1992; Dukes & Mooney 1999; Hellman *et al.* 2008; Rahel & Olden 2008; Huang *et al.* 2011; Diez *et al.* 2012). Shifts in the magnitude and variability of carbon dioxide (CO_2) levels, temperature, and precipitation are altering local conditions, in some cases inhibiting resident species (Walther *et al.* 2002; Root *et al.* 2003; Parmesan 2006). These changes may provide colonization opportunities for non-resident native or non-native species (i.e., species introduced to that location by humans; Richardson *et al.* 2000; Webber & Scott 2012) that are better suited to the new conditions (Dukes & Mooney 1999; Byers 2002; Thuiller *et al.* 2007). For example, projected changes in precipitation and temperature could lead to species turnover rates of more than 40% in European plant communities (Thuiller *et al.* 2005). Although climate change and biological invasions each are altering ecosystem structure and functioning, we lack a general, quantitative understanding of how these drivers interact and could synergistically affect ecosystems in the future.

Non-native species may be poised to take advantage of emerging opportunities for colonization and population growth created by climate change. By definition, non-native species have, given their presence in introduced habitats, already succeeded in colonizing new environments. As a result, many non-native species have traits that are useful for coping with environmental change (Dukes & Mooney 1999; Theoharides & Dukes 2007; Vilà *et al.* 2007), including relatively strong dispersal abilities (Rejmánek & Richardson 1996), minimal reliance on specialized mutualists (van Kleunen *et al.* 2008), rapid growth rates (Grotkopp *et al.* 2010), broad environmental tolerances (Willis *et al.* 2010; Zerebecki & Sorte 2011), and high phenotypic plasticity (Daehler 2003; Davidson *et al.* 2011). In addition, some climatic changes are increasing resource availability (e.g., increased precipitation and atmospheric CO_2) and fluctuations in resource availability (e.g., linked to extreme climatic events; Diez *et al.* 2012), which could facilitate the establishment and spread of fast-growing species, including many of non-native origin (Davis *et al.* 2000; Daehler 2003; Blumenthal *et al.* 2008; González *et al.* 2010; Dukes *et al.* 2011).

Conversely, changes that reduce resource availability, such as decreased precipitation, increased occurrence of drought, or CO_2-driven increases in nitrogen limitation (Daehler 2003; Luo *et al.* 2004), could inhibit non-native species (Bradley *et al.* 2010). Thus, while established non-native species have demonstrated their abilities to persist in new regions, it is not clear whether these species will benefit more than co-occurring native species from changes in climatic conditions.

Relative effects of climate change on native and non-native species are likely to vary widely across ecosystems and taxa. For example, in aquatic systems, elevated CO_2 is associated with decreased pH, often inhibiting calcification and growth (Orr *et al.* 2005). By contrast, elevated CO_2 increases carbon availability and enhances water use efficiency for terrestrial plants, increasing growth of most species (Ainsworth & Long 2005) and sometimes strongly favoring non-native species (Smith *et al.* 2000; Dukes *et al.* 2011). Warming may increase growth rates in temperate aquatic and mesic terrestrial ecosystems, thus promoting fast-growing non-native species (Stachowicz *et al.* 2002; Rahel & Olden 2008; Sorte *et al.* 2010a); however, in arid and semi-arid ecosystems, increased temperatures may exacerbate drought, potentially favoring drought-tolerant natives (Bradley *et al.* 2010; Seager & Vecchi 2010). The net effect of climate change on the success of non-native species is likely to depend on both the degree to which environmental alterations inhibit (or promote) native species (Byers 2002) and the availability of both native and non-native species that are better adapted to new conditions (Bradley *et al.* 2012).

Concerns about how species invasions will interact with climate change have been articulated in several reviews (Dukes & Mooney 1999; Occhipinti-Ambrogi 2007; Thuiller *et al.* 2007; Vilà *et al.* 2007; Hellman *et al.* 2008; Rahel & Olden 2008; Walther *et al.* 2009; Bradley *et al.* 2010). Until recently, however, there were too few studies comparing native and non-native species responses to predicted climatic conditions to conduct meaningful quantitative syntheses. Here, we provide the first meta-analysis of studies comparing the responses of native and non-native species to elevated CO_2, warming, and changes in precipitation, including studies from terrestrial, marine, and freshwater ecosystems. We analyzed 132 studies (from 89 publications) that simultaneously quantified performance for both native and non-native species under ambient and altered climatic conditions (Table 1) to address the following questions:

1. How might climatic changes affect the performance of native and non-native species?
2. Will predicted climatic conditions differentially favor non-native species (i.e., do non-natives respond more positively than native species)?
3. How do absolute and relative responses vary by system and environmental driver, as well as by intrinsic attributes (e.g., response type and life stage) and extrinsic factors (e.g., geography and magnitude of climatic change)?
4. What can the shape of the relationship between performance responses and increasing magnitude of change tell us about which groups of species, under which conditions, exhibit the greatest sensitivity to climate change?

Answering these questions will allow us to assess the combined threat of climate change and biological invasions and to identify drivers that might make particular systems more susceptible to an increase in non-native species. The results of our analyses indicate that altered environmental conditions favored non-native species in aquatic habitats but not in terrestrial habitats. However, non-natives do not appear to be universally poised for increased performance and responded more strongly than native species both to beneficial and detrimental climate changes.

METHODS

We conducted a systematic review of the peer-reviewed literature to support an evidence-based examination of native *versus* non-native responses to projected climate change. Systematic reviews follow a strict protocol to maximize transparency and repeatability while minimizing bias (Pullin & Knight 2009; Stewart 2010). We applied a set of established guidelines from the ecological sciences for undertaking the steps of a formalized systematic review, which included protocol formation, search strategy, data inclusion, data extraction, and analysis (Pullin & Stewart 2006).

Protocol formation and search strategy

We searched ISI Web of Knowledge for topics using a combination of search terms for non-native species, system, and environmental driver of climate change, including changes in temperature, CO_2 levels (with aquatic pH), and precipitation (see Appendix S1 in Supporting Information). We also performed targeted searches for cited references as well as publications based on known ongoing global change studies (Terrestrial Carbon [TerraC] Information System 2011).

Data inclusion

In total, we reviewed approximately 60,000 titles and 3,000 abstracts to identify papers that met three main criteria. (1) Included at least one native and one non-native species (with origin as identified in the papers themselves or through our own literature search) that co-occur in the study location but were not necessarily closely related taxonomically. Non-native species needed to be considered established/naturalized at the study location, but we made no assumptions about species' impacts. (2) Contained at least two treatment levels (i.e., ambient and altered conditions) of a particular climate driver. (3) Reported a measure of performance that fell within the categories of survival, growth, or fecundity.

Data extraction

We identified 89 papers that met our criteria (App. S1, S2), including unpublished data from a dissertation (G. Coffman *unpubl. data*) and our own studies (D. Blumenthal & L. Perry *unpubl. data*). From these papers, we extracted data for 132 unique studies (including 204 native and 157 non-native species) that were run independently with distinct controls. When necessary, we used digital photo analysis software (e.g., ImageJ; Rasband 2009) to estimate values from published figures. When data were presented for multiple time points in a time series, only the end point (longest duration of the study) was included. When more than two treatment levels were established in a single study, or multiple performance measures were reported, they were all included in our analyses. Performance measure categories included survival (note that mortality estimates were converted to survival rates), growth (biomass, size, cover, or photosynthetic rate), and fecundity (number or mass of propagules or reproductive structures). We extracted, when available, mean, sample size, and variance for the performance of each species.

