

Forty years of experiments on aquatic invasive species: are study biases limiting our understanding of impacts?

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Abstract

Invasions by non-native species are a threat to biodiversity because invaders can impact native populations, communities and entire ecosystems. To manage this threat, it is necessary to have a strong mechanistic understanding of how non-native species affect local species and communities. We reviewed 259 published papers (1972–2012) that described field experiments quantifying the impact of aquatic non-native species, to examine whether various types of study biases are limiting this understanding. Our review revealed that invasion impacts had been experimentally quantified for 101 aquatic non-native species, in all major freshwater and marine habitats, on all continents except Antarctica and for most higher taxonomic groupings. Over one-quarter (26%) of studies included tests for impacts on local biodiversity. However, despite this extensive research effort, certain taxa, habitats and regions remain poorly studied. For example, of the over one hundred species examined in previous studies, only one was a marine fish and only six were herbivores. Furthermore, over half (53%) of the studies were from the USA and two-thirds (66%) were from experiments conducted in temperate latitudes. By contrast, only 3% of studies were from Africa and <2% from high latitudes. We also found that one-fifth (20%) of studies were conducted in estuaries, but only 1% from coral reefs. Finally, we note that the standard procedure of pooling or not reporting non-significant treatments and responses is likely to limit future synthetic advancement by biasing meta-analysis and severely limiting our ability to identify non-native species with none or negli-

gible ecological impacts. In conclusion, a future focus on poorly-studied taxa, habitats and regions, and enhanced reporting of results, should improve our understanding and management of impacts associated with aquatic non-native species.

Keywords

Biotic homogenization, alien species, exotic species, review

Introduction

Invasion by non-native species can alter community structure and ecosystem functions with significant impacts on biodiversity (Wilcove et al. 1998; Grosholz 2002; Olden et al. 2004; Bruno et al. 2005; Byers 2009) and large economic (Pimentel et al. 2000), and cultural costs (Lockwood et al. 2007). Efforts to manage and mitigate invasion impacts are contingent on rigorous scientific evidence for the underlying drivers of change (Underwood 1996; Byers et al. 2002; Sutherland et al. 2004). There is debate, however, about whether non-native species cause environmental change, respond to environmental change or do both with complex feedback interactions (Gurevitch and Padilla 2004; Didham et al. 2005; Simberloff 2011). Experimental approaches, where the identity and density of non-native species are controlled, can provide much-needed causal linkages between the non-native species and ecological changes in invaded ecosystems and habitats.

The discipline of invasion ecology has grown immensely in recent decades with papers published across an increasing number of general scientific (ecology, invasion biology, conservation biology) and subject-specific (terrestrial, freshwater and marine) journals. Recently, Pyšek et al. (2008) tallied >2500 papers published on the topic of invasion ecology. Furthermore, it appears that invasion impacts have been reviewed in greater detail for terrestrial than aquatic ecosystems; e.g., recent reviews of plant invasion impact did not include examples from marine seaweeds or seagrasses (cf. reviewed reference listings, Powell et al. 2011; Vilà et al. 2011; Pyšek et al. 2012). To be able to build strong and general impact models and theories across ecosystems it is important that aquatic impact studies are similarly evaluated. Indeed, there is growing scientific evidence that invasions by non-native species are prolific in aquatic ecosystems (Carlton 1996; Hewitt and Campbell 2010; Strayer 2010). Furthermore, even if new aquatic invasions are curbed, impacts from past invaders may continue to increase as lag-phases transition into exponential phases, and ecological interaction “debts” are “collected” over time (Sax and Gaines 2008; Kuussaari et al. 2009). Existing reviews of aquatic invasion impacts have focused so far on specific taxonomic groups (e.g., Ward and Ricciardi 2007; Thomsen et al. 2009; Cucherousset and Olden 2011; Twardochleb et al. 2013), regions (e.g., Ricciardi 2006; Ruiz et al. 2011) or tested specific ecological questions (e.g., Ricciardi and Atkinson 2004; Grosholz and Ruiz 2009; Thomsen et al. 2011). However, to date there has been no synthesis of invasion impacts across non-native taxa, regions and habitats in aquatic ecosystems, thereby limiting our capability to evaluate progress and target research gaps.

Our objectives were to quantify the breadth of field-based experimental studies on invasion impacts in aquatic ecosystems, to identify what species, regions and environments have been targeted in these tests, and whether there have been any general problems relating to their experimental design and data reporting. Analogue reviews have provided important knowledge about research biases in other fields, including climate change, terrestrial ecology, conservation biology and general invasion biology (Pyšek et al. 2008; Darwall et al. 2011; Martin et al. 2012; Wernberg et al. 2012; Kimbro et al. 2013; Sorte et al. 2013).

To achieve our objectives, we reviewed field-based experiments on invasion impacts to identify what species, regions and environments have been targeted in these tests, and whether there have been any general problems relating to their experimental design and data reporting. We hope that this review will stimulate experimental research about aquatic invasion impact and this will lead to the development of new predictive tools in conservation management.

Methods

We searched for peer-reviewed, manipulative aquatic field experiments in Web of Science, Current Contents, and Google Scholar, using various combinations of ‘impact’, ‘effect’, ‘non-native’, ‘non-indigenous’, ‘exotic’, ‘invader’, ‘alien’, ‘aquatic’, ‘marine’, and ‘freshwater’. Reference lists were back-tracked from existing review papers and frequently cited impact studies (e.g. Bruno et al. 2005; Williams and Smith 2007; Byers 2009). We stopped searching on 1st of July 2012 to allow a definitive analysis, as new impact studies are being published every month. Field conditions were defined as any outdoor setting exposed to natural cycles of temperature and light (Martin et al. 2012). We included all studies that quantified impacts on resident organisms by comparing ‘invaded treatments’ to ‘non-invaded controls’ using addition or removal of the non-native species (Thomsen et al. 2011), including whole-lake experiments where non-native species (typically trouts) had been removed or added in well-documented events to specific lakes (treatments) but not to others (controls) (Pope et al. 2009). We also included studies published in non-invasion related contexts, for example impacts of “drift algae”, “turf algae”, or “grazers”, if the manipulated organisms were entirely dominated by non-native species, such as *Gracilaria vermiculophylla*, *Womersley setacea*, and *Littorina littorea*, respectively (Bertness et al. 1999; Airolidi 2000; Thomsen and McGlathery 2006).

First, we evaluated the published research in relation to the *attributes of individual studies*. We categorized whether the journal in which experiments were published targeted general scientists, freshwater, marine, or aquatic biologists (see Suppl. material 1 for detail). We recorded the year of publication and determined whether the experimental design was spatially pseudo-replicated (i.e. with only one ‘spatially independent’ control and/or treatment, Hurlbert 1984), and if the study reported an average invasion impact on resident organisms with an associated measure of

variation (e.g., SD, SE or CL). We specifically identified community impact studies because these are few in numbers but highly valued (Parker et al. 1999; Vilà et al. 2011). For each identified community study we counted if an impact was reported using multivariate structures from graphs (e.g. nMDS plots) or inferential tests (e.g. Anosim) and on univariate biodiversity metrics including taxonomic richness, diversity and evenness.

Second, we evaluated study characteristics related to the *attributes of the non-native species*, that is whether the non-native species was a plant or animal, pre-dominantly occupied the pelagic or benthic realm, was mobile or sessile, whether its trophic position was a plant, filter-feeder, herbivore, omnivore or carnivore, and its taxonomic affiliation. We classified very slow-moving bivalves as sessile taxa, and grouped consumers of macroscopic or microscopic primary producers (the latter group includes sediment eaters and detritivores) together to represent herbivores.

Third, we evaluated study characteristics related to the *attributes of the invaded system*. Here we extracted data about the spatial location of each experiment. Studies that included nested designs or multiple experiments, where study sites were separated by >1 km, were added as independent locations. These data were also grouped into invaded continent and latitude (proxy for climate). We then noted if the invaded system was a freshwater or marine habitat, where estuaries and salt marshes were grouped as marine. This attribute represents the invaded system (instead of the non-native species) because the same non-native species (e.g., the common reed *Phragmites australis*) can impact both marine and freshwater habitats. These two broad habitat types were subdivided into streams, ponds, lakes, wetlands, estuaries, open coast marine sands, rocky intertidal, or rocky subtidal, where wetlands included a few riparian studies, ponds included experiments conducted in outdoor freshwater mesocosms (ponds and mesocosm experiments are both conducted in relatively small enclosed systems), estuaries included both intertidal and subtidal studies, and the rocky subtidal zone included a few coral reef experiments (too few to justify a separate analysis for this habitat, see discussion for detail).

Finally, we examined if taxa were studied in proportion to their ‘recognized occurrence as non-native species’. We used Hewitt and Campbell’s (2010) tally of marine non-native species (this is a ‘grey literature’ report, but represent the most comprehensive tally to date), i.e. we tested if some taxa are well-recognized as non-native species but never studied. This comparison was only done for marine organisms because no master list exists for freshwater non-native species. We first regrouped invaded regions into geographical units used by Hewitt and Campbell (2010; 18 marine provinces based on biological similarity) and then conducted linear regression between our data to data listed in Hewitt and Campbell (2010, Fig. 2 and 11). We used Type 1 regression because our objective was to provide simple predictive models (Quinn and Keough 2002), and we forced the line through the origin because there can be no impact study if there is no invasion (the greater the slope, the more field experiments have been conducted relative to known marine non-native species).

Results

Our initial search suggested that more than 700 aquatic invasion impact studies have been published. However, after excluding reviews (Williams and Smith 2007; Thomsen et al. 2009), indoor lab experiments (Hoeffle et al. 2011), and correlative studies (Staehr et al. 2000; Forrest and Taylor 2003) 259 manipulative field-based impact experiments remained. These peer-reviewed papers experimentally quantified invasion impact on 101 aquatic non-native species and on 4 invasive taxa above the species level ('*Dreissena* mussels', 'trouts', 'predatory fish', and 'crabs', for brevity we also refer to these taxa as non-native 'species'). A total of 20 aquatic non-native species have been experimentally manipulated in more than 5 studies (Suppl. material 1), with 5 species being studied 10 times, including *Carcinus maenas* (a marine crab, 18 studies), 'trouts' (combined effects of freshwater *Oncorhynchus mykiss* and *Salvelinus fontinalis*, 12 studies), *Littorina littorea* (a marine snail, 11 studies), *Pacifastacus leniusculus* (a freshwater crayfish, 11 studies), and *Dreissena polymorpha* (a freshwater mussel, 10 studies).

Evaluating research in relation to *study attributes* revealed that many more papers were published in journals targeting general readers (130) than marine (61), freshwater (41) or freshwater and marine (27) readers. Publications of invasion impact papers increased rapidly for all journal types (Fig. 1a). The first study was published in 1972 (Hurlbert et al.), but very few studies were published in the 1970s (total of 2 species; 3 studies) or 1980s (8; 11). However, experimental approaches to testing invasion impacts became common in the 1990s (28; 43) and increased dramatically in the 2000s (79; 158). From 2010–2012 we identified experiments on 35 species in 44 studies. This trend corresponds to a general exponential decadal increase in published aquatic field-based invasion impact studies ($r^2 = 0.99$, $p = 0.0006$). Of the 259 impact papers, 12 were spatially pseudo-replicated or did not replicate treatment and/or control plots (Fig. 1b) and 22 did not report any variability around reported average impacts (Fig. 1b). We found 68 studies that reported impacts on multivariate or univariate community metrics (Fig. 1c), of which 35 quantified impact with multivariate plots, 32 with multivariate inferential tests, 52 on richness, 23 on diversity and 10 on evenness. Only two of the 68 studies reported all 5 community metrics (Hejda and Pyšek 2006; Albins 2013).

Furthermore, when we evaluated study characteristics in relation to *invader attributes* we found that more experiments have been done on non-native animals (75 species, 185 studies) than plants (30, 76) (Fig. 2a), on benthic (83, 199) than pelagic (22, 64) invaders (Fig. 2b), and on almost the same number of sessile (54, 116) and mobile (51, 143) invaders (Fig. 2c). Subdividing non-native animals into trophic position showed that carnivores (25, 73) were more studied than filter-feeders (27, 46) and omnivores (14, 44), and that few invasive herbivores and detritivores have been studied (10, 29) (Fig. 2d). Of these 10 species, 6 were herbivores with a capacity to denude large vegetation (the mammal *Myocastor coypus*, the bird *Cygnos olor* and the four snails *Littorina littorea*, *Bellamya chinensis*, *Physella acuta*, *Pomacea canaliculata*), whereas the

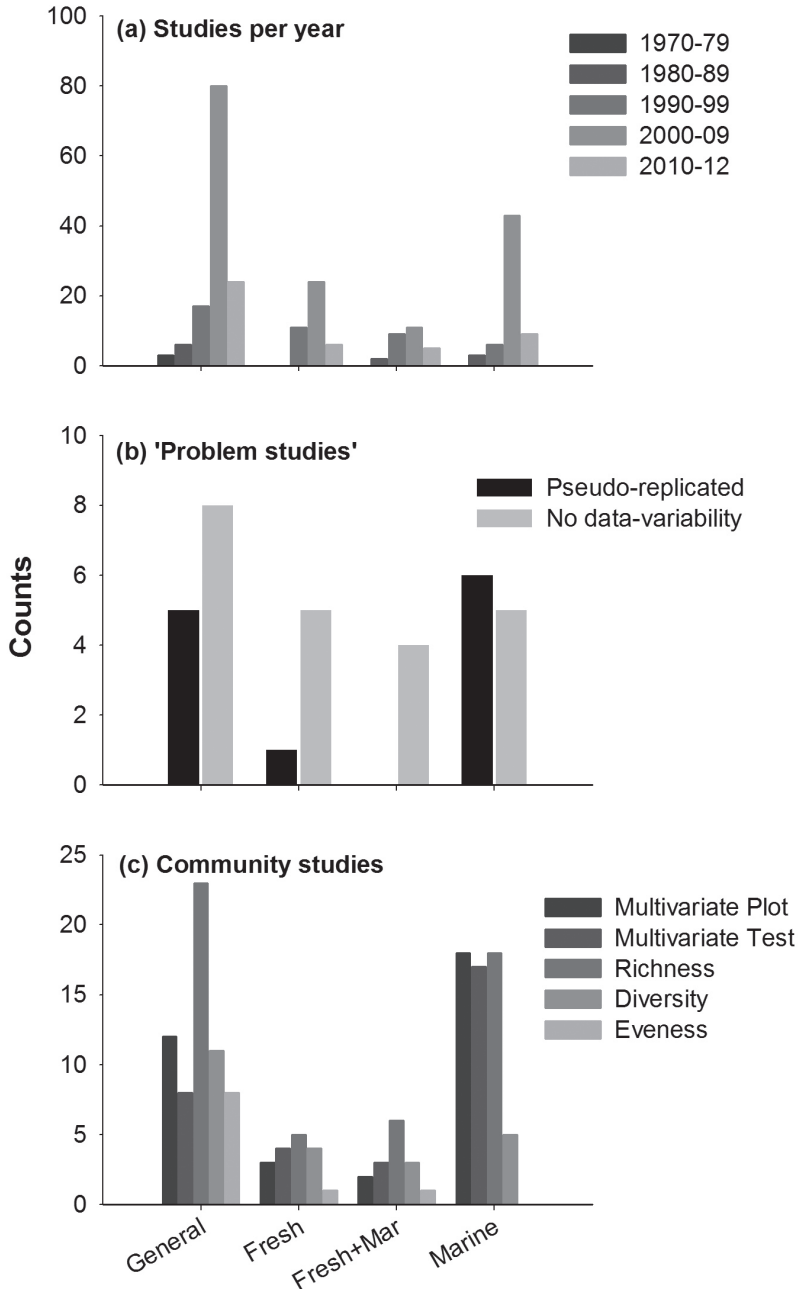


Figure 1. Aquatic invasion impact experiments published in general, freshwater, marine, and both freshwater and marine journals (see S1 for journal classification) **a** decadal trend in publication rates (the last bar only include studies published 2010–12) **b** Studies where the experimental design was spatially pseudo-replicated or did not replicate treatment or control plots, and studies that did not report any measure of variability for impact data **c** Community impact studies that quantified impact with graphical display, multivariate inferential tests, or on taxonomic richness, diversity or evenness.

remaining 4 non-native species were sediment-eaters and detritivorous snails and crustaceans (*Batillaria attramentaria*, *Ilyanassa obsoleta*, *Potamopyrgus antipodarum*, *Limnomysis benedeni*). The most frequent experiments were on non-native fish (20 species, 58 studies - where two studies were from marine systems and the lionfish *Pterois volitans*), vascular plants (20, 38) molluscs (18, 55), crustaceans (16, 53) and algae (10, 39). By contrast, relatively few experiments were on non-native tunicates (8 species, 7 studies), annelids (3, 7), amphibians (3, 5), mammals and birds (3, 5), bryozoans (2, 3), echinoderms (1, 3) or reptiles (1, 3) (Fig. 2e).

Evaluating study characteristics in relation to the *invaded system attributes* showed a strong geographical pattern (Fig. 3); impacts documented in the 259 papers represent studies from 30 countries and were strongly dominated by the USA (60 species; 137 studies). Furthermore, only 9 other countries have tested for impacts of ≥ 5 non-native species, including Australia (13; 21), Germany (8; 7), Brazil (6; 4), Canada (8; 11), Japan (6; 5), New Zealand (6, 5), Italy (5; 12), Spain (5; 10), and France (5; 4). This geographical pattern was also evident when grouped into continental scales; invasion impacts have been tested mainly in North America (59 species, 145 studies), Europe (30; 54), and Australasia (19; 26). Far fewer non-native species have been tested from South America (13; 10), Asia (8; 11), Africa (4; 8) and various islands (4; 5) (Fig. 3, 4a).

We also found a strong geographical pattern along a latitudinal (climate-related) gradient; most studies were from the mid-latitudes of 35–46° (69 species, 171 studies), followed by 23–34° (24; 36) and 47–58° (21; 33). By contrast, few non-native species have been studied from tropical or cold/polar regions (0–22° = 12 species, 14 studies; 59–90° = 5 species, 5 studies – and these studies were all from 59–64° N) (Fig. 3, 4b). Finally, we found that more studies have been conducted in freshwater (59 species, 143 studies) than marine (48; 116) habitats (Fig. 4c), or more specifically, that most aquatic invasive species have been studied in ponds (33; 43, including mesocosm experiments), followed by estuaries (30; 53), streams (18; 43), wetlands (15; 24), rocky subtidal (16; 21, including 3 species and 4 studies from coral reefs), lakes (15; 33), rocky intertidal (12; 32), and sandy open subtidal habitats (7; 11) (Fig. 4d).

