

ANALYZING INVASIVE SPECIES IMPACTS

By

ROBERT CRYSTAL-ORNELAS

A dissertation submitted to the

School of Graduate Studies

Rutgers, The State University of New Jersey

In partial fulfillment of the requirements

For the degree of

Doctor of Philosophy

Graduate Program in Ecology and Evolution

Written under the direction of

Julie L. Lockwood

And approved by

New Brunswick, New Jersey

May, 2019

ABSTRACT OF THE DISSERTATION

Analyzing invasive species impacts

By ROBERT CRYSTAL-ORNELAS

Dissertation Director:

Dr. Julie Lockwood

Due to invasive species' substantial influence on human health, the economy, and the natural environment, invasion ecologists have committed substantial effort to study the variety of impacts caused by invasive species. Impact research has consistently increased since the late 1990s when ecologists published theoretical work on early metrics for calculating impacts. Despite the clear societal benefit of studying and understanding impacts, funding to study impacts are limited. Biases in the taxa, ecosystems, and spatial scales that are studied may undermine our ability to predict invasive species effects. However, there are no syntheses that quantify how these biases influence impact research.

In my dissertation, I investigate patterns in how researchers collect and then publish data about invasive species impacts. In my first chapter, I used a metric for quantifying invasive species impacts to predict the potential distributional range for a recently introduced bird in North America. My analyses suggest that the Pin-tailed Whydah has a substantial amount of available habitat to spread within California and the Antilles. In my second chapter, I conducted a systematic review to identify the impacts, taxa, ecosystems, and spatiotemporal scales that receive a substantial proportion of

impact research. These results suggest that research efforts often focus on a few well-known invasives in forests or on islands while most species have only a single documented impact. In my third chapter, I conducted a cumulative meta-analysis to identify patterns in published evidence accrual for invasive species impacts on richness. In general, the earliest published research on impacts suggests the largest average richness impacts, and repeated studies on the same taxa or in the same ecosystems generally suggest negative, but more moderate average impacts. Taken together, this dissertation highlights the value of producing primary research on invasive species impacts. It also uses syntheses to identify critical research gaps or areas where sufficient evidence has accrued to answer questions about invasive species' impacts on diversity.

ACKNOWLEDGEMENTS

I first thank my advisor, Dr. Julie Lockwood who was the best PhD advisor and mentor I could have hoped for. I always looked forward to our chats and couldn't wait to see what ideas for present or future projects we would draw out on the whiteboard. Julie gave me confidence in my ability to do science and also balance PhD work and the rest of my life—for that I am extremely grateful.

I also thank my PhD committee: Dr. Marci Meixler, Dr. John Wiedenmann, and Dr. Dan Simberloff. I thank each of them for carving out time to provide valuable comments, insights, and encouragement as my dissertation took shape.

I thank my fellow Lockwood lab members: Michael Allen, Jeffrey Brown, Alexandria Safiq, Oliver Stringham, and Rafael Valentin. They improved my research and writing through conversation and edits. They were also so much fun to grab lunch with or play a round of ping pong.

I thank my family, Mary, Don, and Lauren, for always supporting my educational journey even when it included lots of airport trips and months of field work! And I would not have completed this dissertation without the love and support from my partner and best friend Lara and tail wags from our pup Alex.

This dissertation includes one published paper (Chapter I). This is my original work co-authored with my advisor Dr. Julie Lockwood, as well as Dr. Mark Hauber and Dr. Philip Cassey.

Crystal-Ornelas, Robert, et al. "The establishment threat of the obligate brood-parasitic Pin-tailed Whydah (*Vidua macroura*) in North America and the Antilles." *The Condor* 119.3 (2017): 449-458.

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INTRODUCTION

Before non-native species impact native ecosystems, they must be transported, introduced, and eventually establish in a new location (Blackburn *et al.* 2011). Once non-native species are established and cause negative impacts they are called invasive (Lockwood *et al.* 2013). Impacts are generally defined as changes to recipient ecosystems made by invasive species (Lockwood *et al.* 2013; Jeschke *et al.* 2014). The definition of impact as applied to invasion ecology has only recently received a critical evaluation (Jeschke *et al.* 2014). This theoretical framework posits that invasion ecologists must be clear about the context of the impact they measure and describe: (a) whether it is positive or negative, (b) if it is ecological or socio-economic, (c) analytical methods, and (d) the spatiotemporal scale (Jeschke *et al.* 2014). Though Jeschke *et al.* (2014) clarified the definition of impact, the field is still developing cohesion around impact measurement and prediction. In my dissertation, I will explore invasive species impact measurement by: (1) estimating the potential distribution of a recently introduced species, (2) identifying biases in the impact literature, and (3) using meta-analysis to quantify invasive species impacts on diversity over publication years.

Potential distribution of an invasive brood parasitic bird

Initially, invasion ecologists developed qualitative rank-based scoring systems to predict “invasiveness” (Smallwood & Salmon 1992). The metric included elements such as propensity to be introduced and cause damage. Potential to damage was assessed on a scale from “Low” to “High” (Smallwood & Salmon 1992). The user-friendly quality of this metric and the findings paved the way for lists such as “100 of the World’s Worst

Invasive Species” (Lowe *et al.* 2000). Qualitative assessments and “top 100 lists” are useful because their output can be easily translated to action by policy makers and environmentally focused organizations.

Early quantitative impact assessments involved case studies that estimated invasive species impacts on isolated native populations (Kitchell *et al.* 1997). Others relied on broad correlations to show that in many countries there was a negative association between non-native species richness and native species richness (Case 1996). Parker *et al.* (1999) were first to suggest a cohesive theoretical framework for the components of invasive species impacts, based on the following formula:

$$Impact = Range \times Abundance \times Per\ capita\ effect$$

In this equation, impact is a numerical estimate that combines the invasive species’ occupied distribution, abundance, and each individual’s effect. Modifications to the Parker equation recognize that effects and abundance can vary across invaded sites (Thiele *et al.* 2010).

Chapter 1 builds on the work of Parker *et al.* (1999). In this chapter, I estimate the North American geographical range for a non-native bird, the Pin-tailed Whydah (*Vidua macroura*). The whydah is an obligate brood parasite that was recently introduced to two biodiversity hotspots in North America. This study was the first analysis to estimate the whydah’s potential non-native range. To calculate the range, I collected global climate data and occurrences of the invasive species and co-introduced host species in North America. I then created species distribution models to estimate the potential range of this

brood parasitic bird. Based on our preferred model, I found that many islands of the Antilles, Hawaii, Florida, parts of Texas, and the west coast of California all possess suitable climate and hosts for this introduced bird. Future work can focus on completing the Parker equation by estimating the whydah's abundance and per-capita effect on potential host species native to the region where I predict it can establish.

This chapter is published in *The Condor* (Crystal-Ornelas et al., 2017).

Publication bias in invasion ecology

Meta-research is increasingly seen as a way to synthesize the vast amount of ecology research produced each year (Koricheva *et al.* 2013; Gurevitch *et al.* 2018). Recently, systematic review guidelines were developed for ecology (Collaboration for Environmental Evidence 2013). They were quickly adopted by invasion ecologists to synthesize research with more rigor than narrative reviews. However, meta-analysts in invasion ecology are only able to synthesize data on the invasive species and in the ecosystems where research occurs. Therefore, it is possible that invasion ecology experiences a type of publication bias (Cassey *et al.* 2004; Jennions *et al.* 2013) whereby some impacts, species, and locations are studied preferentially over others.

Several key systematic reviews have worked toward characterizing publication bias in invasion ecology. One review explored online invasive species databases and identified the taxa most frequently indicated as invasive worldwide (Turbelin *et al.* 2017). Another recent systematic review showed that invasion ecologists more often hypothesize about boom and bust population dynamics in invaded ecosystems rather than studying the dynamics experimentally (Strayer *et al.* 2017). Finally, Pyšek *et al.* (2008) identified

biases in the taxa that are studied by invasion ecologists. Although previous systematic reviews have identified broad patterns of publication bias in invasion ecology, the field lacks a systematic review that explicitly considers research on invasive species impacts.

In Chapter 2, I conduct a systematic review to assess the strength of publication bias within the impacts literature. Strong publication biases may prevent invasion ecologists from fully understanding the context dependency of invasives' impacts. Compared to previous reviews in invasion ecology, my systematic review is focused solely on the impacts literature and is on a scale larger than any previous impact systematic review. In addition, to adequately explore publications biases I ensured that a large number of studies, and a large variety of taxa and ecosystems were included in the review. For my systematic review, I assembled a database of over 2,200 case studies on invasive species impacts. I found that the impact literature is heavily skewed toward research on impacts at population and community levels, while relatively little research concentrates on genetic and ecosystem impacts. Research tends to be conducted at short timescales and small spatial scales. Also, most invasive species represented in my database have only a single case study measuring their impacts, rather than repeated demonstrations of impact. These publication biases suggest that there are substantial research gaps within the impacts literature that hinder our ability to test the universality of hypotheses and develop theoretical frameworks.

This chapter is formatted for *Ecology Letters* (Crystal-Ornelas & Lockwood In prep).

Invasive species and declines in richness

The presence of invasive species has often been linked with declines in local species richness (Vilà *et al.* 2011; Molloy *et al.* 2017). Despite hundreds of studies on richness impacts, the link between invasive species and richness declines has been debated for decades (Gurevitch & Padilla 2004; Simberloff 2005; Davis *et al.* 2011). We explore whether the debate may stem from declines in published effect sizes over time ('the decline effect') as researchers study richness impacts in a greater variety of taxonomic or ecosystem contexts (Ioannidis 1998; Song *et al.* 2010). The decline effect has received substantial research in the medical field, but remains mostly unexplored in ecological research (but see Jennions & Møller 2002; Leimu & Koricheva 2004).

In chapter 3, I explore the strength of the decline on accumulated evidence for invasive species impacts on diversity. I use a class of meta-analysis called cumulative meta-analysis to explore trends in accumulated evidence between 1999 and 2016. First, I look for evidence of the decline effect across hundreds of case studies documenting diversity impacts. Then, I analyze whether the decline effect is seen across taxonomic or ecosystem subgroups. Within these subgroups, I analyze failsafe ratios and cumulative slopes to identify the year at which sufficient and stable evidence has accumulated for richness impacts.

My cumulative meta-analysis gathered data from 240 publications. I found evidence of the decline effect across all published research on richness impacts. I also found the decline effect within most taxonomic and ecosystem subgroups. Importantly, evidence of the decline effect does not suggest that repeated studies lead to non-significant effects. For example, initial studies on grasses suggested an approximate 70% decrease in invasive species richness. After nearly 40 studies on invasive grasses were

published, the aggregated data suggested a 29% decline in richness. This stable effect size was reached in 2010, and studies on invasive grasses since that year have simply confirmed this decline in richness and have not changed estimates of impact. These findings encourage policymakers and practitioners to rely on accumulated evidence, rather than single case studies.

This chapter is formatted for PRSB and will be submitted there (Crystal-Ornelas & Lockwood In prep).

Taken together, my dissertation advances several key components of the invasion ecology impact literature. Chapter 1 estimates one element of the Parker equation, the geographical range of a non-native brood parasite recently introduced to North America in an effort to predict its long-term potential to become invasive. In Chapter 2, I systematically review the way that invasion ecologists measure invasive species impacts to set the stage for reducing bias found within the field. In Chapter 3, I conduct a cumulative meta-analysis to explore how the decline effect shapes conclusions about invasive species impacts.

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CHAPTER 1: The establishment threat of the obligate brood-parasitic pin-tailed whydah
(*Vidua macroura*) in North America and the Antilles

ABSTRACT

The Pin-tailed Whydah (*Vidua macroura*) is a generalist obligate brood parasite native to Africa, frequently found in the pet trade, which has successfully established exotic populations in two biodiversity hotspots in the Americas. We analyze the whydah's potential future distribution by identifying key locations in the continental U.S., Hawaii, and the Antilles that contain suitable climatic characteristics, host species, and habitat requirements. We used species distribution modeling (MaxEnt) to depict the geographic patterns of possible whydah establishment and compared the predictive power of models that included combinations of climatic data (*climate*), land cover (*habitat*), and localities of historical and one known novel host (*hosts*). The preferred model, the *hosts* model, was the highest performing. The most important variable characterizing whydah distribution in the preferred model was the presence of a frequent historical host that is also established in the Americas, the Common Waxbill (*Estrildid astrild*), followed by a less frequent historical host, the Bronze Mannikin (*Spermestes cucullata*). Our research demonstrates that in the continental U.S., Hawaii, and the Antilles, there are locations that possess the needed exotic host species that may facilitate further invasion by the Pin-tailed Whydah. Given that whydahs are known to exploit over 20 host species from 4 families, clear next steps include assessing the whydah's ability to parasitize novel, native species within the highly suitable areas identified in this research.

INTRODUCTION

Several obligate avian brood parasites have expanded their North American and Antillean range in recent decades and now pose a potential conservation threat to putative native host species in novel areas of their distribution (Pérez-Rivera 1986; Ortega 1998; Dinets *et al.* 2015). Foster parents raising brood parasitic young typically experience losses in their own reproductive success, and some also have reduced annual survival (Rothstein 1990; Hauber 2003; Davies 2010). If these hosts co-evolved with the brood parasite, they may have behavioral or life history counter-measures that can reduce these costs of parasitism (De Mársico & Reboreda 2014). However, when the host is a novel species (i.e., has no co-evolutionary history with the brood parasite) it typically experiences the full (if not increased) costs of parasitism. Some of the range-expanding brood parasites in the Americas involve icterid cowbirds (*Molothrus* spp.), which self-colonized new locations in the wake of, and likely due to, massive land-use transformations (Post & Wiley 1977; Pérez-Rivera 1986; Rothstein 1994; Ortega 1998). Here, we explore the potential for a new addition to this group, the Pin-tailed Whydah (*Vidua macroura*); a species heavily sold in pet markets (Raffaele 1989; Moreno 1997) and one of the few obligate brood parasitic *Vidua* finches that is also a host generalist (Lowther 2016).

The Pin-tailed Whydah (hereafter: whydah) most commonly parasitizes the Common Waxbill (*Estrilda astrild*), but also uses a variety of finch-like birds as hosts in its native range of central and southern Africa (Payne 2005; Lowther 2016). Of the 23 documented hosts in the native range (hereafter called ‘historical hosts’), nearly half have been part of the pet trade, and five of them presently occur as established (locally

breeding) exotic populations in North America and the Antilles (Table 1; Friedmann 1960; Payne 2005; Lowther 2016). These circumstances greatly increase the likelihood that the whydah can become an established exotic member of the avifauna in these regions. Pin-tailed Whydahs have already established breeding and viable exotic populations in Puerto Rico (Raffaele 1989) and, most likely, in southern California (Garrett & Garrett 2016). In Puerto Rico, whydahs were introduced during the 1960s and 1970s through accidental releases as part of the pet trade (Raffaele 1989; Moreno 1997). On the island, they parasitize mostly exotic Orange-cheeked Waxbills (*Estrilda melpoda*), proving that the sequence of events necessary for successful invasion, from transportation to parasitizing hosts in a novel range, is possible. Additionally, whydahs have the ability to host-switch and parasitize novel species, even when the whydah has not evolved nestling mimicry toward these new hosts (Schuetz 2005a; Hauber & Kilner 2006; Lansverk *et al.* 2015). This trait increases the likelihood that Pin-tailed Whydahs will find as suitable hosts other non-African finches also established as exotics in North America and the Antilles. For example, in California whydahs appear to parasitize the exotic Scaly-breasted Munia (*Lonchura punctulata*), an estrildid species native to Asia (Garrett & Garrett 2016).

Species distribution models (hereafter: SDMs) correlate species occurrence records with environmental attributes (e.g., climate, vegetation structure) to create a map depicting relative habitat suitability (Anderson *et al.* 2002; Rodríguez *et al.* 2007; Peterson *et al.* 2011). MaxEnt is a machine learning SDM that has been used extensively to estimate habitat suitability for critically endangered species (Ibáñez *et al.* 2009), the potential geographical range of exotic species (Fernandez & Hamilton 2015), and extent

of suitable habitat in a future altered climate for whole taxonomic groups (Monterrubio-Rico *et al.* 2015). We used MaxEnt to create a map of relative habitat suitability for Pin-tailed Whydahs in the continental U.S., Hawaii, and the Antilles. We consider such a map as a necessary first stage to gauge the threat that Pin-tailed Whydahs pose to native birds in these locations. The maps are not sufficient by themselves to fully calculate invasion risk (see Discussion). However, they do provide a way to quantitatively express where conditions are favorable for whydah occurrence and thus help prioritize monitoring and research efforts that can fully gauge risk (Stohlgren & Schnase 2006).

Initially, we used a standard approach to SDMs to identify locations where the basic climatic requirements of the Pin-tailed Whydah are met. This map is a baseline for where Pin-tailed Whydahs can reasonably be expected to occur in the future, based purely on abiotic requirements. We then extended the SDM to include a Land Use Land Cover (LULC) habitat covariate as a proxy for seeding grasses critical for the whydah's granivorous diet (Raffaele 1989). We consider these abiotic and biotic suitability maps as conservative representations of where whydahs are likely to (at least) establish nascent populations. We then explored SDMs that explicitly recognize that, for the parasitic whydah, even highly suitable habitat will not be occupied if they cannot complete their life cycle by finding suitable host species (Friedmann 1960). We posit that the presence of any host individuals within suitable habitat is sufficient to create an initial bridgehead population of whydahs at that location. This bridgehead population provides the whydah the opportunity to expand to utilize other hosts (if needed), and subsequently grow its population and geographical range. For these SDMs we assumed that whydahs will

parasitize the five historical hosts, and the one known novel host, the Scaly-breasted Munia, that occur in North America and the Antilles (Table 1).

METHODS

Species distribution models, in general, require known occurrence localities of a focal species and quantitative estimates of environmental conditions at these locations. Models are then fitted to environmental conditions at points where the species has been observed. These models can then be used to predict habitat suitability of unsampled locations in geographic space based on abiotic conditions in the model's environmental space (Peterson *et al.* 2011).

MaxEnt is a distribution modeling algorithm that requires geographical coordinates where the focal species is known to be present (Phillips *et al.* 2006; Merow *et al.* 2013). These points are then assigned a variety of attributes, which are provided by the model-builder and are thought by them to reflect environmental factors that dictate habitat suitability. From the attributes of these known-occurrence locations, MaxEnt builds a series of functions that quantitatively create a spatially interpolated map depicting where the species is likely to be found (Elith *et al.* 2011; Peterson *et al.* 2011; Merow *et al.* 2013). Suitability functions are evaluated by the model's ability to differentiate between the locations of known-occurrence vs. a series of randomly selected other locations (i.e., pseudo-absences Phillips *et al.* 2009). The key inputs to MaxEnt are the occurrence records for the focal species, and the factors considered to be relevant

attributes that define suitable locations. We describe this modeling approach below for an invasive brood parasite, the Pin-tailed Whydah.

Pin-tailed Whydah Occurrence Data

We sourced 39,279 georeferenced occurrences of Pin-tailed Whydahs worldwide from the Global Biodiversity Information Facility (GBIF; <http://www.gbif.org/species>). We removed duplicate records or those with missing longitude and/or latitude. Outliers were eliminated through two distinct steps: (1) we confirmed that all records were located within boundaries of the country indicated by the database and not associated with errors in coordinate transcription or museum specimens, and (2) data were filtered by retaining only those points that corresponded to countries with exotic breeding populations of whydahs identified through a literature search (Long 1981; Lever 2005; Garrett & Garrett 2016). Occurrence records were spatially thinned to a nearest-neighbor distance of 3km using *spThin* (Aiello-Lammens *et al.* 2015). We selected a 3km thinning distance based on the home range of the Shaft-tailed Whydah (*Vidua regia*), a congener of the Pin-tailed Whydah (Barnard 1990). In the absence of information on the dispersal range of the Pin-tailed Whydah, we used this information on its congener to estimate a distance beyond which observers are unlikely to record the same individual. Thinning the occurrence records also reduced the possibility that areas with a high density of occurrences due to biased sampling effort contributed a disproportionate amount to model training (see below). Our final whydah occurrence input data included 2,329 points (Figure 1).

Attribute Variables

In an effort to characterize the abiotic conditions conducive to whydah occurrence, we included 19 WorldClim rasters that interpolate climate data for temperature and precipitation at a 5 arc-minute resolution worldwide (Hijmans *et al.* 2005). We used this set of climate variables to depict locations where abiotic conditions are conducive to whydah occurrence.

We recognize that whydahs, being granivorous finches, will be unable to survive in locations without seeding grasses to forage (Raffaele 1989). Thus we utilized the Land Use Land Cover (LULC) database *GlobCover* to depict the location of vegetation that is likely to contain suitable forage (Arino *et al.* 2012). This LULC layer has 22 categories of land use, with 18 that quantify vegetation cover, and the remaining four indicating water (i.e., coastal habitat or river systems), artificial surfaces, ice, and barren areas. We used all 22 categories to identify vegetation and other land cover classes that may be important for predicting whydah distribution. We projected this layer to match WorldClim's 5 arc-minute resolution.

Finally, we included spatially explicit information on the localities of the six known historical or novel host species that occur as exotic populations in the continental U.S., Hawaii, or the Antilles (Table 1). We had two options for doing so (Anderson 2017). The first was to generate SDMs for each host species and use these maps as input into the whydah SDM. The second was to use only the known point-occurrence records for host species as input into the whydah SDM. Both approaches were tested in situations similar to ours where another species' presence is necessary for defining suitable habitat for the focal species (Hof *et al.* 2012; Giannini *et al.* 2013). In these prior studies, the latter approach (using only known point-occurrence records) consistently produced a

better performing model for the focal species (Giannini *et al.* 2013). For the Pin-tailed Whydah, its co-introduced hosts may be far from distributional equilibrium (Elith *et al.* 2010). As the whydah is an obligate brood parasite, the species requires hosts presence and thus realistic models should include only areas of known host occurrence. Host information included occurrence points of 5 known hosts and one recently identified novel host (Scaly-breasted Munia).

Model Set and Selection

Using the above location attributes, we constructed seven SDMs. The simplest were those that used only climate, habitat, or host information (*climate*, *habitat*, *hosts* models; Table 2). We then created four additional models that represented all possible permutations of these three (Table 2). Once the model set was delineated, we evaluated the ability of each to predict Pin-tailed Whydah occurrence and used this information to select the single model that provided the most robust predictions (preferred model).