Data analysis

We ran two parallel sets of analyses: a traditional meta-analysis and a hierarchical analysis. Within the traditional analysis, we assessed general patterns in responses of native and non-native species to changing climate, and we conducted a mixed-model analysis to investigate effects of potential covariates. In addition, we developed a hierarchical approach to explore the relationship of native and non-native species' responses to increasing magnitudes of climate change.

For both approaches, we calculated the effect size (*ES*) of each species' response to climate change as the ratio of the difference between treatment and ambient responses to the average of responses across treatment and ambient conditions, or:

$$ES = (response_{treatment} - response_{ambient}) / (\bar{x}_{response})$$

We used this *ES* instead of the log-response ratio because, while the two metrics are highly correlated (3rd order polynomial $R^2 = 0.99$), our dataset included a large number of zero values, and the required adjustments for log calculations can influence results (Sweeting *et al.* 2004). For the same reasons, we also used this calculation to estimate magnitude of treatment (*MT*); thus, the difference between treatment and ambient conditions for the climate driver (i.e., temperature, CO_2, or precipitation) was:

$$MT = (variable_{treatment} - variable_{ambient}) / (\bar{x}_{variable})$$

These calculations of effect size and magnitude of treatment allowed us to standardize the treatment conditions and responses across the large variety of studies we worked with, including different climate drivers and different responses (i.e., survival, growth, and fecundity). Estimates of both effect size and magnitude of treatment ranged from -2 to 2.

Traditional meta-analysis. We first conducted comparisons to determine the responsiveness to climatic changes across groups and relative differences between native and non-native species. For this analysis, the study was the level of replication, and we pooled *ES* values for individual species, treatment levels, and response types to yield a single ES_{native} and $ES_{non\text{-}native}$ value for each study (i.e., independent comparisons of species' responses, as described above). We then calculated mean effect sizes for the responses of native and non-native species to each climate driver (+ temperature, + CO_2, + precipitation, and - precipitation), both across systems and separately for aquatic (i.e., pooled marine and freshwater) and terrestrial species. We used the jackboot macro in SAS v. 9.2 (SAS Institute 2008) to calculate the bias-corrected bootstrapped 95% confidence interval (based on 999 permutations) for each comparison. Effects on performance of native and non-native species were significant when the bootstrapped confidence intervals did not intersect with zero. To assess whether responses to climate change varied between native and non-native species, we used the methods described above to test for significance of the difference between the responses (i.e., [$ES_{non\text{-}native}$ - ES_{native}] calculated separately for each study).

In addition to the study-level analysis, above, we conducted a parallel analysis at the individual species level that incorporated the variances in measured performance responses. This analysis was comprised of a smaller subset of 69% of the studies that reported variances. Further detail on these methods is provided in Appendix S3.

We also used four mixed models to examine whether, at the species level, *ES* was affected by characteristics of the study treatments, organisms, and environments. Mixed models have been used previously for meta-analyses in a variety of research fields, including ecology (Harsch *et al.* 2009), and offer the flexibility to explore effects of a wide variety of explanatory variables. In all four mixed models, a random effect for the study was used to control for patterns that could be driven only by particular studies. The first model corresponded to the traditional analysis, which addressed whether *ES* varied for native and non-native species between different study systems (i.e., aquatic and terrestrial) and climate drivers (i.e., + temperature, + CO2, + precipitation, and - precipitation). In the second model, magnitude of treatment was added as a covariate to control for differences among studies. The third model included additional study information (treated as fixed effects) that was hypothesized to affect species' responses. These variables were: response type (survival, growth, and reproduction), habitat (forest, grassland, non-grassland herbaceous, aquatic, and other [e.g., desert, shrubland]), geographic location (latitude), and life stage (adult, juvenile, and other). The fourth model was used to specifically test for effects of latitude across study systems and climate drivers.

Mixed models to test for effects of additional explanatory variables were fit in a Bayesian framework using OpenBUGS software (Lunn *et al.* 2009) called from R (R Development Core Team 2011) with the package R2OpenBUGS (Sturtz *et al.* 2005), and all model parameters were given non-informative prior distributions. Bayesian meta-analyses using non-informative priors give comparable estimates to traditional methods while offering flexibility to explore more complex models (Mila & Ngugi 2011). Covariates were considered significant if the 95% interval of their coefficients' posterior distributions did not overlap zero. Differences between native and non-native species were assessed by subtracting estimated regression coefficients for natives from those of non-natives, yielding posterior distributions of the differences between all native and non-native parameters. If the 95% interval of a difference's posterior distribution did not overlap zero, then the responses of native and non-native species were considered significantly different.

Hierarchical analyses. To examine whether the responses of native and non-native species vary with the magnitude of climate change, we modeled the relationship between effect size and magnitude of the treatment (Osenberg *et al.* 1997, 1999). To do this, we first divided species according to whether the direction of their responses indicated a detrimental (negative) or beneficial (positive) effect of climate change on performance. We then used absolute values for both variables when estimating effect size as a function of the magnitude of treatment. We initially explored the relationship between the two variables as well as the effect of duration of treatment by fitting several biologically-plausible functions to the *ES* data (e.g., linear, quadratic, logistic). The best fit relationship (based on lowest Deviance Information Criterion; Spiegelhalter *et al.* 2000) estimated effect size, *ES*, as an asymptotic function of magnitude of treatment, *MT*, with two parameters that describe the maximum effect size and the half saturation constant (see Fig. S4.1 in App. S4). These two parameters have useful biological interpretations that can then be compared between native and non-native species: the maximum effect size is an indicator of species' maximum potential responses to climate change, and the half saturation constant indicates how sensitive species' performances are to an increment of change in climatic conditions.

To test for differences between the responses of native and non-native species under changing conditions, these two parameters were estimated hierarchically. Each parameter's estimates for a particular climate driver (temperature, CO_2, or precipitation) were nested within system (terrestrial or aquatic) and then further nested within an overall estimate for each origin (native or non-native) (App. S4; Clark & Gelfand 2006). This hierarchical structure allowed us to test for significant differences between native and non-native species at each level by calculating the differences between each pair of parameters (i.e., $parameter_{native}$ - $parameter_{non\text{-}native}$). When 95% confidence intervals around these differences did not include zero, the responses of native and non-native species were considered significantly different. Finally, we used these parameter values, their means, and their variance-covariance matrix to predict effect size as a function of magnitude of treatment at each of the three levels. We used Bayesian methods (Gelman & Hill 2007) for running these hierarchical models in OpenBUGS 1.4 (Thomas *et al.* 2006), and simulations (three chains) were run until convergence of the parameters was ensured (~50,000 iterations).

Models were then run for another 25,000 iterations from which posterior parameter values and predicted responses were estimated. Further detail on these methods is provided in Appendix S4.