Finally, when we compared our data to Hewitt & Campbell's compilation of marine non-native and cryptogenic species we found a significant slope, indicating that the number of marine species grouped into different invasive taxa (Fig. 5c; slope = 0.022, $p = 0.0001$, $n = 17$) and invaded biogeographical regions (Fig. 5d; slope = 0.021, $p = 0.0006$, $n = 18$) correlated with number of taxa and regions tested in manipulative field experiments. However, even though the line fit well generally, there were still over and under-represented taxa; for example, experimental studies on molluscs, angiosperms and chordates (mainly tunicates) were over-represented (well above the line), whereas fish, crustaceans and cnidarians were under-represented (well below the line). Similarly, experimental studies from the North East Pacific and the North West Atlantic were over-represented, whereas experimental studies from the Southern Pacific Ocean and the Mediterranean Sea were under-represented. Both regression slopes were small, showing that ca. 2 non-native species had been tested in field impact-experiments for every 100 known non-native marine species.

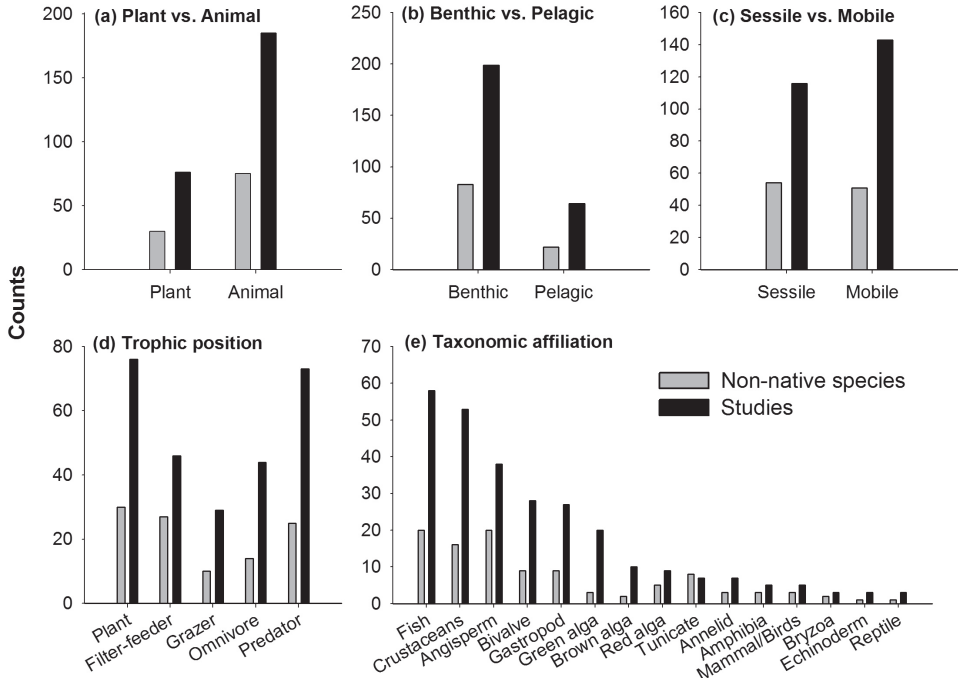


Figure 2. Aquatic invasion impact experiments classified by the attributes of the non-native species. Grey bars correspond to number of invasive species studied (total of 105 taxa); black bars correspond to the number of scientific studies (total of 259 studies). Non-native species were classified as **a** being a plant or animal **b** if they occupy the benthic or pelagic realm **c** if they are sessile or mobile **d** according to their trophic position (mud-eaters were classified as herbivores, as they consume diatoms), and **e** taxonomic affiliation.

Discussion

Virtually all the aquatic invasion examples presented in Charles Elton’s seminal book “The Ecology of Invasions by Animals and Plants” were based on anecdotal or observational data (Elton 1958), yet over the past half-century, intensive field experimentation evaluating the potential impact of non-native species have emerged. Today, invasion impacts have been quantified in field experiments for >100 aquatic non-native species published in at least 259 peer-reviewed papers. From this rapidly growing literature we identified taxonomic groups, regions and habitats that have been poorly studied and where additional experimental data are needed to improve our mechanistic understanding of how non-native species impact resident species, and to guide future research and management priorities. More specifically, we highlight that to provide general impact predictions, more experiments including more non-native species are needed from open coast sandy sediments, coral reefs, polar and tropical regions, the African continent, and on herbivores, as well as marine fish, crustaceans and cnidarians. Furthermore, invasion regulations and management standards are defined and set at the level of country, yet only 10 countries have tested for impacts of

≥5 different non-native species. Addressing these research gaps will allow researchers and managers to build stronger predictive models on how non-native species impact aquatic systems across taxa, habitats and biogeographical regions.

Attributes of individual studies. We found an exponential increase in experimental impact studies over the past few decades. If this trend continues, >500 experimental aquatic impact studies could be published in the next decade. It is vital that this (expensive) effort builds on previous research rather than repeats it; i.e., new experiments should be conducted in a context of the listed studies in the Suppl. material 1. For example, c. 5% of reviewed studies were spatially pseudo-replicated, a design that should be avoided whenever possible (although in some cases this may be impossible, especially for broad-scale studies) (Hargrove and Pickering 1992; Oksanen 2001; Wernberg et al. 2012). Still, this is a low percentage compared to other past ecological research fields (Hurlbert 1984; Wernberg et al. 2012), probably reflecting that experimental invasion biology is a relatively new and modern science (Fig. 1a) and that many non-native species can be manipulated *in situ* in small plots allowing for true replication. We also found that 14% of reviewed studies did not report any measure of variability around reported average impacts; and many more studies reported incomplete data variability (Fig. 1b). Not reporting variability around mean impacts implies that the experiments cannot be included in certain meta-analyses, thereby reducing its value in synthetic frameworks (Gurevitch and Hedges 1999). Given that it is a standard protocol to replicate randomly allocated treatments and controls, it could also be considered standard to report mean impact and associated data variability (if not in a paper then in online appendix) to provide a comparative scientific baseline and to allow for future re-analysis within synthetic frameworks.

We also noted that it was common practice to pool non-significant treatments, to not report non-significant effects, or to report only a subset of quantified responses. If future studies continue to value significance over effect size, for example only reporting significant results (the extreme case being the unknown number of studies that are never published because there are no significant results), the focus will remain on “high-impact invaders” only, thereby limiting our ability to understand contextual differences between high and low invasion impact (Pyšek et al. 2008; Ricciardi and Kipp 2008; Thomsen et al. 2011). We acknowledge that publications should be concise and sacrifice information, but suggest that average values and data variability are reported for all treatments on all responses at least in online appendices. Implementing such practices will make research more transparent and simpler to evaluate, and make it possible to extract unbiased data to build strong synthetic models across studies, ecosystems and habitats (Fernandez-Duque and Valeggia 1993). Almost half of all studies reported impacts on community metrics (Fig. 1c), thereby addressing a previously highlighted research gap (Parker et al. 1999). However, only few studies reported, in the same paper, impacts on 5 community metrics (Hejda and Pyšek 2006; Albins 2013) or showed mean impacts and associated variation from all treatments on all identified taxa (Casas et al. 2004; Ross et al. 2007). Community-impact experiments with extensive data-reporting are important to facilitate a better understanding on how non-native

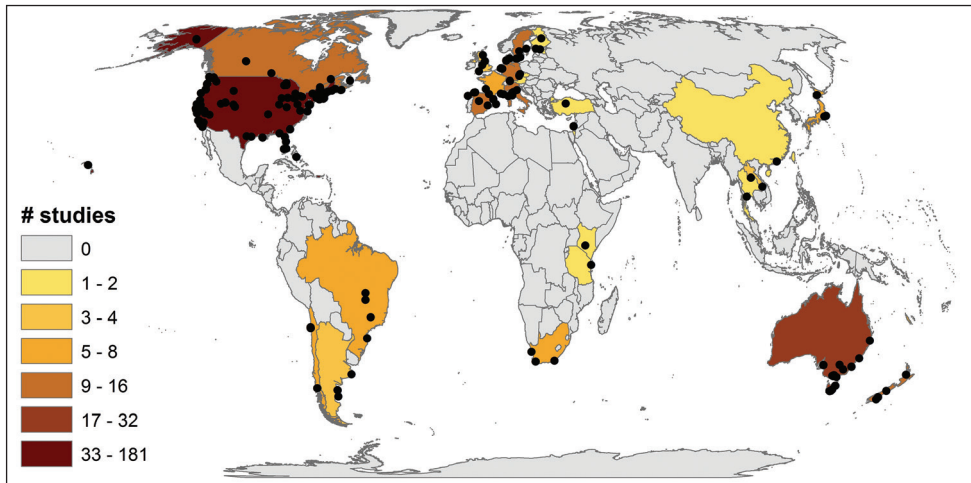


Figure 3. Global distribution of field based aquatic invasion impact experiments ($n = 301$; 259 reviewed studies + 42 extra locations from nested or multiple spatially separated experiments within studies).

species affect resident species because they, within a single environmental context, can quantify direct and indirect, strong and weak, and inter vs. intra-trophic effects.

Our literature list indicates that aquatic impact studies may have been overlooked in invasion biology. As stated in the introduction, reviews of plant invasion impacts have not included examples of impacts of seaweeds or seagrasses (cf. reviewed reference listings, Powell et al. 2011; Vilà et al. 2011; Pyšek et al. 2012), even though we reviewed 42 and 5 experimental impact studies on these two groups of marine invaders, respectively (Suppl. material 1). Similarly, an exhaustive analysis on research bias in invasion biology covering both aquatic and terrestrial systems, experimental and mensurative data, invasion impact and invasion success topics, and field and laboratory methodologies, may have underestimated aquatic invasions (Pyšek et al. 2008). For example, Pyšek et al. (2008) identified the first invasion paper from 1980 (Barrows), but we found, in our more constrained/specific review, three earlier examples (Hurlbert et al. 1972; Lubchenco 1978; Lubchenco and Menge 1978) and identified 2× and 1.3× more studies on invasions from non-native tunicates and *Carcinua maenas*, respectively. If aquatic studies continue to be under-represented in general invasion impact reviews, scientists may miss opportunities to build strong models and theories across ecosystems, and managers, conservationist and politicians who may manage linked terrestrial and aquatic systems may receive biased information about invasion impacts in their regulatory units.

Attributes of the non-native species. More than twice as many non-native animal species than plants have been tested in field impact experiments, most likely reflecting the fact that more non-native animals than plants have been found (Pyšek et al. 2008; Hewitt and Campbell 2010). However, non-native sessile organisms (plants + sessile animals) have been experimentally studied to the same degree as invasive mobile animals, despite the latter being a more species-rich group. Over-representation of

sessile species is not surprising because they are classical ecological test organisms (e.g., Connell 1961), are important in invasion biology because they are transported around the world on ship hulls (Hewitt and Campbell 2010), are relatively simple to manipulate and provide good systems to test invasion theories (Stachowicz et al. 2002; Dunstan and Johnson 2004), and can be habitat-formers and ecosystem engineers with disproportionately large effects on community structures (Crooks 2002; Ward and Ricciardi 2007; Thomsen et al. 2010). We found four times more benthic species studied than pelagic, in part reflecting that there are more of them (they include diverse marine biofouling communities) (Hewitt and Campbell 2010), in part because pelagic organisms are more difficult to control and manipulate in field experiments. It is noteworthy, however, that non-native freshwater fish, many of which are predominantly pelagic, were well-studied, which highlights that mesocosms and caging have successfully been used to quantify impacts of these species.

Analysis across trophic levels revealed that non-native herbivores have been poorly studied. Studies are clearly needed on more aquatic herbivores to better understand, predict and manage their impacts on aquatic plant communities (Lubchenco 1978; Eastwood et al. 2007) and/or provide resource subsidies for higher trophic levels (Trussell et al. 2002). Most experiments on non-native animals were conducted with filter-feeders, for the same reasons listed above for sessile species (most sessile animals are filter-feeders). The plethora of experiments conducted with sessile filter-feeders also highlights a key difference between aquatic and terrestrial invasion ecology in that terrestrial systems have no ecologically equivalent organisms.

Only 2% of recently tallied marine non-native and cryptogenic species have been tested in field impact experiments, demonstrating that basic mechanistic insight on impact is lacking for most marine non-native species. This number varied with taxonomic groups from 0% (e.g. cnidarians, porifera) to 22% (angiosperms). We found few experimental impact studies conducted on non-native cnidarians, porifera, annelids, bryozoans, echinoderms, amphibians, mammals, or reptiles, reflecting in part, that there are few species in these groups (at least for marine organisms, Fig. 5, Hewitt and Campbell 2010). Molluscs, angiosperms and tunicates were over-represented (Fig. 5c) whereas marine fish, crustacean and cnidarians were under-represented. The former taxa are sessile or slow-mobile, easy to manipulate, and typically provide important ecosystem services by controlling ecosystem fluxes and patterns of biodiversity (Crooks 2002; Thomsen et al. 2010), whereas the latter group are more difficult to manipulate; for example, manipulating many non-native marine fish and cnidaria requires large mesocosms/cages, and many crustaceans are small and cryptic. More specifically, invasion impacts of marine fish have only been tested in two studies, both on the decorative territorial lionfish on tropical reefs, even though 166 marine fish invaders have been tallied (Hewitt and Campbell 2010). By contrast, impacts on freshwater fish have been tested on 19 out of the approximately 422 (5%) non-native species that occur globally. There are several possible reasons why there are more experimental studies on freshwater than marine invasive fish. First, based on current estimates, there appear to be more freshwater than marine non-native fish species (this needs to be

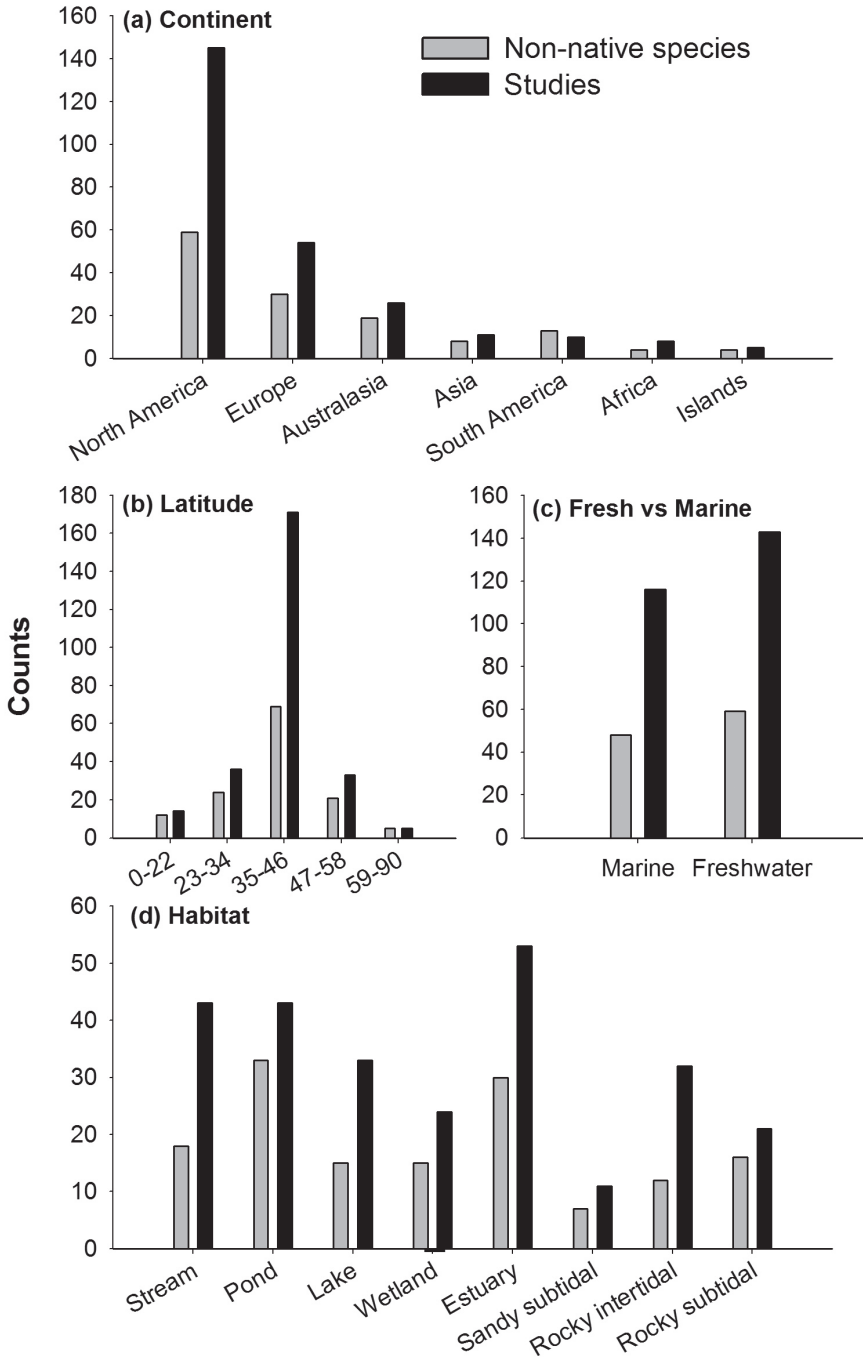


Figure 4. Aquatic invasion impact experiments classified by the attributes of the invaded system. Grey bars correspond to number of non-native species studied out of 105 taxa, and black bars correspond to the number of scientific studies out of 259. The invaded system was classified according to **a** continent **b** latitude **c** if it was a marine or freshwater system, and **d** habitat.

verified in the peer-reviewed literature). Secondly, many non-native freshwater fish are important economically, for recreational purposes, have been intentionally introduced to control diseases and weeds or to establish a fishery (Hofkin et al. 1991; Hart and Pitcher 1995; Pipalova 2006), and occur in less open and more accessible habitats than most marine species. Finally, freshwater fishes are often better adapted to survive in small-scale enclosed mesocosms (i.e. are easier to conduct experiments with) and, due to their enclosed nature, freshwater systems are amendable to whole-lake and whole-stream experiments where invasion densities are manipulated in replicated experiment at the system level (Pope et al. 2009).

Attributes of the invaded system. Not surprisingly, we found strong geographical patterns; many more aquatic invasion impact studies have been done in North America than in other countries or continents. Analysing biogeographical patterns in more detail for marine non-native species revealed a similar pattern; studies from the NE Pacific and NW Atlantic were over-represented (Fig. 4d) compared to most other marine regions. Scientific over-representation from North America, Europe and Australasia, has been documented across ecological sciences, including research on climate changes (Wernberg et al. 2012), terrestrial ecosystems (Martin et al. 2012), conservation (Clark and May 2002; Lawler et al. 2006; Darwall et al. 2011) and invasions (Pyšek et al. 2008). This geographical pattern is likely associated with historical and present-day intensive economic-related activities, such as high transport of goods and people across international borders, and therefore high propagule pressure (Pyšek et al. 2010), that many universities/researchers are located there, and that better historical and taxonomic baseline data makes it easier to identify what is native, cryptogenic and introduced. Note however, that dramatic historical invasions are still being identified also from intensively studied areas (Thomsen et al. 2006; Blakeslee and Byers 2008).