We selected the preferred model by using the sample-size corrected Akaike information criterion (AIC_c) (Burnham & Anderson 2002; Warren & Seifert 2011). Model selection with AIC_c calculates the likelihood of estimated habitat suitability based on occurrence data. The AIC_c approach penalizes more complex models by accounting for the number of parameters used by each MaxEnt model (Swets 1988; Franklin 2009). We selected the preferred model that had the lowest AIC_c score. The preferred model AIC_c score was subtracted from the AIC_c scores of all other models to indicate model relative fit (ΔAIC_c). We identified the most important covariates explaining variation in

whydah relative habitat suitability by determining the covariates that had the highest percent contribution.

For all seven models, we applied a 10% minimum training presence threshold to MaxEnt's continuous output to produce a binary depiction of habitat suitability (Radosavljevic & Anderson 2014). Models were evaluated by testing their performance against 10,000 randomly sampled background points from 5-degree buffers around training occurrences (Elith *et al.* 2011; Van Der Wal *et al.* 2015). Background points should be drawn from an extent potentially occupied by the focal species (Barve *et al.* 2011). The whydah is presently expanding its range, and thus we followed the work of Elith *et al.* (2010) who created SDMs for other invasive species and used a buffer to approximate a 'reachable' extent within which we sample background locations. Next, we created confusion matrices for each binary suitability map to assess their accuracy in terms of correctly identifying suitable vs. unsuitable habitat. We calculated omission rates to identify how often models labeled known suitable habitat as unsuitable. To calculate omission rates, occurrence records were randomly partitioned into calibration (75%) and evaluation (25%) sets. We did not calculate commission rates because background points should not be used to evaluate model fit (Peterson *et al.* 2008).

Methods for incorporating biotic interactions as model covariates have been developed (Anderson 2017). These often involve consensus among several models (Giannini *et al.* 2013). If whydahs, as host generalists, can ultimately exploit a greater range of hosts than they currently do, a model based solely on known-host presence will underestimate their potential distribution and thus invasion risk. We may also underestimate whydah invasion risk if the parasite maintains the same suite of exotic

hosts that it does now, but those hosts themselves expand their ranges. Several co-introduced historical hosts used by the Pin-tailed Whydah are indeed predicted to do so (Stiels *et al.* 2011, 2015). Recognizing the potential for changing biotic interactions, we created a congruence map that relaxes the assumption of host specificity and host range stability by combining suitability predictions for the strict *hosts* model and the more relaxed *climate* model. This approach follows previous work that uses two distribution models to portray variability in the importance of a biotic covariate (Pidgeon *et al.* 2015). We refrain from interpreting poorly performing models, but rather present the congruence map as a potentially more relevant risk map. We obtained a quantitative measure of the whydah's potential distribution by first converting suitability maps to the North America Albers Equal Area Conical projection. We then vectorized each map and used the QGIS (Quantum GIS Development Team 2016) field calculator to determine areas indicating suitability in m² which we converted to km².

RESULTS

Our preferred model for predicting the potential distribution of the Pin-tailed Whydah is the *hosts* model (Table 2). This model had the lowest AIC_c across all permutations of model attributes (AIC_c= 57231). In this model, Common Waxbill and Bronze Mannikin (*Spermestes cucullata*) had the highest percent contributions (48% and 43%, respectively; Table 3). The Scaly-breasted Munia, a known novel host of the whydah, ranked 3rd in percent contribution (3%). Two less frequently used hosts, the Orange-cheeked Waxbill (*Estrilda melpoda*) and Black-rumped Waxbill (*Estrilda troglodytes*) ranked 4th and 5th in percent contribution (3% and 2%, respectively).

Our preferred model (*hosts*) had a relatively high omission error rate (Om. = 0.26; Thresh. = 0.035). Inspection of misclassified points indicated that these points were often near correctly classified locations. Moreover, the model misclassified only two points in the non-native distribution, one in California and one in Florida. The remaining points in the non-native range were correctly classified by our preferred model. The continuous habitat suitability map (Figure 2) demonstrates that the preferred model indicated high suitability in areas where there are one or multiple host species present: the West Coast of the U.S., much of Hawaii, small sections of Texas and Florida, and many islands in the Antilles.

We created a congruence map (Figure 3) using the conservative *hosts* model and the liberal *climate* model to present a risk map showing where the whydah could potentially occur should it begin to exploit hosts other than the six we included here, or if the hosts themselves expand their geographical range. The climate model's highest contributing covariates were maximum temperature in the warmest month (31%) and precipitation in the driest month (17%). As expected, predictions in geographic space were more circumscribed for models built with only host information (27,184 km²) when compared to the *climate* model (58,430 km²). The congruence map further highlighted the high potential of Hawaii and islands in the Antilles to be occupied by Pin-tailed Whydahs (Figure 3).

DISCUSSION

Whether the Pin-tailed Whydah becomes the newest range-expanding brood parasite of conservation concern in North America, Hawaii, and the Antilles hinges primarily on the

presence of suitable host species at the time of their initial establishment. Host information restricts our model to high suitability predicted in southern California, Hawaii, and several islands in the Caribbean. Contrary to previous work that suggests climate and host information provides the best model fit for modeling parasite distribution, our work suggests that for an obligate generalist brood parasitic bird, host information alone provides the best fit.

Of the high-suitability areas we identify in the preferred model, only Puerto Rico and a small fraction of southern California are currently home to established whydah populations. We suggest that Hawaii is poised to harbor a robust Pin-tailed Whydah population if released (again) in large enough numbers. Whydahs were regularly observed as free-living on Oahu during the 1960s through to the 1980s, indicating that they had the opportunity to escape captivity and become free-living in the past. These released individuals either failed to breed at all, or the nascent population they established eventually became locally extinct, possibly due to co-occurring declines in populations of estrildid hosts on Oahu (Pyle & Pyle 2009). Nevertheless, we show that all main islands in the archipelago have large tracts showing suitable climatic conditions for the whydah, with historical host species now well-established within several of these locations (Table 1).

If whydahs can switch to parasitize other exotic finch hosts on Hawaii (e.g., Chestnut Munias (*Lonchura atricapilla*); Pyle & Pyle 2009) or in Florida and the Antilles (e.g., Tricolored Munia (*Lonchura malacca*); Lever 2005) their potential for establishment or range expansion may increase, provided that the climatic and habitat conditions of the region are suitable for occupancy (Duncan *et al.* 2001; Tatem & Hay

2007; Blackburn *et al.* 2009). In contrast, our preferred model may produce unrealistically high suitability estimates if biotic interactions (e.g., novel host species or food sources) are identified as important for whydahs at a smaller scale or extent than our attribute layers can portray (Wisz *et al.* 2013). Given a lack of consensus on methods for incorporating biotic covariates into SDMs (Anderson 2017), we believe that our congruence map best portrays the risk of whydah occurrence by depicting the difference between a highly circumscribed model taking account only of known host locations (*hosts*) and a maximally liberal model constrained only by climatically suitable locations (*climate*).

Since recent whydah introductions are likely due to accidental releases of captive birds in the pet trade (Raffaele 1989; Acevedo & Restrepo 2008), whether this species establishes within these locations depends on the number and spatial location of release events (Lockwood *et al.* 2005). Here we utilize abiotic and biotic predictor variables to estimate potentially suitable habitat, but have no way of depicting the probability of pet owners releasing Pin-tailed Whydahs and thus no suitable proxy for propagule pressure. As a step in this direction, future efforts to quantify establishment probability could estimate import or direct sales data for whydahs within our focal regions and use this as a proxy for propagule pressure (Blackburn *et al.* 2009).

Finally, in evaluating the risk of Pin-tailed Whydahs to native birds in our focal regions we must address their ability and propensity to use native species as their hosts. Pin-tailed Whydahs are remarkably flexible in the hosts they use in their native range (Payne 2005; Lowther 2016), and show the ability to successfully reproduce when expanding their host range (Lansverk *et al.* 2015). In order to reduce the possibility of a

foster parent rejecting their young, Pin-tailed Whydahs mimic the mouth markings of the nestlings of their most frequent host species (Friedmann 1960; Payne 2005; Schuetz 2005b). This brood parasitic adaptation initially would argue that whydahs are likely to be slow (or incapable) of switching to hosts with substantially different nestling gapes. However, mouth markings that are somewhat mismatched to hosts are clearly not prohibiting whydahs from experiencing reproductive success in the native (Payne 2005; Lansverk *et al.* 2015) and exotic range (Garrett & Garrett 2016). For example, Lansverk *et al.* (2015) provide evidence that Pin-tailed Whydahs experience similar reproductive success when parasitizing a novel host in Africa as it does with its more common host.

Despite the flexibility of host use in the Pin-tailed Whydah, we suggest there are notable barriers for whydahs to surmount if they are to exploit as hosts the native avifauna in our focal regions. It is not clear if the whydah is capable of making the jump from their usual small finch hosts to the suite of native species found in the West Coast of the U.S., Florida, Hawaii, or the Antilles. So far, there have been no reports of Pin-tailed Whydahs parasitizing native species in Puerto Rico or southern California, although we found no evidence that anyone has been systematically looking for such events. We suggest that the most likely novel native hosts would be within the fringillid finches (Jetz *et al.* 2012). However, whydahs rarely exploit hosts with the open-cup nests typical of fringillids (Friedmann 1960), and furthermore hosts would need to accept the eggs and have a diet similar to whydahs (Davies 2010). In the Antilles, native *Euphonia* spp. finches build dome-shaped nests that may be more readily parasitized by whydahs, though their frugivorous (rather than granivorous) diet presents another barrier to parasitism (Raffaele 1989).

The question of risk to native avifauna is perhaps better posed as one of addressing how different gape markings, nest construction, and host diet must be before whydahs will either not lay eggs in a host's nest, or whydah nestlings will be rejected by the host parents (Schuetz 2005b). Posing this question in the context of the suite of possible native hosts within suitable whydah habitat we identify here can substantially inform our understanding of the risk whydahs pose to the North American and Antillean avifauna. The locations that we identified here as being suitable for whydah occupancy are native homes to a wide variety of bird species, many of which are threatened with extinction and are naïve to brood parasitism. If Pin-tailed Whydahs were to successfully utilize these hosts, the negative conservation and management impact to these new hosts species could be quite high.

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TABLES AND FIGURES

Table 1. Historical hosts and one known novel host of the Pin-tailed Whydah, frequency of parasitism, occurrence in the pet trade, and whether they have records in North America (Long 1981; Moulton & Pimm 1986; Lever 2005; Payne 2005; Schuetz 2005a; Pyle & Pyle 2009; Aagaard & Lockwood 2016; Birds Express 2016; Finch Farm 2016; Lowther 2016). Occurrence information downloaded from the Global Biodiversity Information Facility (data accessed 20 July, 2016). Species are ordered according to the Clements Checklist (Clements *et al.* 2016) and separated by family (Chesser *et al.* 2016). Species with names in **bold** were included in species distribution model(s). HI = Hawaii, LA = Lesser Antilles, PR = Puerto Rico, sCA = southern California, sTX = southern Texas, FL = Florida.

Host	Frequent or rare host	Traded	Occurrence in North America?
Ploceidae			
Scaly Weaver (<i>Sporopipes squamifrons</i>)	Rare	No	No
Village Weaver (<i>Ploceus cucullatus</i>)	Rare	No	No
Red-collared Widowbird (<i>Euplectes ardens</i>)	Rare	No	No
Long-tailed Widowbird (<i>Euplectes progne</i>)	Rare	No	No
Grosbeak Weaver (<i>Amblyospiza albifrons</i>)	Rare	No	No
Estrildidae			
Swee Waxbill (<i>Coccopygia melanotis</i>)	Rare	Yes	No
Yellow-bellied Waxbill (<i>Coccopygia quartinia</i>)	Rare	Yes	No
Fawn-breasted Waxbill (<i>Estrilda paludicola</i>)	Rare	No	No
Orange-cheeked Waxbill (<i>Estrilda melpoda</i>)	Rare	Yes	Yes (PR, sCA, LA, FL)

Crimson-rumped Waxbill (<i>Estrilda rhodopyga</i>)	Rare	No	No
Black-rumped Waxbill (<i>Estrilda troglodytes</i>)	Rare	Yes	Yes (LA)
Common Waxbill (<i>Estrilda astrild</i>)	Frequent	Yes	Yes (HI, LA)
Black-crowned Waxbill (<i>Estrilda nonnula</i>)	Rare	No	No
Black-cheeked Waxbill (<i>Estrilda charmosyna</i>)	Rare	No	No
Red-billed Firefinch (<i>Lagonosticta senegala</i>)	Rare	Yes	No
Black-bellied Firefinch (<i>Lagonosticta rara</i>)	Rare	No	No
African Firefinch (<i>Lagonosticta rubricata</i>)	Rare	Yes	No
Zebra Waxbill (<i>Sporaeginthus subflavus</i>)	Rare	Yes	No
Bronze Mannikin (<i>Spermestes cucullata</i>)	Rare	Yes	Yes (PR, sCA, sTX)
Magpie Mannikin (<i>Spermestes fringilloides</i>)	Rare	Yes	No
African Silverbill (<i>Euodice cantans</i>)	Rare	Yes	Yes (HI)
Scaly-breasted Munia (<i>Lonchura punctulata</i>)	Rare	Yes	Yes (PR, sCA, GA, LA, FL, HI, sTX)
Fringillidae			
Streaky Seedeater (<i>Serinus striolatus</i>)	Rare	No	No
Emberizidae			
Golden-breasted Bunting (<i>Emberiza flaviventris</i>)	Rare	Yes	No

Table 2. Model selection statistics for combinations of *climate*, *hosts*, and *habitat* covariates. We provide statistics for the models based on a split of occurrence records into training (75%) and testing (25%). Model fit relative to the preferred model is shown by ΔAIC_c . K indicates the number of parameters used by MaxEnt to fit models. The preferred model has $AIC_c = 57231$. Omission error rates assess the frequency at which preferred models incorrectly classified known whydah occurrences.

Model Name	K	ΔAIC_c	Omission Error Rates
<i>hosts</i>	26	0	.26
<i>climate</i> + <i>hosts</i> + <i>habitat</i>	148	516	.13
<i>climate</i> + <i>hosts</i>	146	604	.13
<i>hosts</i> + <i>habitat</i>	42	652	.053
<i>climate</i>	178	3344	.12
<i>climate</i> + <i>habitat</i>	187	3479	.12
<i>habitat</i>	16	17560	.12

Table 3. Variable contribution of the five most important host covariates in the *hosts* model. A stochastic process determines the initial variable contribution (potentially masking variable importance if covariates are highly correlated), thus we provide average values across five model iterations.

Variable	Contribution (%)
Common Waxbill	48
Bronze Mannikin	43
Scaly-breasted Munia	3
Orange-cheeked Waxbill	3
Black-rumped Waxbill	2

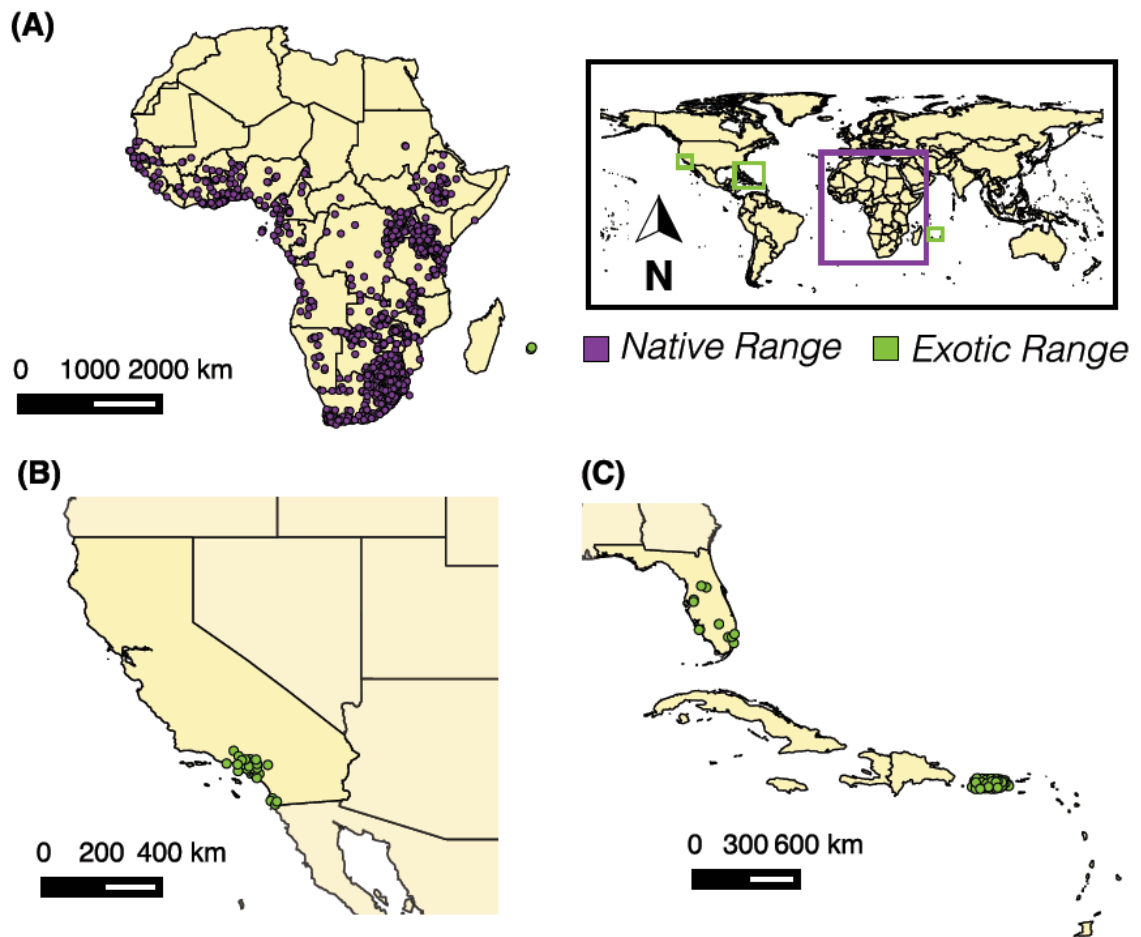


Figure 1. Georeferenced occurrence data for Pin-tailed Whydahs used for generating species distribution models. All localities displayed here ($n = 2,329$) are human observations as reported to the Global Biodiversity Information Facility (GBIF) in both the native range (*purple dots*) and exotic range (*green dots*). We processed all occurrences by removing duplicates, spatially thinning, and excluding countries without established populations (that had no reports of breeding activity). We show the native distribution of whydahs in Africa (A) and exotic populations in California (B), and the Antilles and Florida (C).

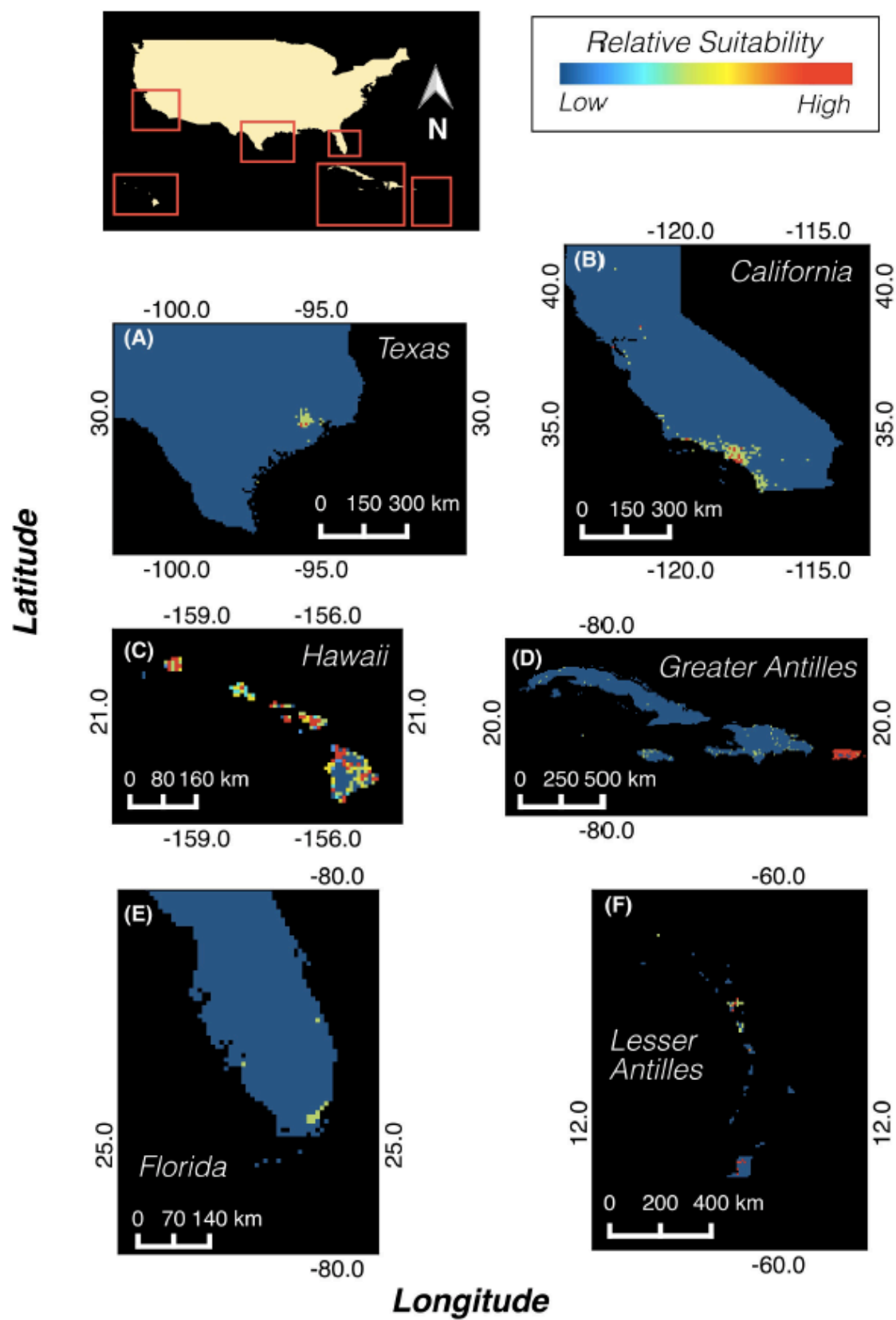


Figure 2. Geographic projection of relative suitability for Pin-tailed Whydah occurrence from the preferred (*hosts*) MaxEnt model for: (A) southern Texas, (B) southern California, (C) Hawaii, (D) the Greater Antilles, (E) southern Florida, and (F) the Lesser Antilles. Warmer colors indicate greater relative suitability for whydah occurrence, given hosts presence.