RESULTS

Our traditional meta-analysis revealed differences in effects of climate change on species performance based upon climate drivers and species origins (Fig. 1). For both native and non-native terrestrial species, increased and decreased precipitation led to positive and negative responses, respectively. Increased CO_2 benefited non-native species overall, which was driven by a positive response of terrestrial (primarily plant; Table 1) species. By contrast, aquatic (primarily animal) species, particularly native ones, tended to be negatively affected by increased CO_2. Temperature effects were non-significant overall and never significant for non-native species. However, there was a positive effect of warming on native terrestrial species and a trend towards a negative effect of warming on native aquatic species. The species-specific results from the variance-weighted analysis always paralleled those from the study-level analysis, with the statistical differences being that the variance-weighted analysis detected significant negative and positive effects of CO_2 enhancement on aquatic and terrestrial natives, respectively, but did not detect significant responses of terrestrial natives under warming or non-natives under increased precipitation (App. S3). The mixed model results presented in Appendix S5 similarly paralleled those presented in Figure 1.

Results of the paired, within-study analysis indicated that non-native aquatic species were significantly favored over native species when temperature was elevated and when CO_2 was increased (Fig. 2). However, in the terrestrial comparisons, no differences were detected between native and non-native species, although non-natives trended towards a more positive response to increased CO_2 and precipitation and a more negative response than native species to decreased precipitation and increased temperature. The mixed model without additional covariates, an unpaired analysis, gave comparable results: here, non-native species were found to respond significantly more positively than natives under elevated temperatures in aquatic systems and under elevated precipitation in terrestrial systems (App. S5).

Of additional factors that we tested *via* the mixed models, treatment magnitude (i.e., level of environmental change) had significant effects on some response variables: both native and non-native aquatic organisms were more negatively affected in studies with exposure to higher levels of warming (App. S5). However, inclusion of treatment magnitude in the mixed models did not alter the basic estimates of response differences for each origin-driver-system group. No additional factors (including performance response type, habitat, latitude, or life stage) had significant effects on native or non-native species responses, although in warmed aquatic systems, the effect of increasing latitude (of the study location) tended to be positive for non-natives but negative for native species (App. S5). Overall, there were no significant differences between native and non-native species in how they responded to these covariates (App. S5).

In our expanded analysis of the relationship of species' performance responses to magnitude of environmental change, we found that non-native species had higher parameter values (i.e., were more responsive to changing climatic conditions) in all comparisons of the maximum effect size parameter (Fig. 3, App. S6). However, in all but two cases, native species were more responsive to increasing treatment magnitude (i.e., had a lower half saturation constant) than non-native species (Fig. 3, App. S6). The groups with the maximum potential performance responses to climate change (i.e., largest estimates of maximum effect size) were, for species responding positively, terrestrial and aquatic non-natives under increased temperature and, for species responding negatively, aquatic non-native species under increased temperature and CO_2. The most responsive groups (i.e., groups with the smallest values for the half saturation constant) were all terrestrial species responding positively to precipitation and native aquatic species responding negatively to increased temperature and CO_2. The only statistically significant differences between native and non-native species ($parameter_{native}$ - $parameter_{non\text{-}native}$; Fig. 3) were both maximum effect size and half saturation constant for aquatic species responding negatively to temperature increase (Fig. 3, App. S6). Overall, although non-significant, our predictive curves of effect size as a function of magnitude of treatment suggested that non-native species tended to respond more strongly both in improved conditions when performance increased as well as in more stressful conditions when performance decreased (Fig. 4 for overall curves, App. S7 for system and driver by system curves).

DISCUSSION

To support proactive ecosystem management in a rapidly changing environment, it is important to understand how ongoing climatic changes are likely to interact with biological invasions. Globally, both factors have been recognized as major drivers of biodiversity loss, and "interactions among the causes of biodiversity change…represent one of the largest uncertainties in projections of future biodiversity change" (Sala *et al.* 2000). The results of our meta-analysis indicate that absolute and relative responses of native and non-native species to climatic shifts depend upon changing temperature and the type and direction of altered resource availability. Non-native species are poised to outperform native species in aquatic ecosystems while responses in terrestrial systems are less consistent.

Effects of changing climate on species performance

Our meta-analysis uncovered largely parallel responses of native and non-native species to climate change when resources were either enhanced or became more limiting. For terrestrial species, of which studies of plants composed the majority of data (other studies were of arthropods), our results highlight a pattern of increased performance in response to elevated CO_2 and precipitation but decreased performance at reduced levels of precipitation. The strong responses of terrestrial species to precipitation are consistent with results from a meta-analysis of ecosystem-level responses to changing water availability (Wu *et al.* 2011). In addition, our finding of a significant increase in performance of non-native (but not native) terrestrial species under enhanced CO_2 is consistent with previous work showing stronger non-native species responses to CO_2 enrichment in some studies (e.g., Smith *et al.* 2000; Belote *et al.* 2004). Elevated temperature also led to increased plant performance, although only significantly for native species. Responses to warming can also be related – although indirectly – to resource availability:

while plants in cold-limited and wet climates may typically benefit from warming, those in water-limited conditions may not (Hoeppner & Dukes 2012). A *post-hoc* comparison indicated that effects of warming (for both native and non-native terrestrial species) tended to be negative in arid, but positive in non-arid, ecosystems; however, we were limited in assessing this potential context-dependency by the small number of studies conducted under relatively dry conditions (i.e., 5 of 26 terrestrial studies).

The negative responses of aquatic species – particularly natives – to changing environmental conditions may be related to resource availability or increased metabolic costs. In aquatic systems, increased dissolved CO_2 is associated with a decrease in pH and changes in water chemistry that make shell formation more difficult and costly (Orr *et al.* 2005). Increased temperature generally leads to increased metabolic rates for both aquatic and terrestrial organisms, particularly ectotherms, which represent all of the species included in these studies. Increased temperature also leads to a decrease in dissolved oxygen in aquatic systems, which then further lowers the tolerance of aquatic animals to warming (Pörtner & Knust 2007). Changes in resource availability could have, then, driven a number of the performance responses that we detected across native and non-native species in both aquatic and terrestrial systems.

Will non-native species be favored under climate change?

We found that performance of aquatic non-native species decreased less than that of co-occurring native species in potential future climatic conditions whereas we found only weak evidence for differential responses in terrestrial ecosystems. The lack of a strong and consistent origin-related response of terrestrial species to climatic factors of global change contrasts with results found, for example, in a meta-analysis of responses to eutrophication: nutrient enrichment consistently favored non-native plants and invertebrates over their native counterparts (González *et al.* 2010). Recognizing distinctions between study designs is important for interpreting differing results across analyses of performance responses to climate change. In this study, we quantified how predicted climatic conditions changed performance of native and non-native species relative to current ambient or average conditions, rather than comparing absolute performance differences between native and non-native species (e.g., González *et al.* 2010). Therefore, our findings for terrestrial species suggest that responses to climate change will not differ between native and non-native species; however, if the current trend is for non-natives to outperform native species, then there is no climate-based reason for this to change in the future. Results from a meta-analysis of performance-related traits in plants yield support for the hypothesis that non-natives outperform native species under current climatic conditions in some settings (van Kleunen *et al.* 2010). Furthermore, in a *post-hoc* analysis of the performance differences between native and non-native plant species in our study (using the effect size *ES* for the ambient $\text{response}_{\text{non-native}}$ *vs.* $\text{response}_{\text{native}}$), we detected a slight non-native performance advantage (0.15 ± 0.08 SE; one-sample *t*-test $t = 1.880$, df = 93, $p = 0.063$). Thus, in terrestrial plant systems, the lack of differential responses to altered conditions would suggest that non-native species are likely to at least retain any prior advantage over native species as the climate changes.

