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Heterogeneity in patterns of survival of the invasive species *Ipomoea carnea* in urban habitats along the Egyptian Nile Delta

Reham F. El-Barougy[1,2], Marc W. Cadotte[1,3,4], Abdel-Hameed A. Khedr[2], Reham M. Nada[2], J. Scott MacIvor[3]

1 *Department of Ecology and Evolutionary Biology, University of Toronto, 25 Willcocks St. Toronto, Ontario, Canada* **2** *Department of Botany, Faculty of Science, Damietta University, Egypt* **3** *Department of Biological Sciences, University of Toronto Scarborough, 1265 Military Trail, Toronto, ON, Canada* **4** *Stake Key Laboratory of Biocontrol, Key Laboratory of Biodiversity Dynamics and Conservation of Guangdong, Higher Education Institutes, College of Ecology and Evolution, Sun Yat-sen University, Guangzhou, PR China*

Corresponding author: *Reham F. El-Barougy* (reham.el.barougy@mail.utoronto.ca)

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Abstract

Plant traits are critical for understanding invasion success of introduced species, yet attempts to identify universal traits that explain invasion success and impact have been unsuccessful because environment-trait-fitness relationships are complex, potentially context dependent, and variation in traits is often unaccounted for. As introduced species encounter novel environments, their traits and trait variability can determine their ability to grow and reproduce, yet invasion biologists do not often have an understanding of how novel environments might shape traits. To uncover which combination of traits are most effective for predicting invasion success, we studied three different urban habitat types along the Nile Delta in Egypt invaded by the Pink Morning Glory, *Ipomoea carnea* Jacq. (Family: Convolvulaceae). Over two years, we measured ten plant traits at monthly intervals along an invasion gradient in each habitat. No single trait sufficiently explained survival probability and that traits linked to invasion success were better predicted by the characteristics of the invaded habitat. While the measured traits did influence survival of *I. carnea*, the importance of specific traits was contingent on the local environment, meaning that local trait-environment interactions need to be understood in order to predict invasion.

Keywords

Invasion success, Exotic species, Survival probability, Morning Glory, Disturbed habitat

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Introduction

Biological invasion is a significant threat to biodiversity and often leads to habitat degradation (Elton 1958, Genovesi and Monaco 2013, Qureshi et al. 2014). There is a great need for efficient tools to predict invasion success and impact on native ecosystems (Funk et al. 2008). Yet, the relative importance of particular life history and functional traits for invasion success and impact is strongly context-dependent and likely to change across environments (Dawson et al. 2009). In cases of significant impact by invasive plants, estimating 'invasiveness' using plant traits that predict plant survival could be used to determine invasion resistance of native plant communities (Ortega and Pearson 2005, Radosevich et al. 2007, Colautti et al. 2014).This is particularly important to understand in urban habitats where urbanization can favor non-native species (McKinney 2006). Urbanization reduces the competitiveness of established vegetation (Wilson and Tilman 1995) and increases the availability of resources (Johnstone 1986, McConnaughay and Bazzaz 1991), which can be exploited by non-native species, further influencing their invasiveness.

At a more basic level, we often lack a basic understanding of how size and life history traits contribute to the successful growth and reproduction of most species and especially non-native species. The attributes that are associated with successful species is undoubtedly correlated with local environmental conditions (Laughlin et al. 2012, Laughlin 2014). For example, Laughlin and colleagues (2012) show how models that match trait values to local climate predict species abundances. Such a relationship between traits and the environment are useful to explain presence/absence or abundance patterns, but little work has been done to see if intraspecific trait variation can explain difference in growth, reproduction, and survival. Further, it is unclear how changes in size-based traits through the growing season and in different environments influence success. What is lacking in our current knowledge is how specific traits or suites of traits influence species performance in different habitats.

A number of studies have shown that invasion success can be linked to specific traits and the degree to which they promote survival in novel environments. These include for example, traits linked with reproduction and dispersal, leaf traits that are believed to reflect competitive strategies, overall resource allocation into growth, and seedling growth patterns (Usher 1988, Pattison et al. 1998, Reichard and Hamilton 1997, Kolar and Lodge 2001, Richardson and Rejmánek 2004, Hamilton et al. 2005, Rejmánek et al. 2005). Leaf traits linked to species success are associated with their ability to capture resources, particularly in environments that are resource limited (Funk and Vitousek 2007). For invasive plants, leaf carbon fixation strategies that improve productivity are closely linked to success in introduced habitats (Wright et al. 2004, Westoby and Wright 2006).

While the search for the attributes that influence species performance and especially invasion would undoubtedly lead to advancing general theory, it is often underappreciated just how sensitive trait-performance relationships can be to local environmental conditions. The appreciation of the importance of intraspecific trait variation has greatly increased in community ecology (Albert et al. 2012, Violle et al. 2012), but our understanding of how specific traits, and their variation, influence plant species growing in different habitats is lacking.