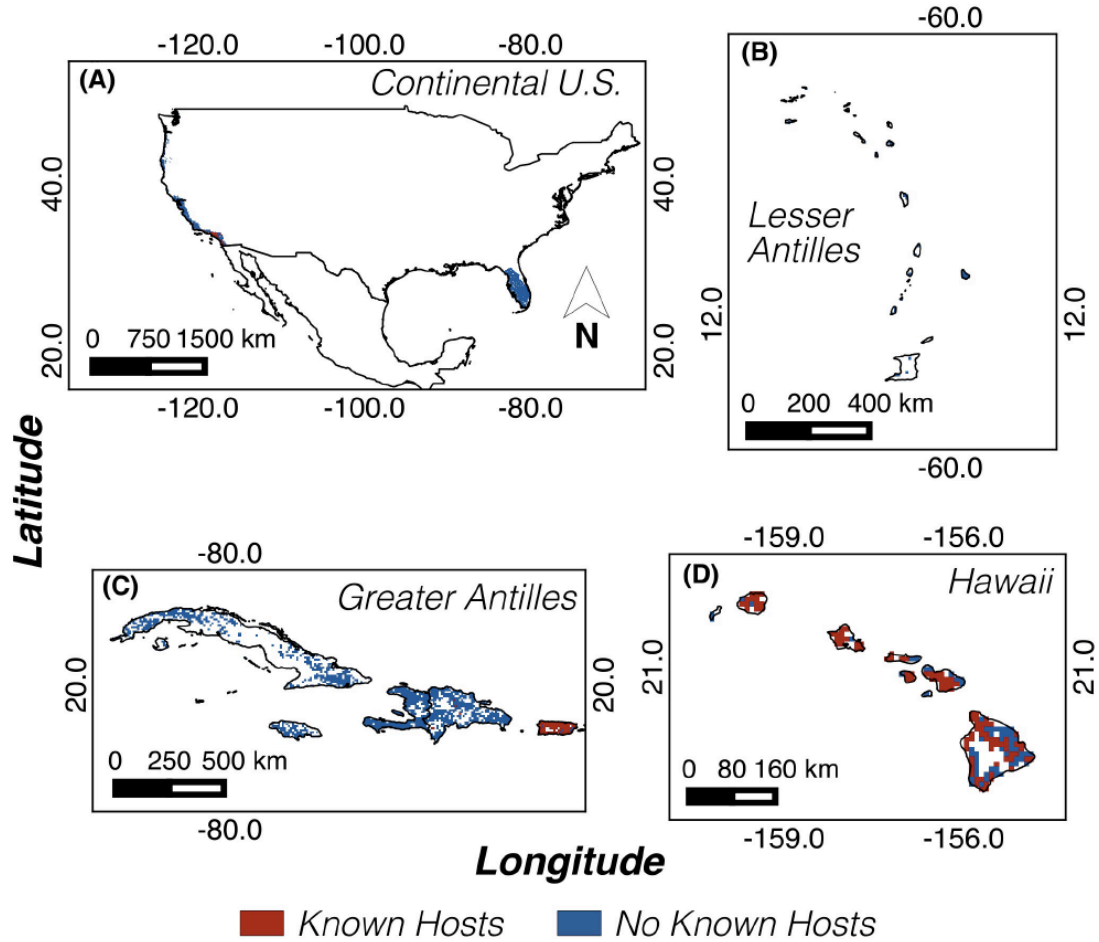


Figure 3. Congruence map showing agreement of *hosts* and *climate* MaxEnt models of suitability for the Pin-tailed Whydah. The *hosts* model is our preferred model. Red indicates areas identified as suitable by the *hosts* model. Blue indicates suitable area from the *climate* model. The more conservative geographical extent outlined in red hinges on the assumption that the whydah will only parasitize the suite of historical hosts and one known novel host we included in the *hosts* model, and that the hosts will not expand their range. The larger area outlined in blue is a more liberal projection that does not include host information. However, this more liberal predicted area may be relevant as a risk map if whydahs begin to use a greater range of hosts, or if the present suite of hosts expand

their range in our focal area. Locations were classified as suitable by a 10% minimum training threshold. We highlight predictions for: (A) continental U.S., (B) the Lesser Antilles, (C) the Greater Antilles, and (D) Hawaii.

CHAPTER 2: What we are missing when we study invasive species impacts: publication bias in ecological effects, taxa, geography, and spatiotemporal scales

ABSTRACT

Research on invasive species' impacts has resulted in thousands of case studies and dozens of meta-analyses. We posit that this substantial body of information is prone to publication bias, which inhibits formulation of impact theories, testing impact hypotheses, and producing robust impact predictions. We built a taxonomically and geographically comprehensive database of over 1,500 research articles on invasive species' ecological impacts published over the past 18 years (1999-2016). We found that, field-wide, published measures of invasive species' impacts are highly skewed toward those measured at the population or community-level with scarce information on other ecological impacts (physiology, behavior). We also show that impact evidence stems most often from one-off studies of single invasive species, most of which are found within a few select countries and ecosystems. This concentration of effort is often not justified based on overall patterns in which species are most impactful and where. Finally, very few species' impacts have been documented across biological scales, or have had their impacts documented beyond very local spatial scales or very short time periods. Our results highlight substantial informational gaps that hinder our ability to incorporate context dependency into theories of invasive species impact, and refine hypotheses and predictive frameworks.

INTRODUCTION

Scientific and public interest in invasive species is driven by these species' sometimes substantial negative ecological impacts (Strayer 2010; Vilà *et al.* 2011; Doherty *et al.* 2016). As efforts to counteract these impacts has grown, so too has the number of publications that document ecological effects or that test hypothesized impact mechanisms (Simberloff 2011). This accumulation of evidence has spurred a recent boon in the production of meta-analyses on invasive species impacts (Appendix S1; Vilà *et al.* 2011; Iacarella *et al.* 2015), and in efforts to formalize impact definitions and build conceptual impact frameworks (Blackburn *et al.* 2014; Jeschke *et al.* 2014). However, existing meta-research and conceptual frameworks can only synthesize the information individual researchers collect. So it follows that if researchers, intentionally or unintentionally, gather data unequally and produce a biased information base (publication bias; Lortie *et al.* 2007; Koricheva *et al.* 2013), this will lead to incomplete conceptual models and hinder the ability of researchers to adequately judge the universality of impact hypotheses (Strayer *et al.* 2006; Reaser *et al.* 2007; Ojaveer *et al.* 2015; Cameron *et al.* 2016). Invasion biology is replete with efforts to identify gaps in knowledge, however most of these efforts have failed to explicitly consider the evidence surrounding measured ecological impacts (e.g., Pyšek *et al.* 2008; Lowry *et al.* 2012), or if it has, considers a single taxonomic group or location (e.g., Vilà *et al.* 2011; Hulme *et al.* 2013; Gallardo *et al.* 2016). It is therefore difficult, if not impossible, to identify publication biases that transcend the field or evaluate bias interactions across taxa, locations, or biological realms (marine, freshwater, terrestrial). We provide this global perspective on the evidence base accumulated for invasive species' ecological impacts here by

compiling and evaluating the most comprehensive database of invasion impact literature to date.

Based on prior, but more circumscribed, systematic synthesis and meta-analysis we posit that four publication biases pervade the invasion impact literature; (1) uneven research effort in recorded impacts across biological scales of measurement and ecological effect types, (2) a tendency toward production of short temporal and local spatial scale analyses, (3) over-representation of particular geographical locations and taxa, and (4) a concentration of effort toward the study of only a subset of ecosystems that have been invaded.

Invasive species' ecological impacts do not have a clear *a priori* expectation of directionality or biological scale (Jeschke *et al.* 2014). Effects can be measured in a uni- or bi-directional manner, and the definition can be value-neutral or informed by human values (Jeschke *et al.* 2014). The issues of directionality and value inform how invasion biology research is perceived and communicated outside the field, and will not be directly addressed in this review. However, the issue of biological scale is pertinent to producing a conceptual impact framework as the task requires integrating cross-scale ecological mechanisms (Parker *et al.* 1999; Ehrenfeld 2010). Additionally, there are a subset of ecological effects directly associated with each biological scale, and thus a bias toward one scale will translate into an incomplete understanding of how ecological effects are mechanistically inter-related (Table 1). For example, population-scale impacts inform understanding of when and why invasive species can alter the fitness and population dynamics of co-occurring native species (Buhle & Ruesink 2009; Jänes *et al.* 2015). However, these effects are likely the more extreme outcomes of effects that originally

manifest at the individual-scale as behavioral or physiological shifts of native individuals in the presence of invasive predators or competitors (Lennox *et al.* 2015). It is thus difficult to create invasive species impact frameworks and comprehensive risk assessments if our evidence base is skewed toward only a few ecological effects within one biological scale.

Related is the ability of syntheses to critically evaluate the large number of impact hypotheses, discarding those with little empirical support and elevating those that have some predictive power (Jeschke *et al.* 2012, 2014). The plethora of hypotheses related to ecological impacts of invasive species can be clearly separated by the biological scale of the underlying ecological effect (Ricciardi *et al.* 2013). An absence of research related to one or more of these scales and effects handicaps our ability to critically evaluate related hypotheses, or generate new more inclusive hypotheses. Thus, we consider publication bias across biological scales and ecological effects to be a key factor inhibiting progress in the field, and we explicitly address how this potential bias manifests across taxa, geographical regions, ecosystem types, and temporal scale of study.

It is widely recognized across ecological disciplines that long-term research uncovers patterns in ecological processes that short-term studies miss (Hobbie 2003; Fischer *et al.* 2010; Haase *et al.* 2018). Within invasion ecology, long-term population dynamics can profoundly influence measured impacts, since ecological effects are often mediated by the invasive species' abundance (Strayer *et al.* 2006). This observation highlights two inter-related issues. First, impacts can vary through time according to a suite of ecological factors that determine the invasive species' population trajectory. Research of short duration is much more likely to miss changes in invasive species

population size or density that may provide the critical context to understanding ecological impacts of that species (Yokomizo *et al.* 2009; Iacarella *et al.* 2015; Cassey *et al.* 2018). Second, if researchers do not indicate the number of years between when they conducted a study and the date at which the invasive species originally entered their study system, it is nearly impossible to place these findings into a time-since-invasion framework to produce a full understanding of how and why impacts may change over time (Strayer *et al.* 2006). For these two reasons, the issue of temporal bias in the invasion impact literature appears repeatedly as a barrier to invasion syntheses (Strayer *et al.* 2006; Cameron *et al.* 2016; D'Antonio & Flory 2017). Here we assess the prevalence of this bias across taxa and ecosystems, and explore whether it is more (or less) pronounced across biological scale and ecological effects.

Another commonly acknowledged publication bias within ecological research is the over-representation of studies conducted at fine rather than broad spatial scales (Mack *et al.* 2007; Fischer *et al.* 2010; Strayer *et al.* 2017; Wood *et al.* 2017). We should expect a similar bias in the invasion impact literature, however to date there has been no systematic assessment of this possibility. As with temporal bias, the ecological factors that mediate invasive species' impacts likely do not manifest equally across all populations of a non-native species (Hulme *et al.* 2013; Ricciardi *et al.* 2013; Courchamp *et al.* 2017). We should further expect that research across a broader spatial scale will average-out finer spatial scale differences in impact, known as the impact-averaging hypothesis (Powell *et al.* 2011; Hulme *et al.* 2013). If the invasion impacts literature is skewed toward providing information predominately at fine spatial scales, efforts to fully

vet impact hypotheses or build universally applicable conceptual models will either inadvertently include this skewed perspective, or deliberately exclude spatial context.

Some of the earliest systematic reviews in invasion ecology documented substantial taxonomic and geographical bias in the published literature, showing that most work focused on herbaceous plants and insects found in North America, Australia, or the European Union (Pyšek *et al.* 2008; Hulme *et al.* 2013). These biases almost certainly apply to the subset of invasion literature focused on ecological impacts, an assertion we test here. Geographic and taxonomic bias may be warranted to some extent, as previous research suggests that the wealthiest countries (in Europe) have more invasive species relative to others (Pyšek *et al.* 2010), and globally some taxa are more prone to movement by humans than others (Pergl *et al.* 2017; Turbelin *et al.* 2017). We may therefore expect that the body of literature on invasive species impacts will focus on geographical locations that are known to have been particularly transformed by invasive species impacts, or suites of species that are considered particularly harmful by conservation organizations. Similarly, we may expect that impact publications will skew towards a focus on the taxa or species that are known to be commonly introduced as non-natives, assuming that these taxa will by chance alone contribute relatively more harmful invasive species (van Wilgen *et al.* 2018). We confront these expectations with comprehensive data that cover all taxa and biological realms, highlighting where these biases may interact with others, especially related to the biological scale and type of ecological effects.

Finally, we note that global historical records indicate that an increase in taxonomic breadth of established non-native species, and an increasingly broad array of

ecosystems being invaded, accompanies the observed recent rise in the rate of species establishment (Essl *et al.* 2011, 2013). The ecological effects that invasive species can manifest are dictated by their life histories, trophic positions, and the abiotic and biotic interactions they experience (Lockwood *et al.* 2013). If most impact information for a single species comes from a single ecosystem, at a single short snapshot of time, it is difficult (if not impossible) to determine how environmental context influences the direction, magnitude, and mechanisms behind its observed impacts. Equally of interest are impact studies undertaken on the same species, but across multiple biological scales and ecological effects. These research threads can be used to develop comprehensive conceptual frameworks of how impacts are propagated from genes through to ecosystems. Thus, we suggest that there is deep and largely unrecognized tension between the need to document the impacts of the same species across geographical regions, biological scales, and temporal scales; versus the need to provide impact information across a wide and growing taxonomic and ecosystem perspective (Hulme *et al.* 2013). Here we evaluate how the existing invasion impact literature has reflected these trade-offs, and what the existing body of literature can tell us about the balance we have thus far achieved relative to these tensions.

METHODS

We performed a literature search in January 2017 using Thomsen Reuters ISI Web of Science ®. We developed search term strings and synonyms intended to be highly sensitive to articles published on the impacts of invasive species while also incorporating any taxa, geographical regions, or ecosystem types. We included only search terms and

articles published in English, and our results are thus subject to greater representation of statistically significant research than if all languages were included (Jüni *et al.* 2002). We used the following combination of search terms: TOPIC = “invasive” AND “impact*”; “introduced species” AND “impact*”; “non-native” AND “impact*”; “exotic” AND “impact*”; “alien” AND “impact*”; “naturalized” and “impact*”; “non-indigenous” AND “impact*”.

These search terms likely did not capture every published article on invasive species impacts. For example, we did not include “effect” or “disturbance” as synonyms for “impact”. Nevertheless, we identified 23,374 candidate articles providing us with confidence that our database gave a comprehensive overview of the literature on invasive species impacts. We limited the range of years for our search from 1999-2016. We chose 1999 as the start of our search since this coincided with the development and publication of initial theories on invasive species impacts (Parker *et al.* 1999), which (in part) spurred a period of growth in primary literature publications on the topic.

Screening and study inclusion–exclusion criteria

Prior to article screening, we developed a set of inclusion criteria where each study had to meet all five criteria to be included (Appendix S2). We used a PICO framework (Populations, Interventions, Control, and Outcomes) to shape our inclusion criteria (Green & Higgins 2005; Moher *et al.* 2009). Articles had to be original research from a natural system published in the primary literature (Population). The article had to clearly state a measured impact from one or more invasive species (Intervention). We did not constrain study design, and thus included experimental, observational, and impact–

control research protocols (Control). For an article to be included, authors had to quantify impacts for an invasive species (i.e., no qualitative assessments of impact; Outcome). We excluded articles that quantified the impact of invasive species on other invasives. We did not restrict study location or taxon as part of screening.

During screening, we checked for consistency with inclusion criteria following steps recommended by *Preferred Reporting Items for Systematic Reviews and Meta-Analysis* (PRISMA) (Moher *et al.* 2009). Owing to the large number of candidate studies, we performed screening in three steps. In the initial step, we checked for consistency with criteria by reading all titles. In the second step, we checked for consistency with all abstracts. In the third screening step, we downloaded and read the full text of remaining candidate articles (N = 1,935). Based on this reading, we decided on their disposition (include or exclude). After the final screening step, we were left with 1,507 articles that we included in our systematic review (Appendix S3). Within this final set of articles, there was a general pattern of increasing publications on invasive species impacts through time, 1999-2016 (Appendix S4).

Data extraction

We used a data form to extract 13 pieces of information pertaining to our hypothesized publication biases (Table 2). We piloted extraction procedures using 10% of the articles after the third screening step (N = 190). One researcher (RCO) was responsible for data extraction. One article could contribute one or more records of invasive species' impact to the database if the authors reported on the ecological effects of more than one species.

One article could also contribute additional case studies if impacts were measured in multiple ecosystems, spatial scales, or countries.

We extracted data on the ecological effects that researchers measured and reported in their articles. We categorized ecological effects into 11 types based on schemes published in previous meta-analyses and reviews on invasive species impacts (Manchester & Bullock 2000; Vilà *et al.* 2011; Lockwood *et al.* 2013). We did not include the related and large literature on socioeconomic effects of invasive species (Pimentel *et al.* 2000; Reaser *et al.* 2007) as these impacts are inherently confounded with human perceptions of value (Ricciardi *et al.* 2013).

Each measured ecological effect can be directly linked to one of five biological scales (genetic, individual, population, community, or ecosystem; Table 1) (Lockwood *et al.* 2013). For example, the ecological effect of hybridization occurs at the genetic scale and ecological effects on diversity occur at the community scale. We developed the linkages between ecological effects and biological scales using classifications provided in previous reviews of invasive species impacts (Vilà *et al.* 2011; Lockwood *et al.* 2013). After we identified each measured ecological effect, we associated the effect with a biological scale. Indirect ecological effects and our “other” category within ecological effects could be linked to all biological scales.

We characterized the temporal scale associated with each recorded impact using four forms of information (Table 2). First, to estimate the length of typical research programs on invasive species impacts, we subtracted the year measurements were first taken in a study from the year that the measurements ended, whenever information was provided by article authors. Second, we recorded the year the invasive species was first

recorded in the country where the study occurred. Third, to document how study design dictated the temporal scale of inference, we estimated how often measurements of impact were recorded, as indicated by the authors. Finally, we recorded the frequency of re-visitation and space-for-time designs employed as these methods can provide a chronosequence of impacts without the infrastructure and funding necessary for long-term research; but it is unknown how often they are implemented in invasion ecology (Thomaz *et al.* 2012).

We recorded the spatial scale of each case study (e.g. lab-based, local, regional, country, global) as indicated by article authors. In general, local research included a small number of measurements from one or several plots. Regional studies typically spanned hundreds of kilometers and crossed multiple state borders (e.g., Pacific lionfish (*Pterois volitans*) impacts along the southeastern coast of the US (Ballew *et al.* 2016)). Research at the country scale measured impacts across the entire range of an invasive species within the country. Global studies aggregated data on impacts from at least two countries. We acknowledge that for higher-order spatial classifications (e.g., country or global), our scheme does not explicitly indicate how measurements were aggregated for analysis, if at all. For example, data collected for a country-wide study could be analyzed as isolated local populations and then compared (Severns & Breed 2014) or data could be aggregated across an entire country (Newson *et al.* 2011). Because of this limitation, we focus our analysis on the frequency of research at different spatial scales rather than the conclusions drawn from their analytical methods. Finally, we recorded the country where the study occurred. If research took place in a lab, we identified the country that contained the study system researchers aimed to replicate with their lab protocols.

We recorded common name, scientific name, and broad taxonomic group for each invasive species using the categorizations developed by Pyšek *et al.*, (2008). We used a Mann Whitney U-test to compare the taxonomic distribution of publications in our database to the distribution found in three other large systematic reviews that explored invasive species impact magnitude, first reports, and online databases (Seebens *et al.* 2017; Turbelin *et al.* 2017; Nentwig *et al.* 2018). We recorded the focal ecosystems of each article based on site descriptions by article authors, categorizing them based on Lowry *et al.*, (2012) with some modification when considering marine habitats. We refined their ‘marine’ ecosystem category into three groups where ‘ocean’ referred to studies in the open ocean, ‘intertidal’ to studies focused within near-shore marine waters and ‘coastal’ to near-shore terrestrial ecosystems (Table 2).

Analysis of interacting biases

We evaluated whether publication biases in ecological effects interacted with publication biases in taxon, ecosystem, temporal, and spatial scales. To do so, we used a Pearson chi-squared test of proportions to compare the overall proportion of case studies that investigated the array of ecological effects to the proportion of case studies when divided by taxa, ecosystem, temporal, or spatial scales (Ballew *et al.* 2016). For example, after we identified overall proportions of ecological effects represented among all case studies, we then explored whether the proportions of ecological effects from all case studies were consistent across taxonomic subcategories. The chi-squared test provided observed and expected case study counts for each taxonomic subcategory (e.g., herbaceous plants, fish, mosses). We show deviations from observed and expected case study counts using ΔN .

Negative values of ΔN mean that the focal taxon (or ecosystem, temporal, or spatial scale) recorded fewer case studies for an ecological effect than expected based on proportions identified across all case studies, and vice versa for positive values of ΔN . When sample sizes were small within subcategories, we estimated p -values using Monte-Carlo simulation (2,000 replicates) to avoid inflated Type I error rates. Significant p -values indicated that proportions within subcategories differed from the overall proportion more than expected by chance. We made multiple comparisons among subcategories, and this potentially increased the probability of committing a Type I error. We used a Bonferroni correction to set more conservative p -values and limit our chances of detecting false positives (Bancroft *et al.* 2007; Koricheva *et al.* 2013).

RESULTS

Ecological effect and biological scale measurement

Across the 2,293 case studies, the biological scale at which ecological effects were measured is heavily skewed toward the community ($N = 643$) and population levels ($N = 1,047$) (Figure 1a). Published information on impacts measured at the individual or genetic biological scale are comparatively very uncommon (Figure 1a). This publication bias in biological scale translates into a similar skew in the underlying ecological effects documented, with the vast majority of case studies measuring diversity, abundance, or fitness impacts and hybridization and habitat change rarely documented (Figure 1a).

We found that the most frequently measured ecological effects varied significantly across major taxonomic groups when compared to the ecological effects measured most often across all case studies (Figure 1b). For example, invasive mollusks'

effects on diversity were studied less often than expected ($\Delta N = -12$), and fitness impacts were studied more often ($\Delta N = +11$) ($\chi^2 = 41.08$, $df = 10$, $N = 162$, $p < 0.001$). The opposite trend was found for herbaceous plants. For plants, diversity impacts were studied more frequently than expected, and fitness impacts were studied less often ($\Delta N = +51$ and $\Delta N = -48$, respectively; $\chi^2 = 106.94$, $df = 10$, $N = 304$, $p < 0.001$). For most major taxonomic subgroups, authors measured ecological effects unequally across subgroups (Figure 1b).