In aquatic ecosystems, our results suggest that non-native species are favored under environmental change relative to native species. Non-native species were less negatively affected by increases in both temperature and CO_2 than co-occurring native species. This dichotomy of non-native performance advantages under climate change in aquatic but not terrestrial systems is an interesting finding but has an important caveat: we were unable to distinguish among differences between native and non-native species that are innate to system (i.e., aquatic or terrestrial) or to life form (i.e., plant or animal). This is because, although we conducted our analyses hierarchically by climate driver (i.e., temperature, CO_2, and precipitation) and system, we necessarily relied on a subset of organisms that are amenable to experimentation and observation, and thus the focus of past study. As a result, there was a disproportionate representation of animals (particularly invertebrates) in aquatic studies (although less so in the CO_2 analyses) and plants in terrestrial studies (Table 1, App. S2). For example, although responses of aquatic species to increased CO_2 were, on balance, negative, this was driven by the negative animal responses: non-native and native aquatic primary producers responded positively in 3/3 and 2/3 of studies, respectively.

Thus, particularly in aquatic animal systems exposed to warming or acidification, non-native species appear to be at a performance advantage relative to co-occurring native species. Mechanisms for this pattern may include differences between native and non-native species in environmental conditions at their geographic origins and their respective physiological tolerances (e.g., see Deutsch *et al.* 2008). For the species compared in several of these studies, compilations of experimental results indicate that the non-natives can tolerate higher – and a broader range of – temperatures (e.g., for the Mediterranean mussel [Lockwood & Somero 2011; Somero 2012] and an assemblage of non-native invertebrates [Zerebecki & Sorte 2011]). Therefore, warming conditions can sometimes becoming more physiologically optimal for particular species (e.g., Witte *et al.* 2010). Furthermore, all of the aquatic experiments were conducted in temperate habitats whereas the majority of the aquatic non-natives originated in warmer locations (e.g., the Mediterranean or northwestern Pacific), indicating that the non-native advantage may derive from a long history of adaptation to higher temperatures. The importance of geography is also illustrated, to some degree, by the mixed model results, which suggest that native species inhabiting cooler (higher-latitude) locations are most negatively affected at increased temperature whereas the non-natives in these locations are poised for more positive performance responses to warming. Unlike the warming comparisons, there are few studies available to assess physiological mechanisms that may explain differential CO_2 or pH tolerances between native and non-native species. It is also interesting to note that patterns of thermal tolerance and latitudinal variation did not lead to differential native vs. non-native performance responses for terrestrial plants (Fig. 2).

The uneven taxonomic and geographic distribution of studies in our database highlights the need for additional study of the responses of native and non-native terrestrial animals and aquatic primary producers to climate change, especially in non-temperate habitats. For example, a recent literature review revealed that only a small fraction of non-native species have been well studied (only 49 out of 892 species were the subject of 10 or more studies), and only in a subset of geographic regions, with Africa and Asia understudied (Pyšek *et al.* 2008). Although we compiled data from a relatively large number of studies for this meta-analysis, our sample sizes were limited for particular combinations of systems and drivers (Table 1). The fact that most non-significant trends matched predictions for differential native *versus* non-native responses (Dukes & Mooney 1999; Rahel & Olden 2008; Bradley *et al.* 2010) suggests that stronger patterns could emerge as more data become available.

Shape and sensitivity of responses to climate change

Beyond the absolute and relative directions of their performance responses, our analyses indicated that non-native species tended to respond more strongly than native species either when conditions became more suitable (increased survival, growth, fecundity, etc.) or when conditions became more stressful (i.e., increased mortality or stunted growth) (Fig. 3). These patterns appear characteristic of opportunistic species that are able to quickly capitalize on increased resources such as enhanced precipitation or elevated CO_2 but, at the same time, may not perform as effectively through stressful periods (Davis *et al.* 2000; Blumenthal 2006). For growth and reproduction, greater responsiveness of non-native species is also consistent with non-native species having higher phenotypic plasticity – and incurring increased cost under resource limitation – as compared to native species (Daehler 2003; Davidson *et al.* 2011). Across our analyses, however, we observed large variability in responses within groups, which led to large variation in predictive curves of performance responses as a function of magnitude of climate change (Fig. 4, App. S7). Given these high levels of variability, statistically significant differences were limited to a single comparison: aquatic species responding negatively to warming. In this case, performance of native species was more responsive to the magnitude of temperature increase but their decreased performance saturated at a lower level (i.e., relatively less impaired), meaning that aquatic non-natives susceptible to warming had a greater scope for responding negatively to warming.

Describing the relationship of performance to magnitude of climate change allows us to project the relative trajectories of native and non-native species under future climatic conditions. Thus, based on our results for aquatic species that were negatively affected by warming, we might predict non-native species to have an initial advantage given that performance of native species declined most under relatively moderate changes in climate. But non-natives would sustain greater effects on performance given their greater response scope as temperatures become increasingly stressful. Furthermore, estimating the slopes of the response curves could allow us to predict relative effects of severely altered climatic conditions outside of the range of climates examined in previous experiments and observations. In summary, given sufficient data, the metrics estimated using this hierarchical approach – sensitivity to magnitude of change and maximum responsiveness – could help us identify ecological thresholds and forecast future ecosystem compositions.

Conclusions

Our systematic review revealed that in aquatic systems, non-native animal species have a strong performance advantage associated with increases in temperatures and CO_2 levels. We also identified weaker trends towards similar patterns with increases in CO_2 and precipitation among terrestrial species. Increasing the disparity in performance between native and non-native species is likely to exacerbate the effects of climate change on community- and ecosystem-level processes, particularly when such non-natives negatively impact resident species. Given our focus on performance measures such as demographic rates (i.e., survival and reproduction) and biomass, components that have the potential to affect abundance, range size, and per capita effects, we might speculate that impacts of aquatic non-native species could be enhanced under elevated temperature and CO_2 (Parker *et al.* 1999). Although, in aquatic systems, negative impacts of non-native species have been most often demonstrated (e.g., Williams & Smith 2007; Sorte *et al.* 2010b), positive impacts could also increase under climate change, and replacement of declining natives might sometimes prove beneficial at the community or ecosystem level (e.g., Crooks 1998). Thus, greater focus on integrating performance measures with an understanding of non-native species' impacts, especially with climate change, is needed for predicting higher-level changes under future climatic conditions. In conclusion, we found that non-native species capitalized on increased resources with environmental change, but they were also negatively affected when conditions became less suitable, and that strong differential effects of climate change on native and non-native species are more likely to be observed among aquatic animals than among terrestrial plants.