This study investigates the aboveground and belowground plant attributes, and especially those that reflect resource allocation, that influence the survivorship of the invasive pink morning glory, *Ipomoea carnea* Jaq. (Family: Convolvulaceae), in three unique urbanized habitats that it invades in the Nile Delta region in Egypt. *Ipomoea carnea* is an annual vine that is native to Central and South America, but occurs worldwide in many habitats, including the Nile Delta where it is invasive (Eid 2002, Shaltout et al. 2010). This species reproduces vegetatively and the reproductive vegetative unit is called ramet (an individual stalk from one individual plant) which originates from a semi-underground organ, the caudex. This type of reproduction is very common and considered as a proxy for the successful invasion of *I. carnea*, additionally it reproduces by seeds and the reproductive unit is called genet which is rarely occurred due to the harsher conditions that required for seed germination. To explore population growth rates of the invasive plant, and how they respond to environmental variation, we used density-independent matrix models (Engelen and Santos 2009, Griffith 2010) to evaluate the survivorship of *I. carnea* in three introduced habitats (Eid 2002, Jerde and Lewis 2007, Bates et al. 2013). We tested three hypotheses 1) there are specific plant traits that predict the survival probability of *I. carnea* along an urbanization gradient 2) there is variation in the survival probability in different urban habitat types which is highest in canal banks habitat followed by roadsides and waste lands, representing an urban gradient, and that 3) leaf traits are the best indicators of the successful invasion of *I. carnea*. Our findings provide valuable information on specific traits that determine invader survival in different novel urban habitat types for a species that is prevalent worldwide.

Methods

Sites

The study area is bound by the main tributaries of the Nile Delta in Egypt, from the Rosetta branch at the west to the Damietta Governorate at the east, the Mediterranean Sea to the north and the Menoufia Governorate to the South. The area of the Nile Delta is about 22,000km^2 and it comprises about 63% of Egypt's productive agricultural area (Abu Al-Izz 1971).

Nine permanent stands in Damietta Governorate were established in each of three different urban habitats where the invasive *I. carnea* occurred: wastelands, roadsides (both with dry-sandy soil) and canal banks (with clay-organic soil) (Shaltout et al. 2010). In each stand, a map was drawn indicating the spatial distribution of above ground vegetative units (ramets) of *I. carnea*. Mean surviving and dead ramets in each stand was recorded monthly.

Plant trait sampling

Ten randomly distributed quadrats (1 × 1 m) were laid down in each stand. The number of *I. carnea* ramets in each quadrat was counted and used to estimate *I. carnea* density per stand (ramets/ m^2). Ten ramets (1 per m^2 plot) were randomly selected and marked using flagging tape to monitor the monthly variation in each of the plant traits. The height from the ground (cm), average diameter (cm), leaf area (cm^2), number of flowering ramets, number of non-flowering ramets, number of leaves, flowers and fruits of the canopy for each permanent marked ramet were estimated monthly.

Three randomly selected ramets were harvested from each stand and their roots, stems and leaves were separated and weighted to determine their fresh weights. The roots, stems and leaves were oven dried at 60°C for three days to determine the dry weight. Mean fresh and dry weights of the roots, stems and leaves of the ramets of each habitat were determined (gm $ramet^{-1}$) and multiplied by the number of ramets (m^{-2}) in each stand to give their standing crop (gm^{-2}) in each habitat (Shaltout and Ayyad 1988, Al-Sodany et al. 2009).

Soil analysis

In each stand, a composite soil sample was collected from beneath invaded and non-invaded canopies from each habitat, each 50 cm deep. These were air dried and passed through a 2 mm sieve to separate gravel and debris. Soil water extracts at 1:5 were prepared for the determination of soil reaction (pH) using a Benchtop pH Meter (Mettler-Toledo).

Statistical analysis

Generalized-multivariable modelling

There were 14 different variables used in generalized multivariable modelling (Table 1). In this analysis, the binomial response variable with two-column was represented by the total observed number of surviving ramets (first column) and dead ramets (second column), while the explanatory variables were represented by plant traits, sampling time and soil (pH) for invaded and non-invaded canopies in the three different urban habitats. We aimed to identify the most parsimonious models that explained which explanatory variables were best for predicting this binomial response variable. To remove potential explanatory variables (predictors), we first constructed a series of models with each of the variables, then we compared the explanatory ability of these models using Akaike's information criterion weights which can be used to interpret which model was the best fit to an observed dataset, among a set of candidate models (Johnson and Omland 2004). We used a chi-square test to test for significance of the model's goodness-of-fit. The best

Table 1. List of measured variables from which the average values were taken from 10 plants per stand in each of the three urban habitats (Canal banks, Wastelands and Roadsides).