We also noted that invasion impacts have been tested with few non-native species for the majority of countries, a typical spatial unit with a specific set of management rules and regulations for invasive species. Given that invasion impacts can depend strongly on the local and regional context (Strayer et al. 2006; Thomsen et al. 2011), this low level of 'invasion impact replication', even at broad country scales, makes it difficult to build predictive impact models for most regions around the world. Latitudinal patterns mirrored patterns observed between continents, oceans and countries with 66% of all studies being conducted within a relatively narrow mid-latitude band. By contrast, few studies were conducted at low or high latitudes, and no studies were conducted beyond 65° - possible reflecting lacking baseline information, few researchers, and logistically challenging environments (Martin et al. 2012) and/or a real pattern of relatively fewer non-native species in polar and tropical regions (in particular for marine systems, Ruiz et al. 1999). However, for freshwater non-native species we expected more field experiments to be conducted in the tropics, because mensurative data suggest relatively large impacts in subtropical and tropical ponds and lakes from intentional fish and crustacean introductions (Miller 1989; Fernando 1991; Ogutu-Ohwayo 1993; Hart and Pitcher 1995) - the textbook case study being how the Nile perch *Lates niloticus* has contributed to

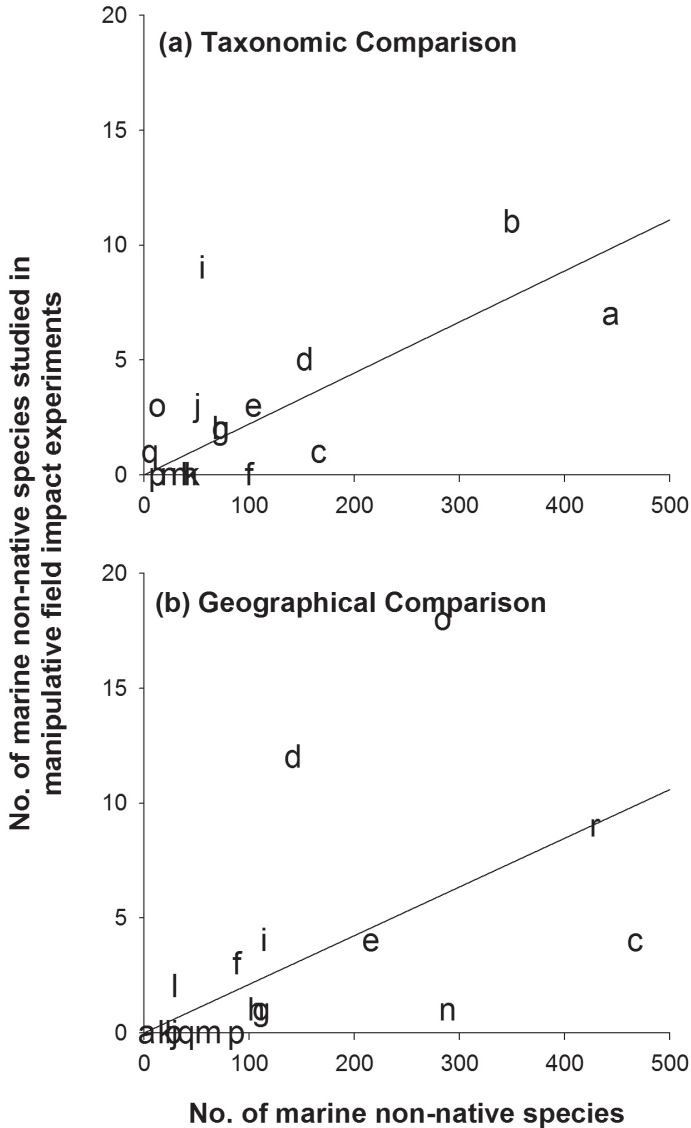


Figure 5. Marine invasion impact experiments classified according to **a** taxonomic identity of the non-native species and **b** invaded biogeographical regions. Graphs depict linear regression between *manipulative marine field-based invasion impact studies* against the total number of *non-native and cryptogenic marine species*, see manuscript text for regression data. Abbreviations (following Pyšek et al. 2008 and Hewitt and Campbell 2010); **a:** a = Arthropoda; b = Mollusca; c = Fish, d = Rhodophyta; e = Annelida; f = Cnidaria; g = Heterokontophyta; h = Ectoprocta; i = Chordata (minus fish); j = Green; k = Bacillariophyta; l = Porifera; m = Dinoflagellates; n = Platyhelminthes; o = Magnoliophyta; p = Protozoa; q = Echinodermata. **b:** a = Antarctica; b = Arctic; c = Mediterranean; d = NW Atlantic; e = NE Atlantic; f = Baltic Sea; g = Wider Caribbean; h = W Africa; i = S Atlantic Ocean; j = Central Indian Ocean; k = Arabian Sea; l = E Africa; m = E Asian Seas; n = S Pacific ocean; o = NE Pacific ocean; p = NW Pacific ocean; q = SE Pacific ocean; r = Australia & New Zealand.

extinction of endemic cichlids fishes (Ogutu-Ohwayo 1993), but supported by little experimental evidence.

Research gaps associated with invaded habitat attributes were less pronounced compared to the geographical patterns, as also noted more generally for all types of invasion studies (Pyšek et al. 2008). Thus, invaded freshwater and marine ecosystems were both represented with more than 100 studies and most aquatic habitat has been included in field based impact studies (Fig. 4d). Still, relatively few experiments have been conducted in sandy open subtidal habitats and on coral reefs. Open sandy habitats have relatively few species in low densities (Defeo et al. 2009) and probably also have few invaders (Hewitt and Campbell 2010) but coral reefs may be significantly understudied. For example, >100 marine non-native species have been registered in Hawaii alone, with many on coral reefs (Coles and Eldredge 2002), and many species have been intentionally introduced for aquaculture, some of which have spread to adjacent reefs (Russell 1983). Alternatively, there may be few outbreaks of non-native species on coral reefs compared to more common outbreaks of native species, including diseases, seaweeds, urchins and sea stars (Lessios 1995; McCook et al. 2001; Bruno et al. 2003). Finally, we found most non-native species to be studied in freshwater ponds, largely because of common use of outdoor mesocosms in freshwater studies (Suppl. material 1), where water, plants and/or animals have been added to tanks to create semi-natural pond test systems [indeed the first identified invasion impact experiment, published in *Science* four decades ago, was a pond-mesocosm experiment (Hurlbert et al. 1972)].

Conclusions

Over the past four decades, invasion impacts have been quantified in field experiments for more than 100 aquatic non-native species published in at least 259 peer-reviewed papers. However, despite this intensive research, our ability to make generalizations and predictions remain limited because impact depends on the specific context that links attributes of the non-native species and the invaded system. Regardless of the large experimental effort, our review revealed substantial gaps in the collective knowledge. Specifically, of the 101 test species, only one was a marine fish and only six were herbivores. Similarly, of the 259 papers, only 3% were from Africa, <2% from high latitudes and only 1% from coral reefs. We therefore recommend that future experiments target these less studied non-native species, regions and habitats. We also noted that it is standard to pool or not report non-significant treatments and responses, a procedure that limits synthetic advancement by biasing meta-analysis and by making it difficult to identify invaders and environmental conditions that result in weak impacts. We therefore also recommend to report non-significant and low impact data with associated data-variability (or for continuous design show scatter-plots with explicit identification of overlapping points) and to report non-pooled impact data for all treatments and responses (even if just in online appendixes). We suggest that our

ability to extrapolate impact assessments across space, time and taxa will increase significantly if these research gaps are targeted. More generally, we argue that impact experiments should manipulate new and novel combinations of different non-native species, different invaded places, different resident organisms, different abiotic conditions and different resource levels, than has already been tested in past experiments (cf. Suppl. material 1). In conclusion, the last 40 years of research activity has provided an excellent starting point to understand invasion impact mechanistically, but we are still far from being able to build generalized and predictive models of invasion impacts on local management scales of most invaders.

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Supplementary material I

List of reviewed references.

Authors: Mads S. Thomsen, Thomas Wernberg, Julian D. Olden, James E. Byers, John F. Bruno, Brian R. Silliman & David R. Schiel

Data type: reference list

Explanation note: References are divided into general (G), freshwater (F), aquatic (FM) or marine (M) journals. References with an asterisk (*) did not replicate or pseudo-replicated either treatment and/or control plots.

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Environmental and economic impact of alien terrestrial arthropods in Europe

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Abstract

In the last few decades, the abundance and importance of invasive alien species have grown continuously due to the undiminished growth of global trade. In most cases, arthropod introductions were unintended and occurred as hitchhikers or contaminants. Alien arthropods can have significant environmental impacts and can be economically costly. To measure these impacts, we expand a generic impact scoring system initially developed for mammals and birds, and applied it to terrestrial arthropods. It consists of six environmental impact categories and six economic impact categories, each with five impact levels. Information on impact was derived from an intensive analysis of published scientific literature. The scoring of the 77 most widely distributed arthropod species alien to Europe revealed the mite *Varroa destructor* as the most harmful species, followed by the Chinese longhorn beetle *Anoplophora chinensis* and the Argentine ant *Linepithema humile*. The highest environmental impact is through herbivory, disease transmission, and ecosystem impacts. The highest economic impact is on agriculture and human infrastructure and administration. The generic impact scoring system allows the impact scores of vertebrates and arthropods to be compared, thus serving as a background for the decision making processes of policy makers and stakeholders.

Keywords

Invasive terrestrial arthropods, non-native, generic impact scoring system, prioritization

Introduction

The number of alien species in Europe has been increasing over the last few decades (DAISIE 2009). Global trade and worldwide travel have offered many species the possibility to spread into distant biogeographic areas they would have otherwise been unable to reach (Pimentel et al. 2005; Nentwig 2007). Following an introduction event, alien species may establish, increase in number and spread (Pyšek and Richardson 2010). It is accepted that propagule pressure, i.e., the number of individuals and introductions as well as their reproductive capacity, is one of the key elements required for understanding the success of alien species establishment (Colautti et al. 2006). With increasing spread, alien species affect native species and the ecosystem (which can be analysed as environmental impact) and the economy (economic impact). Such abundant alien species with high impact are called invasive species following the definition of Blackburn et al. (2011). Along with other drivers of ecosystem degradation such as climate change, pollution and habitat change, biological invasions are seen as one of the main causes of biodiversity decline leading to reduced ecosystem services worldwide (Millennium Ecosystem Assessment 2005). Usually, the larger the population of an invasive species and the faster its spread, the higher its potential impact and the more difficult and expensive it will be to control or eradicate. Therefore, it is highly recommended to react to alien and invasive species as early as possible (e.g., Sakai et al. 2001; Wittenberg and Cock 2001; Leung et al. 2002).

The suitability of a measure or, more generally, the need for a given action in combatting alien species will depend on the circumstances (Pyšek and Richardson 2010). While it is best to prevent introductions of alien species in the first place, once they have established, decisions need to be made regarding the control measures and priorities. The UN Convention on Biological Diversity (1992) recommends to “eradicate those alien species which threaten ecosystems, habitats or species” and Genovesi (2005) even advises to eradicate alien species known to have a high environmental and economic impact, immediately after their first record in a newly invaded area. But how can the impact of an alien and invasive species be measured and comparatively quantified?

Often, the impact of an invasive species is not known for a specific invaded area, but for other invaded areas or its area of origin. Therefore, many approaches to estimate the potential impact of an alien species try to extrapolate from such data to a new situation, often including expert knowledge or expert guess. While there are many assessments of alien species available, it is not intended to provide a comprehensive overview in this paper. Examples include the Australian weed risk assessment, which evaluates the potential of a plant to become an environmental or agricultural weed prior to its introduction (Pheloung et al. 1999) and the risk assessment of alien fish species, which is a quantitative approach to categorize fish species causing high damage (Copp et al. 2005). Zaiko et al. (2011) define a “biopollution level” of invasive species and Kumschick et al. (2012) propose an evaluation system which relies, among others, on the selection and weighting of criteria by stakeholders and decision makers. Recent overviews on the development of risk assessments and their current diversity are given by Essl et al. (2011) and Kumschick and Richardson (2013).

As an alternative to assessments that are based only on expert knowledge, Nentwig et al. (2010) developed a generic impact scoring system, which relies exclusively on published information on the impact of a given species in its invaded area. Generally speaking, information on comparable impacts of a species in its native area can also be used, assuming that a species shows in principle the same behaviour in native and invaded areas (even if adaptation may lead to some flexibility as Wright et al. (2010) suggest). This system was first developed for mammals and later adapted to birds (Nentwig et al. 2010; Kumschick and Nentwig 2010). The strength of this system is its objectivity and reproducibility which allows a scale-independent assessment that can easily be adapted as new knowledge becomes available. By comparing the impact scores of different species, science-based recommendations for prioritization, eradication and other management recommendations are possible.

Interestingly, most of the impact assessment tools for animals deal with vertebrates. Arthropods comprise the majority of all species and can have a huge environmental and economic impact, but have not been considered appropriately. Exceptions are plant pests, assessed by pest risk assessments, which are among the most comprehensive pest risk assessments for alien species (EPPO 2012). Many arthropods are frequent hitchhikers (or stowaways) carried with human transport (e.g., ship and aircraft) and contaminants of specific commodities (Hulme et al. 2008). For example, the Argentine ant *Linepithema humile*, a typical hitchhiker and native to South America, has invaded most continents and is able to displace not only native ants but also affect other arthropods, birds, lizards and mammals through predation, competition for nesting sites or by tending arthropods and plants, thus impacting pollination (Holway et al. 2002; Lach 2007; Davis et al. 2008). Other examples concern species from the whitefly *Bemisia tabaci* species complex, which entered Europe as a contaminant of potted plants. The ability to transmit plant viruses combined with a wide host range has made some of these species limiting factors in the production of food and fibre crops as well as ornamentals in many countries (Jones 2003; Naranjo et al. 1996; Oliveira et al. 2001). Many alien and invasive insects are also of medical importance for humans. The Asian tiger mosquito *Aedes albopictus*, originating from South-East Asia, has invaded Europe and many countries in the Americas, the Middle East, and Africa. It is a vector for many tropical diseases, such as dengue fever (Enserink 2008; Paupy et al. 2009; Schaffner et al. 2009).

In the last few years, the number of publications on alien and invasive insects and their ecological impact has increased continuously. However, two thirds of studies on the ecological impact of alien insects were conducted in North America, indicating that research for Europe is lagging far behind (Kenis et al. 2009). This lack of knowledge is not justified by a lack of importance, when following the analysis of Vilà et al. (2010) mentioning 2481 alien invertebrate species (342 with ecological impact and 601 with economic impact), but only 358 alien terrestrial vertebrate species (109 with ecological impact and 138 with economic impact).

Whereas terrestrial vertebrates have an influence on most aspects of the environment and economy, the main impacts of terrestrial arthropods are considered to be “only” on ecosystems and agriculture (Kenis and Branco 2010; Vilà et al. 2010). Even

if the range of these fields of impact may be assumed to be narrow, the impact of terrestrial invertebrates can be comparable to vertebrates, because the importance of ecosystem services provided by insects is crucial and their disruption can produce enormous costs. To give one example, the global economic value of insect pollination was estimated to be €153 billion and €22 billion for Europe (Gallai et al. 2009).

Having one system for measuring the environmental and economic impact of vertebrates and invertebrates would be highly advantageous. This would allow the impact of alien species to be measured and analysed in a comparative manner, thus enabling management actions to be prioritized between different taxa. Therefore, in this study we modified the generic impact scoring system, initially developed for mammals and birds (Nentwig et al. 2010; Kumschick and Nentwig 2010) to arthropods.

Methods

The generic impact scoring system was developed by Nentwig et al. (2010) for mammals and was subsequently modified for birds (Kumschick and Nentwig 2010). The principle of the generic impact scoring system is the separation of the impacts of invasive alien species into environmental and economic impacts. These two different impact groups are further subdivided into six different categories (Table 1), each with a formal description (Suppl. material 1). For each of these twelve categories, there are five levels of intensity plus a zero impact level for no impact known or detectable. The scoring points represent the intensity level and range from 1 (minor impact) to 5 (major impact), resulting in a maximum of sixty points for species with the highest impact. The description of the twelve categories and the corresponding intensity levels are summarized in the “Handbook of the generic impact scoring system” (Suppl. material 1).

Since the expansion of the scoring system to a species-rich group, arthropods, is best done with a set of species with highest impact, we performed a careful selection of those species which currently exert the highest impact in Europe. Another, more pragmatic reason for such a selection was that it was not possible to screen hundreds of species. We performed this selection in four steps. First, we selected those species which are alien to Europe (i.e., origin outside Europe), leading to the exclusion of species with unknown origin (cryptogenic species) and species alien within Europe. Second, from this list we selected the alien species with the widest distribution in Europe. Because the distribution of a given alien species is generally correlated with its invasiveness, the number of invaded countries is a powerful indicator for the impact of a particular species at a larger scale (Pyšek et al. 2008). Therefore, we compared data about the distribution of alien terrestrial arthropods from the DAISIE database (DAISIE 2012) and from Roques et al. (2010), which provides slightly more recent data. All species that were reported in more than twenty European countries in either of the sources were selected. We defined Europe in a reasonable biogeographical context: the European continent and its islands (without the Azores, Canary Islands, and Madeira), including Ukraine, Belarus and the European part of Russia in the east. Third,

Table 1. Impact categories with respect to environmental and economic impacts. The description of the twelve categories and the corresponding intensity levels are summarized in the “Handbook of the generic impact scoring system” (Suppl. material 1).

1 Environmental impacts
1.1 Impacts on plants or vegetation through herbivory
1.2 Impacts on animals through predation or parasitism
1.3 Impacts on other species through competition
1.4 Impacts through transmission of diseases or parasites to native species
1.5 Impacts through hybridization
1.6 Impacts on ecosystems
2. Economic impacts
2.1 Impacts on agricultural production
2.2 Impacts on animal production
2.3 Impacts on forestry production
2.4 Impacts on human infrastructure and administration
2.5 Impacts on human health
2.6 Impacts on human social life

we ensured that all terrestrial arthropods that appear on the list of the “hundred of the worst alien invasive species” presented on the DAISIE (2012) website were included. Because the spread of a species needs time, our list was completed in a fourth step by adding species first recorded in Europe after the year 2000 and now occur in eight or more countries, according to Roques et al. (2010). This fourth step was undertaken to compensate for a potential data bias concerning the more recently introduced and rapidly spreading species. This resulted in a list of 77 terrestrial arthropod species alien to Europe and invasive in many countries.

The scoring of these 77 arthropod species was carried out using published information from the scientific literature. The literature search was conducted using the ISI Web of Knowledge. As a search string, the scientific species names combined with the following terms of the descriptions of the impact categories were used: herbivory, predation, parasitism, competition, transmission of disease, hybridization, ecosystem, agriculture, livestock, aquaculture, forestry, host, pesticide and human health. Additionally, information on the biology of a species was obtained using the following terms along with the scientific species names: biodiversity, economic impact, yield loss, crop pest, Europe, allergens, economic importance and economic loss.