ACKNOWLEDGEMENTS

We thank J. Kray and J. Heisler-White for assistance with data extraction. Discussions with B. Bradley, R. Early, J. Lawler, and C. Lortie were especially helpful to the development of this project. We are grateful to M. Bracken for analytical assistance and comments. Funding for C.J.B.S. was provided by the Department of Energy (DOE-ER64982 for "Establishment of the Northeast Coastal Watershed Geospatial Data Network"). This study was conducted as part of the Climate & Invasions Working Group with support provided by the National Center for Ecological Analysis and Synthesis, a Center funded by the National Science Foundation (grant #EF-0553768), the University of California, Santa Barbara, and the State of California.

REFERENCES

Ainsworth, E.A. & Long, S.P. (2005). What have we learned from 15 years of free-air CO_2 enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO_2. *New Phytol.*, 165, 351-372.

Belote, R.T., Weltzin, J.F. & Norby, R.J. (2004). Response of an understory plant community to elevated [CO_2] depends on differential responses of dominant invasive species and is mediated by soil water availability. *New Phytol.,* 161, 827-835.

Blumenthal, D. (2006). Interactions between resource availability and enemy release in plant invasion. *Ecol. Lett.*, 9, 887-895.

Blumenthal, D., Chimner, R.A., Welker, J.M. & Morgan, J.A. (2008). Increased snow facilitates plant invasion in mixed grass prairie. *New Phytol.,* 179, 440-448.

Bradley, B.A., Blumenthal, D.M., Early, R., Grosholz, E.D., Lawler, J.J., Miller, L.P. *et al.* (2012). Global change, global trade, and the next wave of plant invasions. *Front. Ecol. Environ.*, 10, 20-28.

Bradley, B., Wilcove, D. & Oppenheimer, M. (2010). Climate change increases risk of plant invasion in the Eastern United States. *Biol. Invasions,* 12, 1855-1872.

Byers, J.E. (2002). Impact of non-indigenous species on natives enhanced by anthropogenic alteration of selection regimes. *Oikos,* 97, 449-458.

Clark, J.S. & Gelfand, A.E. (2006). A future for models and data in ecology. *Trends Ecol. Evol.*, 21, 375-380.

Crooks, J.A. (1998). Habitat alteration and community-level effects of an exotic mussel, *Musculista senhousia*. *Mar. Ecol. Progr. Ser.,* 162, 137-152.

Daehler, C.C. (2003). Performance comparisons of co-occurring native and alien invasive plants: Implications for conservation and restoration. *Annu. Rev. Ecol. Evol. Syst.,* 34, 183-211.

D'Antonio, C.M. & Vitousek, P.M. (1992). Biological invasions by exotic grasses, the grass fire cycle, and global change. *Annu. Rev. Ecol. Syst.,* 23, 63-87.

Davidson, A.M., Jennions, M. & Nicotra, A.B. (2011). Do invasive species show higher phenotypic plasticity than native species and, if so, is it adaptive? A meta-analysis. *Ecol. Lett.*, 14, 419-431.

Davis, M.A., Grime, J.P. & Thompson, K. (2000) Fluctuating resources in plant communities: a general theory of invasibility. *J. Ecol*., 88, 528-534.

Deutsch, C.A., Tewksbury, J.J., Huey, R.B., Sheldon, K.S., Ghalambor, C.K., Haak, D.C. *et al.* (2008). Impacts of climate warming on terrestrial ectotherms across latitude. *Proc. Natl. Acad. Sci. USA*, 105, 6668-6672.

Diez, J.M., D'Antonio, C.M., Dukes, J.S., Grosholz, E.D., Olden, J.D., Sorte, C.J.B. *et al.* (2012). Will extreme climatic events facilitate biological invasions? *Front. Ecol. Environ.,* 10, 249-257.

Dukes, J.S. & Mooney H.A. (1999). Does global change increase the success of biological invaders? *Trends Ecol. Evol.*, 14, 135-139

Dukes, J.S., Chiariello, N.R., Loarie, S.R. & Field, C.B. (2011). Strong response of an invasive plant species (*Centaurea solstitialis* L.) to global environmental changes. *Ecol. Appl.,* 21, 1887-1894.

Gelman, A. & Hill, J. (2007). *Data analysis using Regression and multilevel/hierarchical models*. New York, NY: Cambridge University Press.

González, A.L., Kominoski, J.S., Danger, M., Ishida, S., Iwai, N. & Rubach, A. (2010). Can ecological stoichiometry help explain patterns of biological invasions? *Oikos,*119, 779-790.

Grotkopp, E., Erskine-Ogden, J. & Rejmánek, M. (2010). Assessing potential invasiveness of woody horticultural plant species using seedling growth rate traits. *J. Appl. Ecol.*, 47, 1320-1328.

Harsch, M.A., Hulme, P.E., McGlone, M.S. & Duncan, R.P. (2009). Are treelines advancing? A global meta-analysis of treeline response to climate warming. *Ecol. Lett.*, 12, 1040-1049.

Hellmann, J.J., Byers, J.E., Bierwagen, B.G. & Dukes, J.S. (2008). Five potential consequences of climate change for invasive species. *Conserv. Biol.,* 22, 534-543.

Hoeppner, S.S. & Dukes, J.S. (2012). Interactive responses of old-field plant growth and composition to warming and precipitation. *Glob. Change Biol.,* 18, 1754-1768.

Huang, D., Haack, R.A. & Zhang, R. (2011). Does global warming increase establishment rates of invasive alien species? A centurial time series analysis. *PLoS ONE,* 6, e24733.

Lockwood, B.L. & Somero, G.N. (2011). Invasive and native blue mussels (genus *Mytilus*) on the California coast: the role of physiology in a biological invasion. *J. Exp. Mar. Biol. Ecol.*, 400, 167-174.

Lunn, D., Spiegelhalter, D., Thomas, A. & Best, N. (2009). The BUGS project: Evolution, critique, and future directions. *Statist. Med.*, 28, 3049-3067.

Luo, Y., Su, B., Currie, W.S., Dukes, J.S., Finzi, A.C., Hartwig, U. *et al.* (2004). Progressive nitrogen limitation of ecosystem responses to rising atmospheric carbon dioxide. *BioScience,* 54, 731-739.

Mila, A.L. & Ngugi, H.K. (2011). A Bayesian Approach to Meta-Analysis of Plant Pathology Studies. *Phytopathology*, 101, 42–51.

Occhipinti-Ambrogi, A. (2007). Global change and marine communities: Alien and climate change. *Mar. Pollut. Bull.*, 55, 342-352.

Orr, J.C., Fabry, V.J., Aumont, O., Bopp, L., Doney, S.C., Feely, R.A. *et al.* (2005). Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. *Nature*, 437, 681-686.

Osenberg, C.W., Sarnelle, O. & Cooper, S.D. (1997). Effect size in ecological experiments: the application of biological models in meta-analysis. *Am. Nat.*, 150, 798-812.