Temporal scale bias

We found a strong bias toward short-duration research (< 1 year) within the invasive species impact literature (Figure 2). Furthermore, we show that some ecological effects are measured at even shorter timescales than predicted from all case studies. The ecological effects that were recorded at even shorter durations than expected were behavioral ($\chi^2 = 24.02$, $df = 4$, $N = 125$, $p < 0.001$), hybridization ($\chi^2 = 33.96$, $df = 4$, $N = 55$, $p < 0.001$), and nutrient availability ($\chi^2 = 28.99$, $df = 4$, $N = 227$, $p < 0.001$).

A majority of articles (52%) did not report the year that the non-native species was first introduced to the focal country. We also found that half (50%) of impact effect sizes were based on measurements taken within a single sampling event, or were derived from measurements taken across multiple sampling events in a single year (30%). Just under 20% of all impact measurements were based on samples taken over multiple time periods equal to or exceeding a year. Most case studies had a control/impact sampling design (72%) followed by observational studies (16%) and before-after-control-impact

designs (4%). Some of the least implemented designs were re-visitation (2%) and space-for-time substitution (1%).

Spatial scale bias

We found that most impact measurements were recorded at the local scale (77%) followed by lab research (16%). Impacts recorded at the regional scale occurred much less frequently (5%), with global and country-wide studies being extremely rare (1% and 0.4%, respectively). We also found that, at global scales, nutrient availability and abundance effects garnered significantly less research than predicted by the proportions of ecological effects identified across all case studies ($\Delta N = -3$ and $\Delta N = -3$, respectively; $\chi^2 = 68.91$, $df = 10$, $N = 26$, $p < 0.001$). At local scales, fitness and growth received significantly less impact research than expected based on ecological effect proportions identified across all case studies ($\Delta N = -54$ and $\Delta N = -22$, respectively; $\chi^2 = 37.97$, $df = 10$, $N = 1773$, $p < 0.001$).

Geographical bias

We found substantial evidence for geographical publication bias across the 93 countries represented in our database (Figure 3a). The country with the greatest number of published invasive species' impact measurements was the United States ($N = 840$) followed by Australia ($N = 223$), Canada ($N = 121$), and Spain ($N = 100$). Nearly half of the countries in our database had only 1 or 2 invasive species' impacts published within their borders (41%). It is possible that these geographical publication biases are warranted if they align with countries where invasion-implicated extinctions are

happening. A review of the IUCN database on extinctions showed that most extinctions attributed (at least in part) to invasive species occurred on Australia, New Zealand, and Micronesia (Bellard *et al.* 2016). North America ranks 9th in frequency of species extinction due to invasive species' impacts, yet it appears most often in our impacts publication database. Australia is the only location that simultaneously experiences high native species extinctions due to invasive species' impacts and has a large number of impact case studies in our literature base.

Taxonomic bias

We identified a total of 574 invasive species as having at least one ecological impact measured within at least one publication, with herbaceous plants, trees, and fish dominating the list. The least represented taxa were mosses, fungi, forest pathogens, and bacteria (Figure 3b). At the species-level, few of the 574 invasive species in our database were studied multiple times, and the vast majority only appeared within one or two publications (Figure 4a). The right-skewed distribution of invasive species that is evident in our literature base highlights a strong bias at the species level.

To capture this bias, we compiled a 'Top 10' list of the most frequently studied species (Figure 4b). The most studied species in our database were the cane toad (*Rhinella marina*, N = 50), signal crayfish (*Pacifastacus leniusculus*, N = 40), and red swamp crayfish (*Procambarus clarkia*, N = 39). The species that comprise our Top 10 list from 1999-2016 have not always been the most frequently studied. For example, the cane toad was not part of the Top 10 from 1999-2004 but is so now (Appendix S5). The only species that has remained in the Top 10 from 1999-2016 is rainbow trout

(*Oncorhynchus mykiss*). Of the species where impacts were recorded across multiple studies through time, most decreased in frequency of attention, such as was the case for crested wheatgrass (*Agropyron cristatum*; Figure 4c). A lesser number have had impacts recorded across publications consistently through time such as with the zebra mussel (*Dreissena polymorpha*; Figure 4c). We found that ecological impacts of red swamp crayfish were recorded with increasing frequency across publications in recent years, whereas cane toads increased in frequency for much of the early years but the rate of publication has leveled in recent years.

We investigated how often ecological impacts were studied across multiple biological scales within our Top 10 list of species. As was true overall, population impacts were the most frequently published while genetic and ecosystem level impacts were infrequently published (Figure 4d). Only rainbow trout had their impacts recorded across all five of our biological scales. All other species that comprise our Top 10 list were studied across only three or four biological scales. For example, published cane toad impacts were measured at four biological scales, but we found no studies where their ecosystem impacts have been explicitly recorded and published.

Finally, the species that comprise our own Top 10 list do not match well with other assessments documenting the species most commonly established as non-natives globally, or of the ‘worst’ invasive species in terms of their impacts. Our Top 10 list shared no species in common with Turbelin *et al.*’s (2017) list of the most frequent global invaders. Seebens *et al.* (2017) recorded the number of first records of non-native species globally (1800 to 2014) finding 5,126 first records of invasive insect species, and only 480 crustacean first records. Crustaceans are the taxa represented most often in our Top

10 list. Within Europe, a recently updated list of the 100 worst invaders (Nentwig *et al.* 2018), shares only one species (red-swamp crayfish) with our list. However, when we grouped species into broader taxonomic units, we found that the broad taxonomic distribution in our database generally matched the taxonomic distribution found in lists of the most impactful species, reports of first records, and online databases.

Ecosystem bias

We found that invasive species impacts were most often recorded within forest, lotic, and island ecosystems (N = 440, 349, 265, respectively). In contrast, impacts were seldom recorded within desert (N = 24) or mountain (N = 23) ecosystems. When we explored the interaction between focal ecosystem and the ecological effects that are investigated, we found that, across almost every ecosystem, publication bias was equally strong toward research on diversity and fitness impacts. For example, in forests and lotic ecosystems, diversity and fitness are studied far more than other impacts (Forest: N = 113 and 94, respectively, Lotic: N = 88 and 81; Figure 5). However, in grassland ecosystems, the number of case studies on impacts of invasive plants on native species' fitness was lower than expected ($\Delta N = -26$; $\chi^2 = 48.90$, $df = 10$, $N = 242$, $p < 0.001$). In intertidal ecosystems, there were significantly more studies on fitness impacts than expected ($\Delta N = +14$; $\chi^2 = 35.19$, $df = 10$, $N = 128$, $p < 0.001$). Some combinations of ecosystem and ecological effects received no research (Figure 5). For example, there were no studies examining how invasive species might impact the genetic make-up of co-occurring native species within desert ecosystems.

DISCUSSION

The ecological impacts of invasive species can be substantial, and the growing rate at which species are introduced ensures that ecologists will continue to be confronted with questions about how these impacts occur and what may be done to predict and manage them (Ricciardi & Ryan 2018). It is only recently, however, that invasive species' impacts have been formalized in terms of definition, hypotheses, and measurement schemes (e.g., Jeschke *et al.* 2014). The related spate of published meta-analyses of invasive species' impacts all have had a relatively narrow taxonomic or locational focus (e.g., terrestrial plants (Vilà *et al.* 2011; Hulme *et al.* 2013); seaweeds (Tamburello *et al.* 2015); invasives in Europe (Nentwig *et al.* 2018)), likely reflecting the difficulty in covering the now immense volume of evidence accumulated over decades of research interest (e.g., van Wilgen *et al.* 2018). Nevertheless, it is only through a comprehensive accounting of this evidence base that one can identify gaps in knowledge that transcend taxonomic groups and permit a deep exploration of interactions between publication biases. Here we find evidence for field-wide knowledge gaps on invasive species' impacts that, if left unaddressed, can handicap progression toward comprehensive impact theories, hypotheses filtering, and production of better risk predictions.

We show that the biological scale at which invasive species impacts are measured is heavily weighted toward population and community levels no matter the geographical location or biological realm into which the invasive species exists, or its taxonomic affiliation. Our results suggest that there is a particular deficiency in knowledge related to impacts promulgated at the individual and genetic levels. We acknowledge that technological advances have led to a recent burgeoning of hybridization impact research

(Martin-Albarracin *et al.* 2015; Lavoie 2017; Mallet 2018) which we did not capture here possibly due to limitations presented by our search terms. Despite the recent increase of research on genetic impacts, we found that over decades of research studies tended to focus on community and population effects and this may be warranted given that previous meta-research indicates that invasive species can drive native species toward extinction and lead to decreases in native species fitness (Vilà *et al.* 2011; Jauni & Ramula 2015; Mollot *et al.* 2017). Similarly, certain ecological effects may rightly dominate publications within taxonomic groups because these taxa cause large and specific impacts (e.g., buff-tailed bumblebees, *Bombus terrestris*, interfering with pollination networks (Morales *et al.* 2013)). For this reason, it may not be fruitful to study every species across all ecological effect types or all biological scales. However, it seems unlikely that community and population level impacts are more common than individual or ecosystem impacts in nature. This skew in research effort is certainly mirrored in, or is mirroring, the preponderance of existing impact hypotheses that invoke population or community ecology theories (Ricciardi *et al.* 2013). Indeed, our results identify a species-level effect bias for even the best studied species, suggesting that, despite decades of research, we are still a long way from fully documenting how and which ecological impacts propagate across biological scales and how ecological effects may be inter-related.

Possibly the most data-poor area within invasion ecology relates to how invasive species impacts change over time (Strayer *et al.* 2006). We show that fully two-thirds of published research measured impacts over a year or less, and half of all published work failed to indicate when their measurements were taken relative to time since initial

establishment of the focal invasive species. These deficiencies occur across all taxa, biological realms, and geographical locations of research. The absence of even moderately long-term impact studies is concerning given that the invasive species' abundance, and the native species it interacts with, will vary through time; sometimes dramatically so (e.g., lags and collapses; Aagaard & Lockwood 2016; Strayer *et al.* 2017). Long-term ecological research is difficult to fund and sustain, which is surely a central reason why this publication bias exists. We found that space-for-time substitution and re-visitation research designs are vastly underused, however, despite their ability to make important additions to the understanding of how impacts change over time.

By exploring the interaction between temporal and ecological effect biases, we found that no ecological effects had more long-term studies than we predicted from the overall trend. However, hybridization, behavioral, and nutrient availability effects were even more heavily skewed toward short-term research than may be expected. This interacting bias of timescale and ecological effect suggests that either there are *a priori* often unstated reasons that these three ecological effects should be more pronounced within, or restricted to, short timescales, or that their longer timescale effects have simply been ignored. Overall, our results suggest that invasion scientists are not yet capable of comprehensively describing how ecological impacts change over time for even a single ecological effect (D'Antonio & Flory 2017; Strayer *et al.* 2017).

We show that two-thirds of all invasive species impact research occurs at local spatial scales as identified by article authors, with few studies conducted at regional or global scales. Very little research has analyzed how invasive species impacts change when the spatial scale of research moves from fine to broad (c.f., Powell *et al.* 2011). Our

systematic review suggests that nearly every ecological effect will benefit from investigation at broader spatial scales. With such research investment comes a stronger understanding of how tightly impact magnitude is tied to the spatial scale of research (Guerin *et al.* 2018). The current informational base of invasion ecology is so strongly biased toward fine spatial scale research that the field lacks the empirical evidence to create a robust predictive impact framework that accounts for spatial scale dependency.

That the invasion literature has a pronounced geographic and taxonomic bias is well documented (Pyšek *et al.* 2008), and not surprisingly, we find such biases in the subset of literature focused on measuring ecological impacts. We found a small number of studies on invasive pathogens, and highlight this as a potential limitation posed by search terms that did not adequately capture research in disease ecology (Anderson *et al.* 2004; Wikelski *et al.* 2004; Crawl *et al.* 2008). The degree to which these publication biases influence efforts to formalize an impact theory or create efficient policy depends on whether the locations most at risk, and the more impactful species, are the subject of most research. We show that neither condition is generally true. Our Top 10 most studied species are not regularly listed among the world's most widespread or 'worst', nor are the locations where most impacts are researched the locations that are known to be quite vulnerable to invasive species impacts. The exception may be mammals introduced to islands, and the large number of impact case studies centered in Australia; both of which have received considerable attention according to our review, and based on other evaluations, warrant this attention.

Another possibility is that the species in our Top 10 most-studied list, or those studied within North America, Europe, and Australia, may be considered 'models' that

can inform theory development and policy approaches. The extent to which this may be the case depends on whether these species have truly generalizable impacts, rather than simply being frequently studied species within funding-rich countries that have idiosyncratic effects and impact mechanisms. We suggest that ecologists must consider carefully whether geographical and taxonomic publication bias is helping or hindering the generation of a general understanding of invasive species' impacts.

Related, we show that most species appear in our impacts database only once or twice (Hulme *et al.* 2013). One-off species case studies can be misleading since, in general, the earliest published effect sizes on a subject are overinflated (the Proteus phenomenon) (Ioannidis & Trikalinos 2005). Thus, replicate studies on a topic may be necessary before the effect size under investigation settles to a more accurate (and often lower) estimate. Of course, scientific replication is costly and incentivized much less than novel experiments or information on newly invasive species (Ioannidis & Khoury 2014). However, a lack of replication within species can be perilous in invasion science if policy, risk analysis, or land management regimens are based on single case study evidence (Ioannidis 2005). Nevertheless, there is an argument to be made that spreading research effort across a wide variety of species is justified as each species brings new information relative to the context in which they have become invasive. As the rate of non-native species establishment continues to accelerate across most taxonomic groups (Essl *et al.* 2011), a legitimate question is how fast we can expect research effort and funding to expand in response and whether such an expansion is necessary for production of conceptual models, risk assessments or hypothesis filtering.

Few systematic reviews have been comprehensive enough to highlight the stark ecosystem bias in invasion ecology we document here. We found that nearly half of the impact research to date is conducted within forests, on islands, and within lotic ecosystems. These ecosystems are known invasion hotspots largely because for centuries they have housed large human population centers (forests), or have been subjected to purposeful species introduction efforts (lotic and island ecosystems) (Fuller 2003; Cucherousset & Olden 2011; Turbelin *et al.* 2017). However, as the human footprint expands into a wide variety of ecosystems (deserts, mountains, arctic), then the prevalence of invasive species in even geographically remote and environmentally harsh ecosystems also expands (Dean *et al.* 2002; Chown *et al.* 2012; Pauchard *et al.* 2016). There is certainly good reason to expect that invasive species' impacts in deserts, for example, will be different than those observed in lakes or forests (e.g., Vilà *et al.* 2011; Hirsch *et al.* 2016; Schirmel *et al.* 2016). The near total lack of information on invasive species in these ecosystems therefore deprives the field of needed ecological context surrounding impacts.

Related, the ecosystems that we show as severely under-documented in terms of invasive species impacts have considerable ecological value, with several receiving designation as world heritage sites or are considered biodiversity hotspots (Goudie & Seely 2011; Critical Ecosystem Partnership Fund 2018). Isolated desert and mountain ecosystems, for example, are the mainland analogs to island communities, and they may be equally vulnerable to invasive species impacts (Pyšek *et al.* 2017; Pauchard *et al.* 2018). However, due to a lack of research in these ecosystems, it is not yet clear how often endemic species in desert or mountain ecosystems encounter invasive species. As

invasive species appear in a wider variety of ecosystems, our results show there is a clear need for more evidence on how endemics that occupy island-like niches in desert and mountain ecosystems will respond to increased pressure by invasive species.

A comprehensive and unbiased base of published scientific evidence on invasive species impact is a necessary prerequisite to the creation of a theoretical framework, assessing the universality of mechanistic hypotheses, and providing accurate risk analyses (van Wilgen *et al.* 2018). Without this knowledge base, invasive species impacts can appear so complex that efforts to reach broader conclusions are discouraged (Courchamp *et al.* 2017; Cassey *et al.* 2018). Our results, combined with other more circumscribed data synthesis efforts, provide compelling evidence that there are substantial gaps in the evidence base for invasive species ecological impacts. Some of these gaps are relatively straight-forward to fill, albeit this will require a shift or expansion in commitment of resources (e.g., toward longer temporal and broader spatial scale research). Other gaps represent knowledge-based tensions that we suggest require explicit debate within the field so that a balance may be struck between the need for replication within ecosystems and taxa, and the need to expand our understanding of the context dependency of invasion impacts.

ACKNOWLEDGMENTS

We thank D. Simberloff, M. Meixler, J. Wiedenmann, M. Allen, J. Brown, A. Safiq, O. Stringham, R. Valentin, and J. Sadowski for helpful discussions and/or comments.

Funding statement: R.C.O was funded by a Rutgers University Ecology and Evolution grant.

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TABLES AND FIGURES

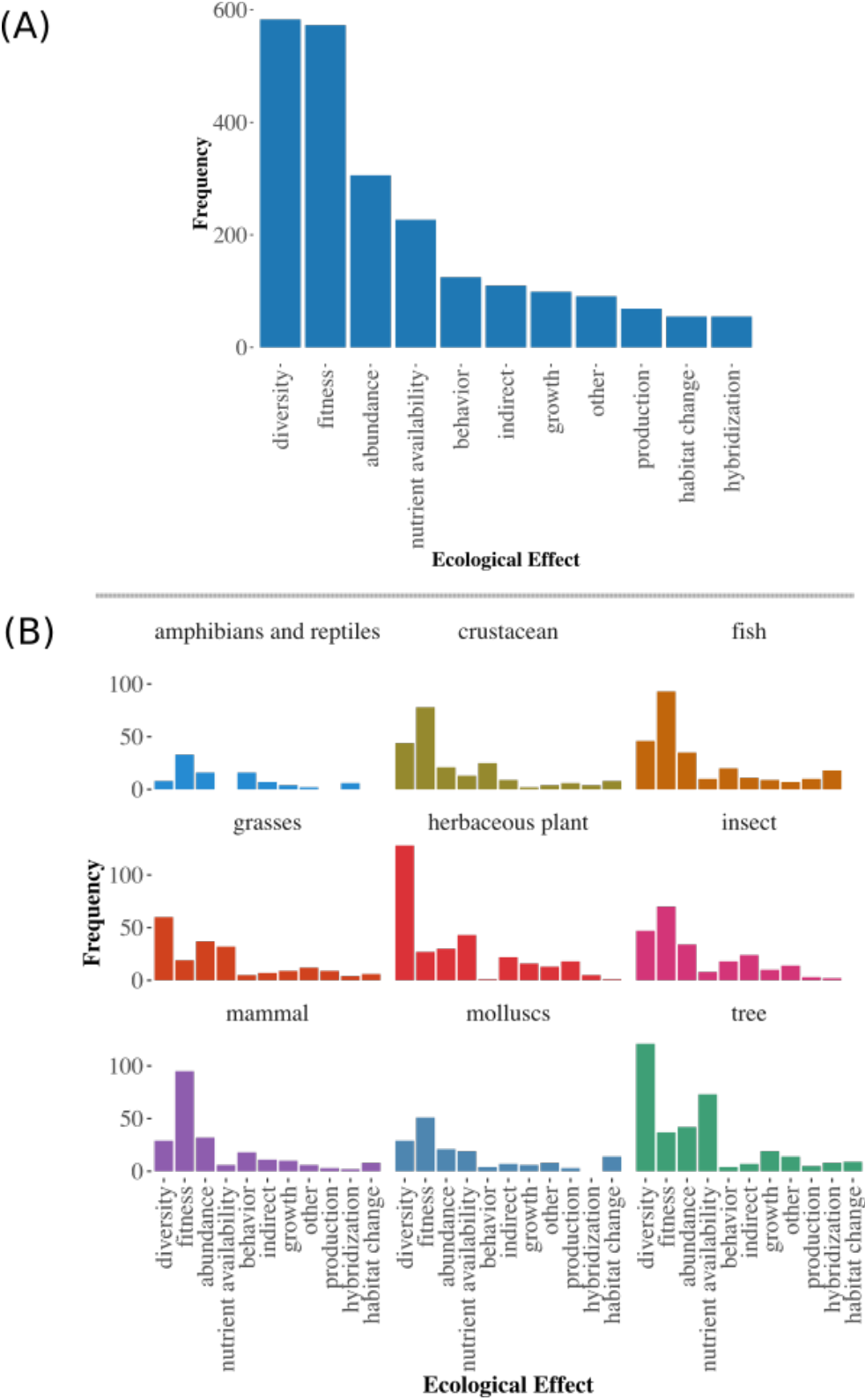


Figure 1

(A) Frequency of ecological effects studied in the invasion impacts literature. Each article in this review could contribute more than one case study to our analyses if researchers measured multiple ecological effects ($N = 2,293$). The x-axis lists different ecological effects that were the focus of case studies. (B) We explored the interaction of publication biases in ecological effects and taxonomic groups. In this figure, we show taxa whose distribution of case studies in ecological effects significantly differed from the distribution predicted across all case studies.