From these publications (Suppl. material 2), the information relevant to species impact was translated to the particular impact level of the scoring system, ranging from 0 to 5 (Suppl. material 1). For completeness, we also cross-checked the information obtained from the literature search with general overview articles available in databases on alien and invasive species. These included the Invasive Species Compendium (CABI 2012), the Global Invasive Species Database (GISD 2012), the European Network on Invasive Alien Species (NOBANIS 2012), the European and Mediterranean Plant Protection Organization (EPPO 2012) and DAISIE (2012).

It was necessary to modify the definitions used in the vertebrate version of the “Handbook of the generic impact scoring system” to adapt this method to arthropods (Suppl. material 1). In general, this led to broader impact definitions or descriptions per impact category. These modified descriptions made it possible to assign all published impact reports to an appropriate impact category and impact level. Since we consider the repeatability of the results of this scoring process to be very important, the second author tested this by independently scoring a number of randomly chosen species. The test showed a very good match of the final scores, which differed by no more than one or two impact points per species.

Results

The 77 invasive alien arthropod species we selected belong to 13 orders and 38 families of insects, myriapods and mites (Table 2). Hemiptera and Coleoptera comprise most species (64%) whereas many orders are represented by only one or a few species, such as Acari, Blattodea and Chilopoda (Figure 1a). These 77 species have a combined total impact of 449.5 impact points, which is distributed among the higher taxa more or less according to the number of species. Only Hemiptera and Hymenoptera seem to produce an overall lower impact (42% of species have 28% of impact points), whereas Acari (4% of species, *Varroa destructor*, *Panonychus citri* and *Brevipalpus obovatus*) have 11% of total impact (Figure 1b).

Overall, 183.5 impact points (41%) originated from environmental impacts and 266 impact points (59%) originated from economic impacts. Among environmental categories, invasive alien arthropods had the largest impact on the ecosystem (20% of total impact), followed by impact through herbivory (10%). Impact through hybridization was not reported. From an economic point of view, the main impacts of invasive alien arthropods were on agriculture (29%) and on human infrastructure and administration (18%). Only *Varroa destructor* showed an impact on animal production resulting in 1% of the total impact (Figure 2).

The five most harmful invasive alien species are the mite *Varroa destructor*, the Argentine ant *Linepithema humile*, the Chinese longhorn beetles *Anoplophora glabripennis* and *A. chinensis*, and the harlequin ladybird *Harmonia axyridis*. In the categories of environmental impact *Varroa destructor*, *Linepithema humile* and *Harmonia axyridis* are the most harmful species, whereas in the categories of economic impact, the highest scoring species are *Varroa destructor*, the citrus red mite *Panonychus citri* and both *Anoplophora* species (Table 2).

Using the impact data for mammals and birds from the studies by Nentwig et al. (2010) and Kumschick and Nentwig (2010), it is possible to compare the impacts of these three taxa. Figure 3 illustrates the mean environmental and economic impacts of the 20 highest scoring mammals, birds and arthropods. It shows that the impact increases from birds, with the lowest (average environmental impact 4.4; economic impact 2.4) to arthropods with a medium impact (environmental impact 6.4; eco-

Table 2. Environmental, economic and total impact scores of all selected 77 invasive alien arthropod species. Impact categories 1.1 to 1.6 refer to environmental impact (1.1 on plants or vegetation through herbivory, 1.2 on animals through predation or parasitism, 1.3 on other species through competition, 1.4 through transmission of disease or parasites to native species, 1.5 through hybridization, 1.6 on ecosystems) and impact categories 2.1 to 2.6 refer to economic impact categories (2.1 on agricultural production, 2.2 on animal production, 2.3 on forestry, 2.4 on human infrastructure and administration, 2.5 on human health, and 2.6 on human social life).

Class / Order	Family	Species	Impact categories													Total	
			1.1	1.2	1.3	1.4	1.5	1.6	2.1	2.2	2.3	2.4	2.5	2.6			
Acari	Trombidiformes	<i>Brevipalpus obovatus</i>	1.5	0	0	2	0	0	3	0	0	0	0	0	0	0	6.5
		<i>Panonychus citri</i>	0.5	0	0	0	0	3	5	0	0	3	2.5	0	0	14	
	Varroidae	<i>Varroa destructor</i>	0	5	0	5	0	5	5	5	0	3.5	1	1	30.5		
Chilopoda	Henicopidae	<i>Lamycetes emarginatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0		
Diplopoda	Paradoxosomatidae	<i>Oxidus gracilis</i>	1	0	0	0	0	3	0	0	0	0	0	0	4		
Blattodea	Blattidae	<i>Periplaneta americana</i>	0	0	0	0	0	2.5	0	0	0	3	0	5.5			
	Anobiidae	<i>Pinus tectus</i>	0	0	0	0	0	3	0	0	3	0	0	6			
	Anthicidae	<i>Omonadus floralis</i>	0	0	0	0	0	1.5	0	0	0	0	0	1.5			
Bostriidae	Carabidae	<i>Stricticomus tobias</i>	0	0	0	0	0	0	0	0	0	0	0	0			
		<i>Rhyzopertha dominica</i>	0	0	0	0	0	2	3.5	0	1	3	0	0	9.5		
		<i>Trechicus nigriceps</i>	0	0	0	0	0	0	0	0	0	0	0	0	0		
Coleoptera	Cerambycidae	<i>Anoplophora chinensis</i>	3.5	0	0	0	0	4	3.5	0	4	3	0	3	21		
		<i>Anoplophora glabripennis</i>	3	0	0	0	0	4	0	4	3	0	3	17			
		<i>Acanthoscelides obrectus</i>	2	0	0	0	0	3	3	0	0	2	0	0	10		
Chrysomelidae	Chrysomelidae	<i>Bruchus pisorum</i>	1	0	0	0	0	3	4	0	0	2	0	0	10		
		<i>Bruchus rufimanus</i>	1	0	0	0	0	0	1	0	0	0	0	0	2		
		<i>Callosobruchus chinensis</i>	1	0	0	0	0	3	4	0	0	2.5	1	0	11.5		
		<i>Diabrotica virgifera</i>	0	0	0	0	0	3	4	0	0	3	0	0	10		
		<i>Leptinotarsa decemlineata</i>	1	0	0	0	0	3	3	0	0	3.5	0	0	10.5		
Coccinellidae	Cryptophagidae	<i>Harmonia axyridis</i>	0	4	2	0	0	3	2	0	0	2.5	2	1	16.5		
		<i>Caenoscelis subdeplanata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0		
		<i>Sitophilus oryzae</i>	0	0	0	0	0	3	4	0	0	3	0	0	10		
Nitidulidae	Nitidulidae	<i>Cartodere nodifer</i>	0	0	0	0	0	0	0	0	0	0	0	0	0		
		<i>Carpophilus marginellus</i>	0	0	0	0	0	0	1	0	0	0	0	0	1		

Class / Order	Family	Species	Impact categories													Total
			1.1	1.2	1.3	1.4	1.5	1.6	2.1	2.2	2.3	2.4	2.5	2.6		
Hymenoptera	Diaspididae	<i>Saissetia oleae</i>	0	0	0	0	0	2	3	0	0	2	0	0	7	
		<i>Aspidiotus nerii</i>	0	0	0	0	0	1	2	0	0	0	0	0	3	
		<i>Diaspidiotus perniciosus</i>	1	0	0	0	0	3	4	0	0	3	0	0	11	
	Membracidae	<i>Stictocephala bisonia</i>	1	0	0	0	0	1	0	0	0	0	0	0	2	
		<i>Pseudococcus viburni</i>	1	0	0	1	0	0	3	0	0	1	0	0	6	
	Aphelinidae	<i>Aphytis mytilaspidis</i>	0	0	0	0	0	1	0	0	0	0	0	0	1	
		<i>Encarsia formosa</i>	0	0	0	0	0	1	0	0	0	0	0	0	1	
		<i>Copidosoma floridanum</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	
	Encyrtidae	<i>Leptomastix dactylopi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	
		<i>Hypoponera punctatissima</i>	0	0	0	0	0	0	0	0	0	0	0	0	1	
	Formicidae	<i>Linepithema humile</i>	2	2	4	0	0	4	2	0	0	3	0	0	17	
		<i>Monomorium pharaonis</i>	0	0	0	0	0	1	0	0	0	1	2	2	6	
		<i>Megastigmus spermotrophus</i>	0	0	0	0	0	0	0	0	2	0	0	0	2	
Arctidae	<i>Hyphantria cunea</i>	2	0	0	0	0	1	2	0	1	1	0	1	8		
	<i>Sitotroga cerealella</i>	0	0	0	0	0	2	3	0	0	2	0	0	7		
Lepidoptera	Gelechiidae	<i>Tuta absoluta</i>	2	0	0	0	0	3	5	0	0	3.5	0	0	13.5	
		<i>Spodoptera littoralis</i>	0	0	0	0	0	3	3	0	0	2.5	0	0	8.5	
	Tineidae	<i>Tinea translucens</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	
Siphonaptera	Ceratophyllidae	<i>Grapholita molesta</i>	0	0	0	0	0	4	4	0	0	2	1	0	11	
		<i>Nosopsyllus fasciatus</i>	0	1	0	2	0	0	0	0	0	0	1	0	4	
Thysanoptera	Thripidae	<i>Frankliniella occidentalis</i>	2	0	0	3	0	3	4	0	0	3	1	0	16	
		<i>Heliothrips haemorrhoidalis</i>	2	0	0	0	0	2	3	0	1	2	0	0	10	
		<i>Parthenothrips dracaenae</i>	2	0	0	0	0	0	2.5	0	0	0	0	0	4.5	
		Total	43.5	13	6	30	0	91	132.5	5	14	79	20.5	15	449.5	

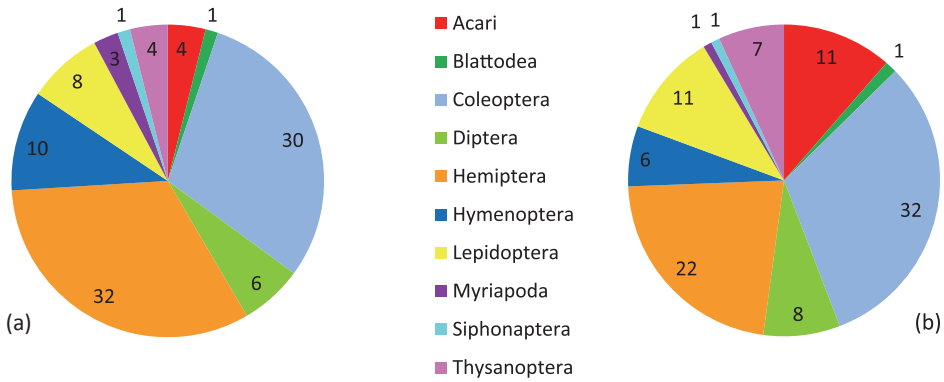


Figure 1. (a) Percentage of species representing a particular higher taxon of terrestrial invasive alien arthropods and (b) percentage of the impact points of these taxa of the total impact points produced by terrestrial arthropods (77 species). This comparison indicates that the impact of some taxa is higher than estimated from their frequency.

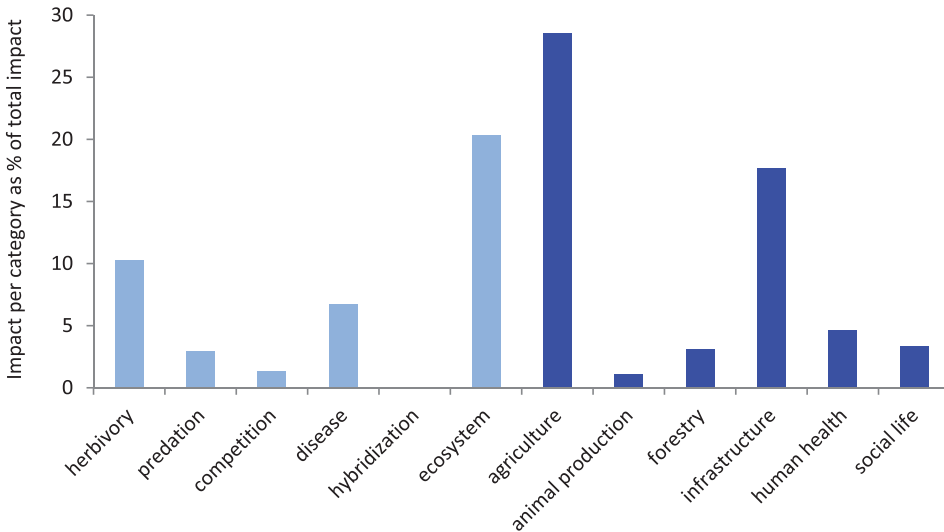


Figure 2. Distribution of the impacts (%) of 77 species of invasive alien arthropods among six impact categories each in the field of environmental (light blue) and economic impact (dark blue).

conomic impact 7.9) to mammals with the highest overall impact (environmental impact 11.4; economic impact 10.7). For the environmental categories, arthropods reach the highest scores by influencing ecosystems (mean 3.2), while mammals score highest due to their impact on herbivory and the transmission of diseases (means of 3). The highest impact of birds is through hybridization with native species (mean 2.2) (Figure 4). Among all categories of economic impact, arthropods score the highest for their impact on agriculture (mean of 3.2) and human infrastructure and administration (mean

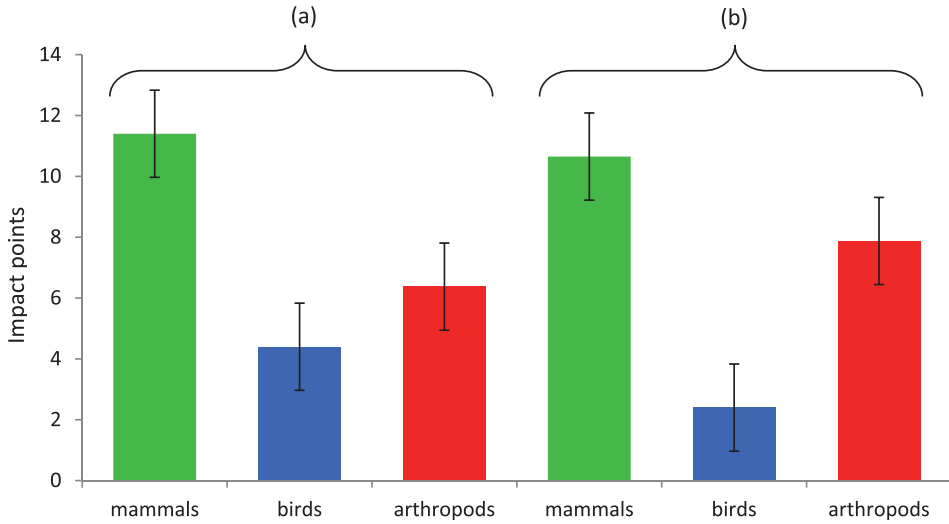


Figure 3. The mean impact and standard deviation of the 20 highest scoring species of mammals, birds and arthropods for environmental impact (a) and economic impact (b). Bird and mammal data from Kumschick and Nentwig (2010).

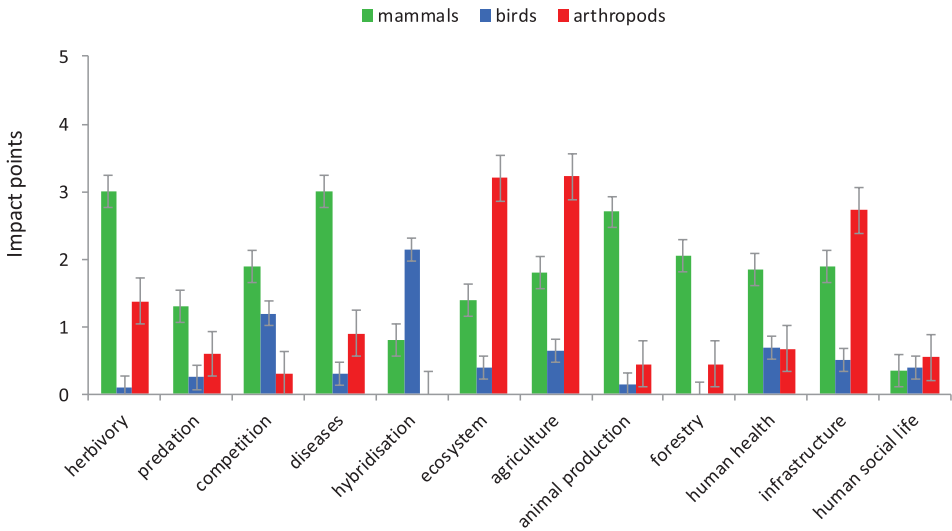


Figure 4. The mean impact and standard deviation of the 20 highest scoring species of mammals, birds and arthropods for the different categories of environmental and economic impact. Bird and mammal data from Kumschick and Nentwig (2010).

of 2.7), and mammals reach similarly high values of 2.7 by their impact on animal production. The scores of birds were also very low in these categories (means of 0–0.7) (Figure 4).

Discussion

In this study, we modified the generic impact scoring system developed by Nentwig et al. (2010) for vertebrates, in such a way that it can also be applied to arthropods. By adapting the definitions of the twelve categories of environmental and economic impact to apply to arthropods, we were able to express the impact of the most invasive alien arthropod species in a comparative manner as impact points. In order to end up with robust results guaranteeing reproducibility and broad acceptability, only published information from scientific journals was used. By summing up the corresponding scoring points of each category, a ranked list of the analysed arthropod species was created, ranging from highest to lowest impacts. These values reflect the current state of knowledge and can therefore be easily adapted over time as new knowledge becomes available. If no information is available (neither from other invaded areas nor from its native area), the generic impact scoring system cannot be applied, but this would also be the case with any other assessment approach. The great advantage of the system presented here is its broad applicability and the possibility to compare vertebrates and arthropods. This prioritisation list can serve as a background for decision makers and can facilitate the creation of policies and decision processes. With further enhancement of this system, it should even be possible to translate the environmental and economic impacts of every invasive alien species into general scoring points, regardless of the taxonomic group.

Environmental and economic impact categories

The comparison of the overall impact of invasive alien arthropods on the environment and economy shows a large impact on the economic categories, mainly agriculture and human infrastructure and administration. Since the 1960s, the importance and value of merchandise trade has accelerated enormously, but this has also led to an increase in the introduction of alien species (Hulme 2009). The degree of trade is a significant indicator of the number of alien species present and the rate of new introductions into a region (Levine and D'Antonio 2003; Westphal et al. 2007; Roques et al. 2010). Most invasive alien arthropods have been introduced as contaminants or as stowaways (Hulme et al. 2008) and many of them benefit from cultivation and husbandry, or escape from their natural enemies (Mack et al. 2000). As a consequence, invasive alien arthropods have a major impact on agriculture (Roques et al. 2010), which results in economic losses and requires the application of pesticides to reduce these losses. Since pesticides have to be developed, produced and regulated, this explains why agricultural pests also have a strong impact in the category "human infrastructure and administration". The use of (nonspecific) pesticides also leads to the loss of many non-target organisms, some of which play important roles in ecosystem functions. Therefore, the impact of alien agricultural pests usually also causes an impact on ecosystem level.

