

Do invasive species perform better in their new ranges?

JOHN D. PARKER,^{1,19} MARK E. TORCHIN,² RUTH A. HUFBAUER,³ NATHAN P. LEMOINE,⁴ CHRISTINA ALBA,⁵
DANA M. BLUMENTHAL,⁶ OLIVER BOSSDORF,⁷ JAMES E. BYERS,⁸ ALISON M. DUNN,⁹ ROBERT W. HECKMAN,¹⁰
MARTIN HEJDA,⁵ VOJTĚCH JAROŠÍK,^{5,11} ANDREW R. KANAREK,¹² LYNN B. MARTIN,¹³ SARAH E. PERKINS,¹⁴
PETR PYŠEK,^{5,11} KRISTINA SCHIERENBECK,¹⁵ CARMEN SCHLÖDER,² RIEKS VAN KLINKEN,¹⁶ KURT J. VAUGHN,¹⁷
WYATT WILLIAMS,^{3,20} AND LORNE M. WOLFE¹⁸

¹Smithsonian Environmental Research Center, 647 Contee Wharf Road, Edgewater, Maryland 21037 USA

²Smithsonian Tropical Research Institute, Box 0843-03092, Balboa, Ancon, Republic of Panama

³Department of Bioagricultural Sciences and Pest Management and Graduate Degree Program in Ecology, 1177 Campus Delivery, Colorado State University, Fort Collins, Colorado 80523 USA

⁴Florida International University, Department of Biology, 3000 NE 151st Street, North Miami, Florida 33181 USA

⁵Department of Invasion Ecology, Institute of Botany, Academy of Sciences of the Czech Republic, CZ-252 43, Pruhonice, Czech Republic

⁶USDA–ARS, 1701 Center Avenue, Fort Collins, Colorado 80526 USA

⁷Institute of Plant Sciences, University of Bern, Altenbergrain 21, CH-3013 Bern, Switzerland

⁸Odum School of Ecology, University of Georgia, 140 E. Green Street, Athens, Georgia 30602 USA

⁹School of Biology, Faculty of Biological Sciences, University of Leeds LS2 9JT United Kingdom

¹⁰Department of Biology, University of North Carolina, 408 Coker Hall, 120 South Road, Chapel Hill, North Carolina 27599 USA

¹¹Department of Ecology, Faculty of Science, Charles University in Prague, CZ-128 44 Viničná 7, Prague 2, Czech Republic

¹²National Institute for Mathematical and Biological Synthesis, University of Tennessee, 1122 Volunteer Boulevard, Ste 106, Knoxville, Tennessee 37996 USA

¹³Department of Integrative Biology, SCA 110, University of South Florida, 4202 East Fowler Avenue, Tampa, Florida 33620 USA

¹⁴Cardiff School of Biosciences, Sir Martin Evans Building, Museum Avenue, Cardiff CF10 3AX United Kingdom

¹⁵Department of Biological Sciences, California State University, Chico, California 95929 USA

¹⁶CSIRO Ecosystem Sciences, 41 Boggo Road, Dutton Park, Queensland 4102 Australia

¹⁷Landowner Stewardship Program Audubon California, P.O. Box 733, Winters, California 95694 USA

¹⁸Department of Biology, Georgia Southern University, Statesboro, Georgia 30460 USA

Abstract. A fundamental assumption in invasion biology is that most invasive species exhibit enhanced performance in their introduced range relative to their home ranges. This idea has given rise to numerous hypotheses explaining “invasion success” by virtue of altered ecological and evolutionary pressures. There are surprisingly few data, however, testing the underlying assumption that the performance of introduced populations, including organism size, reproductive output, and abundance, is enhanced in their introduced compared to their native range. Here, we combined data from published studies to test this hypothesis for 26 plant and 27 animal species that are considered to be invasive. On average, individuals of these 53 species were indeed larger, more fecund, and more abundant in their introduced ranges. The overall mean, however, belied significant variability among species, as roughly half of the investigated species ($N = 27$) performed similarly when compared to conspecific populations in their native range. Thus, although some invasive species are performing better in their new ranges, the pattern is not universal, and just as many are performing largely the same across ranges.

Key words: animal invasion; biogeography; comparative demography; invasion paradox; invasive species; plant invasion.

INTRODUCTION

Although many species have been introduced outside of their home ranges, relatively few introduced species become abundant and widespread in the new ranges (Mack et al. 2000). Identifying the mechanisms driving

profound invasions when they do occur is the focus of a large body of empirical and theoretical literature in invasion biology (van Kleunen et al. 2010a, Blackburn et al. 2011, Gurevitch et al. 2011), with most hypotheses assuming that success is acquired as a result of novel ecological and evolutionary dynamics in the introduced range. For example, introduced species are hypothesized to benefit from escaping natural enemies (Mitchell and Power 2003, Torchin et al. 2003), hybridization with natives (Ellstrand and Schierenbeck 2000), purging of genetic load (Facon et al. 2011), novel biochemical weapons (Callaway and Ridenour 2004), invasional

Manuscript received 18 October 2012; revised 12 December 2012; accepted 3 January 2013. Corresponding Editor: E. T. Borer.

¹⁹ E-mail: parkerj@si.edu

²⁰ Present address: Oregon Department of Forestry Private Forests Division, 2600 State Street, Building D, Salem, Oregon 97310-0340 USA.

meltdowns (Simberloff and Von Holle 1999, Parker et al. 2006), or interactions among these factors.

As an indicator for whether introduced populations are benefiting from novel conditions, numerous studies have focused on whether organism size, fecundity, and abundance are increased in the new range (Hierro et al. 2005, van Kleunen et al. 2010a). In support, individuals in introduced populations can indeed be larger (Crowley 1987, Grosholz and Ruiz 2003, Jakobs et al. 2004), more fecund (Grigulis et al. 2001, Stastny et al. 2005), and more abundant (Freeland 1990, Hinz and Schwarzlaender 2004, Prati and Bossdorf 2004, Hierro et al. 2005, Vila et al. 2005, Herrera et al. 2011). These differences have been linked to novel conditions as a way of explaining invasion success (e.g., Torchin et al. 2001, Mitchell and Power 2003, Alba and Hufbauer 2012).