Osenberg, C.W., Sarnelle, O., Cooper, S.D. & Holt, R.D. (1999). Resolving ecological questions through meta-analysis: Goals, metrics, and models. *Ecology*, 80, 1105-1117.

Parker, I.M., Simberloff, D., Lonsdale, W.M., Goodell, K., Wonham, M., Kareiva, P.M. *et al.* (1999). Impact: Toward a framework for understanding the ecological effects of invaders. *Biol. Invasions*, 1, 3-19.

Parmesan, C. (2006). Ecological and evolutionary responses o recent climate change. *Annu. Rev. Ecol. Evol. Syst.*, 37, 637-669.

Pörtner, H.O. & Knust, R. (2007). Climate change affects marine fishes through the oxygen limitation of thermal tolerance. *Science*, 315, 95-97.

Pullin, A.S. & Knight, T.M. (2009). Doing more good than harm- Building an evidence-base for conservation and environmental management. *Biol. Conserv.*, 142, 931-934.

Pullin, A.S. & Stewart, G.B. (2006). Guidelines for systematic review in conservation and environmental management. *Conserv. Biol.*, 20, 1647-1656.

Pyšek, P., Richardson, D.M., Pergl, J., Jarosík, V., Sixtová, Z. & Weber, E. (2008). Geographical and taxonomic biases in invasion ecology. *Trends Ecol. Evol.,* 23, 237-244.

R Development Core Team (2011). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at: http://www.R-project.org/.

Rahel, F.J. & Olden, J.D. (2008). Assessing the effects of climate change on aquatic invasive species. *Conserv. Biol.,* 22, 521-533.

Rasband, W.S. (2009). ImageJ. U. S. National Institutes of Health, Bethesda. Available at: http://rsb.info.nih.gov/ij/.

Rejmánek, M. & Richardson, D.M. (1996). What attributes make some plant species more invasive? *Ecology,* 77, 1655-1661.

Richardson, D.M., Pyŝek, P., Rejmánek, M., Barbour, M.G., Panetta, F.D. & West, C.J. (2000). Naturalization and invasion of alien plants: concepts and definitions. *Divers. Distrib.*, 6, 93-107.

Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C. & Pounds, J.A. (2003). Fingerprints of global warming on wild animals and plants. *Nature*, 421, 57-60.

Sala, O.E., Chapin III, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R. *et al.* (2000). Global biodiversity scenarios for the year 2100. *Science*, 287, 1770-1774.

SAS Institute. (2008). SAS Version 9.2. SAS Institute, Cary, NC.

Seager, R. & Vecchi, G.A. (2010). Greenhouse warming and the 21st century hydroclimate of southwestern North America. *Proc. Natl. Acad. Sci. USA,* 107, 21277-21282.

Smith, S.D., Huxman, T.E., Zitzer, S.F., Charlet, T.N., Housman, D.C., Coleman, J.S. *et al.* (2000). Elevated CO_2 increases productivity and invasive species success in an arid ecosystem. *Nature,* 408, 79-81.

Somero, G.N. (2012). The physiology of global change: linking patterns to mechanisms. *Ann. Rev. Mar. Sci.*, 4, 39-61.

Sorte, C.J.B., Williams, S.L. & Zerebecki, R.A. (2010a). Ocean warming increases threat of invasive species in a marine fouling community. *Ecology,* 91, 2198-2204.

Sorte, C.J.B., Williams, S.L. & Carlton, J.T. (2010b). Marine range shifts and species introductions: comparative spread rates and community impacts. *Glob. Ecol. Biogeogr.,* 19, 303-316.

Spiegelhalter, D.J., Best, N., Carlin, B.P. & Linde, A.V.D. (2000). Bayesian measures of model complexity and fit. *J. Royal Statist. Soc. B*, 64, 583-639.

Stachowicz, J.J., Terwin, J.R., Whitlatch, R.B. & Osman, R.W. (2002). Linking climate change and Biol. Invasions: Ocean warming facilitates nonindigenous species invasions. *Proc. Natl. Acad. Sci. USA,* 99, 15497-15500.

Stewart, G. (2010). Meta-analysis in applied ecology. *Biol. Lett*., 6, 78-81.

Sturtz, S., Ligges, U. & Gelman, A. (2005). R2WinBUGS: A Package for Running WinBUGS from R. *J. Statist. Software*, 12, 1-16.

Sweeting, M.J., Sutton, A.J. & Lambert, P.C. (2004). What to add to nothing? Use and avoidance of continuity corrections in meta-analysis of sparse data. *Statist. Med.*, 23, 1351-1375.

Terrestrial Carbon (TerraC) Information System. (2011). University of Florida, Gainesville. Available at: http://TerraC.ifas.ufl.edu. Last accessed 14 October 2011.

Theoharides, K.A., & Dukes, J.S. (2007). Plant invasion across space and time: factors affecting nonindigenous species success during four stages of invasion. *New Phytol.,* 176, 256-273.

Thomas, A., O'Hara, B., Ligges, U. & Sturtz, S. (2006). Making BUGS open. *RNews*, 6, 12-17. <http://cran.r-project.org/doc/Rnews/>.

Thuiller, W., Richardson, D.M., Pyšek, P., Midgley, G.F., Hughes, G.O. & Rouget, M. (2005). Niche-based modeling as a tool for predicting the risk of alien plant invasions at a global scale. *Glob. Change Biol.*, 11, 2234-2250.

Thuiller, W., Richardson, D.M. & Midgley, G. (2007). Will climate change promote alien plant invasions? In: *Biological Invasions* (ed. Nentwig, W.). Springer-Verlag, Berlin, pp. 197-211.

van Kleunen, M., Manning, J.C., Pasqualetto, V. & Johnson, S.D. (2008). Phylogenetically independent associations between autonomous self-fertilization and plant invasiveness. *Am. Nat.*, 171, 195-201.

van Kleunen, M., Weber, E. & Fischer, M. (2010). A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecol. Lett.,* 13, 235-245.

Vilà, M., Corbin, J.D., Dukes, J.S., Pino, J. & Smith, S.D. (2007). Linking plant invasions to global environmental change. In: *Terrestrial Ecosystems in a Changing World* (eds. Canadell, J., Pataki, D. & Pitelka, L.). Springer, New York, pp. 93-102.

Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C. *et al.* (2002). Ecological responses to recent climate change. *Nature,* 416, 389-395.

Walther, G.R., Roques, A., Hulme, P.E., Sykes, M.T., Pyšek, P., Kuhn, I. *et al.* (2009). Alien species in a warmer world: risks and opportunities. *Trends Ecol. Evol.,* 24, 686-693.

Webber, B.L. & Scott, J.K. (2012). Rapid global change: implications for defining natives and aliens. *Glob. Ecol. Biogeogr.*, 21, 305-311.

Williams, S.L. & Smith, J.E. (2007). A global review of the distribution, taxonomy, and impacts of introduced seaweeds. *Ann. Rev. Ecol. Evol. Syst.,* 38, 327-359.

Willis, C.G., Ruhfel, B.R., Primack, R.B., Miller-Rushing, A.J., Losos, J.B. & Davis, C.C. (2010). Favorable climate change response explains non-native species' success in Thoreau's woods. *PLoS ONE,* 5, e8878.