During this study it became obvious that our overall knowledge of the impact of invasive alien arthropods on the environment is insufficiently documented in the scientific literature (compare also Kenis et al. 2009). Therefore, we assume that the current impact in environmental categories is probably underestimated. Information about predation on or parasitism of native species was available in the literature for *Varroa destructor*, *Linepithema humile* and *Harmonia axyridis*. However, for ten of the other eleven predacious or parasitic species, no information could be found, indicating that more research is needed in this field. The same is true for impact through hybridization: in all species analysed here, we had to state “no impact known”, but we believe that this is mainly a knowledge gap. Allopatric speciation is common in arthropods and when human-assisted dispersal overcomes the natural separation of species, this can lead to hybridization (Sanchez-Guillen et al. 2013). Previous analyses showed that alien mammals have some impact on native mammals through hybridization (Nentwig et al. 2010) and alien birds exert an even higher impact (Kumschick and Nentwig 2010). Schierenbeck and Ellstrand (2009) found that hybridization in plants can be an evolutionary stimulus for invasiveness and that hybridization could be an explanation for the time lag between the first introduction of a species and the beginning of an invasion. Hybridization with native species and/or multiple introductions of an alien species produces a genetic advantage in favour of the invasive species, finally leading to the exclusion of native species (Rhymer and Simberloff 1996; Vilà et al. 2000; Largiadèr 2007). This is supported by the findings of Colautti et al. (2006) that propagule pressure is a significant predictor of invasiveness. Even if alien arthropods may encounter fewer closely related species in invaded areas than alien vertebrates, the genetic impact of invasive alien arthropods is largely unexplored. Following studies on hybridization of native and introduced bees and bumblebees (Labrador et al. 1999; Jensen et al. 2005), we may assume that in the near future there will be more examples demonstrating the impact of hybridization of alien arthropods with native species.

Mammals, birds and arthropods

The comparison between these three different taxonomic groups showed mammals to have the highest overall impact on the environment and economy (Figure 3). The impact scores of alien arthropods, however, may be underestimated due to a bias towards arthropod species with relevance for the economy and human health (Kenis et al. 2009). This resulted in a knowledge gap regarding the other impact categories of alien arthropods. Arthropods reach the highest impact in three connected categories (agriculture, ecosystem and human infrastructure and administration, Figure 4), with mean scores higher than 3, which is not reached by mammals in any category. Our list of the top 20 arthropods may change towards a higher impact score once some of the important pest species recently imported into Europe and currently rapidly spreading (e.g., *Vespa velutina* and *Drosophila suzukii*) are included.

Necessity and opportunities of the generic impact scoring system

Creating a prioritization list for the three taxonomic groups analysed so far (mammals, Nentwig et al. 2010; birds, Kumschick and Nentwig 2010; arthropods, this study), the Canada goose *Branta canadensis* scores the highest, followed by the muskrat *Ondatra zibethicus*, the sika deer *Cervus nippon* and the Varroa mite *Varroa destructor*. All these species score higher than 30 points, indicating a very serious impact on the environment and economy in Europe. The fact that the four highest scoring species belong to different taxonomic groups (one bird, two mammals and one arthropod) demonstrates the need for a prioritization tool that allows the impacts of different taxonomic groups to be compared. Decision making processes about the management of invasive alien species are usually not restricted to taxonomic borders and therefore need to include all groups that occur in a given area. We are convinced that a generalized approach in combination with our simple “currency” of impact points as a general unit for environmental and economic impacts is a broadly applicable method for prioritizing alien species.

The generic impact scoring system is characterized by relying on already available and published scientific information (not expert opinion). The impact point system implies that all impact categories are (at least initially) of equal importance. Definitions of impact categories and impact intensities as provided in the Handbook (Supplementary material) make the results reproducible and transparent. In a second approach, the results can be weighted, restricted to given areas, or modified according to expert opinion. This is the major difference compared to other prioritization systems, such as those of Smallwood and Salmon (1992) and Bomford (2003). These systems weight the categories differently and place more weight on agricultural impacts. Kumschick et al. (2012) proposed a system to prioritize invasive alien species that largely depends on expert opinions and management opinions, while also allowing selected categories to be weighted.

Another important point in the engagement against invasive alien species is the coordination of measures undertaken by different European countries (Hulme et al. 2009). The impact scoring system is basically scale-independent, which means that it can be conducted for a country in which a given species is not yet present but has the potential to invade. This allows early reactions and in combination with knowledge about the pathways of introduction, the invasion of such a species can be prevented (Hulme 2006). Prevention measures are much less costly than combatting an invasive alien species once it has established (Hulme 2009). Up to now, successful eradications were mostly restricted to alien vertebrates on islands. In Europe, only a small number of successful eradications have taken place and no invertebrates were included (Genovesi 2005; 2007). A cautionary example is the initial lack of pathway analyses and coordinated measures against *Varroa destructor*. The situation might have developed differently with today’s prioritization information available at that time.

A current example concerns the repeated introductions of the Chinese longhorn beetle *Anoplophora glabripennis* to Europe (Carter et al. 2009). It has a total of 21 impact points and exerts a very high impact on forestry and forest ecosystems. In many European countries, the general public is informed by newspaper articles in the daily

press reporting on the enormous impact of these beetles and the cost of local eradication campaigns. Mentioning the relatively high impact score of the species and drawing attention to a comparison with other high-impact invasive alien species could help to justify such means and to increase the acceptance of eradication activities in the public opinion.

Conclusion

A sound knowledge is needed for policy and decision makers to control invasive alien species. The introduction of species known to have a high impact should be avoided or, if already introduced they should be eradicated as soon as possible. The core challenge is the limited possibility to know about the invasiveness of a given species in advance. The generic impact scoring system can help to translate scientific knowledge regarding environmental and economic impacts into easily comparable impact scoring points, leading to a prioritization list across different taxonomic groups. In this study, the generic impact scoring system was applied to terrestrial arthropods in order to enhance and broaden the applications of the system, which was developed for vertebrate groups. Further applications to other taxonomic groups will result in an enhancement of the generic impact scoring system approach and a broader usage of science-based tools in invasion management.

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Supplementary material 1

Handbook of the scoring system for the impacts of alien species

Authors: Sibylle Vaes-Petignat, Wolfgang Nentwig

Data type: other

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Link: doi: 10.3897/neobiota.22.6620.app1

Supplementary material 2

Literature used to score 77 terrestrial arthropod species

Authors: Sibylle Vaes-Petignat, Wolfgang Nentwig

Data type: other

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Invasion of yellow crazy ant *Anoplolepis gracilipes* in a Seychelles UNESCO palm forest

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Abstract

The mature palm forest of the Vallée de Mai, a UNESCO World Heritage Site, on the Seychelles island of Praslin, is a unique ecosystem containing many endemic species, including the iconic coco de mer palm *Lodoicea maldivica*. In 2009, the invasive yellow crazy ant *Anoplolepis gracilipes* was recorded for the first time within the palm forest, raising concern about its potential impacts on the endemic fauna. This research aimed to: (1) assess the current distribution and spread of *A. gracilipes* within the palm forest; (2) identify environmental variables that are linked to *A. gracilipes* distribution; and (3) compare endemic species richness and abundance in *A. gracilipes* invaded and uninvaded areas. *Anoplolepis gracilipes* was confined to the north-east of the site and remained almost stationary between April 2010 and December 2012, with isolated outbreaks into the forest. Infested areas had significantly higher temperature and humidity and lower canopy cover. Abundance and species richness of the endemic arboreal fauna were lower in the *A. gracilipes* invaded area. Molluscs were absent from the invaded area. The current restricted distribution of *A. gracilipes* in this ecosystem, combined with lower abundance of endemic fauna in the invaded area, highlight the need for further research to assess control measures and the possible role of biotic resistance to the invasion of the palm forest by *A. gracilipes*.

Keywords

Endemic arboreal species, coco de mer palm, geckos, invasive alien species, islands, molluscs, World Heritage Site, Western Indian Ocean

Introduction

Ants are highly successful invaders, particularly on islands (Ingram et al. 2006; Cerdá et al. 2012). Their invasion is of concern to conservationists due to their broad range of impacts (e.g., Holway et al. 2002; O'Dowd et al. 2003; Lach and Hooper-Bui 2010) and the difficulties of eradicating them once established (Silverman and Brightwell 2008; Hoffmann et al. 2011). Impacts of invasive ants can include direct effects such as displaced vertebrate (Feare 1999; Holway et al. 2002 and references therein), non-ant invertebrate (Lubin 1984; Hill et al. 2003; Causton et al. 2006), and ant species (Walker 2006; Hoffmann and Saul 2010; Roura-Pascual et al. 2010), and indirect effects on key ecological functions such as frugivory (Davis et al. 2010), pollination and seed dispersal (Hansen and Müller 2009), and seedling recruitment and litter breakdown in a forest ecosystem (O'Dowd et al. 2003). The yellow crazy ant *Anoplolepis gracilipes* is ranked amongst the top 100 worst global invasive species (Lowe et al. 2000) and is responsible for catastrophic ecological impacts on islands (O'Dowd et al. 1999; O'Dowd et al. 2003).

In the Seychelles, *A. gracilipes* was first recorded in 1962 on the main island of Mahé (Lewis et al. 1976). The species had spread to the neighbouring island of Praslin by 1975 and was eradicated from this island shortly afterwards (Haines and Haines 1978a, b). Since then, despite control measures on Mahé, its range across the Seychelles islands has expanded and, by 2000, the species occurred on nine of the central islands, including Praslin (Hill et al. 2003).

Although the impacts and ecology of *A. gracilipes* have been well documented in degraded habitats in the Seychelles (Haines and Haines 1978a, Hill et al. 2003), little is known about this ant's invasion potential in endemic palm forest ecosystems. Praslin, the second largest granitic island of the archipelago, is home to Seychelles' native mature palm forest. This habitat represents one of the last island palm forest ecosystems in the world and hosts many species that are endemic to Praslin or the Seychelles (Beaver and Chong-Seng 1992; Fleischer-Dogley et al. 2011). The forest is dominated by the iconic coco de mer palm *Lodoicea maldivica*. This palm species, famous for producing the largest seeds in the plant kingdom, has been fundamental in driving the evolution of endemic fauna species, many of which are restricted to *L. maldivica* habitat (Noble et al. 2011). Moreover, the most pristine area of palm forest, the Vallée de Mai, renowned globally for its natural beauty, is a major visitor attraction and brings considerable financial benefit to the Seychelles, and to Praslin in particular. Threats to the ecological integrity of this habitat, including those from invasive species, therefore have potential economic as well as conservation implications.

Anoplolepis gracilipes was identified in the Vallée de Mai for the first time in August 2009 (L. Chong-Seng & P. Matyot, pers. comm.). Here, we present research into the distribution of *A. gracilipes* over the subsequent 2.5 year period in the Vallée de Mai palm forest, and its potential impact on a key group of animals in the ecosystem, the arboreal vertebrate and invertebrate palm specialist species. The overall aim of this research was to determine the distribution and spread of *A. gracilipes* in the Vallée de Mai

over time and improve understanding of its impact on endemic arboreal species in this unique palm forest. Given the extent of *A. gracilipes*' impacts elsewhere, we expected that the fauna associated with *L. maldivica* would be less abundant where *A. gracilipes* was present. We specifically ask: (1) what are the distribution, spread rate, and activity levels of *A. gracilipes* in the palm forest?; (2) Which environmental variables are associated with *A. gracilipes* distribution?; and (3) Are there differences in the number of species and abundance of endemic arboreal fauna between *A. gracilipes* invaded and uninvaded areas of the Vallée de Mai?

Methods

Study site and species

The study was conducted in the Vallée de Mai (19.5 ha; 4°19'S, 55°44'E) which is located in Praslin National Park (342 ha; Fig. 1). The Vallée de Mai was inscribed as a natural UNESCO World Heritage Site in 1983 for its unique and globally important habitat. The vegetation consists of low-intermediate elevation palm forest dominated by *L. maldivica*. A strip of cleared vegetation with trimmed introduced and native trees is maintained around the area as a firebreak. Outside the firebreak, the vegetation is mixed with more native and introduced broadleaf species. There is a network of paths used by visitors throughout the Vallée de Mai which are regularly swept and kept free of leaf litter. The Seychelles has a tropical climate and experiences temperatures of 24–32 °C and average rainfall of *ca.* 200 mm/month.

Anoplolepis gracilipes originates from either central east Africa or Asia but now has a pan-tropical and subtropical distribution. The species is a generalist and opportunistic consumer, which will predate and scavenge a variety of food sources. Workers make up >80% of the individuals in the nest and exhibit extensive foraging 24 h/day year round in areas where the climate does not hinder ant activity (Haines and Haines 1978a, Abbott 2005; Abbott 2006). The species can reach very high densities (e.g. supercolony densities can reach >2000 ants per m², Abbott 2005) and has been documented to spread at an average rate of 125 m/year on Mahé (Haines and Haines 1978a).

Distribution, ant activity and environmental variables

The main fieldwork was conducted over a 12-week period between March and June 2010. Fieldwork included surveys on ants and the arboreal endemic fauna and recordings of environmental variables. In addition, two ant distribution surveys were conducted in April 2012 (end of the wet season) and December 2012 (end of the dry season). To determine the distribution of *A. gracilipes*, a grid of fifty 10×10 m quadrats (~2.5% of the total area) throughout the valley was surveyed. Quadrats were spaced 75×75 m apart and sampled along parallel N-S transects spanning the entire study

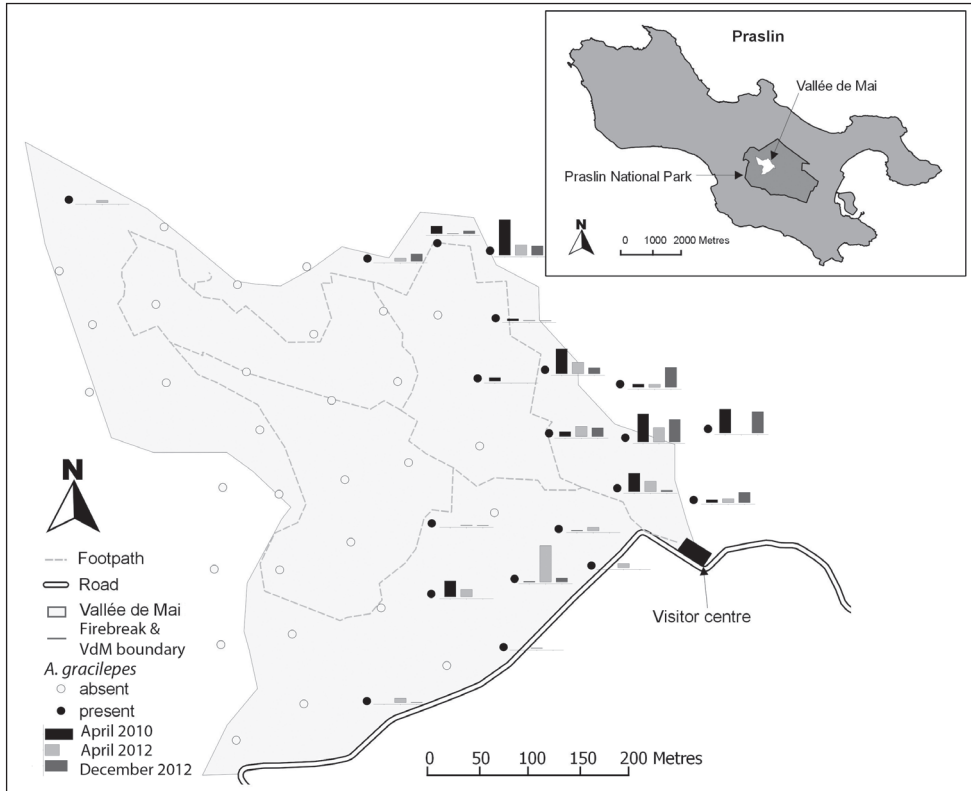


Figure 1. The distribution and abundance of *Anoplolepis gracilipes* in the Vallée de Mai, Seychelles. Circles indicate the sample locations and the presence (closed) or absence (open) of *A. gracilipes* within 10×10 m quadrats. In April 2010 and December 2012 *A. gracilipes* were observed at 14 locations, and in April 2012 ants were recorded from 18 locations in the Vallée de Mai. Bars next to full circles show relative *A. gracilipes* activity in April 2010 (black), April 2012 (light grey) and December 2012 (dark grey), and are drawn to the same scale.

area. Quadrats located in water or on large boulders were shifted to the nearest suitable adjacent area. Hereafter, the area of the Vallée de Mai with *A. gracilipes* is referred to as ‘invaded’ and the area without *A. gracilipes* as ‘uninvaded’.

We used ant activity counts to quantify *A. gracilipes* abundance. We were not able to apply the more standard pitfall methods to assess *A. gracilipes* abundance because the terrain of the Vallée de Mai consists of thick, multi-level palm leaf litter and boulders; therefore we adapted the method used by Abbott 2005. Using this method limits comparisons with other studies but allows for standardised assessment within the Vallée de Mai. In all three surveys, ant activity was measured by placing a 15×15 cm laminated white sheet on the ground or into the leaf litter with an absorbent cotton pad soaked in 15% sugar solution in the centre. We allowed a 3-min settling period before counting all *A. gracilipes* individuals crossing the sheet within three minutes. The number of individuals that crossed each sheet per minute is referred to as ‘ant

activity'. Five ant activity counts were taken per quadrat, one at each corner and one in the centre, and the mean value of each quadrat was used in the analysis. Ant activity was only recorded in fair weather conditions (not during rain or shortly afterwards) between 0800–1600 h when ant activity remained constant (Cuthbert 2010).

At each ant count location we recorded canopy cover, ground surface temperature (recorded to 0.1 °C with a thermometer in the shade on the ground) and relative humidity (humidity meter 'Rapitest', Stanton Hope, Essex). Canopy cover was assessed by counting the number of quarters of a 10×4 cm tube that showed canopy when looking vertically upwards at each ant count location. A quarter was counted only if more than half of that quarter was covered by the canopy. Each counted quarter therefore represents a maximum of 25% canopy cover, i.e., 0 quarters = 0% canopy cover, 2 quarters = 50% canopy cover etc. Records from each ant count location were averaged to produce mean canopy cover, temperature and relative humidity per quadrat.

We also assessed canopy use by *A. gracilipes* via tree trunks for each quadrat in the invaded area by searching trunks for one minute each and recording presence/absence of *A. gracilipes* on five randomly selected adult trees in each invaded quadrat. No other ant activity was recorded on trunks in quadrats in either area.