In contrast, other studies show no difference in performance between the native and introduced ranges (Thébaud and Simberloff 2001, Firn et al. 2011), sometimes despite large differences in biotic conditions (e.g., Adams et al. 2009, Lamarque et al. 2012). These patterns suggest the alternative hypothesis that invasion success may reflect the inherent properties of certain species rather than novel conditions. For example, many invasive species are characterized by traits related to widespread dispersal and rapid growth (van Kleunen et al. 2010b), and widely abundant invasive and native species often share similar traits (Lind and Parker 2010, van Kleunen et al. 2010a). If invasion success better reflects species-specific traits rather than novel conditions per se, it suggests that some invasive species may be ecologically dominant in both their introduced and native ranges, a prediction that has received surprisingly little attention in the literature (Firn et al. 2011). For example, most biogeographical studies of the performance of introduced organisms have to date focused on naturalized but not necessarily highly invasive species (e.g., Thébaud and Simberloff 2001, Firn et al. 2011), or on just a few archetypal invaders (e.g., Prati and Bossdorf 2004, Herrera et al. 2011). We thus currently lack an understanding of whether highly invasive species, defined as those exhibiting local dominance (Richardson et al. 2000b) or negative impacts on native species (Parker et al. 1999), are experiencing disproportionate success in their new ranges or performing similarly regardless of range.

To determine whether individuals of invasive introduced species are generally larger, more fecund, or more abundant in their novel ranges, we quantitatively evaluated population data from both the native and introduced range for 53 introduced species that are considered to be invasive, including 36 species categorized as among the “World’s Worst Invasive Alien Species” (Lowe et al. 2004). This set of species is not intended to be exhaustive or rank species based on their impact, but rather to represent a group of introduced species that have had well-documented impacts on

biological diversity or human activities. We searched the literature to find performance data in both the introduced and native ranges for a diverse array of plant growth forms, including herbs, shrubs, and trees, and a range of animals, including birds, amphibians, reptiles, fishes, and invertebrates, broadening the taxonomic focus of previous studies. We also asked whether any differences in demography were explained by the time elapsed since initial introduction, and whether a species’ introduction was intentional or accidental, as both of these factors are also thought to help explain relative success of invasive populations (Richardson et al. 2000a, Miller et al. 2002, Pyšek and Jarošík 2005, Chrobock et al. 2011).

MATERIAL AND METHODS

Literature review

As a starting point for collecting data on species considered to be invasive, we used a list of “100 of the World’s Worst Invasive Alien Species” (Lowe et al. 2004), which are described as having a “serious impact on biological diversity and/or human activities.” We excluded eight microbial species from the list because their life histories and morphologies would make demographic comparisons difficult relative to other taxa. We also excluded three mammals (domestic cats *Felis catus*, goats *Capra hircus*, and pigs *Sus scrofa*) that have been domesticated for so long that the identification of free-ranging native populations was not possible.

For each of the remaining 89 species, we searched in ISI Web of Science (1960–present) to obtain data for the following metrics in both native and introduced populations: (1) individual organism size (e.g., biomass, length per individual, or some standardized measure of size such as stem width, and other metrics), (2) organism reproductive traits (e.g., offspring per individual, gonadosomatic index, inflorescence size, seed mass, seed bank, and other traits), and (3) population abundance (e.g., density, cover, biomass, and other values). We also searched the references of returned papers for additional sources and prominent invasive species’ web sites (e.g., the Global Invasive Species Database). Importantly, because we wanted to examine the traits of species under the conditions they would typically experience in a natural setting in both ranges, we excluded studies conducted in artificial settings, such as greenhouses, common garden or field experiments, and laboratory experiments.

We further expanded our data set by collecting comparative data for additional introduced species that were not on the list of the World’s Worst Invasive Alien Species. This search returned data for an additional 16 species (15 plant species), all of which are also considered “invasive” by various sources (e.g., Randall 2002) (*available online*).²¹ One important distinction between the data we compiled on some of the World’s

²¹ www.invasiveplantatlas.org

Worst Invaders and the latter search is that many of the papers we found documenting the performance of the World's Worst Invaders were conducted by different researchers across ranges, and thus were not explicitly focused on making biogeographical comparisons. In contrast, all studies uncovered in our second search were explicitly interested in making biogeographical comparisons using the same methods in both ranges. Thus, in addition to expanding our data set, this second group of "targeted" comparative biogeographical studies (hereafter termed BIO studies) served to evaluate whether patterns seen in the World's Worst invaders (hereafter termed WW studies) could be artifacts of varying experimental methodology across studies. Overall, we found comparable data from both the native and the introduced range for a total of 53 species (37 on the list of the WW studies, and 16 from more targeted BIO studies), from 221 publications, and over 100 countries and territories (see Supplement).

From each study we recorded the mean value for each metric of interest, with population or site as the unit of replication. A single paper could thus have multiple entries for the same metric if they investigated multiple populations per range. We entered data directly from tables where possible, or calculated the means from figures. If temporal data were presented, we took the mean of all data points. Some metrics were measured in multiple formats within and across ranges. Population abundance data, for example, could be variously presented as density, cover, and/or biomass per area. Rather than arbitrarily selecting one of these metrics, we kept all measures of performance, and we made biogeographical comparisons only for metrics that were measured in both ranges. We first calculated the mean for each unique metric (e.g., cover, density, mass per organism, and so forth) in the introduced and native ranges, respectively, and then calculated the log response ratio of performance for each unique metric in the introduced divided by the native range. Positive values indicate increased performance in the introduced range, and negative values indicate decreased performance. Each unique metric was assigned to one of three different categories reflecting broad parameters thought to be important to invasion success: organism size, reproductive performance, and population abundance (see Supplement).

Statistical analyses

Observations from multiple unique metrics were nested within species, and the number of comparisons varied among species; thus we used a Bayesian hierarchical model to estimate mean species' parameters and overall "hyperparameters" describing the overall effect size (Appendix). A Bayesian model is ideal for meta-analyses where observations are nested within higher groups, some groups have few observations, and designs are unbalanced (Sutton and Abrams 2001, Conlon et al. 2007). In contrast, traditional meta-

analyses use bootstrapping resampling to estimate confidence intervals, and thus confidence intervals cannot be estimated for species with a single comparison of performance in the introduced vs. native range. Bayesian hierarchical models, however, still provide posterior credible intervals for all parameters even when individual sample sizes are small; thus all data can be used to inform the overall means. Another important difference is that rather than threshold *P* values associated with traditional frequentist statistical approaches, the Bayesian approach results in exact probabilities of a certain outcome. In this case, we were interested in the probability of increased performance in the introduced range; thus we assessed statistical significance as the posterior probability that the log response ratio of performance in the introduced over the native range was greater than zero.