Witte, S., Buschbaum, C., van Beusekom, J. E. E. & Reise, K. (2010). Does climatic warming explain why an introduced barnacle finally takes over after a lag of more than 50 years? *Biol. Inv.,* 12, 3579-3589.

Wu, Z., Dijkstra, P., Koch, G.W., Peñuelas, J. & Hungate, B.A. (2011). Responses of terrestrial ecosystems to temperature and precipitation change: a meta-analysis of experimental manipulation. *Glob. Change Biol.*, 17, 927-942.

Zerebecki, R.A. & Sorte, C.J.B. (2011). Temperature tolerance and stress proteins as mechanisms of invasive species success*. PLoS ONE,* 6, e14806.

SUPPORTING INFORMATION

Additional Supporting Information may be downloaded via the online version of this article at Wiley Online Library (www.ecologyletters.com).

Appendix S1 Search terms for the systematic review and references for papers included in the meta-analysis.

Appendix S2 Table summarizing studies included in the meta-analysis.

Appendix S3 Results of variance-weighted meta-analysis.

Appendix S4 Methods for the hierarchical analysis of response as a function of magnitude of the climate treatment.

Appendix S5 Results of mixed models used to assess effects of potential covariates.

Appendix S6 Posterior mean parameter values for the hierarchical analyses.

Appendix S7 Results of hierarchical analyses by system and climate driver.

FIGURE LEGENDS

Figure 1 Performance responses of native (black circles) and non-native species (gray triangles) to drivers of climate change (including elevated temperature, CO_2, and precipitation, and decreased precipitation). Effect sizes are given as average *ES* (difference-to-mean ratio; see *Methods*) for studies of aquatic species (Aq), terrestrial species (Terr), or both (All). Error bars are bias-corrected bootstrapped 95% CIs, and asterisks denote *ES*'s that are different from zero and, thus, significant responses of groups to potential future climatic conditions. Sample sizes are given in Table 1.

Figure 2 Differences in effect sizes (*ES*'s; i.e., performance responses) between native and non-native species. Values are mean differences between groups ± bias-corrected bootstrapped 95% CIs within studies of aquatic species (Aq), terrestrial species (Terr), or both (All). Asterisks denote *ES* differences between native and non-native species that are significantly greater (non-natives favored) or less than zero (natives favored). Sample sizes are given in Table 1.

Figure 3 Responsiveness to treatment magnitude (i.e., magnitude of climatic change) of native (black circles) and non-native species (gray triangles) given as posterior mean values (and 95% CIs) for the parameters of the hierarchical analyses. The maximum effect size is indicative of the maximum change in performance with climate change whereas a lower half saturation constant indicates greater sensitivity to increasing magnitude. Parameters were estimated at the overall, system, and driver-within-system levels separately for negative and positive responses to altered climatic conditions for terrestrial (T) and aquatic (A) species. Asterisks denote statistically significant differences between natives and non-native species.

Figure 4 Observed (symbols) and predicted effect size (mean middle lines, and 95% PI lower and upper lines) as a function of magnitude of climate-change treatment. Responses were analyzed separately for (a) negative and (b) positive responses of native (black circles and solid lines) and non-native species (gray triangles and dashed lines).

TABLES

Table 1 Sample sizes for the traditional meta-analysis of performance responses to climate change (with difference-to-mean ratio *ES*) presented in Figures 1 and 2. Studies, as defined by independence of controls, were the unit of replication used in the analyses. Distribution of life forms is given as the percentage of studies for each driver and system combination focused on plants; the rest of the studies are of animals.

Climate Change Driver	**Papers (*N*) / Studies (*N*)**		**Native Species (*N*) / Non-native Species (*N*)**		**Life Form Distribution (% Studies of Plants)**	
	Aquatic	**Terrestrial**	**Aquatic**	**Terrestrial**	**Aquatic**	**Terrestrial**
+ Temperature	13 / 20	23 / 26	24 / 17	68 / 64	5%	88%
+ CO_2	5 / 8	19 / 23	5 / 5	58 / 42	38%	100%
+ Precipitation	-	18 / 23	-	43 / 26	-	100%
- Precipitation	-	30 / 35	-	43 / 37	-	97%