Impacts on endemic fauna

Preliminary observations suggested that *A. gracilipes* frequently used the palm forest canopy, which is dominated by large *L. maldivica* leaves. Because most of the endemic arboreal fauna of the Vallée de Mai is closely associated with *L. maldivica*, we expected any interference between *A. gracilipes* and endemic arboreal species to occur predominantly on *L. maldivica*. We assessed the effect of *A. gracilipes* presence by surveying eight species of arboreal endemic fauna likely to be directly affected by *A. gracilipes*, which were recorded from all parts of the palm forest prior to the invasion of *A. gracilipes*. The species surveyed were the day geckos *Phelsuma astriata* and *P. sundbergi*, the three species of bronze gecko *Ailuronyx seychellensis*, *A. tachyscopaeus* and *A. trachygaster*; and three arboreal molluscs *Vaginula seychellensis*, *Stylodonta studeriana* and *Pachnodus pralines*. The high density of *L. maldivica* in the Vallée de Mai and almost constant flowering of males provides a reliable food resource for these and other species. Surveys were made on 60 randomly selected trees (20 males, females and juveniles) of *L. maldivica* in each the invaded and uninvaded area. On each tree, a 5-min thorough search of the trunk, all stems, undersides of leaves and fruit/flowers was conducted with binoculars (magnification: 8×42) recording the number of individuals of each of the eight species.

Analysis

We used a logistic regression model to test the influence of environmental variables on *A. gracilipes* distribution. Dfbeta statistics, similar to Cook's distance in linear models,

is a measure of influence of individual points on logistic regression analysis (Belsley et al. 2005). Two outliers with $dfbeta > 1.0$ strongly influenced the logit coefficient and were thus removed from our analysis. To examine the effect of environmental variables on *A. gracilipes* activity in the invaded area, we ran a generalised linear model (inverse Gaussian distribution) with *A. gracilipes* activity as response and canopy cover, temperature and humidity as explanatory variables. Full factorial generalised linear models (negative binomial with log-link distribution) and pairwise comparisons were used to determine the effects of area (invaded or uninvaded) and tree type (male, female or juvenile) on species richness and abundance of endemic species. Counts of endemic arboreal species in invaded and uninvaded areas were compared by Chi-square tests. All statistical tests were conducted in SPSS 16.0.

Results

Ant distribution and activity

In 2010, *A. gracilipes* was confined to the north-east part of the Vallée de Mai, occurring in 14 of the 50 (28%) quadrats (Fig. 1). In April 2012, *A. gracilipes* expanded its range to occupy 18 quadrats, including 12 of the 14 previously occupied, with the range expansion being from the firebreak in the east and north-east and from the road along the southern border. This was followed by a range contraction in December 2012 to 14 previously occupied quadrats (Fig.1). The activity of *A. gracilipes* is lowest in the south-east and highest near the firebreak in the east close to the visitor centre, bordering the Vallée de Mai (Fig. 1). There was no change in mean ant activity (\pm SE) in the invaded area across surveys (2010: 3.55 ± 0.88 individuals/ min^{-1} ; April 2012: 2.18 ± 0.58 ; December 2012: 2.57 ± 0.69 ; paired Wilcoxon test $p > 0.1$; range: 0.07 – 10.9). Mean *A. gracilipes* activity in invaded quadrats at the edge of the Vallée de Mai ($N=6$; 4.83 ± 0.94) was higher than those inside the forest ($N=8$; 0.87 ± 0.31 ; Wilcoxon test $p > 0.0036$; Fig. 1) in December 2012, but not in 2010 and April 2012, suggesting a shift in ant abundance towards the firebreak in December 2012.

Ant occurrence and environmental variables

Invaded areas were characterised by higher humidity (invaded vs. uninvaded: $75.8 \pm 0.8\%$ vs. $72.9 \pm 0.5\%$ mean \pm SE), lower canopy cover ($2.5 \pm 0.2\%$ vs. $3.0 \pm 0.1\%$), and slightly higher temperature (27.6 ± 0.13 °C vs. 27.5 ± 0.083 °C; Table 1), but variation of *A. gracilipes* activity within invaded areas was not related to temperature ($\chi^2_{3,10} = 0.04$, $p = 0.83$), canopy cover ($\chi^2_{3,10} = 1.21$, $p = 0.27$) or humidity ($\chi^2_{3,10} = 0.17$, $p = 0.69$).

Anoplolepis gracilipes was observed primarily on the ground but was recorded on 35% (54 of 153) of trees in invaded quadrats, most commonly on introduced *Cinnamomum verum* (20%), followed by *L. maldivica* (13%). Overall, the relative abundance of intro-

Table 1. Logistic regression analysis showing the effect of environmental variables on the likelihood of *Anoplolepis gracilipes* presence or absence within quadrats in the Vallée de Mai ($N = 47$) ($R^2 = 0.63$ (Nagelkerke), model $\chi^2 = 26.16$, classifies 94% correctly).

	Coefficient	SE	Wald χ^2	Odds ratio	95% CI for Odds ratio		P
					Lower	Upper	
Temperature	2.68	1.13	5.67	14.6	1.61	132	0.017
Canopy cover	-2.36	0.96	6.05	0.094	0.014	0.619	0.014
Humidity	0.745	7.45	7.45	2.11	1.22	3.60	0.006
Constant	-125	48.4	6.61	0.000			0.010

duced broadleaf trees was more than four times higher in the invaded (native:introduced = 6.75:1) than the uninvaded area (1.57:1). We opportunistically observed *A. gracilipes* tending two species of honeydew-producing hemipterans, the soft scales *Pulvinaria ur-bicola* (Coccidae) and *Icerya seychellarum* (Margarodidae). Both species are introduced to the Seychelles and were tended on endemic and introduced dicotyledonous trees in and close to the firebreak. We randomly checked several hundred palm leaves during the study period and observed no tended hemipterans on any of the palm species.

Impacts on endemic arboreal fauna

The endemic arboreal species displayed considerable variation between the invaded and uninvaded areas (Fig. 2). The molluscs *V. seychellensis*, *S. studeriana* and *P. pralines* were less abundant or absent where ants occurred ($\chi^2 = 69$, $p < 0.0001$; $\chi^2 = 9.8$, $p < 0.01$; $\chi^2 = 8.3$, $p < 0.01$, respectively). The white slug *V. seychellensis* was common in the uninvaded area but entirely absent from the invaded area. Of the geckos, only the dwarf bronze gecko *A. tachyscopaeus* was significantly less abundant in the invaded area ($\chi^2 = 7.2$, $p < 0.01$). Abundance of the four species with the greatest differences between invaded and uninvaded areas showed no relationship with humidity or canopy cover (all $r < 0.01$, $p > 0.05$). Overall, mean species richness (invaded: 0.44 ± 0.08 ; uninvaded: 1.1 ± 0.10 ; $\chi^2_{5,114} = 0.25$, $p = 0.002$) and abundance (invaded = 46; uninvaded = 166; $\chi^2_{5,114} = 17.01$, $p < 0.001$) of endemic arboreal species on *L. maldivica* were lower in the invaded compared to uninvaded areas. There was no significant main effect for endemic species richness ($\chi^2_{5,114} = 0.245$, $p = 0.89$) and abundance ($\chi^2_{5,114} = 0.614$, $p = 0.74$) on male, female and juvenile *L. maldivica* within the invaded and uninvaded areas (Fig. 3). Although the abundance of endemic arboreal species on female *L. maldivica* trees was similar in *A. gracilipes* invaded and non-invaded areas ($p = 0.54$), abundance on males and juveniles ($p < 0.001$) in the invaded area was significantly lower (area \times tree type interaction effect; $\chi^2_{5,114} = 6.50$, $p = 0.039$; Fig. 3). There was no significant interaction effect between tree type and area in the number of endemic arboreal species ($\chi^2_{5,114} = 2.73$, $p = 0.25$).

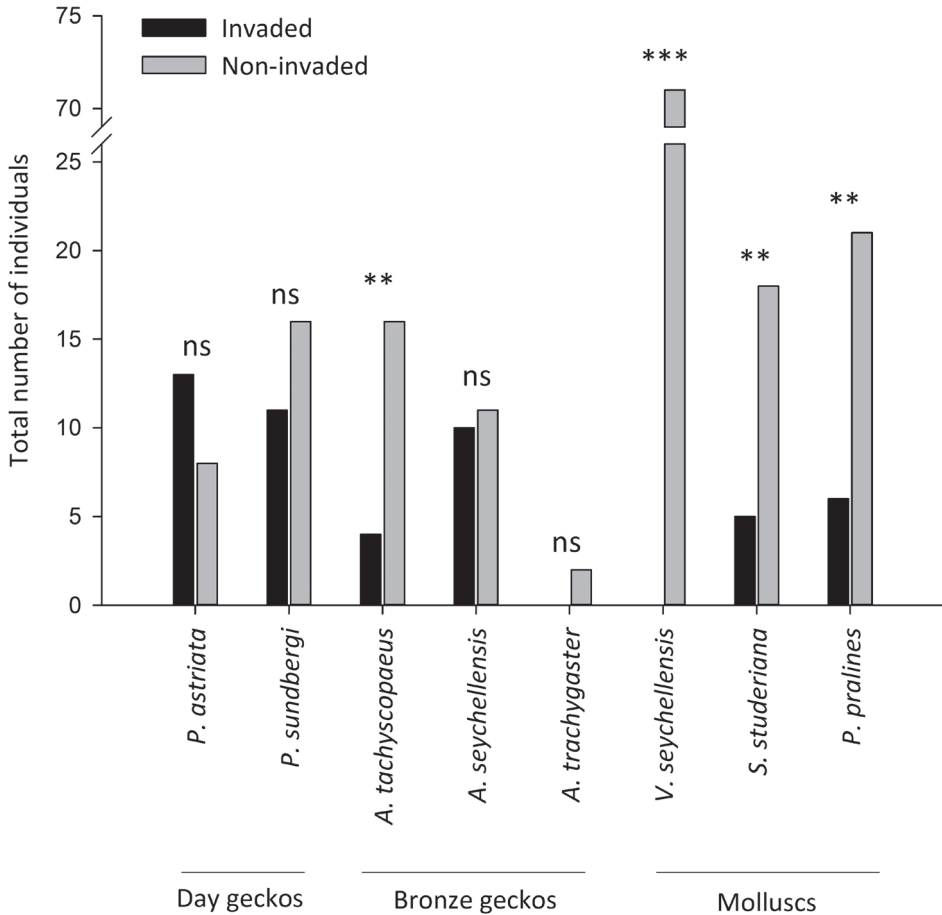


Figure 2. Abundance of eight endemic species in the *A. gracilipes* invaded and uninvaded areas: Number of observed individuals of eight species of endemic arboreal species on *Lodoicea maldivica* palms in the *Anoplolepis gracilipes* invaded ($N = 60$ trees) and uninvaded areas ($N = 60$ trees) within the Vallée de Mai. Counts were compared by chi-square test and levels of significance indicate: ns = non-significant, * < 0.05, ** < 0.01, *** < 0.001.

Discussion

Although *Anoplolepis gracilipes* has occurred across Praslin for at least the last decade and is present in Praslin National Park, there were no reports of the species occurring inside the Vallée de Mai until 2009. Despite its documented ability to rapidly cover large areas in high densities under optimal conditions (Hill et al. 2003; O’Dowd et al. 2003), the current distribution of *A. gracilipes* in the Vallée de Mai appears to be in a dynamic equilibrium and is restricted to the north-east of the reserve, with highest activity levels close to the firebreak and the visitor centre. This confined and relatively stable distribution invokes several possible explanations.

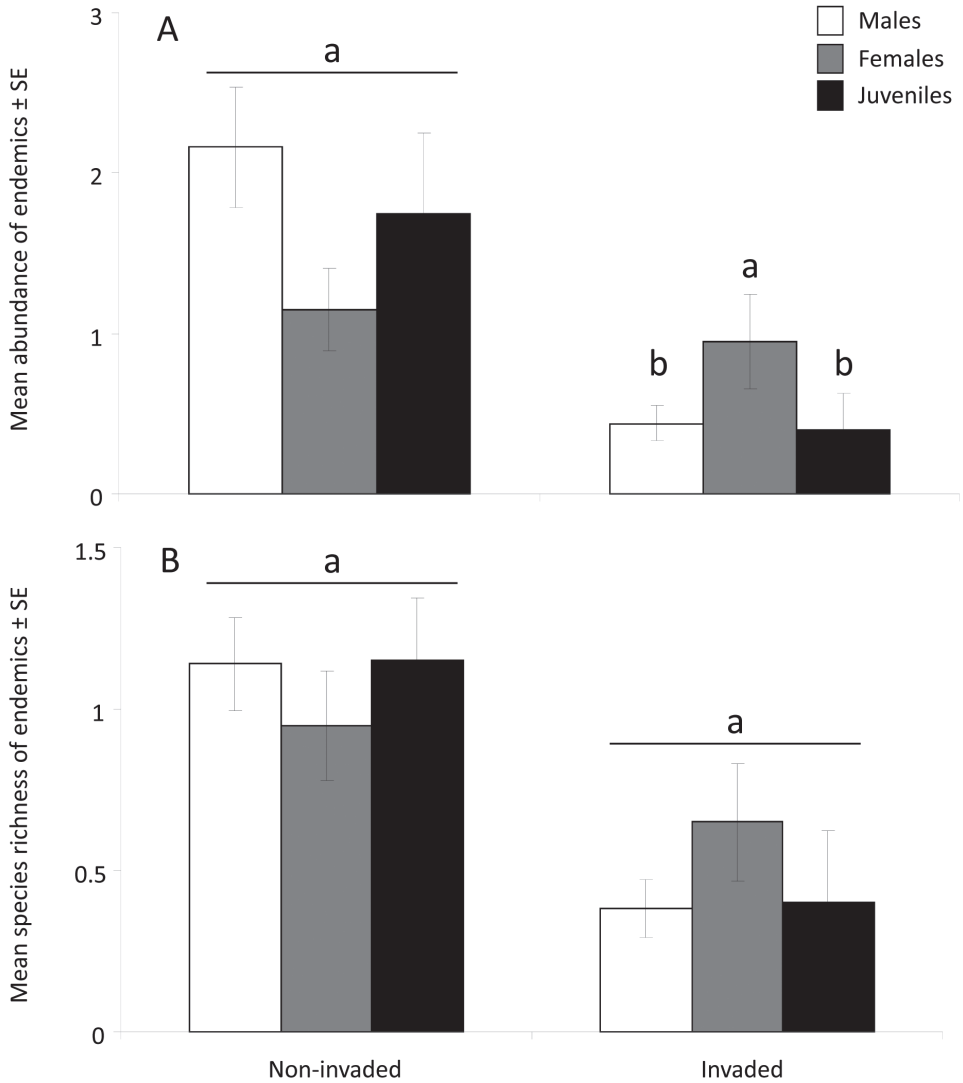


Figure 3. Differences in endemic species abundance and richness between the invaded and uninvaded areas and across tree classes. **(A)** Mean abundance and **(B)** species richness of endemic arboreal species in *A. gracilipes* invaded and uninvaded areas are similar between 20 male, female and juvenile *L. maldivica* palms in the Vallée de Mai. Different small letters indicate significant differences in between-area comparisons (invaded vs. non-invaded) but not within-area comparisons. Full statistics are presented in the text.

Firstly, the occurrence of *A. gracilipes* in the Vallée de Mai may be due to localised introduction and disturbance close to the palm forest. Repeated introductions and anthropogenic disruption of ecosystems both increase the likelihood of successful species invasions (Lockwood et al. 2005; Roura-Pascual et al. 2011; Bacon et al. 2014). The current distribution of *A. gracilipes* in the Vallée de Mai includes the visitor centre and entrance

area and it is possible that the recent construction of this centre (2007–2009) facilitated *A. gracilipes* establishment and invasion into the palm forest, through both the transport of *A. gracilipes* with construction materials and anthropogenic disturbance at the forest edge. The highest *A. gracilipes* activity and a continuous increase in activity throughout the study period close to the visitor centre suggest that the disturbance has generated favourable conditions, such as high carbohydrate supply, good abiotic conditions and potentially lower biotic resistance, for the establishment and spread of *A. gracilipes*. Similar findings were reported by Drescher et al. (2007) in Borneo where ant densities were highest in anthropogenically disturbed sites. This raises questions about reasons for the unfavourable conditions for colony establishment and growth in non-degraded forest inside the reserve.

Secondly, the lack of population growth in the Vallée de Mai may be due to a shortage of liquid sugary substances, which is an important energy source for workers, especially during invasions (Savage et al. 2011; Shik and Silverman 2013). To secure large quantities of carbohydrates, *A. gracilipes* establishes a mutualism with hemipterans, which provide a reliable source of honeydew as food (Delabie 2001; Abbott and Green 2007; Blüthgen and Feldhaar 2010). In the Vallée de Mai, hemipterans, such as introduced *Pulvinaria urbicola* and *Dysmicoccus* sp., which are invasive elsewhere in Seychelles (Gaigher et al. 2011), were rarely observed on palms (CKB, pers. obs.). This may explain why *A. gracilipes* made substantially lower use of trees in the Vallée de Mai (35%), compared to the numbers observed by O'Dowd et al. (1999) who recorded 98.5% of trees being utilised by *A. gracilipes* on Christmas Island. Similarly, Haines and Haines (1978b) reported 59–100% of trunks occupied by *A. gracilipes* at four sites on Mahé, Seychelles. The lack of hemipterans on palms may restrict the spread of *A. gracilipes* to the boundaries of the mixed forest where broadleaved vegetation and associated hemipterans are abundant (Haines and Haines 1978a). Of the trees that are used in the Vallée de Mai by *A. gracilipes*, 20% were the introduced broadleaf *C. verum*, which is disproportionately high compared to its relative abundance (2.9%; SIF, unpubl. data), suggesting an active preference for *C. verum* in the palm forest.

Thirdly, biotic resistance may also explain the observed stable population of *A. gracilipes* in the Vallée de Mai. There is little and ambiguous information on the role of native ant species in conferring biotic resistance to the invasion of exotic ant species. Both Way (1953) and Hoffmann and Saul (2010) concluded that habitat suitability, and not the presence of native ants, is the strongest predictor of invasive *A. gracilipes* distribution. The invasion of other ants, such as the Argentine ant *L. humile* in Portugal, however, was prevented by dominant native ants in cork oak plantations and pasture habitat (Way et al. 1997). Whether native ant species have the potential to limit *A. gracilipes* invasion in the Vallée de Mai palm forest is unknown, but the effect of native ants may be largest at early stages of invasion when population size of *A. gracilipes* is still relatively small (Menke et al. 2007). According to biotic resistance theory (Elton 1958), native communities should have higher biotic resistance and therefore be less susceptible to invasion than degraded habitat where native ant species numbers have been reduced. At least 10 native ant species occur in the Vallée de Mai. While this is a relatively low number of species compared to ant communities on mainlands it is among the best

habitat types for ants on Praslin (B. Fisher, pers. comm.). This richness in native ants may not confer biotic resistance, but it suggests that the habitat is suitable for a variety of ant species, which are likely to compete for resources with the generalist *A. gracilipes*.