Within a species, observations were allowed to vary around the species mean with normally distributed errors:

$$y_{ij} \sim \mathcal{N}(\bar{\beta}_i, \sigma^2)$$

where y_{ij} is the j th observation of species i , $\bar{\beta}_i$ is the mean of species i , and σ^2 is within-species variance. To estimate the effects of organism type (i.e., plant/animal) and WW/BIO status on species' log response ratios (RR), we included an additional level of hyperparameters in the model where species means were modeled as a function of organism type and WW/BIO status:

$$\bar{\beta}_i \sim \mu + \Delta \text{organism}_i + \gamma \text{WW/BIO}_i$$

where μ is the overall mean, Δ is the effect of being a plant vs. animal, and γ is the effect of being a World's Worst invader vs. a BIO invader. Thus, prior to estimating effects of organism type and World's Worst status, observations were nested within species to account for the fact that observations within a species are likely correlated and therefore not independent.

Redundant parameterization was used to speed convergence of parameters (Gelman and Hill 2007). All modeled parameters were assigned uninformative priors from a wide normal distribution ($\mu = 0$, $\sigma^2 = 1000$). These priors represent a conservative a priori uncertainty as to whether nonnative species respond better, worse, or the same in their introduced ranges (e.g., Firn et al. 2011). We used four Monte Carlo Markov chains; each chain had a "burn-in" of 10 000 iterations. Convergence of chains was verified using probability density plots. Posterior distributions of mean log response ratios for each species and the overall mean were generated by saving every 10th value of 10 000 MCMC samples from the posterior distribution. To indicate the degree to which a species mean was "shrunk" to the overall mean because of few observations within a species, we estimated pooling factors for each species in the analysis following Gelman and Hill (2007). If significant shrinkage was observed, we ran unpooled models to calculate the exact change in the

estimated effect size due to Bayesian modeling (Gelman and Hill 2007), and then we compared pooled and unpooled models to estimate whether the results were qualitatively different.

We ran separate models for each data category of size, reproduction, and population abundance; and then a final model for the pooled data set of all observations combined. Pooling data across the different metrics increased the number of replicates within species substantially, allowing us to accurately model both the species and overall means. To specifically examine the hypothesis that introduced species exhibit increased performance in their introduced ranges, we calculated the one-tailed probability that the log response ratio was >0 ($P_{(RR)} > 0$) for each species within each data category, for all group means, the overall mean, and for the pooled data set. We also used contrasts to compare means for WW plants against BIO plants, which provided some estimate of whether methodological differences were driving any observed patterns. A second contrast of WW plants vs. WW animals tested whether plants vs. animals were more likely to exhibit enhanced performance.

In addition to the mean response across ranges, we also examined whether variability in size, reproduction, and abundance differed in the introduced compared to the native range. Some work has suggested larger variability in the introduced range (Jakobs et al. 2004, Hinz et al. 2012), potentially reflecting higher plasticity or postintroduction evolution in introduced populations (Blossey and Nötzold 1995, Bossdorf et al. 2005). For this comparison, we removed any species with fewer than three replicates per unique metric and then calculated the coefficient of variation (CV) of each metric for each species, resulting in 46 comparisons across 20 species, which we then further collapsed into mean (\pm SE) values for each species. We then plotted the introduced range CV against the native range CV, with values above the 1:1 line having higher population level variance in the introduced range and vice versa.

For each species, we also estimated the date of introduction to the region of interest from the source paper or through other published sources. Similarly, we also listed whether each species was accidentally or intentionally introduced when information was available. We then used a Bayesian t test, allowing for nested parameters as described above, assessing whether intentionally introduced species performed better in their new ranges relative to accidentally introduced species. Three species were intentionally introduced into some locations, but accidentally introduced into others, resulting in more than 53 species in this comparison. To assess whether differential performance attenuated with residence time, we regressed the log response ratio of each unique metric against time since invasion separately for each introduced population or metric against the mean value for that metric across all reported values in the native range. We also analyzed whether performance

for plants/animals differed by mode of introduction or residence time using a single ANCOVA with mode of introduction and plant/animal status as fixed factors, and residence time as a covariate. Bayesian analyses were conducted using JAGS v3.2 and the “rjags” package in R v2.13 (Plummer 2012).

RESULTS

Hierarchical Bayesian modeling showed that these 53 invasive species were strongly likely ($P_{(RR>0)} \geq 0.942$) to be larger and more fecund in their introduced ranges relative to conspecifics in their native ranges, but less likely ($P_{(RR>0)} = 0.860$) to be more abundant (Fig. 1). For size specifically, there was a high probability ($P_{(RR>0)} = 0.962$) that the 35 introduced species for which we found size data were larger in their new ranges. However, only World’s Worst (WW) invaders (both animals and plants) were strongly likely ($P_{(RR>0)} \geq 0.974$) to show larger sizes, whereas plants from the targeted biogeographical studies (BIO) showed no tendency to be larger in their introduced ranges ($P_{(RR>0)} = 0.310$; Fig. 1). At the species level, 23 species were at least 92% likely to be larger in the introduced range, whereas 12 species were likely to be of similar size in the introduced and native range (i.e., 50% credible intervals crossing zero). Notably, however, there were some uncertainties in the species-level estimates, as evidenced by pooling factors ≥ 0.90 for numerous species (Appendix: Table A1), suggesting significant “shrinkage” to the group mean. To analyze the extent to which this might influence the results, we re-ran the analysis as an unpooled model using only the raw means. The Bayesian estimated mean response ratio for each species differed from the raw mean by only 0.01 ± 0.44 (mean \pm SD) across all 35 species. Moreover, only nine species had raw means that did not fall within the Bayesian credible intervals, and the difference between the estimated and raw means for these species was only -0.13 ± 0.71 . Thus, it is unlikely that shrinkage due to small sample size for some species dramatically influenced the estimates of size at the overall or species level.

We found comparably collected reproductive data for only 21 species, but across these species there was a high probability ($P_{(RR>0)} = 0.942$) of increased reproductive performance in the introduced range (Fig. 1). In contrast to size comparisons, increased reproductive performance was driven by differences for both BIO and WW plants, but not WW animals. At the species level, only four species were at least 95% likely to exhibit greater reproductive performance in their introduced range, whereas 12 species had reproductive traits that did not differ substantially between native and introduced ranges (Fig. 1). Reproductive performance comparisons were not influenced by shrinkage (Appendix: Table A1).