Figure 1

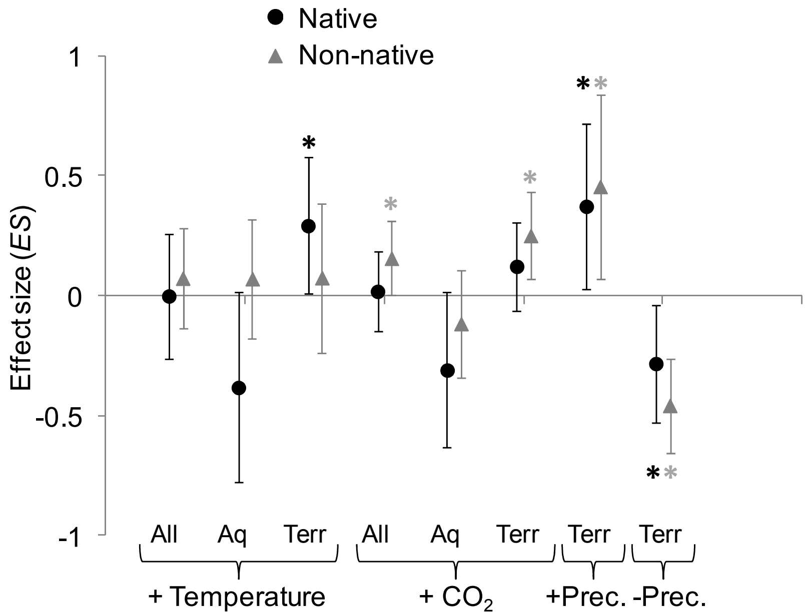
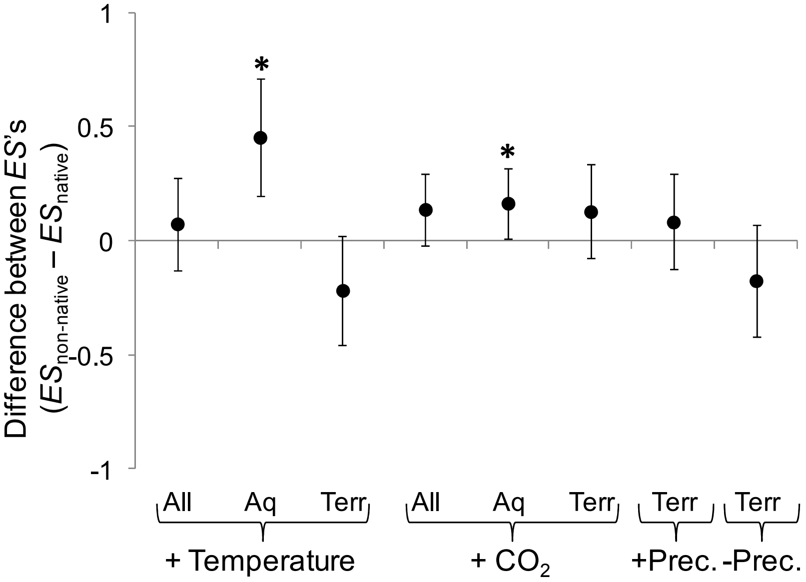
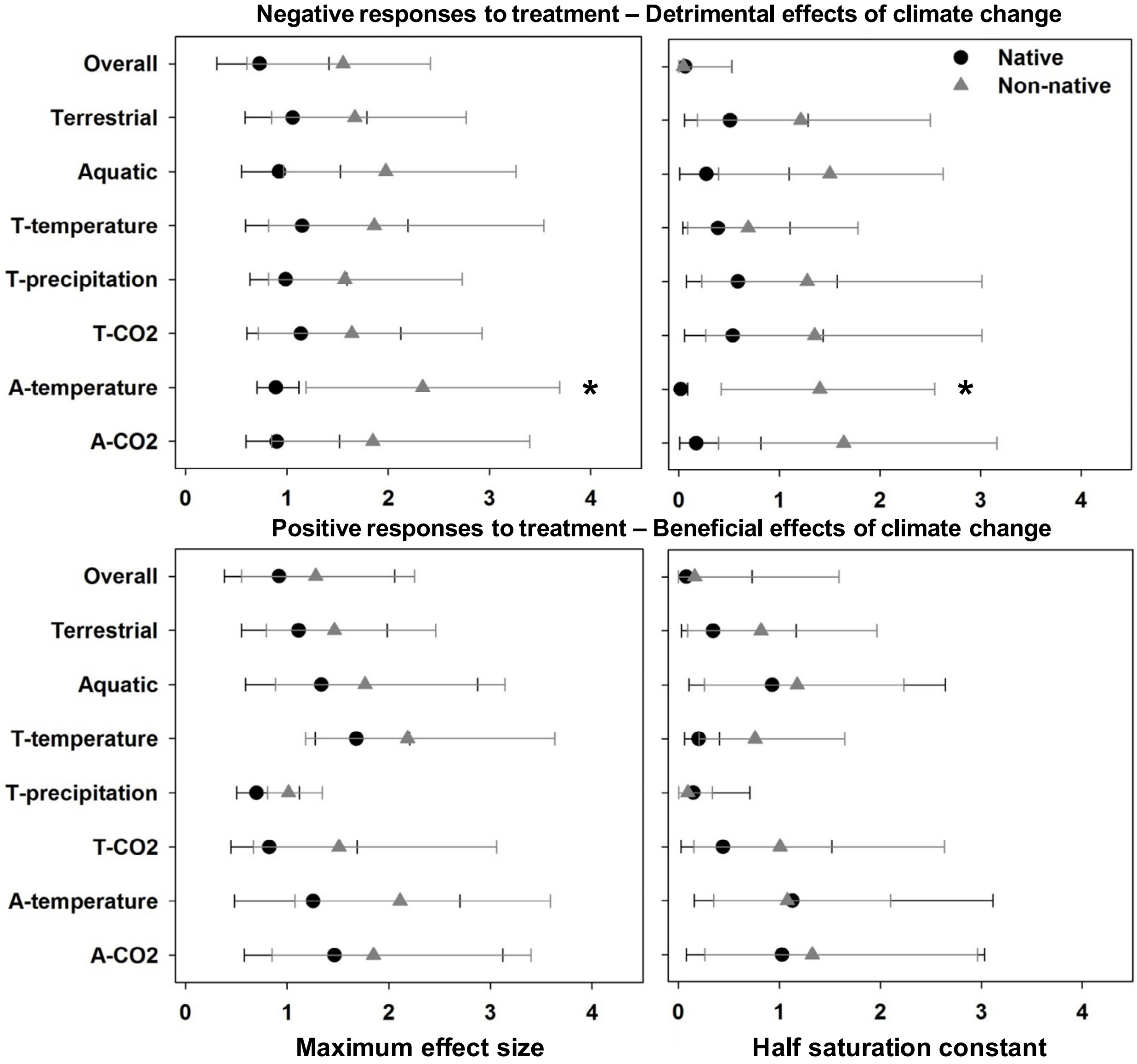

● Native
▲ Non-native
Effect size (ES)
1
0.5
0
-0.5
-1
*
*
*
* *
* *
All
Aq
Terr
All
Aq
Terr
Terr
Terr
+ Temperature
+ CO_2
+Prec.
-Prec.

Figure 2



Difference between ES's ($ES_{non\text{-}native} - ES_{native}$)
1
0.5
0
-0.5
-1
*
*
All
Aq
Terr
All
Aq
Terr
Terr
Terr
+ Temperature
+ CO_2
+Prec.
-Prec.

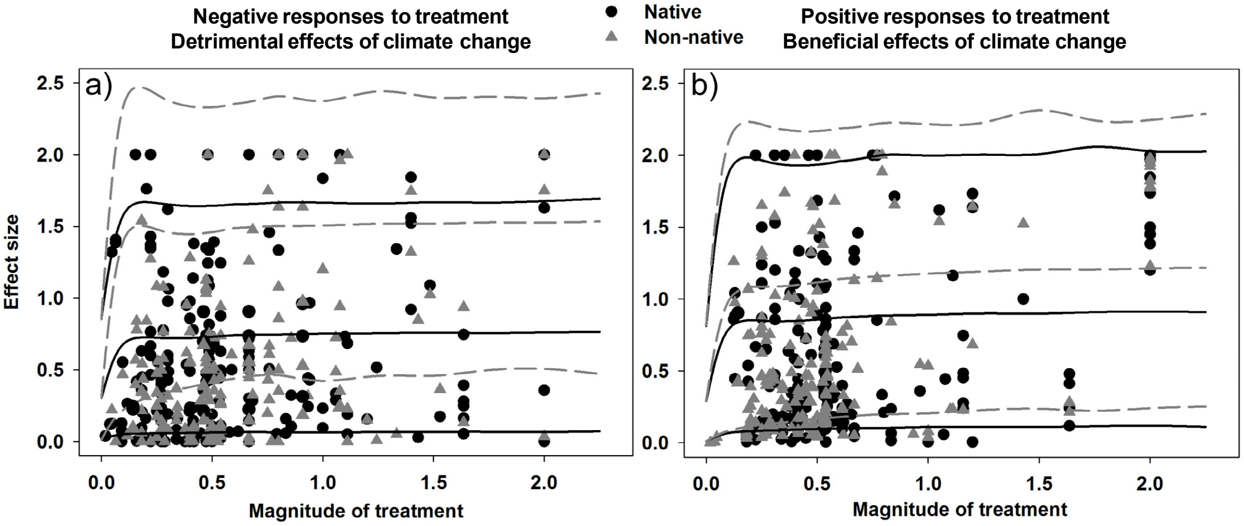
709 **Figure 3**



710

711

Figure 4


Negative responses to treatment
Detrimental effects of climate change
● Native
▲ Non-native
Positive responses to treatment
Beneficial effects of climate change
a)
b)
Effect size
0.0
0.5
1.0
1.5
2.0
2.5
0.0
0.5
1.0
1.5
2.0
Magnitude of treatment
Magnitude of treatment