A final explanation for the apparent dynamic equilibrium of the *A. gracilipes* population concerns abiotic conditions. Hoffmann and Saul (2010) showed that habitat suitability is the primary determinant of *A. gracilipes* incursions, and climatic variables, especially temperature and humidity, are important factors determining ant distribution (Torres 1984; Porter 1988; Hölldobler and Wilson 1990; Krushelnycky et al. 2005). In the Vallée de Mai, higher humidity and temperature and lower canopy cover were correlated with *A. gracilipes* presence. The interior of the palm forest is characterised by dense canopy cover and lower temperatures. Cold and wet conditions have been shown to affect foraging activity of other invasive ant species such as the Argentine ant in Hawaii (Krushelnycky et al. 2005). Nevertheless, the total differences in temperature and humidity between invaded and uninvaded areas in our research are so small (e.g., ground temperature difference was only 0.07 °C) that they are unlikely to affect the behaviour of the invasive *A. gracilipes* (Chong and Lee 2009).

We observed marked variation between the presence of *A. gracilipes* and several arboreal species. The number and abundance of endemic arboreal species was lower on *L. maldivica* in invaded areas, and the effect was particularly strong for molluscs, which were abundant throughout the palm forest prior to the arrival of *A. gracilipes* (NB, pers. obs.). To our knowledge this is the first record of *A. gracilipes* invasion coinciding with the disappearance of native molluscs, although cause and effect could not be confirmed. Further spread of *A. gracilipes* through the palm forest could threaten the viability of these species and the relationship between molluscs and palms in this forest. The absence of the slug *V. seychellensis*, a *L. maldivica* specialist, from the invaded area is particularly concerning. Effects of *A. gracilipes* on native species were also recorded on Mahé, where fewer terrestrial reptiles occurred in *A. gracilipes* invaded areas (Haines and Haines 1978a). It is not known whether *A. gracilipes* actively prey upon or aggressively exclude endemic arboreal species in the Vallée de Mai. Our observations suggest that *A. gracilipes* excludes endemic arboreal species from male *L. maldivica* trees, which provide a rich pollen food source for many arboreal species including geckos and molluscs. *Anoplolepis gracilipes* may, however, be attracted to male trees not due to direct pollen resources but to the dead and decaying small invertebrates which accumulate at the base of the catkins (Cuthbert 2010; C. Kaiser-Bunbury pers. obs.).

Conclusion

Island endemics are typically at higher risk of extinction (Gaston 1998) and invasive species can accelerate this process (Wanless et al. 2007; Medina et al. 2011). Attempts to reverse these processes, by controlling the spread and impact of invasive species have been undertaken worldwide (Veitch et al. 2011). Once an invasive species is established it is often difficult to eliminate or prevent further spread (Lewis et al. 1976; Krushelnycky et

al. 2004). In the case of *A. gracilipes* in the Vallée de Mai, further research into control or exclusion options, impacts and potential biotic resistance to ant invasion are required in addition to continued monitoring of distribution and abundance. Chemical control poses a considerable risk to non-target species, such as endemic ants. We therefore advise promoting and researching resistance of the palm forest by, for example, creating and maintaining conditions which restrict *A. gracilipes* populations, such as the removal of introduced broadleaf trees which host high numbers of introduced hemipterans, and targeted control of ant nests in the most disturbed habitats. Removal of introduced trees, however, must be carried out with great care to limit canopy gaps and soil disturbance which favour *A. gracilipes* and other invasive plant and animal species. Future research should experimentally assess and quantify parameters that ensure the resistance of the unique Vallée de Mai palm forest and its co-evolved plant and animal species.

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Aztec introduction of the great-tailed grackle in ancient Mesoamerica: Formal defense of the Sahaguntine historical account

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Abstract

The historical account of Aztec Emperor Auitzotl's introduction of the great-tailed grackle *Quiscalus mexicanus* into the Valley of Mexico (1486–1502) is significant because it documents human translocation of wild birds in Mexico over 500 years ago, before the Spanish Conquest of that land. In the present paper, which defends the account from writings that dispute it, I first review the evidence of how the account was obtained and show that its many details are consistent with what is known from other sources about both the great-tailed grackle and the Aztecs (Nahuas). I then review and examine all published criticisms of the account and explain in detail why they are wrong. The critics have to date presented no persuasive evidence to support their speculation that the Aztecs confused, or might have confused, a natural invasion for an introduction. In contrast to these critics, Bernardino de Sahagún's research group in the 1500s presented a highly credible, peer-reviewed historical account that documented Aztec introduction of the great-tailed grackle. The pioneering work of these Renaissance Mexican scholars continues to stand as one of the most important records of invasive alien species introduction in ancient times.

Keywords

Ahuitzotl, alien birds, archeobiota, cryptogenic birds, exotic birds, great-tailed grackle, introduced birds, invasive alien species, IAS, invasive birds, Mexico, non-native birds, *Quiscalus mexicanus*, translocated birds

Introduction

The introduction of the exotic great-tailed grackle *Quiscalus mexicanus* into the Valley of Mexico by Aztec Emperor Auitzotl, was reported by Mexican scholars in the sixteenth century, in one of the earliest scientific works on the fauna and flora of the New World (Sahagún [1577] 1979; Haemig 1978, 2011, 2012). Their historical account of this ancient avian translocation, however, was lost to science for centuries because of dispersal and confiscation of their manuscripts during the Inquisition and, later, the secretive policies of Spanish colonial authorities.

Consequently, it was not until four hundred years after its writing that the account and its implications were finally presented and discussed in an international scientific journal (Haemig 1978). Because biologists had long assumed that introductions of exotic wild birds in the western hemisphere occurred only after European colonization, the revelation of this ancient translocation surprised the scientific world and caused many to wonder how many other birds had been translocated by humans in ancient times (Haemig 1978; Tella 2011).

Today, the account faces a new challenge: Critics have written three papers questioning to various degrees its veracity (Remsen and Cardiff 1990; Christensen 2000; Peer 2011). The most recent (Peer 2011) claims that the great-tailed grackle was only “purportedly introduced” by the Aztecs, and “could also have spread to the area without human assistance.” Peer (2011) presents no evidence to explain why he doubts the historical account. Instead, he confidently urges readers to “see Remsen and Cardiff (1990)” who disputed the historical account because their “personal experience with South American indigenous peoples” was “sprinkled with cases of amusing, but obviously erroneous, explanations of past and present natural phenomena”.

But Mexico is not located in South America, nor is it correct to judge all indigenous people as unreliable just because some may be so. The sixteenth-century chroniclers of Auitzotl’s introduction of the great-tailed grackle were well-educated scholars who used the most rigorous and demanding research techniques of their time to assess the truth and veracity of the information they collected (Lopez Austin 1974; Haemig 2012). They were not naïve fools who believed everything they were told, but rather careful and thoughtful researchers who collected information from reliable sources and verified it using peer review (Haemig 2012). Furthermore, these scholars were fluent in the Aztec (Classical Nahuatl) language and had access to many credible sources of information that are no longer available to us, including distinguished experts from Auitzotl’s time, pre-Hispanic pictorial manuscripts that accurately recorded historical events, and surviving members of the Aztec dynastic family (Sahagún [1577] 1982; Haemig 2012).

Therefore, before we believe the claims of those who assert that this ancient bird introduction never happened, we should critically examine their arguments to see if their evidence and reasoning are sound. Accordingly, in the present paper, I carefully consider the claims made by the critics and reply to each one.

I begin with an opening statement that reviews how, when and where the historical account was obtained and the basic facts of Auitzotl’s introduction of the great-

tailed grackle. I then show that the details of the historical account are consistent with what other sources say about both the great-tailed grackle and the Aztecs. Next, I examine the claims and arguments made by those who deny the grackle introduction, and explain in detail why I believe them to be wrong. I then make concluding remarks in the discussion.

This paper is the third in a series of three recent articles that I have written on Auitzotl's introduction of the great-tailed grackle. In the first paper (Haemig 2011), I conducted a four-stage analysis of this ancient bird translocation. In the second paper (Haemig 2012), I investigated the origin of the historical account and the team of scholars that collected it. Now, in this third paper, I review the evidence and defend the historical account from its critics.

Opening statement

During the years 1561–1565, a research group of Mexican scholars collected information in Tlatelolco on a large number of bird species. They were writing a regional work on Mexican birds that would eventually be part of a comprehensive encyclopedia about the Spanish colony of New Spain (Mexico). While gathering data on the great-tailed grackle, they were told by their expert consultants and collaborators that this bird was not native to the area but had instead been introduced there by Aztec Emperor Auitzotl before the Spanish Conquest (Haemig 2012).

Sometime during the years 1486–1502, Auitzotl (also spelled Ahuitzotl) commanded that great-tailed grackles be brought to the Valley of Mexico from Aztec provinces in the Huastec (Teenek) and Totonac regions of Mexico (Haemig 1978, 2011). After the grackles were transported to the Valley of Mexico and released there, the Aztecs made two additional human interventions to ensure establishment of these exotic birds: (1) supplemental feeding and (2) protection from human harassment and predation (Haemig 1978, 2011). Nurtured and guarded by Mexico's most powerful ruler and his people, the grackles soon established themselves in their new home, multiplied and spread to other areas (Haemig 1978, 2011).

The research group that collected this information was led by Bernardino de Sahagún, an academic clergyman who had studied at the University of Salamanca in Spain (Anderson 1982). The other members of the research group, all native Mexican scholars, were either graduates and/or faculty members of the Royal College of the Holy Cross (El Imperio Colegio de la Santa Cruz) (Sahagún [1577] 1982; Haemig 2012). This College, located in Tlatelolco, was an elite European-style school that was a center for advanced learning and research in New Spain (Haemig 2012).

When Sahagún's research group were told the details of Auitzotl's introduction of the great-tailed grackle, they wrote them down in the Aztec language into a document now known as the *Manuscript of Tlatelolco* (Appendix A.1) Although the account they recorded does not specifically say that it is based on eye-witness-testimony, we cannot exclude that possibility. The account quotes the words of Aztec people guarding the

introduced great-tailed grackles, suggesting eyewitness testimony (Appendix A.2) and/or use of a pre-Hispanic pictorial manuscript that was itself based on one or more eyewitness sources (Appendix A.3). In addition, the research group later revealed that the city where they were then working (Tlatelolco), was one of the sites where Auitzotl had introduced the great-tailed grackles 59–79 years earlier (Haemig 2011).

Nevertheless, to further verify the authenticity of the account, Sahagún's research group had it peer reviewed by bird experts in another city where Auitzotl introduced the great-tailed grackle: the Aztec capital Tenochtitlan (Haemig 2011, 2012). After successfully passing this peer review, the research group wrote the historical account into a document now known as the *Manuscript of 1569*, which is regarded as the finished Aztec language version of their work (Appendix A.4). During the 1570s, the research group copied the Aztec texts of the entire great-tailed grackle account, together with a Spanish translation that included the scholia (i.e. glosses, explanations, critical comments, grammatical explanations, Appendix A.5) into the encyclopedia known today as the *Florentine Codex* (Appendix A.6). The complete bilingual texts of the historical account from the *Florentine Codex* read as follows:

Aztec Text (English Translation): It is named *teotzanatl* [divine, genuine, or marvelous grackle, see Appendix A.7] because it did not live here in Mexico in times of old. Later, in the time of the ruler Auitzotl it appeared here in Mexico. For he commanded that they be brought here from [the provinces of] Cuextlan [and] Totonacapan. It was made known especially that those which came here were to be fed. But when they multiplied, they scattered, they traveled everywhere, they ate everywhere. They eat lizards. And when they were still esteemed, no one might throw stones at them. If anyone stoned them, they chided one another; the common folk said to one another, "What are you doing over there? Do not shout at, do not stone the lord's birds!" (Sahagún [1577] 1963, p. 50).

Spanish Text: Llámanse teotzanatl que quiere decir ave rara, o tzanatl preciosa: Porque no son naturales desta tierra: No ha muchos años que vinieron a estas partes; cuando era señor Auitzotl vinieron a estas partes de México, por su mandado fueron traídas de las provincias de Cuextlan y Totonacapan. Y entonces tenían cargo de dar las de comer. Y como comenzaron a multiplicarse derramáronse por todas las comarcas de México. Estas comen lagartijas y otras sabandijas semejantes. A los principios nadie las usaban matar, ni tirar: porque estaba vedado por el señor. (Sahagún [1577] 1979, Volume 3, Book 11, folios 53v–54r).

Comparing the *Florentine Codex's* chapter on birds to the texts of the earlier *Manuscript of Tlatelolco*, we find that the *Codex* contains over thirty new bird accounts that are not present in the *Manuscript of Tlatelolco*, as well as significant new information on many birds already present in the latter (e.g. *Itzquauhтли*, *Mixcoaquaauhтли*, *Itztlhotli*, *Chiqujmoli*, *Chachalacametl*). These many changes to the bird chapter, which appear both before and after the account of Auitzotl's introduction of the great-tailed grackle, were added by the peer reviewers in Tenochtitlan. They confirm Sahagún's statement that the *Tenochca* (people of Tenochtitlan, Appendix A.8) "amended and added many things to the twelve books" at that time (Sahagún [1577] 1982, p. 55), and also leave little doubt that the *Tenochca* scrutinized the grackle account (Appendix A.9). That

the *Tenochca* were familiar with the male great-tailed grackle is proven by the fact that this bird is specifically mentioned as a size model in the *Florentine Codex's* account of the *Chachalacametl* (Sahagun [1577] 1963, 1979), which was written in Tenochtitlan.

That the grackle account successfully passed the peer review process in Tenochtitlan is shown by the following facts: (1) The details of the introduction of the great-tailed grackle, as told in the Aztec and Spanish texts of the *Florentine Codex* (above), are not significantly different from those of the *Manuscript of Tlatelolco* (Haemig 2011, 2012), (2) No alternate account of the great-tailed grackle was added to the manuscript in Tenochtitlan, as was done for several bird accounts from Tlatelolco that the *Tenochca* judged unsatisfactory (e.g. *Atotolin*, *Atapalcatl*, *Itzquauhtli*, *Mixcoaquauhtli*, *Tolcomoctli*). (3) The account lacks warning phrases (Haemig 2012) that the research group used to alert the reader to doubtful information such as fables.

The account of Auitzotl's introduction of the great-tailed grackle is thus a peer-reviewed historical account, collected and authenticated by a professionally-trained research group within a human lifetime of the grackle translocation (Haemig 2012). The existence of this peer-reviewed historical account means that the evidence for Auitzotl's introduction of the great-tailed grackle is considerably better than what exists for many birds currently thought to have been translocated by humans (See examples in Long 1981; Lever 2005; Blackburn et al. 2009).

Compatibility with other sources

The credibility of the historical account is further enhanced by the fact that there is nothing in its content that casts doubt on its veracity. Its many details are consistent with what other sources tell us about both the Aztecs and great-tailed grackles.

For example, other historians confirm that the Aztecs moved many different kinds of organisms outside their natural ranges (Haemig 1978, 2011). In one particularly illuminating case, Auitzotl's mentor and closest advisor, Tlacaelel, persuaded an earlier Aztec emperor, Montezuma I, to create a large garden-park of exotic tropical plants south of the Aztec capital at Huaxtepec, in what is today northern Morelos (Duran [1581] 1994; Haemig 2011). Among Tlacaelel's many reasons for recommending that exotic plants be translocated to this area was his curiosity to see if the plants could thrive outside their natural ranges. In addition, he argued persuasively that "it will cost us little to find out" (Duran [1581] 1994; Haemig 2011, p. 394). Consequently, Montezuma commanded that many different species of tropical plants be brought to Huaxtepec from Cuertlaxtla (located in present-day Veracruz) to create this garden-park. Over forty professional gardeners from Cuertlaxtla, along with their wives and families, moved to Huaxtepec with the exotic plants so that the latter could be successfully established using horticultural methods from Cuertlaxtla (Duran [1581] 1994; Tezozomoc [1598] 1997).

We also know from other sources that the great-tailed grackle is not the only introduced bird species recorded from the Valley of Mexico. Nineteenth-century ornitholo-

gists listed about a dozen other exotic bird species as occurring there, including two icterids (*Amblycercus holosericeus*, *Cassiculus melanicterus*) and several species of parrots (Herrera 1888; Peterson and Narvarro-Sigüenza 2006; Haemig 2010). Whether or not these other species were also introduced by Aztec rulers is unknown. Since pre-Hispanic times, large numbers of exotic birds have been sold in the market places of Mexico City (Cortés [1520] 1971), so these species could be descended from escaped cagebirds and even date from more recent times. Nevertheless, the presence of so many exotic bird species in the Valley of Mexico suggests that this area, which is one of the great cradles of human civilization, has also been a theater for exotic bird introduction.

The reference in the historical account to common people protecting the grackles is also consistent with information from other sources. Haemig (2011, p. 392) explains:

“Diego Durán tells us that by 1486, the year Auitzotl became emperor, the Aztec nation was so well organized that there were special functionaries ‘for every activity, even minor ones... There were even officials in charge of sweeping. The order was such that no one was allowed to interfere with the work of another or express an opinion since he would be rebuffed immediately’ (Durán ([1581] 1994, p. 309)... Auitzotl was unique among Aztec emperors in that he promoted common people to official positions that had previously been held only by nobles (Durán [1581] 1994). When Auitzotl’s successor, Montezuma II, became emperor, he removed common people from official positions, reversing the gains that commoners had made under Auitzotl (Durán ([1581] 1994). Because Auitzotl opened up Aztec society for the lower classes, he was popular with them. Consequently, the common people may have enthusiastically protected “the lord’s birds” not just out of fear and respect, or because it was their job to protect the grackles, but also out of gratefulness and love for their emperor.”

The historical account states that the grackles were brought from Cuextlan and Totonacapan and released in the Valley of Mexico. Here again, we find consistency with other sources: the race of the great-tailed grackle inhabiting the Valley of Mexico (*Q. m. mexicanus*) is the same as that which inhabits Cuextlan and Totonacapan (Haemig 1978).

The historical account further states that the great-tailed grackles introduced by Auitzotl became invasive and ubiquitous:

“But when they [the introduced grackles] multiplied, they scattered, they traveled everywhere, they ate everywhere” (Aztec text – Sahagún [1577] 1963, p.50).

“And when they [the introduced grackles] began to multiply, they spread themselves through all the territories of Mexico” (Spanish text – Sahagún [1577] 1979, vol. 3, book 11, folios 53v-54r).

These descriptions sound very much like the great-tailed grackle we know today, which is greatly expanding its geographic range (Phillips 1950; Dinsmore and Dinsmore 1993) and is widespread in urbanized environments (González Oreja et al. 2007; Ortega-Álvarez and MacGregor-Fors 2009; Carbó-Ramírez and Zuria 2011; González Oreja 2011; Pineda-Lopez et al. 2013).

The historical account mentions that people had to be restrained from shouting at the introduced great-tailed grackles, suggesting that these birds had become pests. (The

account also states that people had to be prevented from throwing stones at the grackles and killing them, but in these latter cases it is unclear if the grackles were wanted dead because they were pests or to obtain their valuable feathers). Great-tailed grackles in modern times are often persecuted as pests too and humans sometimes shout and throw stones at them. So once again the details of the historical account resonate completely with current knowledge and experience.