On average, there was a lower probability ($P_{(RR>0)} = 0.860$) that introduced species were more abundant in their new ranges, as all three groups (WW plants, WW

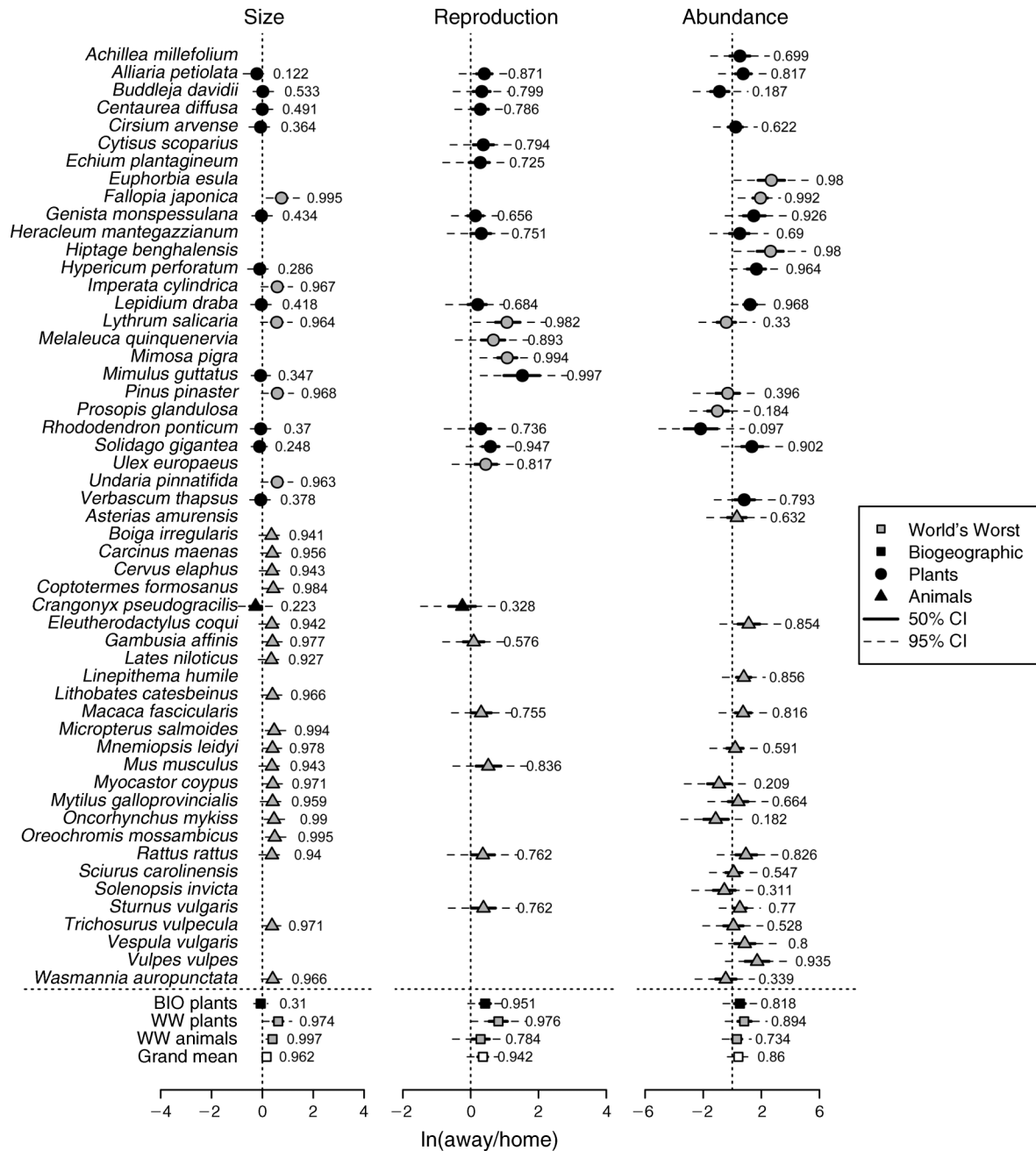


FIG. 1. Response ratios depicting medians with 50% and 95% Bayesian credible intervals (CI) of 53 invasive species for various responses in native and introduced ranges: organism size, reproduction, and population abundance (data not available for all responses for all species). The x-axis is the log of the ratio of measurements in the introduced (away) vs. measurements in the native (home) ranges. Positive numbers indicate enhanced performance in the introduced range. Numbers to the right of credible intervals indicate the one-tailed probability that the response ratio is >0. WW species are from the World's Worst Invasive Aliens list; BIO species are from targeted biogeographical comparisons. Note that some credible intervals are smaller than the symbols and thus not visible.

animals, and BIO plants) were only moderately likely to be more abundant in their introduced range ($P_{(RR>0)} \geq 0.734$). Similar to findings for reproductive traits, the patterns were weaker for WW animals ($P_{(RR>0)} = 0.734$) than WW plants ($P_{(RR>0)} = 0.894$). Only 8 of 33

species were strongly likely to be more abundant in their new ranges ($P_{(RR>0)} \geq 0.90$), seven of which were plants, and 13 showed no tendency to be more or less abundant across geographic ranges (Fig. 1). Shrinkage effects were negligible (Appendix: Table A1).