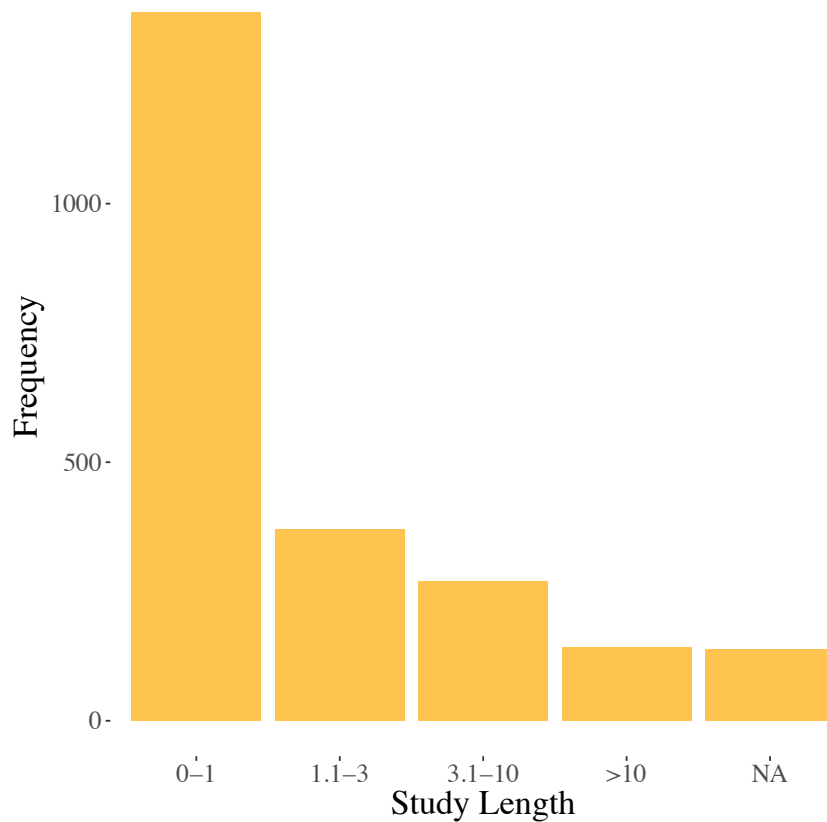
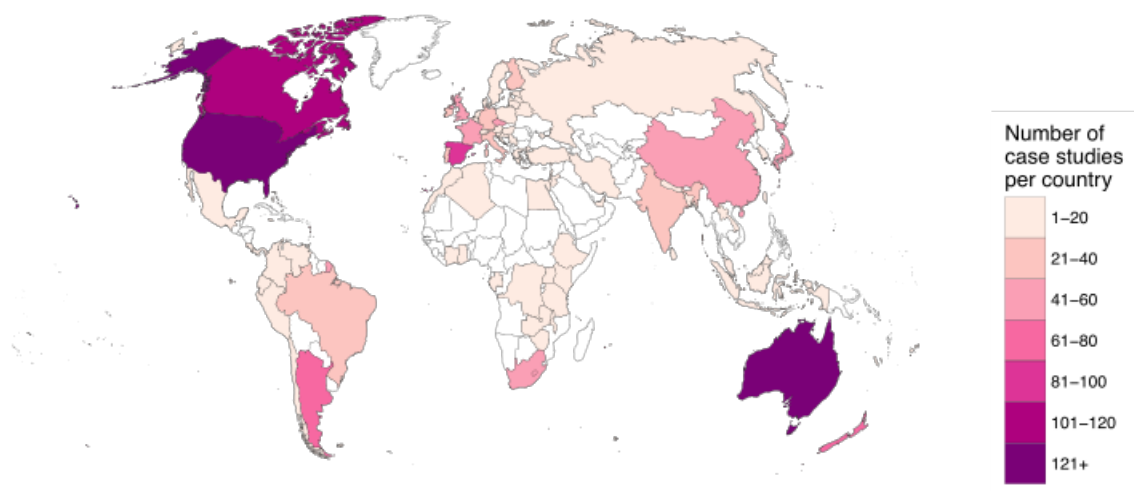


Figure 2

Length of case studies measuring invasive species impacts. We calculated study length by subtracting the year the first measurements were taken from the year the study ended. In this figure, NA represents studies for which researchers did not provide a start and/or end date.

(A)



(B)

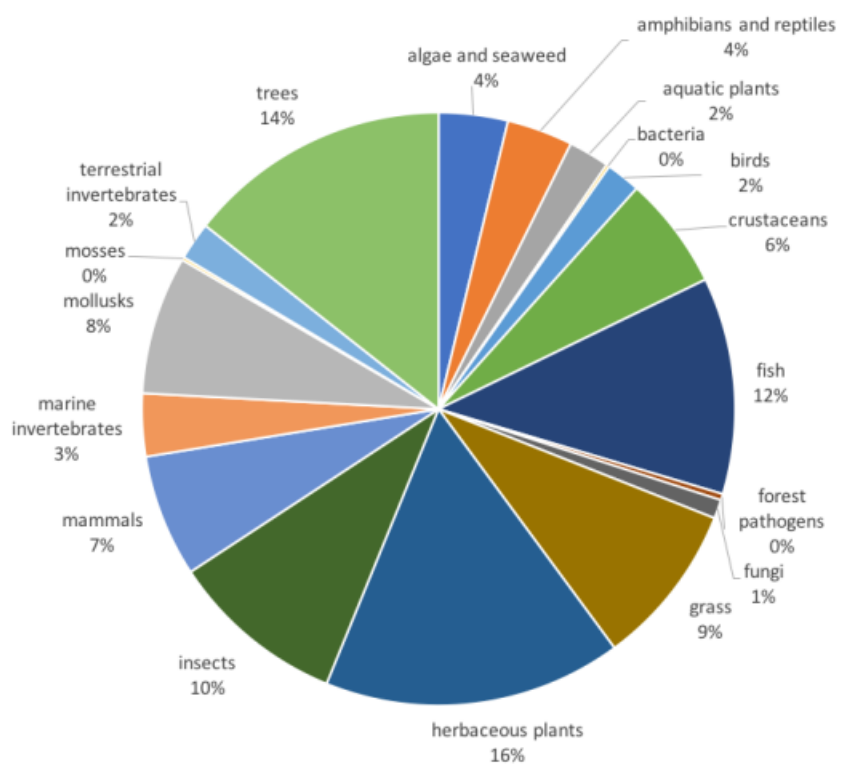


Figure 3

(A) Geographic publication bias in the invasive species impact literature from 1999-2016.

Darker colors indicate a greater number of case studies attributed to a country. We extracted country-level data from each case study and matched the country with a corresponding International Organization for Standardization (ISO) country code. There are no ISO codes for waters, so we selected corresponding countries based on the closest or associated country reported by the researchers (e.g., research that happened in Ugandan portion of Lake Victoria). (B) Taxonomic bias in invasion impacts literature. We standardized taxonomic categories to a previous invasion ecology systematic review (Pyšek *et al.* 2008). This figure includes only unique occurrences of each species in our database of relevant case studies (i.e., each species counted only once; N = 574).

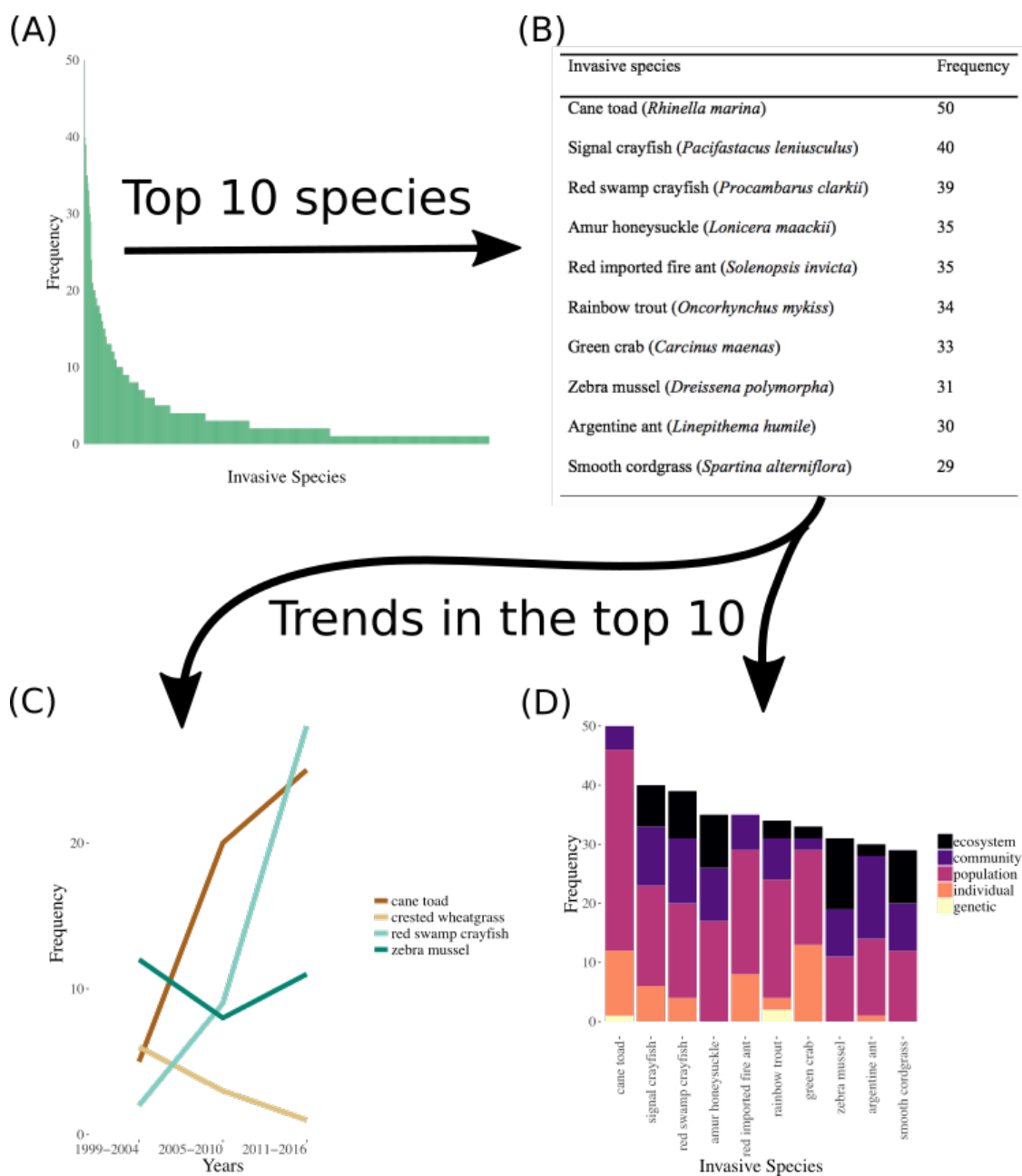


Figure 4

(A) The frequency distribution of all invasive species that were the subject of case studies from 1999-2016. This figure contains one bar for each of the 574 invasive species included in our systematic review. The height of each bar corresponds to the number of

case studies attributed to each species ($N = 2,293$ case studies). (B) The top 10 invasive species studied from 1999-2016. We recorded the number of times each invasive species was the focus of a case study. (C) When invasive species are the focus of multiple case studies, how often they are studied each year changes over time. Each line represents one of four frequently studied invasive species. The lines also depict four possible trajectories of invasive species research intensity over time. For ease of visualizing, we binned all case studied into 6-year increments. Over 18 years, some invasive species: (1) declined in frequency of study, (2) remained relatively constant, (3) leveled off at a high number of studies, and (4) continued to increase. (D) We examined the Top 10 invasive species and asked whether any species had been studied across all 5 biological scales: genetic, individual, population, community, and ecosystem. Each bar represents one of the top 10 most frequently studied invasive species. The height of each bar indicates how many case studies focus on the species. Each bar is divided by biological scales. Only rainbow trout were studied across all 5 biological scales.

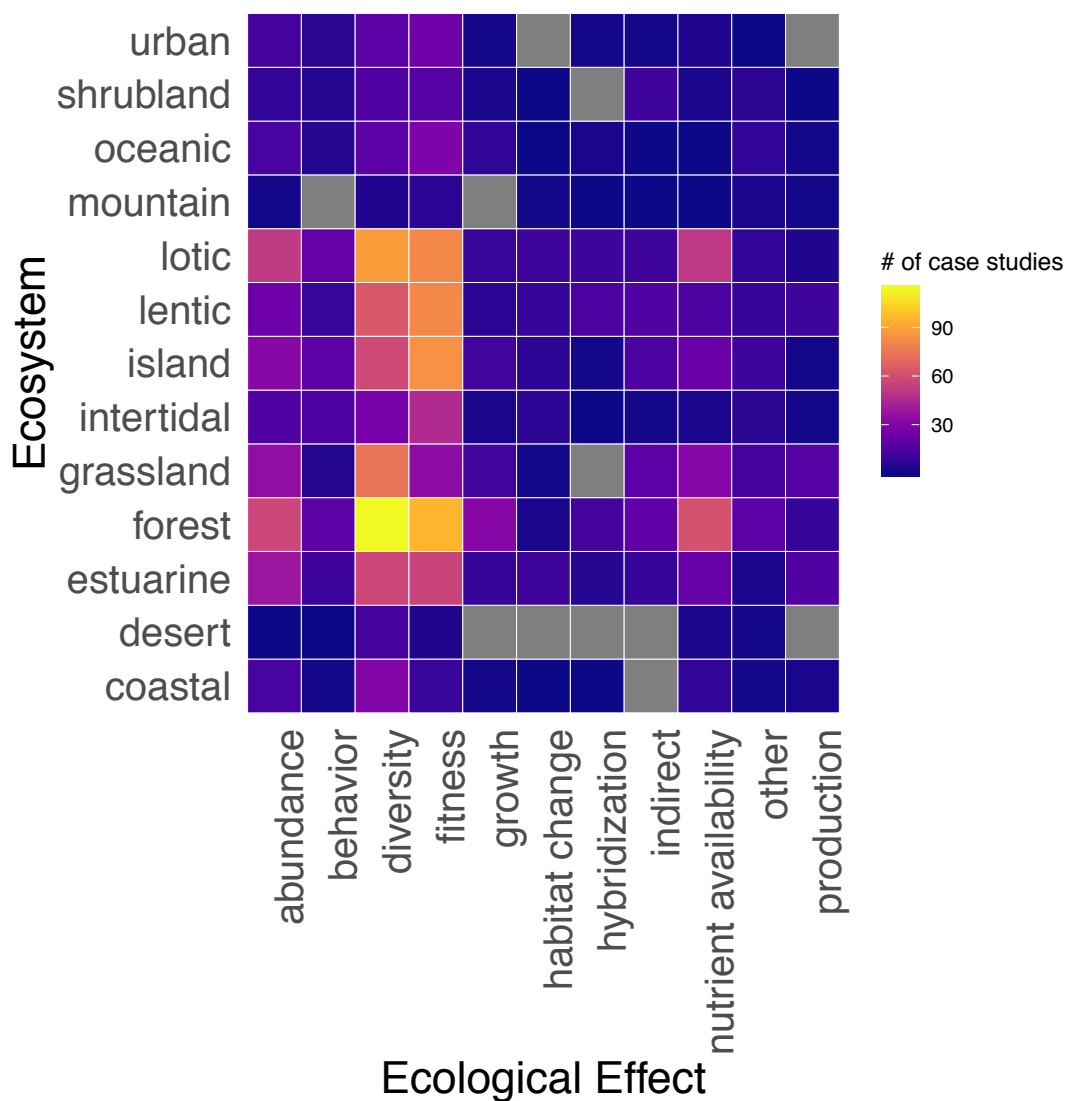


Figure 5

This heatmap shows the number of case studies that explored combinations of ecosystem and ecological effects. Warmer colors indicate that a greater number of case studies have been focused on the paired ecosystem and ecological effect. Cooler colors indicate a low number of case studies on combinations of impact and ecosystem. Gray blocks show where our systematic review identified no research on combinations of ecological effects and ecosystems.

Table 1

We show how ecological effects are linked to broader biological scales. We created this classification scheme from previously published reviews on invasive species impacts (Vilà *et al.* 2011; Lockwood *et al.* 2013). Two ecological effects, “indirect effects” and “other”, could be associated with all biological scales.

Biological scale	Ecological impact
Genetic	Hybridization
Individual	Behavior, growth
Population	Abundance, fitness
Community	Diversity
Ecosystem	Nutrient availability, habitat change, production

Table 2

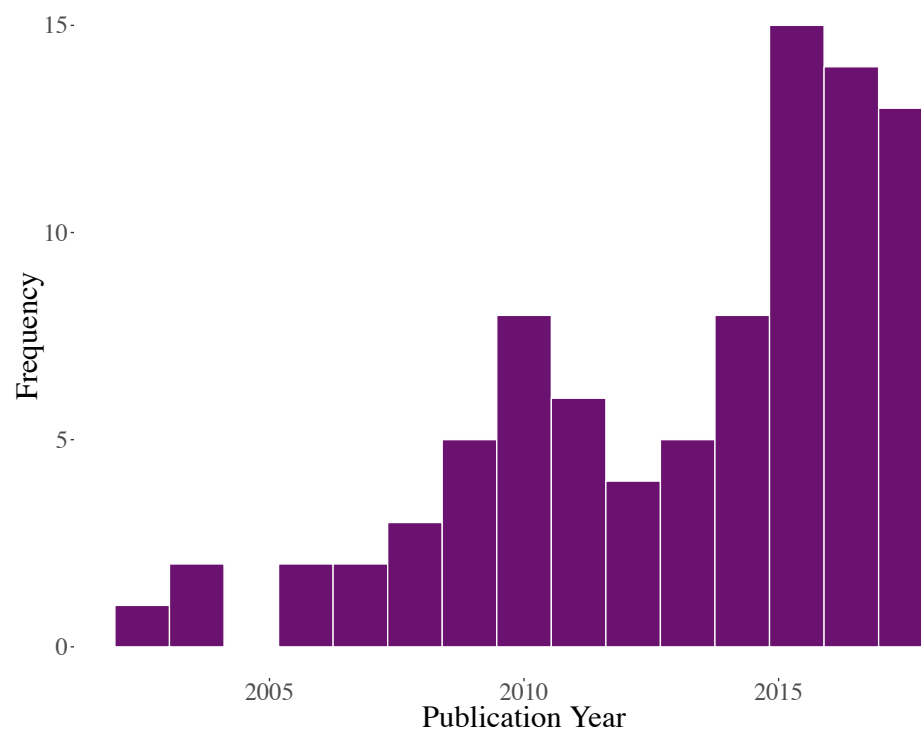
We provide the categories and definitions for data extracted from case studies included in this systematic review. When we constrained input for categories, we listed all potential subcategories. Several of the subcategories were based on previous systematic reviews in related fields, and in these instances, we provide relevant references.

Bias Assessed	Category	Description and subcategories
	Unique study code	#####-Lastname-Year
	Publication year	Publication year
Impacts	Biological scale	Genetic, individual, population, community, ecosystem (Lockwood <i>et al.</i> 2013)
	Ecological effect	Abundance, behavior, diversity, fitness, growth, habitat change, hybridization, indirect, nutrient availability, other, production (Manchester & Bullock 2000; Vilà <i>et al.</i> 2011; Lockwood <i>et al.</i> 2013)
Temporal	Study length	Year study ended – year study began
	Sampling frequency	Once, annual, less than annual, more than annual

	Study design	Observation, Before-After, Control-Impact, Before-After-Control-Impact, space-for-time, re-visitation
Spatial	Spatial scale	Lab, local, regional, country, global (as indicated by article authors)
Geographical	Country	Name of country where study system is located. If study is a lab experiment, include the country that lab is replicating.
Taxonomic	Common name	Invasive species common name
	Latin name	Invasive species Latin name
	Taxa	Invasive species taxa. Algae and seaweed, amphibian and reptile, aquatic plant, bird, crustacean, fish, forest pathogen, fungi, grasses, herbaceous plant, insect, mammal, marine invert, mollusks, terrestrial invert, tree Expanded from (Pyšek <i>et al.</i> 2008)
Ecosystem	Ecosystem	Ecosystem where research occurred.

Ocean, forest, grassland, desert, lotic,
lentic, estuarine, island, coastal,
shrubland, mountain, urban, intertidal
Expanded from (Lowry *et al.* 2012)

APPENDICES



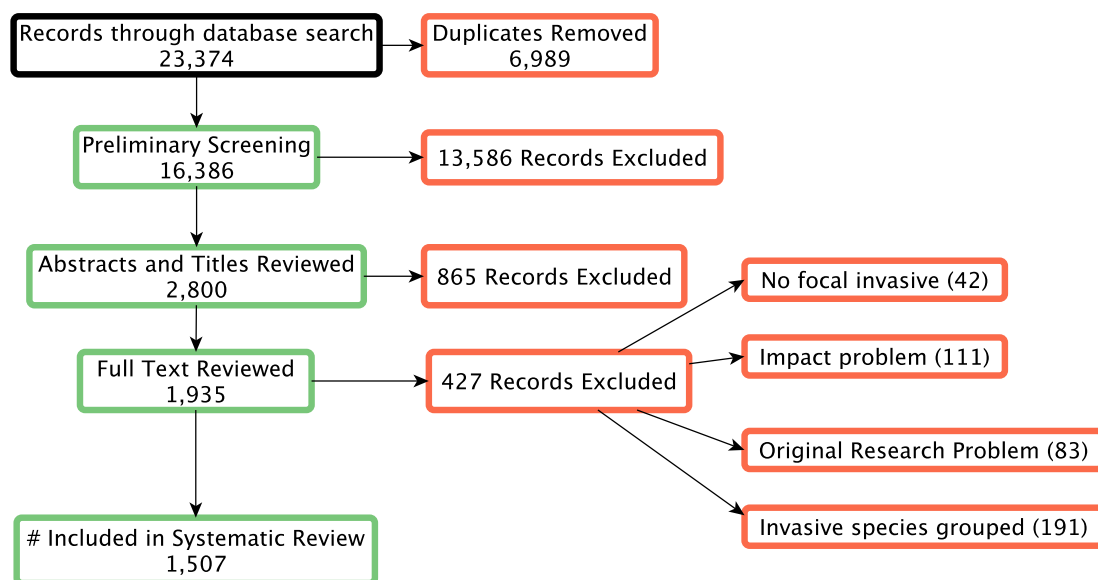
Appendix S1

We compiled a comprehensive database containing meta-analyses on invasive species impacts. To assemble the database, we searched Web of Science from 1999-2017. We used the same set of search terms outlined in the methods section of this manuscript but substituted the word “meta-analysis” for “impact.” We added the search string “invasion ecology AND meta-analysis”. The first meta-analyses on invasive species impacts appeared in the early 2000s. From 1999-2017 there were 90 meta-analyses on invasive species impacts. After a small number of initial evidence synthesis publications, the number of meta-analyses on impacts has risen over time.

Appendix S2

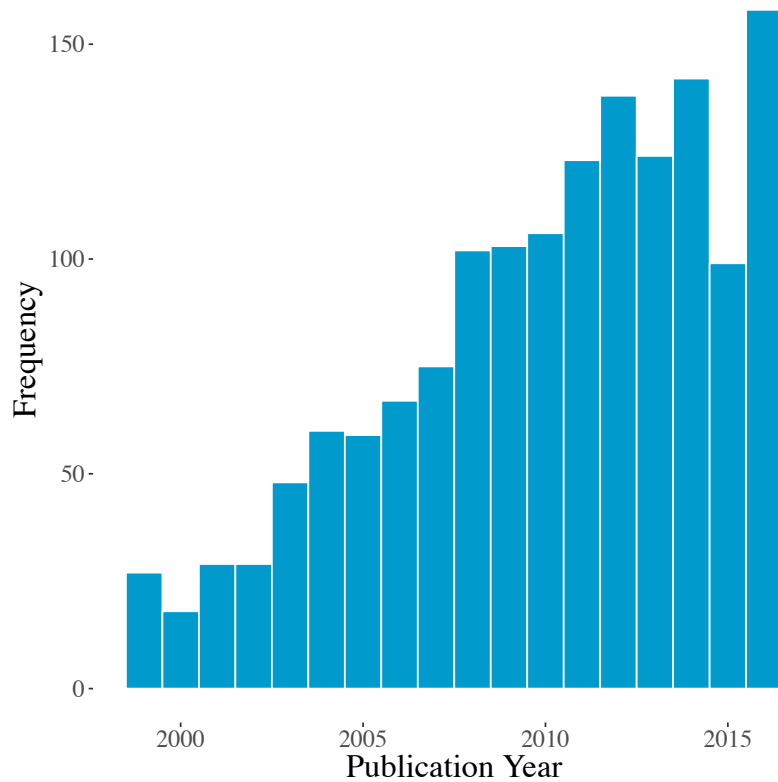
Inclusion criteria for this systematic review. We defined inclusion criteria prior to beginning the systematic review. Once the criteria were developed, we used them during all three screening steps. We compared each article against the criteria to justify inclusion or exclusion.