Critique of dissenting views

Remsen and Cardiff (1990) disputed the historical account. Because all subsequent authors who have questioned the historical account (Christensen 2000; Peer 2011) continue to cite and rely heavily on Remsen and Cardiff's paper, it is essential to review and answer all of its points. Remsen and Cardiff's criticisms of the historical account fall into four categories: (1) caricature of the *Florentine Codex*, (2) objection to the use of indirect observations, (3) objection to the presentation of evidence that conflicts with the hypothesis of natural invasion, and (4) objection to the use of information from indigenous peoples. Let us now examine in detail these criticisms.

Caricature

A significant part of Remsen and Cardiff's critique of the historical account consists of distorted and inaccurate descriptions. They caricature the *Florentine Codex* as "a friar's 1577 collection of animal stories", belittle the peer-reviewed historical account as "folklore", and call the highly-civilized and literate Aztecs "primitive peoples".

Remsen and Cardiff's (1990) caricature of the *Florentine Codex* gives the impression that this work is hopelessly out-of-date, written by a non-scholar, and contains no useful scientific information. Like most caricatures, it is inaccurate because it omits many important details and trivializes others. For example, while it is true that Sahagún was a (Franciscan) friar, Remsen and Cardiff neglect to mention that he was also a serious scholar, teacher and leader of a distinguished academic research group (Lopez Austin 1974; Anderson 1982; Nicolau d'Olwer 1987; Leon-Portilla 2002). In 1536, Sahagún helped found the Royal College of the Holy Cross (described above) in Tlatelolco. While working at this college, Sahagún taught the brightest children of the former native nobility and mentored several who went on to become distinguished scholars.

Later, during a twenty year period (1558–1577), Sahagún directed the General History Project, which culminated in the writing of a peer-reviewed encyclopedia (the *Florentine Codex*) that contained a wealth of important new information about Mexico that was unknown to science. Comparing him to other friars of his time, Anderson, (1982, p. 41) wrote: "While Sahagún clearly reflected the views and methods of his time and of his order, he nevertheless stands absolutely unique... Even when compared

with his ablest contemporaries he excelled any of them in his ability to organize, train, use, and direct effectively a team of emerging native scholars.”

Remsen and Cardiff’s caricature also leaves the false impression that the *Florentine Codex* was written by one person. In reality, this encyclopedia was produced by a group of scholars in collaboration with indigenous experts in the various topics studied. While Sahagún was the leader of the project, much of the research and fieldwork was done by four distinguished trilingual scholars: Martin Jacobita, Antonio Valeriano, Alonso Vegerano, and Pedro de San Buenaventura (Sahagún [1577] 1982). Because Sahagún was the only member of the research group that was a clergyman, it is inaccurate and misleading to characterize the authorship of the *Florentine Codex* as a “friar’s” work.

Third, the *Florentine Codex* is far more than a “collection of animal stories.” Covering a wide variety of topics, it contains the first scholarly descriptions of flora and fauna for many species in the New World. In the prologue to Book Eleven of the *Florentine Codex*, where the account of Auitzotl’s introduction of the great-tailed grackle is found, Sahagún ([1577] 1982, p. 87) summarizes the contents of this volume as follows: “In it, recorded in the Mexican language, are the better known and most utilized animals, birds, fish, trees, herbs, flowers, and fruits which exist in all this land - their characteristic properties and traits, exterior and interior.”

The account of Auitzotl’s introduction of the great-tailed grackle is found in Chapter Two of Book Eleven. This chapter focuses on birds and describes many species. Included are not only physical descriptions and names but also other information, such as habitat, song, nesting habits, eggs, behavior and interactions with humans. Thus, among other things, Chapter Two of Book Eleven is a serious scholarly attempt to summarize the better known and most utilized birds of the Spanish colony of New Spain. Because its Aztec texts were finished in 1569, three years before Francisco Hernandez came to New Spain, it may be the earliest-known regional avifaunal work on the birds of Mexico.

Indirect observations

As shown in the previous section, the *Florentine Codex*’s bird chapter is a regional avifaunal work. Regional works on birds review and summarize the existing state of knowledge of birds in a given area, and so are usually based at least partially on the work of others. Important historical information, such as the introduction of exotic bird species, is often mentioned in regional works and is almost never based on the direct observations of the authors themselves (e.g. Berger 1972; Cramp et al. 1977-1996; AOU 1998). It is therefore astonishing to read that Remsen and Cardiff (1990, p. 973) criticize the historical account because, in their words, it comes from “Aztec informants (and not the friar’s direct observations)”.

Although Peer (2011) gave credence to Remsen and Cardiff’s argument by uncritically quoting it, he failed to note that Remsen and Cardiff themselves use indirect sources and so could be accused of imposing a double standard. For example, a year before Remsen and Cardiff (1990) criticized “the friar” for reporting the great-tailed

grackle's introduction without directly observing it, Remsen reported in a regional work on Bolivian avifauna that two bird species of that county were introduced (Remsen and Traylor 1989). Like Sahagún's research group, Remsen and Traylor (1989) did not directly observe the introduction of these two exotic species by humans, but had instead obtained their knowledge of these birds' introduced status indirectly, from sources which they knew to be reliable.

Six years after criticizing "the friar", Remsen et al. (1996) published another regional work, this time on vireo migration in Louisiana. In that paper, Remsen and Cardiff stated that some of the data they used were not based on their own direct observations but instead came from amateur bird watchers. They explained, "Some previously unpublished observations were obtained from the card file of unusual bird sightings reported to the regional editors of *Audubon Field Notes - American Birds - National Audubon Society Field Notes* (Remsen et al. 1996, p. 123)."

Because Remsen and Cardiff use indirect information that they judge to be reliable, it is hard to understand why they object to Sahagún's research group doing the same. More important, it is quite common in scientific work to use reliable indirect information. For example, most modern-day scientific papers have a section titled "References" or "Literature Cited" where the authors cite sources that contributed indirectly to the work. Most also have a section titled "acknowledgements", where unpublished sources that contributed indirect information, such as museums, databases, other researchers, etc. are thanked. While direct observations are the ideal, they are not always necessary nor even possible. In the present case, Sahagún's research group was not able to travel back in time to Auitzotl's reign to witness the grackle introduction directly, and so had to depend upon interviews and/or pictorial manuscripts. Needless to say, all good data, whether direct or indirect, gain more credibility when they are peer reviewed by experts, as was the account of Auitzotl's introduction of the great-tailed grackle (Haemig 2012).

The natural invasion hypothesis

Some critics have suggested that the Aztecs confused, or may have confused, a natural invasion of great-tailed grackles for an introduction (Remsen and Cardiff 1990; Christensen 2000; Peer 2011). However, none of these critics have presented evidence that such confusion happened or that a natural invasion occurred during Auitzotl's reign.

In an earlier paper (Haemig 2012), I showed why it is highly unlikely that the historical account is the result of confusion. The investigative methods used by Sahagún's research group were designed to avoid, detect and correct any possible confusion. For example, the research group consulted and collaborated with native experts that had reputations for integrity. If any of their consultants and collaborators in Tlatelolco had really become confused, it is likely that the research group would have discovered the confusion when the account was peer reviewed in Tenochtitlan. Furthermore, many

Table 1. Examples of bird species that occur in both North America and Europe. Note that the existence of species native to both continents (Column 1), does not rule out the existence of species introduced by humans to one or both of the continents (Columns 2, 3 and 4). Data from AOU (1998) and Cramp et al. (1977–1996).

Species natural to both continents	Species natural to Europe but introduced in North America	Species natural to North America but introduced in Europe	Species introduced to both continents
Mallard (<i>Anas platyrhynchos</i>)	Mute Swan (<i>Cygnus olor</i>)	Canada Goose (<i>Branta canadensis</i>)	Mandarin Duck (<i>Aix galericulata</i>)
Willow Grouse (<i>Lagopus lagopus</i>)	Grey Partridge (<i>Perdix perdix</i>)	Wild Turkey (<i>Meleagris gallopavo</i>)	Pheasant (<i>Phasianus colchicus</i>)
Barn Owl (<i>Tyto alba</i>)	Rock Dove (<i>Columba livia</i>)	Northern Bobwhite (<i>Colinus virginianus</i>)	Monk Parakeet (<i>Myiopsitta monachus</i>)
Winter Wren (<i>Troglodytes troglodytes</i>)	Starling (<i>Sturnus vulgaris</i>)	Ruddy Duck (<i>Oxyura jamaicensis</i>)	Common Myna (<i>Acridotheres tristis</i>)
Sand Martin (<i>Riparia riparia</i>)	House Sparrow (<i>Passer domesticus</i>)		
Waxwing (<i>Bombycilla garrulus</i>)			

details of the grackle translocation are given in the account. If confusion had really occurred, one would expect to find differences in the various details in the texts from the two cities. Instead, there were no substantive differences between the Aztec and Spanish texts written before and after peer review (Haemig 2011, 2012).

Remsen and Cardiff (1990) argued that since other bird species colonized the Mexican Highlands without human help, the great-tailed grackle must also have done so. They wrote, “the Mexican Plateau region inhabited by the grackle is also inhabited by disjunct, highland populations of other normally lowland species...for which a hypothesis of human introduction is untenable (p. 973).” Therefore, they concluded, the great-tailed grackle’s distribution was “readily explained within the context of broader distribution patterns, and that there is no need to invoke human intervention (p. 973).”

Remsen and Cardiff’s argument is based on the assumption that similar distributions are the result of similar dispersal histories. However, this is not always true. Consider the following examples: Europe and North America, like the highlands and lowlands of Mexico, have many bird species in common. Some are native to both continents, while others are native to one continent and introduced on the other (Table 1). If we follow Remsen and Cardiff’s reasoning that the presence of species native to both areas rules out the possibility of there also being birds native to one of the areas but introduced in the other, we would erroneously conclude that the starling (*Sturnus vulgaris*), house sparrow (*Passer domesticus*) and mute swan (*Cygnus olor*) invaded North America naturally. Likewise, the presence of naturally-occurring neotropical birds in Florida, like the mangrove cuckoo (*Coccyzus minor*), snail kite (*Rostrhamus sociabilis*), shiny cowbird (*Molothrus bonariensis*) and smooth-billed ani (*Crotophaga ani*) does not prove that other neotropical birds there, such as the spot-breasted oriole (*Icterus pectoralis*), were not introduced by humans.

Remsen and Cardiff (1990), as well as Christensen (2000) and Peer (2011), cite the great-tailed grackle's modern invasion of areas in the United States (Wehtje 2003) as evidence to support the natural invasion hypothesis. However, this fact does not disprove Auitzotl's introduction of the great-tailed grackle, and can just as easily be used to support the introduction hypothesis because it confirms a claim made by the historical account: that the introduced grackles multiplied and spread to other areas.

Finally, I must comment on Remsen and Cardiff's oft-quoted argument that "there is no need to invoke human intervention" because the great-tailed grackle's presence in the "Mexican Plateau region" is "readily explained within the context of broader distribution patterns" (p. 973). I find this argument to be unconvincing. Remsen and Cardiff are in essence telling us to ignore good evidence (a credible historical account) because it threatens their favorite hypothesis.

Indigenous sources

Remsen and Cardiff (1990) concluded their critique of the historical account by attacking its source. Noting that the account came from indigenous peoples, they argued that such peoples cannot be trusted because they sometimes make errors. Remsen and Cardiff explained:

"Although the plausibility and detail of the latter [the historical account] are intriguing, we regard such folklore with distrust. Our personal experience with South American indigenous peoples as well as with "educated" peoples is sprinkled with cases of amusing, but obviously erroneous, explanations of past and present natural phenomena, in spite of detailed and accurate knowledge of natural history in other cases (Remsen and Cardiff 1990, p. 973)."

I know of no other case in the introduced species literature where a credible historical account documenting bird introduction (and even identifying the person responsible for the introduction) has been questioned using negative stereotypes of folk groups. I also find it amazing that Remsen and Cardiff (1990) categorize indigenous peoples separately from "educated" peoples as though indigenous peoples are never educated.

Over the years, I have met other individuals who dispute the historical account because it comes from indigenous sources. Seldom, if ever, does anyone accuse Europeans, or their descendants, of confusing natural invasions with introductions. Yet, as soon as American Indians are identified as the source of information, critics tell us that the information cannot be trusted, that the Aztecs might have been confused - in spite of the fact that the historical account was collected and verified by professionally-trained scholars (Lopez Austin 1974; Haemig 2012). The old falsehood that American Indians are more easily confused than others and cannot keep their facts straight has been a powerful, enduring myth in the Americas, one used for centuries to cover up crimes against native peoples such as treaty violations, war provocations, genocide and land theft, and to argue that surviving Indians need colonial authorities to manage their lands, resources and histories. As professional scientists, we need to recognize that prejudices such as these can hinder the search for truth.

Discussion

I am sometimes asked why Sahagún's research group did not collect and preserve specimens of the great-tailed grackle for us to examine. The answer is that they lived long before the era of scientific collecting and so, like most scholars of their time, modeled their work instead after classical giants like Pliny and Aristotle.

Furthermore, when Sahagún's research group worked in the 16th century, the methods and technologies for long-term preservation of bird skins (with their feathers) had not yet been invented (Walters 2003). Stresemann (1975, p. 27) writes that before the 18th century "many birds, dead and alive," were shipped to Europe but "none of the birds lasted very long: ...the dried skins, which no one knew how to impregnate, were eaten by moths and dermestids". Thus, even if Auitzotl's Aztecs or Sahagún's research group could have predicted future research methodologies and tried to save skins of grackles for us to inspect today, it is doubtful if those specimens would have survived the centuries.

Although Sahagún's research group did not preserve specimens of the great-tailed grackle, they wrote an excellent, detailed description of it (Sahagún [1577] 1979, vol. 3, book 11, folios 53v-54r, Sahagún [1577] 1963, p.50). Their description matches the great-tailed grackle and leaves no doubt that the bird which the Aztecs called *Teotzánatl* is *Quiscalus mexicanus* (Appendix A.7).

Today, we have better scientific methods and technologies than Sahagún's research group had when they worked over four hundred years ago. Yet, and this is humbling to admit, Sahagún's research group had a least one advantage over us: They lived in Mexico at a time when experts from Auitzotl's reign were still alive and when many pre-Hispanic pictorial manuscripts were still extant. In other words, they had access to good sources of information that are no longer available to us, and they tapped these sources using the best scholarly research methods of their time. I therefore believe that, unless convincing evidence to the contrary can be presented, we have a greater likelihood of knowing the truth about Auitzotl's introduction of the great-tailed grackle if we trust the careful work of Sahagún's research group rather than the speculations of persons living today, over 400 years later.

Some critics claim that "insufficient evidence" has been presented to prove that the great-tailed grackle was introduced into the Valley of Mexico by Aztec Emperor Auitzotl (Remsen and Cardiff *in* Christensen 2000). That claim is debatable, since there are different opinions as to what constitutes sufficient evidence. But at least Sahagún's research group presented a highly-credible, peer-reviewed historical account - better documentation than what is available for many birds currently classified as introduced. In contrast, the proponents of the natural invasion hypothesis have to date presented no historical account of grackles naturally invading the Aztec capital during Auitzotl's reign, and have failed completely in their attempts to discredit the *Florentine Codex's* account of introduction.

There is no evidence for natural invasion of the Valley of Mexico by great-tailed grackles during the reign of Auitzotl. On the other hand, there is good evidence for intro-

duction by Aztecs. That evidence comes from the authentic historical account preserved in the *Florentine Codex*. It is hard to find a more credible and reliable ancient source than this encyclopedia, for it was the product of many years of research by the top scholars of sixteenth-century Mexico, who used the most rigorous and demanding methods of investigation for their time, including peer-review, to ensure that their work was truthful and reliable (Haemig 2012). If we throw out the historical account of Auitzotl's introduction of the great-tailed grackle, we must in all fairness throw out much of mankind's history of the ancient world, for a great amount of the latter was collected and recorded under far less rigorous standards than that employed by Sahagún's research group.

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Appendix

- A.1. The original *Manuscript of Tlatelolco* is preserved today in the Biblioteca de la Real Academia de la Historia in Madrid, Spain (Haemig 2012). A facsimile copy of the page from that manuscript with the account of Auitzotl's introduction of the great-tailed grackle can be seen in Sahagún [1565] 1907, folio 259v. It is written in Aztec (classical Nahuatl).
- A.2. Sahagún's research group collected much of their information from Aztec elders who, in their youth, may have been eyewitnesses to Auitzotl's introduction of the great-tailed grackle (Sahagún [1577] 1979, 1982; Haemig 2011, 2012).
- A.3. Sahagún ([1577] 1979, 1982) stated specifically that some of the information his research group collected came from extant pre-Hispanic pictorial manuscripts. For example, writing of his group's earlier fieldwork in Tepepulco during the years 1558-1561, Sahagún mentioned that their consultants and collaborators there gave them "all the matters we discussed in pictures, for that was the writing they employed in ancient times" (Sahagún [1577] (1982) p. 54). Another historian, Diego Duran, wrote that by 1486, the year Auitzotl became emperor, the Aztec nation was so well organized that officials kept records of everything: "This nation had a special functionary for every activity, even minor ones. *Everything was so well recorded that no detail was left out of the accounts and registers*" [emphasis mine] (Duran [1581] 1994, p. 309). Because the introduction of the great-tailed grackle was the result of a specific command by the emperor, it may have been considered important enough to be documented in pictorial manuscripts.
- A.4. The *Manuscript of 1569* is now lost, however its Aztec texts were copied into the *Florentine Codex* during the 1570s (Sahagún [1577] 1979, 1982; Dibble 1982).
- A.5. The Spanish texts in the bird chapter of the *Florentine Codex* are critical abstracts of the Aztec language bird accounts that appear to incorporate, among other things, details from the Aztec texts as well as additional information including comments added during peer-review in Tenochtitlan. In 1569, Sahagún specifically stated that it had not yet been possible to provide the *Manuscript of 1569* with the scholia and Spanish translations (Sahagún [1577] 1982, p.46). At that time, it was intended to make three columns on every page: one column each for the Aztec text, Spanish Text and the scholia (Sahagún [1577] 1982, p.51). However, when the *Florentine Codex* was later produced, each page contained only two columns, one for the Aztec text and one for the Spanish text with scholia.
- A.6. A facsimile copy of the *Florentine Codex's* pages with the account of Auitzotl's introduction of the great-tailed grackle in both the Aztec and Spanish texts can be seen in Sahagún [1577] 1979, vol. 3, book 11, folios 53v-54r.
- A.7. Martin del Campo (1940) identified the *Teotzanatl* as the Great-tailed Grackle. See Christensen (2000) and the Appendix of Haemig (2010) for confirmation of this identification.

- A.8. To avoid confusion, I use the word *Tenochca* rather than Sahagún's *Mexicanos*, because it is clear from sentences proceeding and following the quoted passage that Sahagún uses *Mexicanos* in a very restricted sense to mean only people of Tenochtitlan (Sahagún [1577] 1982, p.41).
- A.9. The many changes seen in the Aztec text of the *Florentine Codex* (compared to the *Manuscript of Tlatelolco*) also show that these texts were copied from the *Manuscript of 1569* rather than the *Manuscript of Tlatelolco* (Sahagún [1577] 1979, 1982).