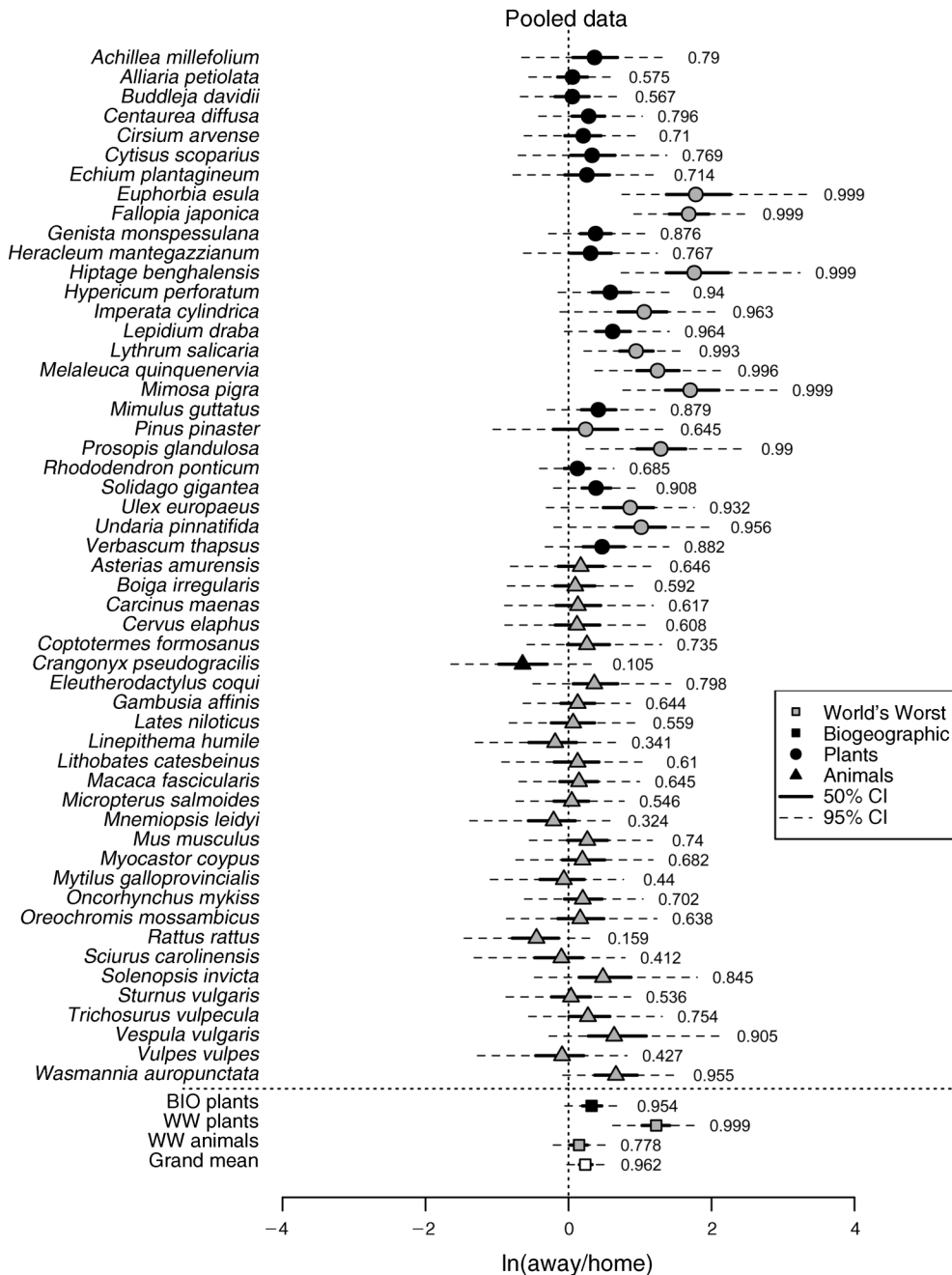


FIG. 2. Response ratios depicting medians with 50% and 95% Bayesian credible intervals (CI) for 53 individual species for pooled responses across the categories of size, reproduction, and abundance. Positive numbers indicate enhanced performance in the introduced (away) range. Numbers to the right of credible intervals indicate the one-tailed probability that the response ratio is greater than zero. WW are species from the World's Worst Invasive Aliens list; BIO are species from targeted biogeographical comparisons.

When we pooled data from all three separate metrics, there was a high probability ($P_{(RR>0)} = 0.962$) of increased performance in the new range across all 53 species (Fig. 2). Overall, both BIO plants and WW plants were likely to perform better in the introduced range ($P_{(RR>0)} \geq 0.95$), while WW animals showed a weaker trend ($P_{(RR>0)} \geq 0.78$). When broken down by

species, 15 of 53 invasive species were strongly likely to perform better in their new ranges ($P_{(RR>0)} \geq 0.91$), but 27 showed no tendency to perform better or worse in their introduced ranges (i.e., 50% credible intervals crossing zero; Fig. 2). There were no shrinkage effects (Appendix: Table A1). Contrasts also showed that WW plants were likely to perform better than BIO plants,

and WW plants were likely to perform better than WW animals (Appendix: Fig. A1). In addition, with relatively few exceptions, there was roughly equal variance in introduced vs. native populations across all metrics (Appendix: Fig. A2).

There were no performance differences due to mode of introduction, as both accidentally ($N = 27$) and intentionally ($N = 28$) introduced species showed on average a similarly increased performance in their new ranges (Fig. 3). Additionally, time since introduction did not appear to be a strong factor in performance, as there was no relationship between the performance differential of individual populations and the estimated number of years since they were introduced ($R^2 = 0.003$, $P = 0.40$, linear regression; Fig. 3). There were also no significant effects when we partitioned these data by plant/animal status and by mode of introduction in a single ANCOVA (all $P \geq 0.18$).

DISCUSSION

While our overall result suggests that invasive species perform better in their introduced relative to their native range, there was considerable variation across species. Across all data for 53 species, we found a 96% likelihood of enhanced performance in their introduced ranges, including strong increases in organism size ($P_{(RR>0)} = 0.96$), and reproductive performance ($P_{(RR>0)} = 0.94$), along with a more modest increase in abundance ($P_{(RR>0)} > 0.86$; Fig. 1). These patterns suggest that the process of introduction or novel conditions in new ranges can enhance performance, at least for some species. Although support for this phenomenon is increasing at the species level (e.g., Herrera et al. 2011), to our knowledge this is the first evidence of this pattern across numerous invasive species, disparate plant and animal taxa, and utilizing a suite of performance metrics. Importantly, the general patterns of increased performance of introduced populations belied substantial variation among taxa and species. Increases in overall performance were stronger for plants vs. animals (Fig. 2; Appendix: Fig. A1), and roughly half the species we investigated showed little evidence of increased performance. This finding suggests considerable uncertainty in assuming that invasive species are performing better in their new ranges, and most invasive species might be performing relatively similarly despite potentially large differences in ecological and evolutionary conditions (Hufbauer and Torchin 2007).

Our findings indicated that plants performed consistently better in the introduced range, but animals often had smaller differences in performance. In contrast, previous literature reviews have suggested that both plants and animals exhibit increased performance in their introduced ranges. For example, a literature review by Hinz and Schwarzlaender (2004) found evidence that plants often exhibited increased performance in their introduced ranges, while a separate study by Freeland

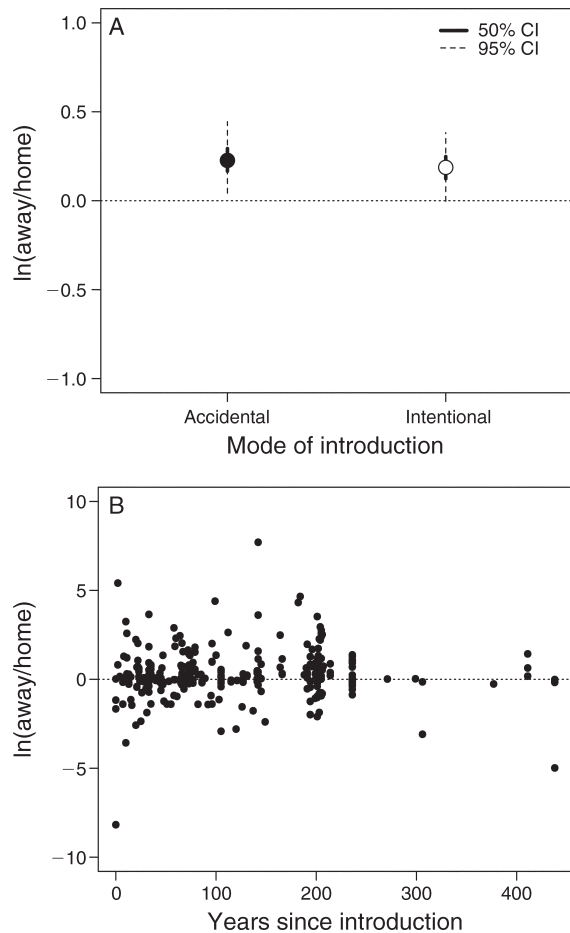


FIG. 3. Comparison of performance (all metrics combined) between accidentally ($N = 27$) and intentionally ($N = 28$) introduced species (A) in their introduced vs. native range, and (B) plotted vs. time since introduction.