Criteria	Rationale
Original research from natural systems (Population)	Exclude reviews, meta-analyses, and other forms of research synthesis Exclude research in artificial environments Include mesocosms if there is natural system analog
Focal invasive species (Intervention)	If more than one invasive species, separate case study Exclude large undifferentiated assemblages Do not include invasive human diseases
Study design (Control)	Studies can be observational or case/control
Impact (Outcome)	Must have a clearly defined ecological impact If more than one impact, separate case study If impact is measured at multiple spatial scales, separate No impacts hypothesized or on other invasive species
After 1999 (Other)	Publications after Parker et al.'s (1999) work on impacts



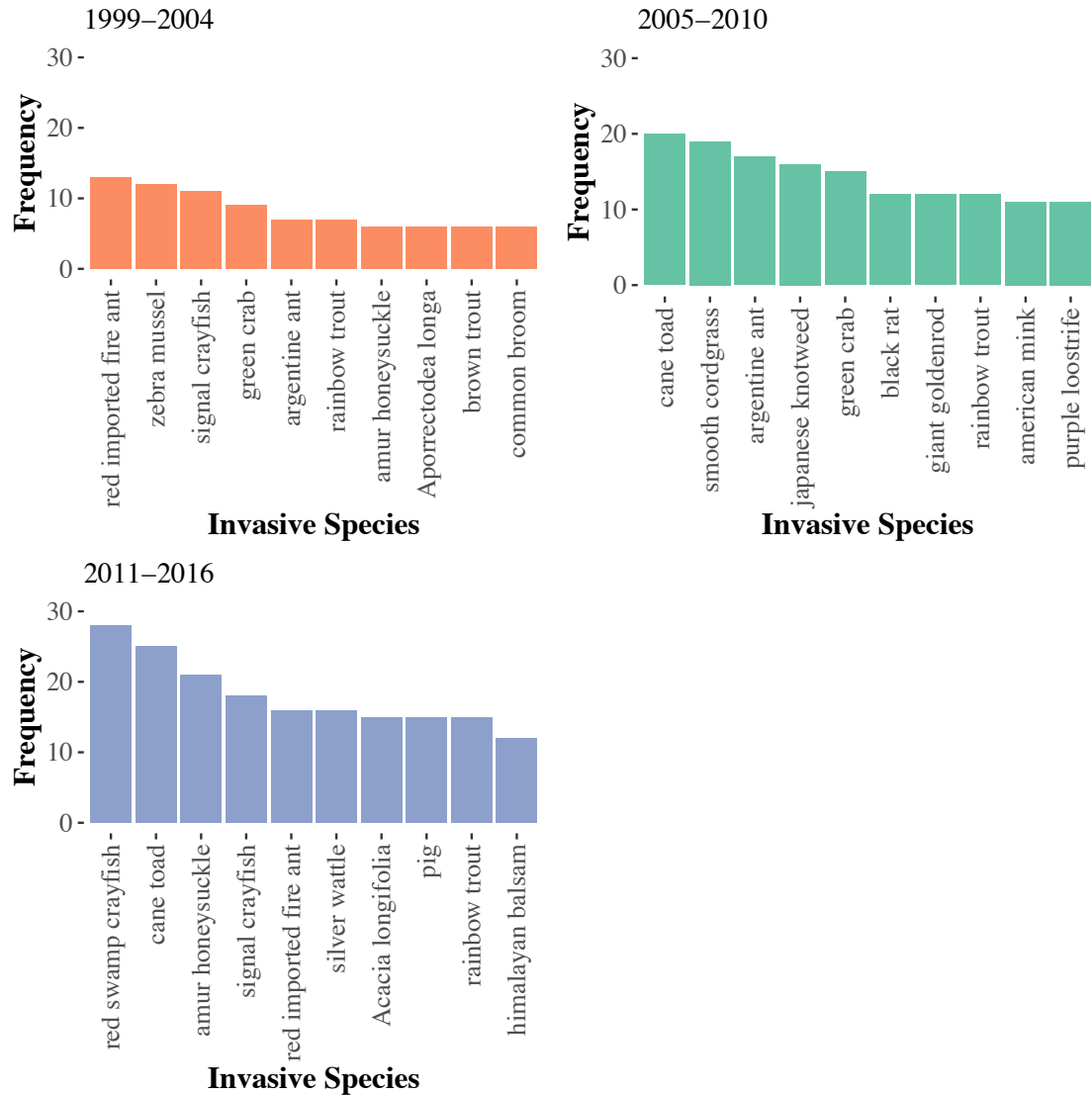
Appendix S3

Flowchart depicting articles included or excluded during each of three screening steps. We selected articles for the systematic review based on Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) standards (Moher *et al.* 2009). We modified the PRISMA-recommended flowchart by including multiple screening steps. Numbers in green boxes represent the number of studies included at each screening step. Numbers in red boxes indicate the studies that were excluded at each screening step.



Appendix S4

The number of articles included in this systematic review by year ($N = 1,507$). These articles passed all three screening steps against the inclusion criteria. Publication years ranged from 1999-2016 to correspond with early theoretical work on invasive species impacts by Parker et al. (1999).



Appendix S5

The ten most frequently studied species from 1999-2016 in six year increments. The only species that is consistently in the top 10 across all years included in this systematic review is rainbow trout (*Oncorhynchus mykiss*). Cane toads (*Rhinella marina*), the species with the largest number of case studies overall, was not part of the top ten until 2005.

CHAPTER 3: Invasive species are associated with an average decrease in richness

ABSTRACT

One of the principal supposed impacts of invasive species is that they reduce local species richness where they occur. Because these reductions are associated with loss of ecosystem services and species endangerment, the field has amassed a large volume of evidence on this link. We used cumulative meta-analysis to synthesize evidence from 240 published articles evaluating whether this cumulative evidence base generally supports, or refutes, this association. We also tracked if evidence accumulation lowered the mean effect size of invasions on richness through time (decline effect), including if, and when, accumulated evidence reached sufficiency, indicating that the mean effect direction (positive or negative) was unlikely to be reversed by unpublished research. We also identified whether or not the mean effect size reached a threshold of stability over publication years. Finally, we explored if any observed decline effect was driven by publication bias or by the inclusion of more species or ecosystems in the evidence base over time. We found a clear decline in the cumulative mean effect of invasive species on richness as evidence accumulated between 1999 to 2016. Despite this decline, evidence of an average negative association was stable and sufficiently robust to unpublished studies by 2007, showing a 21% mean richness decrease by 2016. Our analysis of the decline effect suggested that the decline reflected inclusion of varied ecosystems as evidence amassed over time. Within ecosystem and taxonomic subgroups we found variability in levels of the decline effect, sufficiency compared to unpublished research,

and stability, and this variability highlights the challenges posed in summarizing ecological evidence through meta-analysis.

1. Introduction

Ecologists have produced hundreds of studies on the relationship between invasive species presence and declines in local species richness (Vilà *et al.* 2011; Hulme *et al.* 2013; Cameron *et al.* 2016; Schirmel *et al.* 2016), however the relationship remains highly debated (Gurevitch & Padilla 2004; Simberloff 2005; Davis *et al.* 2011; Mollot *et al.* 2017; Pauchard *et al.* 2018; Schlaepfer 2018). Standard meta-analysis has shed needed light on the collective evidence for, or against, this relationship within specific taxonomic groups and ecosystems (e.g., Vilà *et al.* 2011; Tamburello *et al.* 2015). However, to date no one has evaluated evidence of an association (magnitude and direction) using information from all studied taxa and ecosystems. We do so here. We also evaluate if, and why, mean effect magnitude declines as the evidence base informing it grows; termed the ‘decline effect’ (Ioannidis 1998; Ioannidis & Trikalinos 2005; Jeschke *et al.* 2012). Even if a decline effect is observed, it may not be strong enough to overturn the mean effect direction (positive, negative) of the initial findings. If so, establishing when the accumulated evidence stabilizes around a largely static mean effect magnitude (*stability*; Muellerleile & Mullen 2006; Cook 2014; Love *et al.* 2018), is key to recognizing consensus on the mean effects of invasive species. Because unpublished results may alter the direction of mean effect sizes computed through meta-analysis (Schooler 2011; Sanchez-Tojar *et al.* 2018), we identify whether enough evidence exists in the published literature so that the direction of the mean effect is unlikely to be reversed by unpublished studies (*sufficiency*; Muellerleile & Mullen 2006; Kuppens & Onghena 2012; Love *et al.* 2018).

The decline effect is the result of pioneering publications tending to report very large ('astonishing') statistical effect sizes (Song *et al.* 2010; Schooler 2011), and then as more research is published on the same topic, publications report smaller magnitude effects. If the decline effect is strong enough, mean effects can drop so low that they become indistinguishable from zero or switch direction from positive to negative or vice versa (Ioannidis & Trikalinos 2005). Cumulative meta-analysis (CMA; Lau *et al.* 1992; Leimu & Koricheva 2004) is well suited for detecting the decline effect, as it sequentially estimates a mean effect size for a proposed relationship as evidence is published over years. Thus, mean effect sizes are re-computed with each addition of published evidence. CMAs are commonly used in the medical literature to evaluate how evidence accumulates in favor of, or against, treatment options as relevant studies are initiated and then completed through time. We acknowledge that meta-analysis, particularly within ecological research, can obscure important true study-level variation (Whittaker 2010; Ioannidis 2016; Morrissey 2016). We emphasize that mean effect sizes from CMA (and other forms of meta-analysis) should be understood for what they are, an averaged effect size across heterogeneous studies rather than a universal effect that will manifest identically across intricate ecological systems with deviations from the mean effect size based on some sort of error. CMAs are rarely used in ecology even though they can highlight the allocation of research effort over time (Jennions & Møller 2002). In the context of invasive species and richness declines, we use CMA to evaluate the extent to which a few, early studies report astonishing large mean effect sizes (Ioannidis 2005; Schooler 2011). We also quantitatively estimate the degree to which mean effect

magnitude lowers, and whether mean effect magnitude changes direction as more evidence has accumulated through time.

Three main reasons are proposed for the decline effect (Song *et al.* 2010; Jeschke *et al.* 2012). First, the earliest studies on a new scientific discovery may survive peer review only if they demonstrate statistically significant and large magnitude effects (Jennions & Møller 2002; Song *et al.* 2010). For example, in the medical literature, research with non-significant or low effect size findings can take twice as long to publish compared to research with significant and large effects (Song *et al.* 2010). Second, and related, when articles demonstrating non-significant or low magnitude effects are eventually published, they tend to appear in low-impact journals, which are slower to publish and receive less attention (Murtaugh 2002; Nakagawa *et al.* 2017). Finally, as interest in the research question grows, publication biases weaken and evidence comes from a greater variety of contexts (Coyne & de Voogd 2012). Here, we consider the context to have widened as the taxonomic identity of invasive species, and the ecosystems that are invaded, expands beyond those considered in early published studies.

Using CMA results from medicine (Ioannidis & Trikalinos 2005; Schooler 2011) and qualitative assessments of the decline effect in invasion ecology (Jeschke *et al.* 2012) as guiding expectations, we predict that we will find a decline effect in the magnitude of mean richness decline associated with the presence of invasive species. We also explore whether high-magnitude effects tend to be published earlier than low-magnitude effects, and if low-magnitude effects tend to appear in lower-impact journals. Finally, because invasive taxa and ecosystems are not studied equally (Crystal-Ornelas & Lockwood In

prep; Pyšek *et al.* 2008; Hulme *et al.* 2013) we explore the strength of the decline effect within different taxonomic groups and ecosystems.

2. Methods

2.1 Article search

We developed an *a priori* systematic search and screening protocol to locate articles that investigated invasive species associations with changes in local species richness. We used Thomson Reuters ISI Web of Science ® to locate articles from 1999-2016 in English. We conducted the search in January 2017. Initially, we used the following search terms to locate articles on invasive species impacts published from 1999-2016: TOPIC = “invasive” AND “impact*”; “introduced species” AND “impact*”; “non-native” AND “impact*”; “exotic” AND “impact*”; “alien” AND “impact*”; “naturalized” and “impact*”; “non-indigenous” AND “impact*”. This search was part of a larger systematic review, and full details on database development are provided by Crystal-Ornelas & Lockwood (In prep). Because we limited our search to articles written in English, the individual effect sizes we incorporated into this meta-analysis are more likely to be statistically significant and large (Jüni *et al.* 2002).

2.2 Inclusion criteria and screening

Our initial search identified over 23,000 articles that potentially investigated invasive species impacts on natural ecosystems. We removed duplicate articles and then conducted three screening steps to locate articles that included information on invasive species impacts on richness (Figure 1). First we screened articles based on titles, then

abstracts, and finally we screened the full text of all remaining articles. A single article could contribute multiple impact measurements to our database. We developed an *a priori* set of inclusion criteria to screen articles that measured impacts on richness (Table 1). We used a Population, Intervention, Control, and Outcome framework to shape our inclusion criteria (Huang *et al.* 2006; Pullin & Stewart 2006). First, each article had to identify at least one invasive species and the invasive species had to be present within a natural ecosystem rather than agriculture or aquaculture systems (Population). All articles had to include replicate plots or study sites where invasive species were present (Intervention). The intervention could not be an assemblage of invasive species, but rather had to focus on the impacts of a single invasive species on richness. The study had to have a control group where the invasive species was either not present or present at very low densities (Control). We extracted measurements of species richness or higher order taxonomic richness (Outcome). If we did not include higher order richness measurements we would have disproportionately removed studies for taxonomic groups where species identification is more challenging or communities are hyper-diverse (e.g., crustaceans, fish, and insects). While there are critiques of using richness to quantify biodiversity, particularly for groups of taxa that are not well-known, richness is a frequently used metric in primary research and meta-analysis (Gaertner *et al.* 2009; Mollot *et al.* 2017). After completing all screening steps, we included 240 articles that published 334 richness measurements (Figure 1).

2.3 Data extraction

We extracted 14 pieces of data from each publication (Table 2). The data either describe study characteristics (e.g., publication year, country, and focal invasive species) or quantitative measurements (e.g., mean richness, sample size, and standard deviation).

We identified the article's first author, publication year, and the journal where the article was published. We used the SCImago Journal and Country Rank database (SCImago 2018) to associate each publication with a journal rank (called the SCImago Journal Rank or SJR) for the year the article was published. The SJR is similar to a journal's impact factor but accounts for citations over more years than impact factors and captures a broader array of citations by using the SCOPUS database (Falagas *et al.* 2008; SCImago 2018). We used taxonomic classifications based on a previous systematic review in invasion ecology (Pyšek *et al.* 2008). We divided the 'plant' category from Pyšek *et al.* (2008) into aquatic plants, grasses, herbaceous plants, and trees. We also differentiated between terrestrial and marine invertebrates. We identified the ecosystem where each study took place based on a classification provided in Lowry *et al.* (2012). We expanded their 'marine' classification to distinguish between open ocean ('ocean'), nearshore marine ('rocky intertidal' or 'sandy intertidal'), and nearshore terrestrial ('coastal').

We selected the response ratio (RR), a metric that compares continuous outcomes from two groups, as the effect size for our meta-analysis (i.e., $RR = \text{invaded site richness} / \text{control site richness}$; Hedges *et al.* 1999; Lajeunesse 2011; Blakey *et al.* 2018). For each study, we compared the average richness of sites with relatively high abundance of the focal invasive species to the average richness of non-invaded or low invasive-abundance control sites. To calculate RR , we extracted three pieces of data from invaded and control

treatments: mean richness, standard deviation, and sample size. In many cases, control site invasive species density was zero (i.e., no invasive species present), and in other cases authors indicated density was lower than in the high invasive species treatment. Control groups could be uninvaded sites, sites where invasives were eradicated, or sites with data prior to invasive species establishment. When researchers provided a gradient of densities for the invaded treatment, we followed previous authors and extracted richness measurements from the highest density treatment (Howard *et al.* 2017). If changes in richness were recorded over multiple years, we extracted only richness values from the most recent date to avoid non-independent sampling (Castanho *et al.* 2015; Howard *et al.* 2017; Tekiela & Barney 2017).

We used the natural log of the *RR* when performing statistical analyses because it is more suitable for use in random effects models than is proportion (Koricheva *et al.* 2013; Schwarzer *et al.* 2015). After computing mean effect sizes, we back-transformed the natural log of the *RR* to show percent increase or decrease in richness owing to the presence of the invasive species (Ferreira *et al.* 2015). We calculated a 95% confidence interval (CI) around each *RR* value. Richness values between treatment and control groups showed a non-zero mean effect when 95% CIs around the mean effect sizes excluded zero. We implemented meta-analytic models using R packages (R Development Core Team 2017) *metafor* (Viechtbauer 2017) and *metaviz* (Kossmier *et al.* 2018).

For many articles, the data we needed to compute the *RR* were included in figures rather than in the text. If data were in bar plots or scatter plots, we used *WebPlotDigitizer* (Rohatgi 2018) to extract mean and standard deviation. When data were presented in box plots, we obtained mean richness values from the text or authors and extracted standard

deviation from boxplots using the R package *metaDigitiseR* (Pick *et al.* 2018). While some error is associated with data extraction from figures, experimental tests have validated programs similar to *WebPlotDigitizer* and *metaDigitiseR* and found that trained researchers could extract data using software-assisted extraction tools with 99% accuracy (Flower *et al.* 2016). We extracted richness measurements from supplemental information if provided by authors. If the data were not found in text, figures, or supplemental information, we e-mailed the corresponding author and requested the missing data (N = 38 requests, N = 30 responses).

A relatively small number of articles (N = 12) provided richness measurements and sample sizes for invaded and control treatments but did not provide an associated measure of variation. Though imputation decreases the precision of results, meta-analyses with imputation outperform those where articles with missing data are excluded (Koricheva *et al.* 2013; Ellington *et al.* 2015; Weir *et al.* 2018). We imputed all missing standard deviations (N = 13 control and N = 13 invaded) using the R package *mice* (Buuren & Groothuis-Oudshoorn 2011). The missing standard deviations for invaded sites were calculated based on *mice*'s Bayesian linear regression (Schafer 1997) fit to the available mean richness and sample sizes for invaded sites. We used the same procedure for imputing missing control site standard deviations but imputed from mean richness and sample sizes for control sites.

2.4 Meta-analytic models

We first conducted a CMA using all of the available richness impact measurements (N = 334). Then, we divided the 334 measurements by their focal invasive taxonomic groups

based on Pyšek *et al.* (2008) and performed CMAs within these taxa. Finally, we divided measurements by the ecosystem in which research took place and conducted CMAs within the ecosystem subgroups based on Lowry *et al.* (2012).

In CMA, articles are chronologically ordered from earliest to latest year of publication, and a single effect size is initially calculated using only the first published effect. Then, a new mean effect size is calculated using data published each new year (Koricheva *et al.* 2013). As is suggested for ecological meta-analysis, we calculated mean effect sizes using random effects models fit with restricted maximum likelihood estimation (Koricheva *et al.* 2013; Schwarzer *et al.* 2015). Mean effect sizes were weighted using the inverse-variance method (Schwarzer *et al.* 2015) so that more precise individual effect size estimates (i.e., studies with lower variance) were given greater weight when we calculated mean effect sizes (Koricheva *et al.* 2013).

We used CMA to test for a decline effect using *RR* for all taxa and ecosystems that had five or more published effect sizes available across the entire period of record (Rothstein *et al.* 2006). We identified when sufficiency was achieved using the failsafe ratio (Muellerleile & Mullen 2006; Love *et al.* 2018). This ratio is calculated using the failsafe number (i.e., the number of null results that would be need to be published in order to overturn the mean effect size; Rosenberg 2005) divided by Rosenthal's $5(k)+10$ standard (Rosenthal 1979), where k is the number of measurements in the database. A failsafe ratio greater than 1.0 indicates that accumulated evidence has reached sufficiency. We calculated failsafe ratios using chronological accumulation of evidence as we did for calculating cumulative mean effect size (see above).

We identified the year when new published measurements added into a CMA did not substantially alter mean effect magnitude (*stability*) by calculating cumulative slopes for the CMA. To do so we fit a linear model to the CMA forest plot each time a new study was chronologically added to the analysis (Muellerleile & Mullen 2006; Love *et al.* 2018). Following guidelines by Muellerleile & Mullen (2006), our threshold for stability is when the slope of the regression line fit to the data was between $\beta = \pm 0.005$.

We used a linear model to test whether early articles were published in higher impact journals than were more recent articles. We also used a linear model to determine if a correlation existed between SJR and magnitude of published effect sizes. We used generalized linear models with a logit link function to identify whether mean effect magnitude diminished as scientists studied a greater variety of taxonomic or ecosystem contexts (controlling for the number of measurements published each year).

3. Results

The number of publications on how invasive species presence links to species richness increased from 1999-2016 (Appendix S1). The final year in our database (2016) contributed the greatest number of articles ($N = 29$). There were 166 invasive species represented in our database. The most frequently studied were amur honeysuckle (*Lonicera maackii*; $N = 16$) and Himalayan balsam (*Impatiens glandulifera*; $N = 9$). Of the 166 species, 69% were plants and 31% were animals. Across all species, 49% had only a single richness impact measurement in our database. Over half (56%) of the measurements were recorded in four countries: U.S. ($N = 109$), Australia ($N = 33$), Canada ($N = 27$), and New Zealand ($N = 20$) (Appendix S2).

All Taxa

We found evidence of a decline effect across all 334 measurements of invasive species impacts on richness published between 1999 and 2016 (Figure 2a). The mean effect size from the first year in our database (1999) suggested that invasive species presence was associated with a large mean decline in local richness ($\ln(RR) = -1.00$, $N = 5$, $p = 0.0293$, $CI = -2.44, -0.437$). This translates to an average 63% richness decrease. After we sequentially included more published evidence, mean effect size magnitude quickly decreased and the associated confidence interval around the mean effect narrowed ($\ln(RR) = -0.232$, $N = 334$, $p < 0.0001$, $CI = -0.288, -0.175$). As of 2016, accumulated evidence suggests invasive species presence results in a 21% mean decrease in local richness.