(1990) found that populations of six introduced mammal species in Australia were often more abundant than their respective native populations. Moreover, Jeschke and Strayer (2005) found that introduced animals were more likely than plants to establish and spread in their new ranges. Our findings could reflect the potential to gather more precise data on plants, which “stand still and wait to be counted” (Harper 1977). However, the same result could occur if plants are generally more plastic than animals (Bradshaw 1972), leading to a greater ability to respond to new conditions in the introduced range.

Interestingly, WW plants performed better in their introduced ranges than did BIO plants. This pattern could reflect real differences among the investigated species or methodological differences among studies. For example, species on the list of the World’s Worst Invasive Aliens may indeed be more “invasive,” hence their inclusion on the list. One caveat, however, is that most of the studies we found for WW species were separate studies for each range and were generally

conducted by disparate research groups, likely using different methodologies. Thus, it is possible that the WW comparisons could be biased toward finding larger differences if only the most problematic populations of introduced species were intentionally selected for study. In contrast, the same research groups conducted the BIO studies in both ranges with the express intent of determining differences in performance. Thus, BIO studies often controlled for environmental differences across ranges and sampled haphazardly among populations to minimize the possibility of selecting “outlier” populations (e.g., Herrera et al. 2011). Despite these methodological differences, there were few differences in variability among BIO–WW populations (Appendix: Fig. A2), and qualitative patterns for WW plants and BIO plants were similar with the exception of organism size. Thus, even if biases in WW plant studies overestimated the magnitude of increased reproduction, abundance, and overall performance, they did not fundamentally change the sign of the effect.

Roughly half the species included in our study (27/53) performed similarly when compared to conspecifics in their native range (Fig. 2). This result suggests that most introduced species might be performing relatively similarly across ranges despite profound differences in ecological or evolutionary pressures. Indeed, Firn et al. (2011) evaluated home and away abundances of 26 plant species across 39 sites in eight countries and found no consistent increase in plant abundance. Similarly, our study showed only a relatively modest likelihood of increased abundance in the introduced range. This similarity is made more striking by the fact that Firn et al. (2011) studied mostly “noninvasive” species (only 10 of the 26 species were considered invasive), whereas all 26 plant species in our study are considered invasive. Our results also match well with Firn et al. (2011) when we examined the dramatic species-level variation in performance in both ranges. In both studies, roughly half of the investigated species had similar performance between the native and introduced ranges (Fig. 2). Similar equivocal findings for species within the models for organism size, reproductive traits, and pooled analyses emphasize our primary conclusion that although invaders may *on average* be performing better, the overall pattern appears to be driven by relatively few introduced species exhibiting strong differences. Hence, the widely presumed “away-field advantage” for introduced species (e.g., Callaway and Ridenour 2004) may be relatively uncommon or fairly small in magnitude, even among a group of introduced species considered invasive.

One critical finding of our work is that we were not able to find comparative data for a majority of species labeled as the world’s worst invaders (60%, or 53/89). In particular, there was a general lack of data from the native ranges of species, pointing out that invasion biologists still need more studies from the native ranges of introduced species to better understand the invasion

process. Although this has been pointed out repeatedly (Hierro et al. 2005, van Kleunen et al. 2010a), the lack of data from the native range indicates a continued systematic bias toward studying invaders primarily in their introduced ranges. Funding may in part drive this discrepancy, as agencies may be more likely to support research on a species novel to a range, rather than something that is considered native. However, by partnering with scientists around the world and by forming international research networks (e.g., the U.S. National Science Foundation supported the Global Invasions Network that led to this paper), and by engaging in citizen-science efforts such as the “Global Garlic Mustard” survey (*available online*)²² data from the native range of introduced species may become more accessible, advancing a more rigorous understanding of invasion dynamics.

Our comparison of intentionally vs. accidentally introduced species suggests that both pathways generate invaders that are likely to flourish in their new ranges. However, these comparisons may have juxtaposed species that have already passed through important filters (human selection and environmental filtering) that would have accentuated differences in mode of introduction. For example, intentionally introduced species often exhibit better performance in their new ranges if humans carefully select species to be compatible with the new environment (Mack 2000, Chrobock et al. 2011). Likewise, accidental introductions would presumably not have this selection effect, but the well-established species in our study have already passed nonrandomly through the environmental filters that can prevent invasions (Pyšek et al. 2011). Thus, it is possible that differences in mode of introduction are more important in the establishment phase of introductions than the already established species we investigated.

Our data examining temporal dynamics of invasion did not show strong patterns of residence time. In contrast, some invasion models predict that after an initial population expansion phase, the success of an introduced species may diminish over time either due to an accumulation of natural enemies (Hawkes 2007, Blakeslee et al. 2009, Mitchell et al. 2010), or from environmental changes, such as is in the case of the recent collapse of the Argentine ant (*Linepithema humile*) in New Zealand (Cooling et al. 2012). However, we did not see a tendency for species to converge toward similar performance in the introduced and native ranges over time (Fig. 3), although we note that we still need more studies on long-established introduced species to fully flesh out this pattern.

In conclusion, although our data generally support the idea that invasive species exhibit increased performance in their introduced range, roughly half of the invasive species we investigated performed similarly

²² <http://www.garlicmustard.org/>

between the home and away ranges. One implication of this finding is that novel ecological and evolutionary conditions in the introduced range may only partly explain success in a new range. Indeed, there has been much recent progress in determining the traits that make some species invasive across a range of environmental conditions, with growing evidence that many successful introduced species share similar traits with successful native species (Pyšek and Richardson 2007, Lind and Parker 2010, van Kleunen et al. 2010b). Coupled with our findings and those of Firn et al. (2011), this highlights the notion that species' traits, and particularly the interaction between traits and environmental context, may be a better predictor of invasion success than novel conditions alone.