We found that our aggregated dataset that included all effect sizes reached sufficiency for richness decreases in 1999, when the failsafe ratio exceeded and remained above 1.0 until the end of the publication record (2016). Thus, accumulated evidence for a negative non-zero mean effect of invasive species on local richness was, as of 1999, unlikely to be overturned by unpublished evidence (Figure 2b). Mean effect size magnitude, however, did not stabilize until 2007 when all subsequent published effect sizes beyond this year did not substantially change the mean effect magnitude from around 21% (Figure 2c).

Mechanisms of the decline effect

We did not find an association between publication year and SJR ($\beta = 0.0126$, $SE = \pm 0.0134$, $p = 0.347$, $r^2 = 0.00268$; Appendix S3a). Also, we found no association between published effect sizes and SJR ($\beta = 0.0816$, $SE = \pm 0.104$, $p = 0.434$, $r^2 = 0.00186$; Appendix S3b). Similarly, our generalized linear model suggested that an increase in the number of invasive species included in the cumulative evidence pool per year did not explain the decline effect ($\beta = 1.85$, $SE = \pm 2.06$, $p = 0.383$). However, we did find a trend of declining mean effect magnitude when more ecosystems were included in the evidence base over time, albeit this trend was not statistically significant ($\beta = 2.50$, $SE = \pm 1.34$, $p = 0.0798$).

Taxonomic and Ecosystem Subgroups

There was not enough evidence for us to calculate CMAs for four taxonomic groups (< 5 measurements) of invasive species: amphibians and reptiles, birds, marine invertebrates, and terrestrial invertebrates. For the remaining 10 taxonomic groups, we show that several exhibited a decline effect yet still had a negative mean effect on local richness (Figure 3). For example, the first five publications on the impacts of invasive trees on local richness (between 2000-2003) suggested a large negative mean effect ($\ln(RR) = -0.389$, 32% mean decrease, $p = 0.0232$, $CI = -0.690, -0.0870$). By 2016, however, additional accumulated evidence showed a more moderate magnitude mean effect ($\ln(RR) = -0.209$, 19% mean decrease, $p = 0.0001$, $CI = -0.312, -0.106$). The evidence showing invasive trees are associated with an average decline in richness reached sufficiency in 2001 (Figure 4) and stability in 2007 (Figure 5).

Published research for some invasive species taxonomic groups exhibited the opposite of a decline effect. For example, conflicting reports in the first five publications on how invasive insects link to local richness (1999-2003) resulted in a non-significant mean effect size ($\ln(RR) = -0.428$, $p = 0.172$, $CI = -1.14, 0.286$). By 2016, however, a total of 27 published effects were available and the cumulative evidence base showed a 41% mean decrease in richness at sites with invasive insects present ($\ln(RR) = -0.522$, $p = 0.0284$, $CI = -0.984, -0.0597$). Accumulated evidence for invasive insects reached sufficiency in 2003 (Figure 4), yet the available data suggests that stability in mean effect size magnitude has not yet been reached (Figure 5).

When we synthesized published effect sizes on invasive algae, aquatic plants, fish, and mollusks we found that the mean effect size for these taxonomic subgroups did not differ from zero (Figure 3). Of these taxa, invasive aquatic plants and mollusks have a relatively small number of published effects that met our inclusion criteria ($N = 8$ and $N = 7$, respectively). Accordingly, we show that mean effect sizes for these subgroups have yet to stabilize (Figure 5). Invasive algae have received enough publication attention that we could synthesize data from over 20 articles. Nevertheless, the evidence accumulated to date shows that, when taken together, the invasive algae in our database have no clear mean effect on local richness (i.e., mean effect size did not differ from zero; $N = 22$, $p = 0.507$, $CI = -0.311, 0.159$; Figure 3). Despite a relatively large number of publications, the failsafe ratio for invasive algae does not indicate the accrued data have sufficient (Figure 4) or stable (Figure 5) mean effect sizes when we aggregated published data.

We found a decline effect for invasive species' mean effects on forest species richness (Figure 6). Between 1999 and 2006, invasive species in forests had a mean effect

of a 44% decrease in richness ($\ln(RR) = -0.581$, $p = 0.0346$, $CI = -1.11, -0.0487$). By 2016, the synthesized data suggested a 19% mean decrease ($\ln(RR) = -0.208$, $p = 0.0016$, $CI = -0.334, -0.0814$). Despite sufficiency being reached in 2004, the RR for invasive species in forests has not yet stabilized around a mean effect size. We also identified a decline effect for mean effect sizes within lotic ecosystems (Figure 6); however, in this case sufficiency was reached in 2001 (Figure 7) and a stable mean effect on richness was reached in 2007 (Figure 8; $\ln(RR) = -0.259$, 23% mean decrease, $p < 0.0001$, $CI = -0.368, -0.149$).

4. Discussion

For decades, invasion ecologists have debated whether invasive species are associated with declines in local species richness (Gurevitch & Padilla 2004; Clavero & Garcíaberthou 2005; Schlaepfer 2018). Using one of the largest databases of effect sizes on invasive species richness impacts to date, we used cumulative meta-analyses (CMA) to show a stable and sufficient mean effect size of a 21% richness decrease at invaded sites compared to control sites. Invasion ecology has been criticized when replicate studies fail to match the findings of early publications (Davis *et al.* 2011; Schlaepfer *et al.* 2011), and our results show that mean effect magnitude has declined as evidence accumulates through time. Evidence syntheses indicate that the decline effect is common (Ioannidis 1998; Schooler 2011; Jeschke *et al.* 2012), and we should expect sometimes widely diverging impact measurements when we synthesize early research on ecological relationships. CMA provides a formal, quantitative way to synthesize evidence for a suspected mean invasive species impact and detecting points of sufficiency and stability for mean effects.

Contrary to expectations from medical research, we did not find evidence that SJR was correlated with year of publication or published effects (Murtaugh 2002; Rothstein *et al.* 2006). Also, individual published effects did not diminish as ecologists conducted research across a larger variety of taxa or ecosystems (Krist 2018). We recognize that our CMAs are an indirect test of publication bias against non-significant impacts because we cannot explicitly test our database of published results to a set of non-published effect sizes. However, a publication bias against non-significant results remains the simplest explanation for why early studies show inflated effects of invasive species on richness (Jennions & Møller 2002; Song *et al.* 2010). One way to directly test the number of studies that go unpublished owing to researcher and editor decisions is through preregistration of experimental methods and statistical analyses (Collaboration for Environmental Evidence 2013; Ioannidis 2014). Preregistration is beginning to take hold in biological sciences (e.g., <https://osf.io>; <https://www.environmentalevidence.org/>), and permits a comparison of the analyses proposed by researchers and the results that are ultimately published.

We found that evidence for mean effect magnitude sufficiency and stability manifested differently within taxonomic and ecosystem groups. This result is unsurprising given the context-dependency of invasive species impacts (Vilà *et al.* 2011; Pyšek *et al.* 2012; Ricciardi *et al.* 2013), though it contradicts the published literature on the decline effect in medicine (Ioannidis 1998; Schooler 2011). We emphasize that meta-research, by definition, aggregates publications through a relatively coarse synthesis to make generalizations from available evidence (Gurevitch *et al.* 2018; Peng *et al.* 2019). Thus, the mean effect sizes produced through our meta-analyses likely obscure important

impacts presented in primary publications (Whittaker 2010). For example, our CMA on invasive algae found that as more evidence accumulated, mean effects were not significantly different from zero (confirming findings by Tamburello *et al.* 2015). However, within the cohort of studies that we synthesized, the individual publications that comprise our meta-analysis suggested that invasive algae can locally decrease richness when introduced (e.g., McKinnon *et al.* 2009; Smith *et al.* 2014). Thus, while the goal of CMA, stability, and sufficiency metrics is to identify broad patterns across publications (Gurevitch *et al.* 2018), we should expect that primary publications will continue to reach conclusions that rightly deviate from the mean effects that we identify here.

We found high levels of variation in the decline effect within ecosystems, indicating that some ecosystems may be more likely to show larger declines in richness than others. Most ecosystems that received 35 or more richness impact measurements (forest, lotic, grassland, and island), showed sufficient, although not often stable, negative mean effect sizes. The lack of stability in mean effect magnitude for some ecosystems is likely due to early and highly contradictory published effects (Ioannidis & Trikalinos 2005; Krist 2018). Our results suggest that future research within ecosystems is warranted in most cases so as to reach stability in mean effect magnitude.

The context-dependency of invasive species impacts (Ricciardi *et al.* 2013) means that syntheses, even those that have a taxonomic or ecosystem focus, may mask important findings from individual publications. Providing a single mean effect size through traditional meta-analyses clearly ignores an assessment of evidence accumulation, sufficiency, and stability. Cumulative meta-analysis provides a more

nuanced exploration of how evidence from published research converges on sufficient and stable mean effect sizes over years of published research.

Acknowledgments: We thank D. Simberloff, M. Meixler, J. Wiedenmann, and the Lockwood lab for helpful discussions and/or comments. We thank the many researchers that contributed data to this meta-analysis either through their manuscripts or by email.

Competing interests: The authors declare no competing interests.

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Table 1

Description of the inclusion criteria we used during article screening. We used a Population, Intervention, Control, Outcome framework to develop our inclusion criteria. An article had to meet all six criteria to be included in our cumulative meta-analysis.

Criteria	Description
Invasive species of interest (Population)	We did not restrict invasive species taxa. However, impact had to be attributed to at least one invasive species. If article included more than one invasive species, we counted each separately.
Sites with invasive species (Intervention)	Research had to include replicate study sites that contained invasive species.
Sites without invasive species (Control)	Research had to include replicate study sites that lacked invasive species, or had invasive species at low densities.
Richness (Outcome)	We extracted data on richness (species richness or higher order richness) from both intervention and control sites.
Publication date (Other)	1999-2016
Language (Other)	English

Table 2

We extracted 14 pieces of data surrounding each effect size measurement included in our cumulative meta-analysis. Some of the categories allowed for open responses (e.g., journal name) while others had a pre-defined set of possible entries (e.g., broad taxonomic group). When categories included pre-defined entries, we provide them here along with relevant citations.

Data	Description
Unique article identifier	#####-Author-Year
Publication year	Year
Invasive species common name	Common name
Invasive species Latin name	Latin name
Invasive species broad taxonomic group	Algae and seaweed, amphibians and reptiles, aquatic plant, avian, crustacean, fish, grasses, herbaceous plants, insect, mammal, marine invert, mollusks, terrestrial invertebrates, trees. Categories expanded from (Pyšek <i>et al.</i> 2008).
Ecosystem	Ecosystem where study took place. Ocean, forest, grassland, desert, lotic, lentic, estuarine, island, coastal, shrubland, mountain, urban, rocky intertidal, sandy intertidal, multiple.

	Categories expanded from (Lowry <i>et al.</i> 2012)
SCImago Journal Rank	Journal ranking metric corresponding to associated journal and publication year (SCImago 2018)
Country	Country where research took place
Mean (Control)	Mean richness for uninvaded sites
SD (Control)	Standard deviation for uninvaded sites
Sample size (Control)	Sample size for uninvaded sites
Mean (Invaded)	Mean richness for invaded sites
SD (Invaded)	Standard deviation for invaded sites
Sample size (Invaded)	Sample size for invaded sites

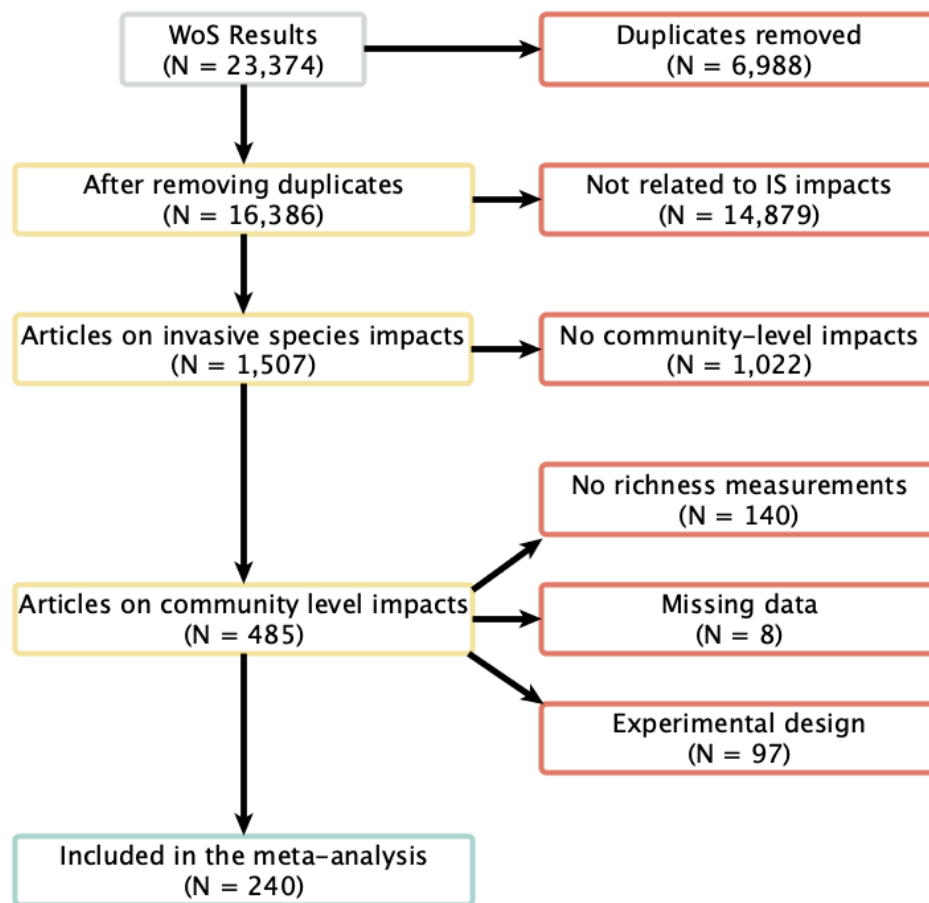


Figure 1

The PRISMA diagram (Moher *et al.* 2009) graphically displays our screening process used in this meta-analysis. Our initial literature search (as described in Crystal-Ornelas & Lockwood In prep) identified over 23,000 potential articles relevant to our meta-analysis. Each of the yellow boxes indicates a screening step where publications were checked for consistency with screening criteria (Table 1). When articles were excluded, we provide reasons for exclusion in red boxes. We excluded articles based on experimental designs if they lacked control groups or did not have replicate control and invaded sites because these designs were not in line with conditions needed for computing the meta-analytic effect size. A total of 240 articles and 334 measured impacts of invasive species presence on local richness were retained for our cumulative meta-analysis.

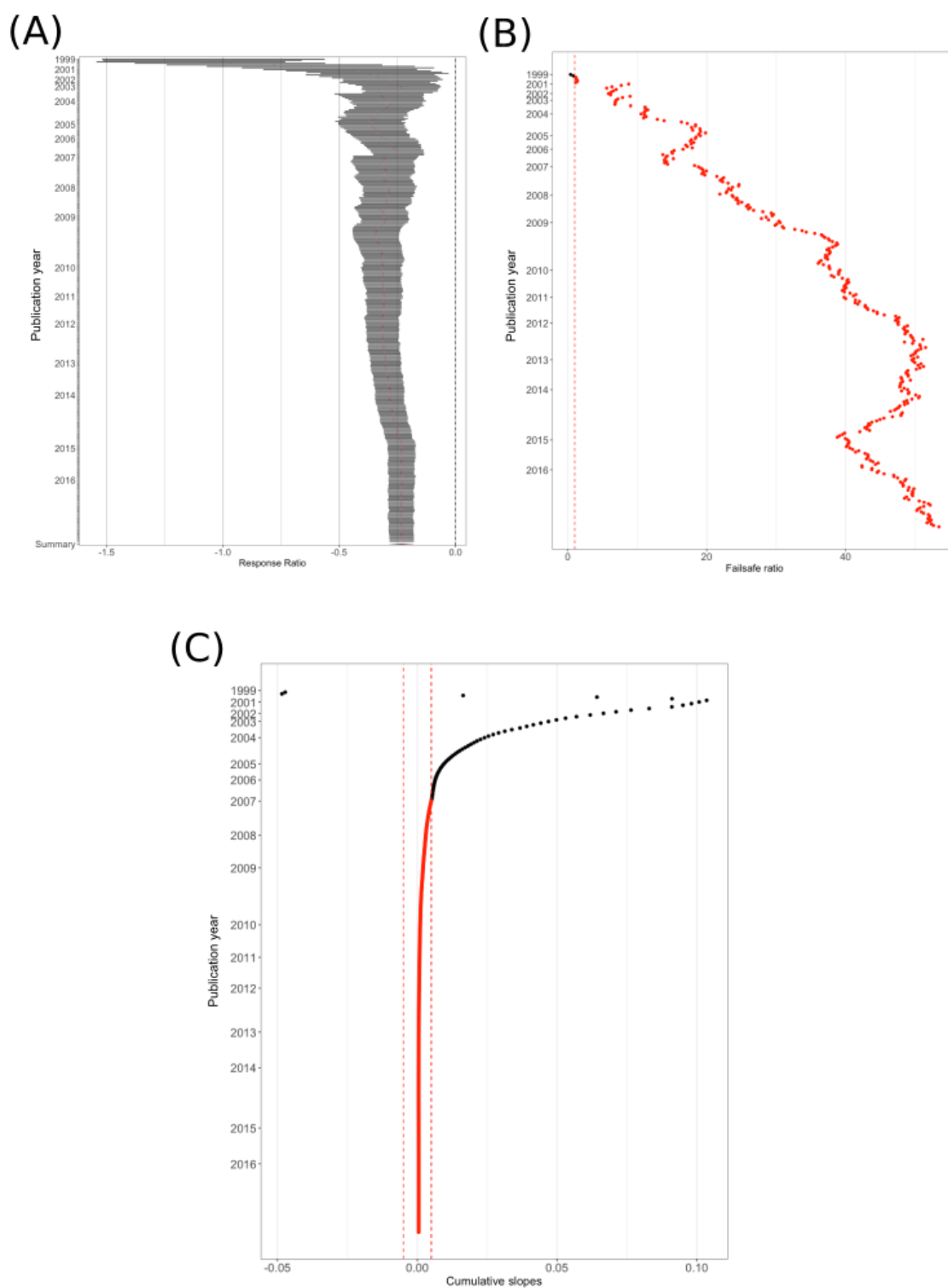


Figure 2

(A) Forest plot of our cumulative meta-analysis on the link between invasive species and local richness. Each point represents an estimate of mean effect size calculated using all published data up to and including that year, along with associated 95% confidence intervals. The last horizontal bar indicates the mean effect size calculated using all published information up to 2016 (N = 334). (B) Plot of failsafe ratio as a function of accumulated evidence. Red dots show years in which the failsafe ratio indicated sufficiency, and black dots show years in which this ratio did not show sufficiency. By 1999, it was very unlikely that unpublished null results could overturn the cumulative evidence for a mean decrease in richness in the presence of an invasive species. (C) Plot depicting annual change in response ratio as new evidence is added to the mean effect size calculation each year. Here red dots indicate cumulative slopes that are within ± 0.005 of zero (vertical red lines), and black dots otherwise. The overall CMA reached stability at a mean effect magnitude of about 21% drop in richness in 2007.

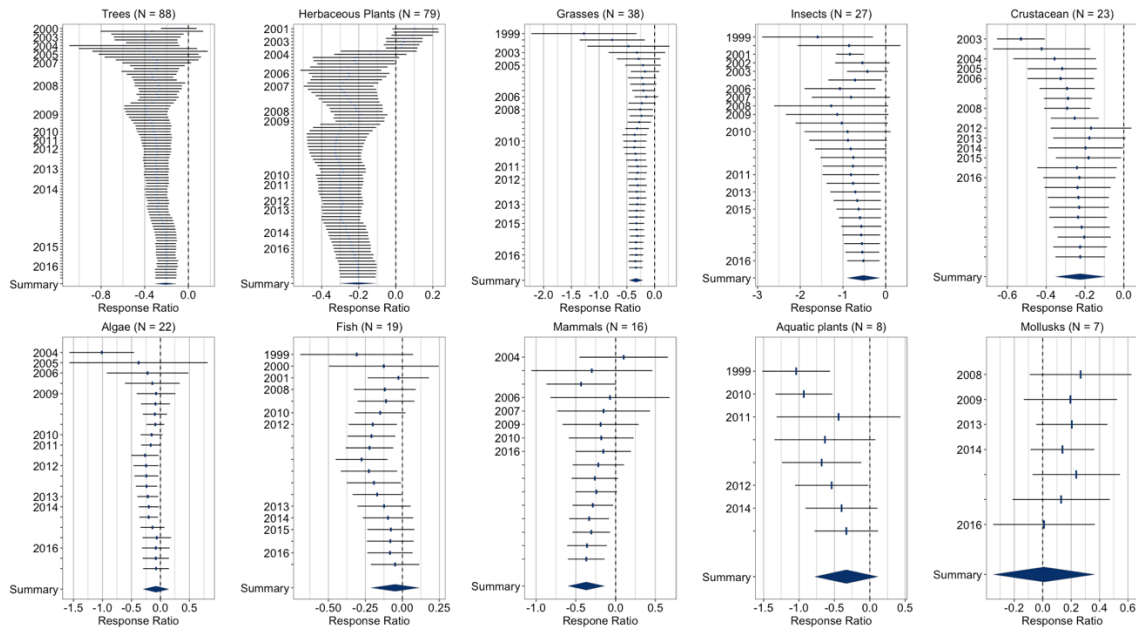


Figure 3

Forest plots of published mean effect sizes for invasive taxonomic groups on local richness. Early published effect sizes of invasive herbaceous plants, insects, and mammals on local richness tended to contradict one another in magnitude and direction (positive, negative), however as evidence accumulated mean effect magnitude and direction declined and stabilized at negative values. Conversely, invasive species in other groups (e.g., aquatic plants and algae) initially reported large mean decreases in richness in the presence of an invasive species, but accumulated evidence currently shows no mean effect. We also highlight that mean effect sizes for fish have generally overlapped zero across all years included in our CMA.

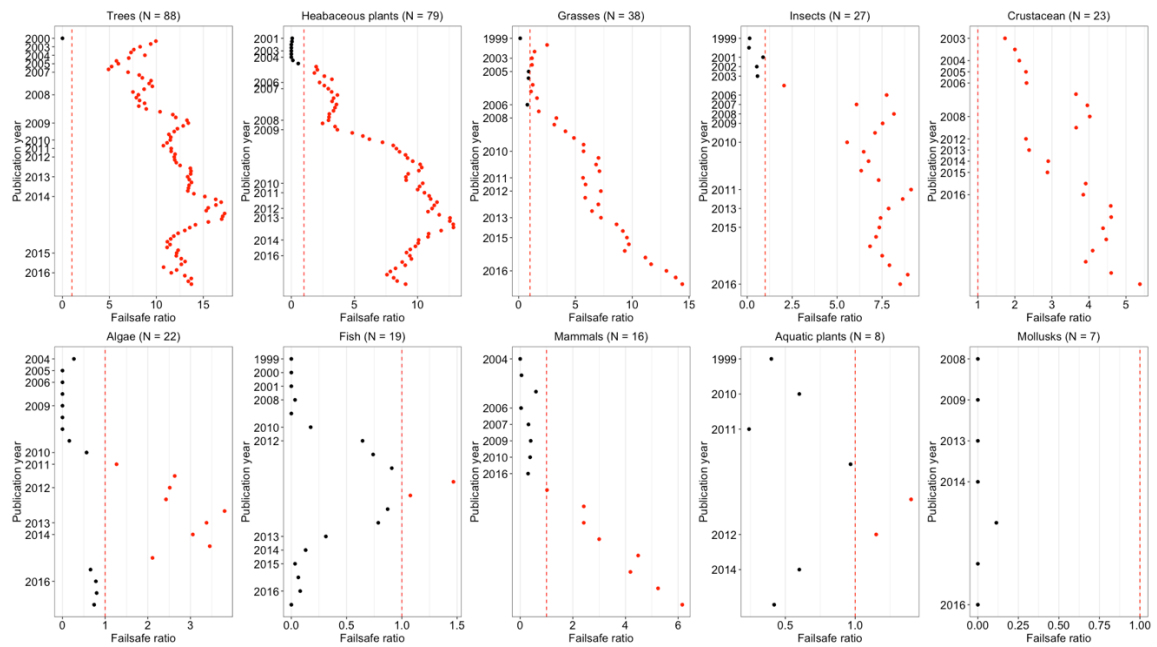


Figure 4

Failsafe ratio plots for taxonomic groups of invasive species. Some taxa (e.g., trees and herbaceous plants) reached sufficiency within the first several years of published research. Other taxa have had fewer publications on their impacts (e.g., algae and mollusks) and have not yet reached sufficiency.

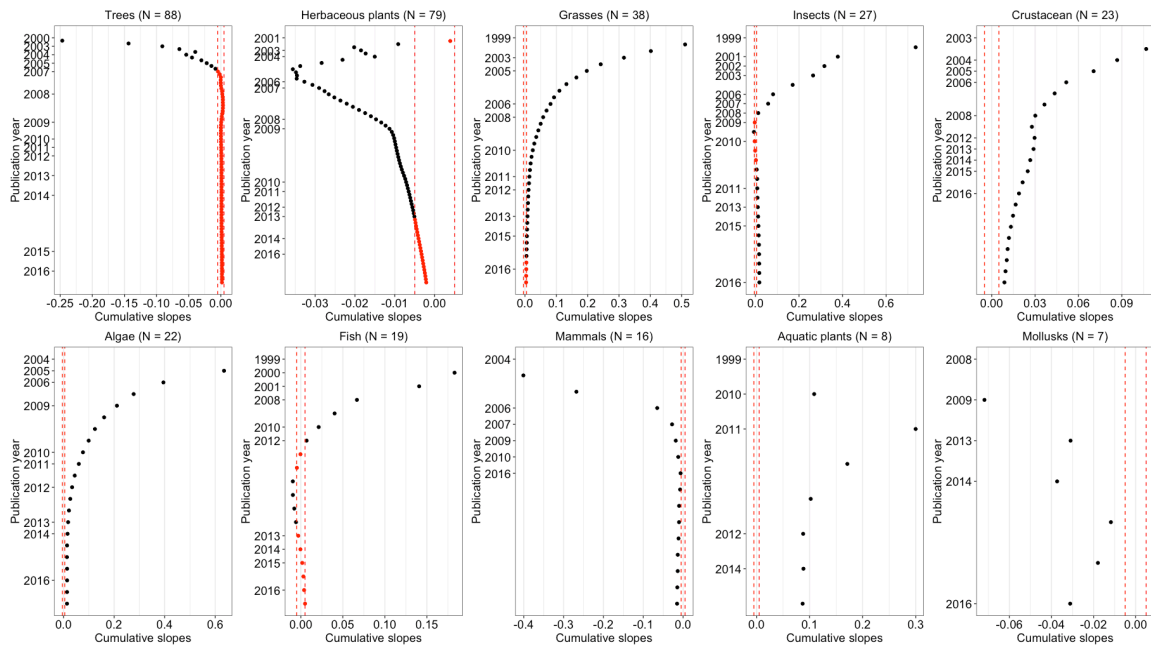


Figure 5

Mean effect stability plots for taxonomic groups of invasive species. Only four taxonomic groups have reached stability in mean effect magnitude (fish, trees, herbaceous plants, and grasses). For all other groups, as evidence continues to accumulate, mean effect magnitude will shift. The more cumulative evidence, the more likely mean effect magnitude reaches stability.

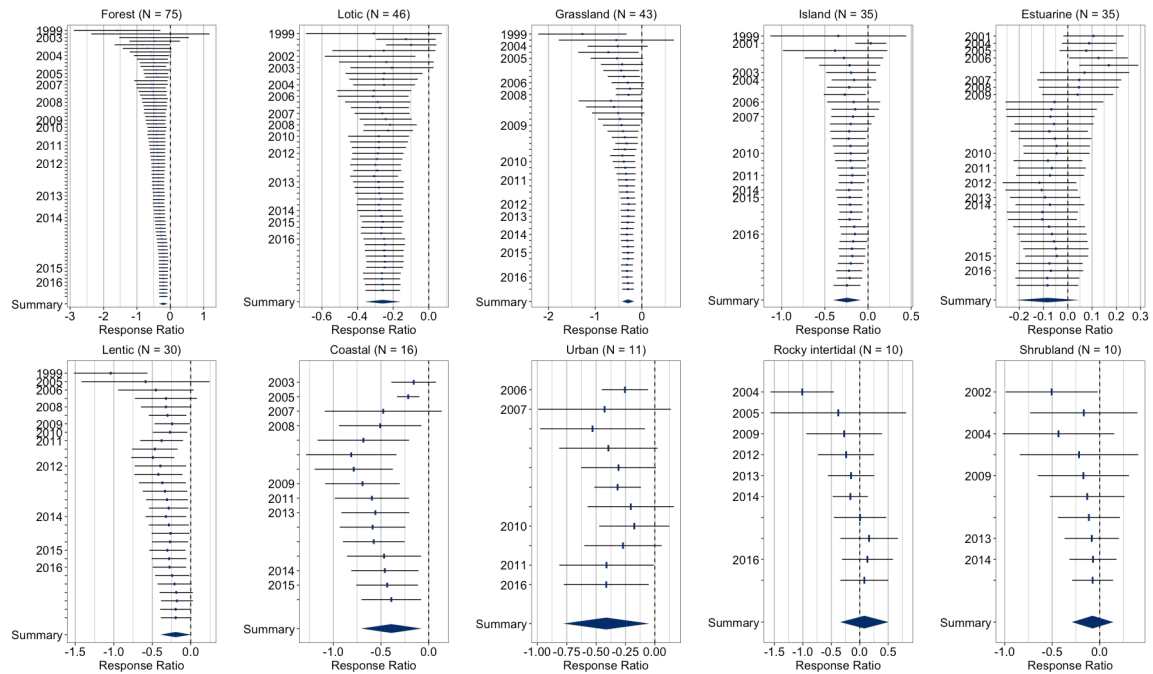


Figure 6

Forest plot showing how overall mean effect size shifts as new evidence accumulates on invasive species associations with richness within particular ecosystems. Some ecosystems, particularly those with over 35 measurements, exhibit patterns typical of the decline effect, with final measurements suggesting a significant negative mean effect on richness. For ecosystems with fewer published measurements (e.g., rocky intertidal and urban), mean effect size has moved from strongly negative to overlapping zero.

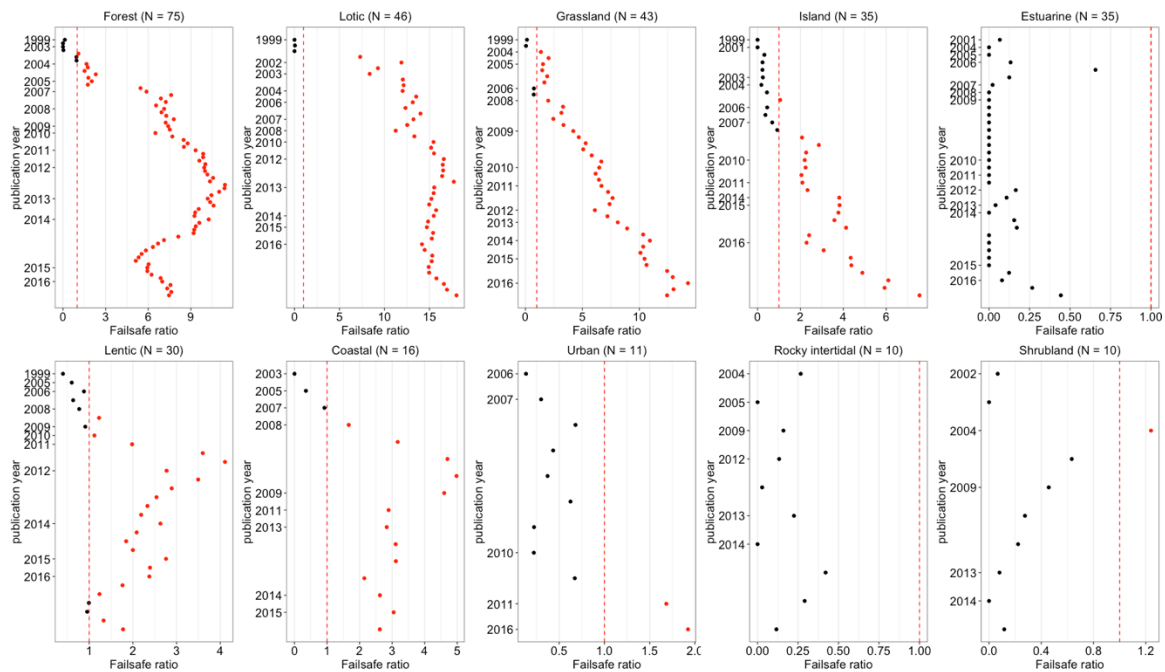


Figure 7

Sufficiency plots for invasive species impacts on richness within ecosystems. For most ecosystems, accumulated evidence shows sufficiency to suggest a negative mean effect of invasive species on local richness within 10 years of initial publication. However, for ecosystems with few published effect sizes (e.g., rocky intertidal, shrubland), sufficiency has not been reached.

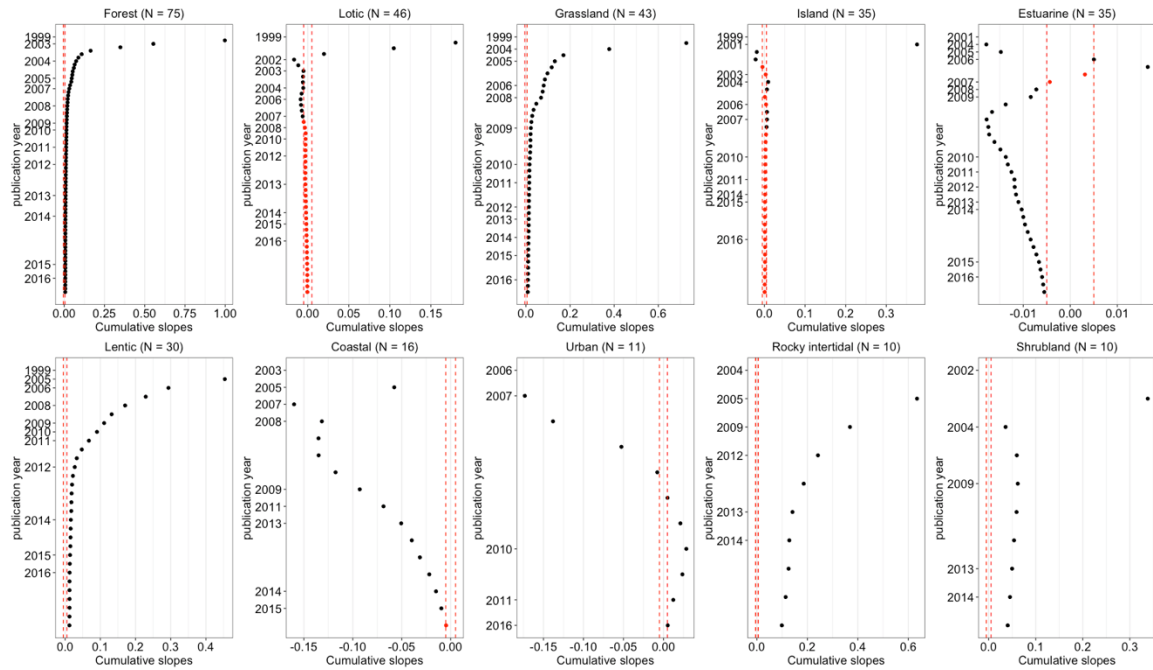
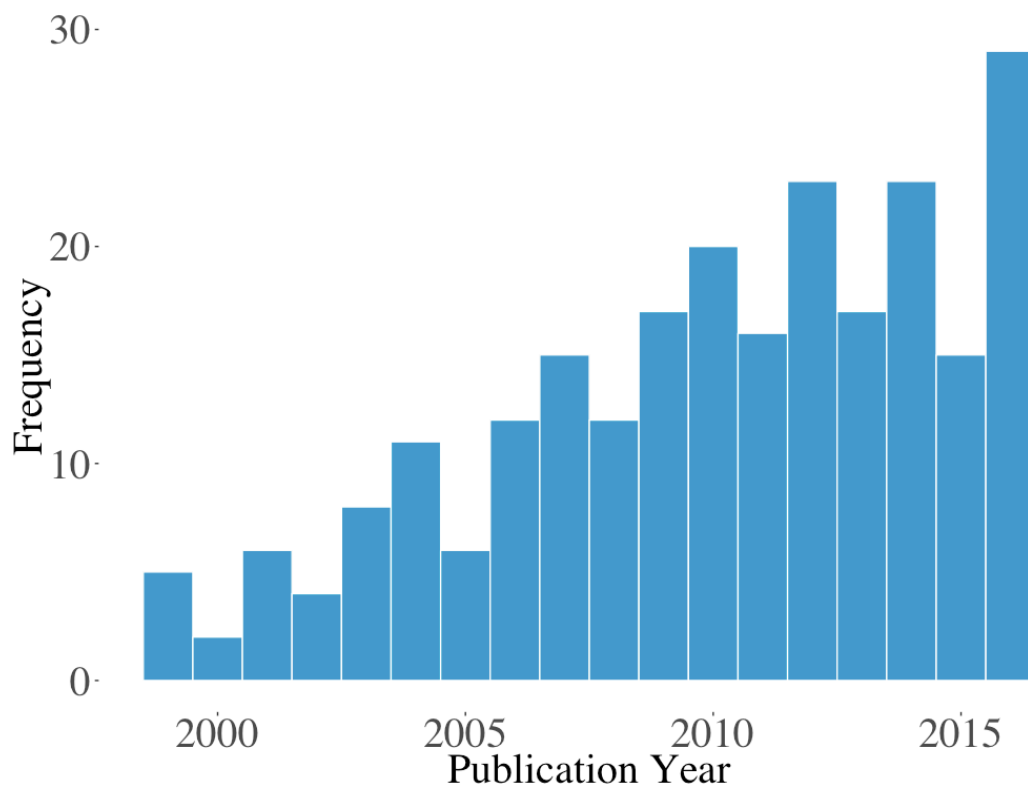
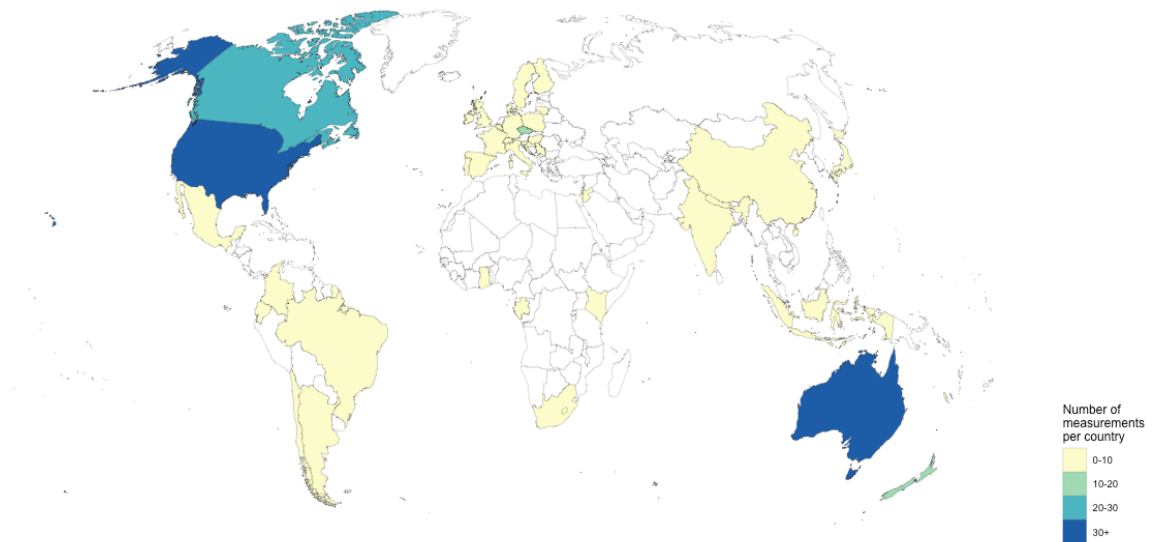


Figure 8

Mean effect stability plots across ecosystems. Only lotic and island ecosystems show a stable mean effect of invasive species on local richness. In all other ecosystems, mean effects are expected to shift toward stability with additional research.

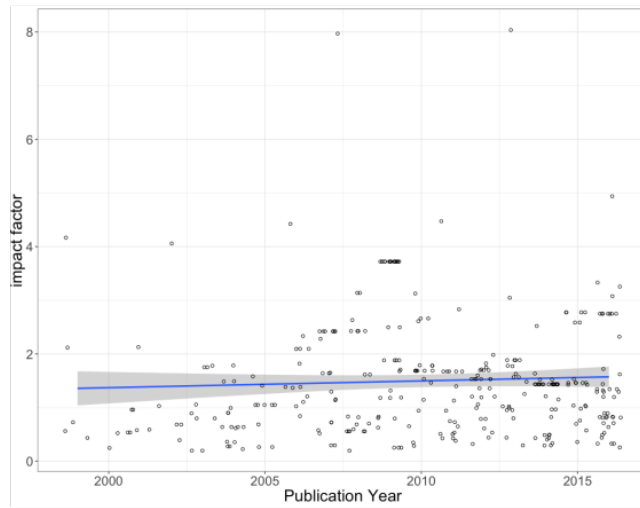
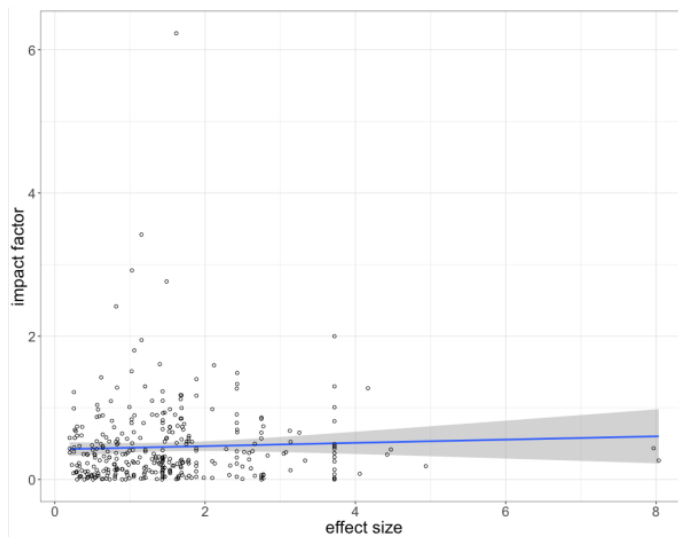
APPENDIX**Appendix S1**

Our database synthesized evidence on the association between invasive species presence and changes in local richness from research published between 1999 and 2016. About 5 publications per year appeared in the early 2000s accelerating to over 20 per year after 2010. The most recent year in our database (2016) had the most published articles on richness impacts ($N = 29$).



Appendix S2

This map shows the spatial distribution of published measured effect sizes of invasive species on local richness within our database ($N = 334$). Our data show a strong geographical bias toward research in the USA ($N = 109$), Australia ($N = 33$), Canada ($N = 27$), and New Zealand ($N = 20$).

A**B**

Appendix S3

We produced linear models that assess the relationship between SCImago Journal Rank (SJR) and (a) publication year and (b) effect size. We found no association between SJR and publication year ($\beta = 0.0126$, $SE = \pm 0.0134$, $p = 0.347$, $r^2 = 0.00268$) or between published effect sizes and SJR ($\beta = 0.0816$, $SE = \pm 0.104$, $p = 0.434$, $r^2 = 0.00186$).

CONCLUSION

Invasive species can negatively impact human health, the economy, and the natural environment and research on these effects can help to predict or prevent impacts. My dissertation research includes an individual case study that predicts the spread of a recently introduced species and two syntheses that use published research to provide broad assessments of the impact literature. In Chapter 1, I make an initial prediction for the spread of the Pin-tailed Whydah (*Vidua macroura*), an exotic songbird that has recently formed established populations in the US and the Antilles. The Pin-tailed Whydah is a brood parasite and has the potential to cause declines in native bird populations. In chapter 2, I performed a systematic review and found that most invasion research is performed on a small number of well-studied species, in the forests of North America. This research tends to be short in duration and at small spatial scales. Invasive species impacts are thought by some researchers to be too context-dependent to predict, however my research suggests this conclusion may be premature because there are many contexts within invasion ecology that have thus gone unstudied. In chapter 3, I extracted data on invasive species richness impacts from 240 publications. I identified a decline effect whereby the earliest studies on richness impacts showed large negative mean effects. Dozens of measurements were needed over a period of around 10 years before published mean effects stabilized at a value smaller than the initial, yet still negative. The implication is that policy and practice developed from single case studies may be based on overinflated findings. Overall, my dissertation advances a more comprehensive understanding of invasive species impacts and highlights research gaps that require more attention to better predict and understand the impacts of invasive species.