ACKNOWLEDGMENTS

Authorship: John Parker, Mark Torchin, and Ruth Hufbauer initiated the hypothesis. All authors designed the research agenda, prepared the database, and edited the article. Nathan P. Lemoine analyzed the data, and John Parker, Mark Torchin, and Ruth Hufbauer wrote the article.

We thank Jess Shue, Christian Latimer, Emily Myron, Madalin Parepa, Lauren Richie, and Hannah Wilbur for data entry and verification. This work was supported in part by the Global Invasions Network NSF RCN DEB-0541673 and an NSF REU site grant (NSF-DBI 0851303). Petr Pyšek and Vojtěch Jarošík were supported by grants no. P505/11/1112 and 206/09/0563 (Czech Science Foundation), long-term research development project no. RVO 67985939 (Academy of Sciences of the Czech Republic), and institutional resources of the Ministry of Education, Youth and Sports of the Czech Republic. Petr Pyšek acknowledges the support by Praemium Academiae award from the Academy of Sciences of the Czech Republic. Alison Dunn acknowledges support from NERC (NE/G015201/1). Andrew R. Kanarek acknowledges support from NSF Award #EF-0832858. Lynn B. Martin acknowledges NSF-IOE 0940275. Oliver Bossdorf was supported by the SNF grant 31003A_122408. Ruth A. Hufbauer acknowledges support from the Colorado Agricultural Experiment Station and NSF RCN DEB-0541673.

LITERATURE CITED

- Adams, J. M., W. Fang, R. M. Callaway, D. Cipollini, and E. Newell. 2009. A cross-continental test of the Enemy Release Hypothesis: leaf herbivory on *Acer platanoides* (L.) is three times lower in North America than in its native Europe. *Biological Invasions* 11:1005–1016.
- Alba, C., and R. Hufbauer. 2012. Exploring the potential for climatic factors, herbivory, and co-occurring vegetation to shape performance in native and introduced populations of *Verbascum thapsus*. *Biological Invasions* 14:2505–2518.
- Blackburn, T. M., P. Pyšek, S. Bacher, J. T. Carlton, R. P. Duncan, V. Jarošík, J. R. U. Wilson, and D. M. Richardson. 2011. A proposed unified framework for biological invasions. *Trends in Ecology and Evolution* 26:333–339.
- Blakeslee, A. M. H., C. L. Keogh, J. E. Byers, A. M. Kuris, K. D. Lafferty, and M. E. Torchin. 2009. Differential escape from parasites by two competing introduced crabs. *Marine Ecology-Progress Series* 393:83–96.
- Blossey, B., and R. Nötzold. 1995. Evolution of increased competitive ability in invasive nonindigenous plants—a hypothesis. *Journal of Ecology* 83:887–889.
- Bossdorf, O., H. Auge, L. Lafuma, W. E. Rogers, E. Siemann, and D. Prati. 2005. Phenotypic and genetic differentiation between native and introduced plant populations. *Oecologia* 144:1–11.
- Bradshaw, A. D. 1972. Some of the evolutionary consequences of being a plant. *Evolutionary Biology* 5:25–47.
- Callaway, R. M., and W. M. Ridenour. 2004. Novel weapons: invasive success and the evolution of increased competitive ability. *Frontiers in Ecology and the Environment* 2:436–443.
- Chrobok, T., A. Kempel, M. Fischer, and M. van Kleunen. 2011. Introduction bias: Cultivated alien plant species germinate faster and more abundantly than native species in Switzerland. *Basic and Applied Ecology* 12:244–250.
- Conlon, E. M., J. J. Song, and A. Liu. 2007. Bayesian meta-analysis models for microarray data: a comparative study. *BMC Bioinformatics* 8:1–21.
- Cooling, M., S. Hartley, D. A. Sim, and P. J. Lester. 2012. The widespread collapse of an invasive species: Argentine ants (*Linepithema humile*) in New Zealand. *Biology Letters* 8:430–433.
- Crawley, M. J. 1987. What makes a community invisable? Pages 429–453 in A. J. Gray, M. J. Crawley, and P. J. Edwards, editors. *Colonization, succession, and stability*. Blackwell, Oxford, UK.
- Ellstrand, N. C., and K. A. Schierenbeck. 2000. Hybridization as a stimulus for the evolution of invasiveness in plants? *Proceedings of the National Academy of Sciences USA* 97:7043–7050.
- Facon, B., R. A. Hufbauer, A. Tayeh, A. Loiseau, E. Lombaert, R. Vitalis, T. Guillemaud, J. G. Lundgren, and A. Estoup. 2011. Inbreeding depression is purged in the invasive insect *Harmonia axyridis*. *Current Biology* 21:424–427.
- Firn, J., et al. 2011. Abundance of introduced species at home predicts abundance away in herbaceous communities. *Ecology Letters* 14:274–281.
- Freeland, W. J. 1990. Large herbivorous mammals: exotic species in Northern Australia. *Journal of Biogeography* 17:445–449.
- Gelman, A., and J. Hill. 2007. *Data analysis using regression and multilevel/hierarchical models*. Cambridge University Press, Cambridge, UK.
- Grigulis, K., A. W. Sheppard, J. E. Ash, and R. H. Groves. 2001. The comparative demography of the pasture weed *Echium plantagineum* between its native and invaded ranges. *Journal of Applied Ecology* 38:281–290.
- Grosholz, E. D., and G. M. Ruiz. 2003. Biological invasions drive size increases in marine and estuarine invertebrates. *Ecology Letters* 6:700–705.
- Gurevitch, J., G. A. Fox, G. M. Wardle, Inderjit, and D. Taub. 2011. Emergent insights from the synthesis of conceptual frameworks for biological invasions. *Ecology Letters* 14:407–418.
- Harper, J. L. 1977. *Population biology of plants*. Academic Press, New York, New York, USA.
- Hawkes, C. V. 2007. Are invaders moving targets? The generality and persistence of advantages in size, reproduction, and enemy release in invasive plant species with time since introduction. *American Naturalist* 170:832–843.
- Herrera, A. M., R. I. Carruthers, and N. J. Mills. 2011. Introduced populations of *Genista monspessulana* (French broom) are more dense and produce a greater seed rain in California, USA, than native populations in the Mediterranean Basin of Europe. *Biological Invasions* 13:369–380.
- Hierro, J. L., J. L. Maron, and R. M. Callaway. 2005. A biogeographical approach to plant invasions: the importance of studying exotics in their introduced and native range. *Journal of Ecology* 93:5–15.
- Hinz, H. L., and M. Schwarzlaender. 2004. Comparing invasive plants from their native and exotic range: What can we learn for biological control? *Weed Technology* 18:1533–1541.
- Hinz, H. L., M. Schwarzlaender, J. L. McKenney, M. G. Cripps, B. Harmon, and W. J. Price. 2012. Biogeographical comparison of the invasive *Lepidium draba* in its native,

- expanded and introduced ranges. *Biological Invasions* 14: 1999–2016.
- Hufbauer, R., and M. Torchin. 2007. Integrating ecological and evolutionary theory of biological invasions. Pages 79–96 in W. Nentwig, editor. *Biological invasions: ecological studies* 193. Springer-Verlag, Berlin, Germany.
- Jakobs, G., E. Weber, and P. J. Edwards. 2004. Introduced plants of the invasive *Solidago gigantea* (Asteraceae) are larger and grow denser than conspecifics in the native range. *Diversity and Distributions* 10:11–19.
- Jeschke, J. M., and D. L. Strayer. 2005. Invasion success of vertebrates in Europe and North America. *Proceedings of the National Academy of Sciences USA* 102:7198–7202.
- Lamarque, L. J., S. Delzon, M. H. Sloan, and C. J. Lortie. 2012. Biogeographical contrasts to assess local and regional patterns of invasion: a case study with two reciprocally introduced exotic maple trees. *Ecography* 35:803–810.
- Lind, E. M., and J. D. Parker. 2010. Novel weapons testing: Are invasive plants more chemically defended than native plants? *PLoS One* 5.
- Lowe, S., M. Browne, S. Boudjelas, and M. DePoorter. 2004. 100 of the world's worst invasive alien species: selection from the Global Invasive Species Database. In T. I. S. S. Group, editor. *Species Survival Commission of the World Conservation Union*. IUCN, Gland, Switzerland.
- Mack, R. N. 2000. Cultivation fosters plant naturalization by reducing environmental stochasticity. *Biological Invasions* 2: 111–122.
- Mack, R. N., D. Simberloff, W. M. Lonsdale, H. Evans, M. Clout, and F. A. Bazzaz. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications* 10:689–710.
- Miller, A. W., C. L. Hewitt, and G. M. Ruiz. 2002. Invasion success: does size really matter? *Ecology Letters* 5:159–162.
- Mitchell, C. E., D. Blumenthal, V. Jarošík, E. E. Puckett, and P. Pyšek. 2010. Controls on pathogen species richness in plants' introduced and native ranges: roles of residence time, range size and host traits. *Ecology Letters* 13:1525–1535.
- Mitchell, C. E., and A. G. Power. 2003. Release of invasive plants from fungal and viral pathogens. *Nature* 421:625–627.
- Parker, I. M., et al. 1999. Impact: toward a framework for understanding the ecological effects of invaders. *Biological Invasions* 1:3–19.
- Parker, J. D., D. E. Burkepile, and M. E. Hay. 2006. Opposing effects of native and exotic herbivores on plant invasions. *Science* 311:1459–1461.
- Plummer, M. 2012. Bayesian graphical models using MCMC. Page Interface to the JAGS MCMC library, CRAN. R Foundation for Statistical Computing, Vienna, Austria.
- Prati, D., and O. Bossdorf. 2004. A comparison of native and introduced populations of the African Ragwort *Senecio inaequidens* D.C. in the field. Pages 353–359 in S. Breckle, B. Schweizer, and A. Fangmeier, editors. *Results of worldwide ecological studies*. Verlag Gunter Heimbach, Stuttgart, Germany.
- Pyšek, P., and V. Jarošík. 2005. Residence time determines the distribution of alien plants. Pages 77–96 in Inderjit, editor. *Invasive plants: ecological and agricultural aspects*. Birkhäuser Verlag-AG, Basel, Switzerland.
- Pyšek, P., V. Jarošík, and J. Pergl. 2011. Alien plants introduced by different pathways differ in invasion success: unintentional introductions as a threat to natural areas. *PLoS One* 6:e24890.
- Pyšek, P., and D. M. Richardson. 2007. Traits associated with invasiveness in alien plants: where do we stand?. Pages 97–125 in W. Nentwig, editor. *Biological invasions*. Springer, New York, New York, USA.
- Randall, R. 2002. *A global compendium of weeds*. Meredith, Australia.
- Richardson, D. M., N. Allsopp, C. M. D'Antonio, S. J. Milton, and M. Rejmanek. 2000a. Plant invasions—the role of mutualisms. *Biological Reviews* 75:65–93.
- Richardson, D. M., P. Pyšek, M. Rejmanek, M. G. Barbour, F. D. Panetta, and C. J. West. 2000b. Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions* 6:93–107.
- Simberloff, D., and B. Von Holle. 1999. Positive interactions of nonindigenous species: invasional meltdown? *Biological Invasions* 1:21–32.
- Stastny, M., U. Schaffner, and E. Elle. 2005. Do vigour of introduced populations and escape from specialist herbivores contribute to invasiveness? *Journal of Ecology* 93:27–37.
- Sutton, A. J., and K. R. Abrams. 2001. Bayesian methods in meta-analysis and evidence synthesis. *Statistical Methods in Medical Research* 10:277–303.
- Thébaud, C., and D. Simberloff. 2001. Are plants really larger in their introduced ranges? *American Naturalist* 157:231–236.
- Torchin, M. E., K. D. Lafferty, A. P. Dobson, V. J. McKenzie, and A. M. Kuris. 2003. Introduced species and their missing parasites. *Nature* 421:628–630.
- Torchin, M. E., K. D. Lafferty, and A. M. Kuris. 2001. Release from parasites as natural enemies: increased performance of a globally introduced marine crab. *Biological Invasions* 3:333–345.
- van Kleunen, M., W. Dawson, D. Schlaepfer, J. M. Jeschke, and M. Fischer. 2010a. Are invaders different? A conceptual framework of comparative approaches for assessing determinants of invasiveness. *Ecology Letters* 13:947–958.
- van Kleunen, M., E. Weber, and M. Fischer. 2010b. A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecology Letters* 13:235–245.
- Vila, M., J. L. Maron, and L. Marco. 2005. Evidence for the enemy release hypothesis in *Hypericum perforatum*. *Oecologia* 142:474–479.

SUPPLEMENTAL MATERIAL

Appendix

Hierarchical Bayesian model description, tables of pooling factors, and figures showing WW/BIO contrasts and coefficient of variation in the introduced vs. native range ([Ecological Archives E094-087-A1](#)).

Supplement

Studies used in the analysis plus performance data from the introduced and native ranges of 53 species ([Ecological Archives E094-087-S1](#)).