Variable	Units	code
Total surviving and dead ramets	-	y
Sampling month	-	M
Leaf area		LA
Diameter	cm	D
Height	cm	H
Number of all leaves	-	NL
Leaf biomass	gm/M^2	LB
Number of flowering ramets	-	Flr
Number of non-flowering ramets	-	NFlr
Number of flowers	-	Fl
Shoot biomass	gm/M^2	SB
Root biomass	gm/M^2	RB
Soil pH under canopy (invaded areas)	-	PhU
Soil pH outside canopy (non-invaded areas)	-	PhO

models were filtered according to 1) lower values of AIC, 2) higher values of model probability (AW), 3) higher *p* values of chi-square test ($p>0.05$). We checked diagnostic plots (e.g. residual versus fitted plots) for potential outliers and data trends. We were not only interested in the best single variable explaining the rate of survival probability, but also combining all plant traits in multi-variable models (see Suppl. material 1).

For each urban habitat, we assessed the observed survival probability based on the ratio between the observed number of surviving ramets and total ramets (including surviving and dead ramets), while the fitted survival probability was assessed from each multivariable model as fitted values. We tested the difference between the observed and fitted survival probability values for all multivariable models to confirm that the difference between observed and fitted values from the best model was very low. Further, for each modelled trait, we assessed which trait values tended to have higher or lower survival probabilities. All analyses were completed using R v.3.2.2 (RStudio Team 2015).

Odds ratio (OR)

We modelled the probabilities of survival as a function of the plant traits and environmental variables in different habitats and to do this we used odds ratio to predict the upper and lower limit of the ratio of the probability of success (survival) and the probability of failure (death) for each modelled variable. Odds ratios were also used to test for possible associations between different environmental variables. If the OR is equal to 1, there is no association. If the OR is (> 1and <1), then there is a possible statistical association between them (Morris et al. 1988, McHugh 2009, Szumilas 2010). The odds ratios were computed in R using functions *confint* and *exp* in the MASS package.

Results

There was a highly significant effect of habitat on survival probability of *I. carnea* with lower survival probability in wastelands and roadsides compared to canal banks which showed a remarkably highly survival probability. For adult ramet mortality, wasteland and roadside had the highest, while canal banks had the lowest (Fig. 1a).

Generalized Multivariable modelling

Comparing the mean plant trait values and abiotic variables in different habitats, forty generalized linear models were constructed (Suppl. material 1). The most parsimonious model explaining the binomial response variable (the total surviving and dead ramets) in *I. carnea* in the canal banks site included sampling time (month), number of non-flowering ramets, root biomass, number of flowers, number of flowering ramets and leaf area (AW = 0.606, AIC = 102.3). For wastelands, the best model (AW = 0.756, AIC = 189.41) included leaf biomass, root biomass, stem diameter, number of leaves

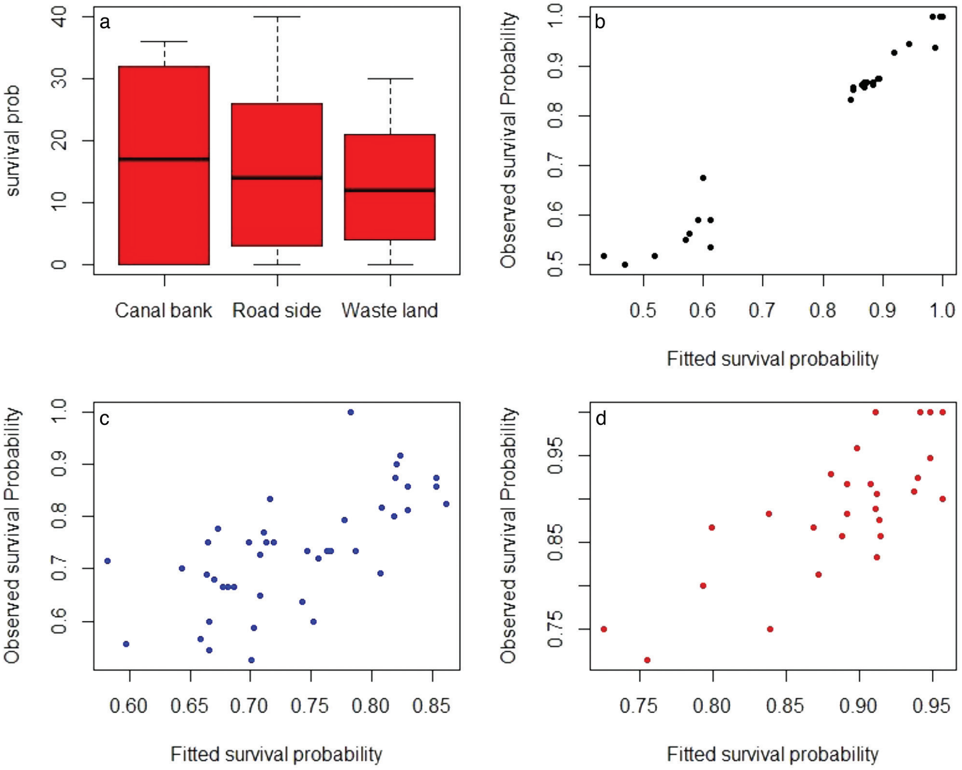

Figure 1. a Comparison between the mean of observed survival probability at habitat level **b–d** the relationship between fitted survival probabilities from the three top models and survival probabilities from the actual observed data in canal banks, roadsides and wastelands respectively.

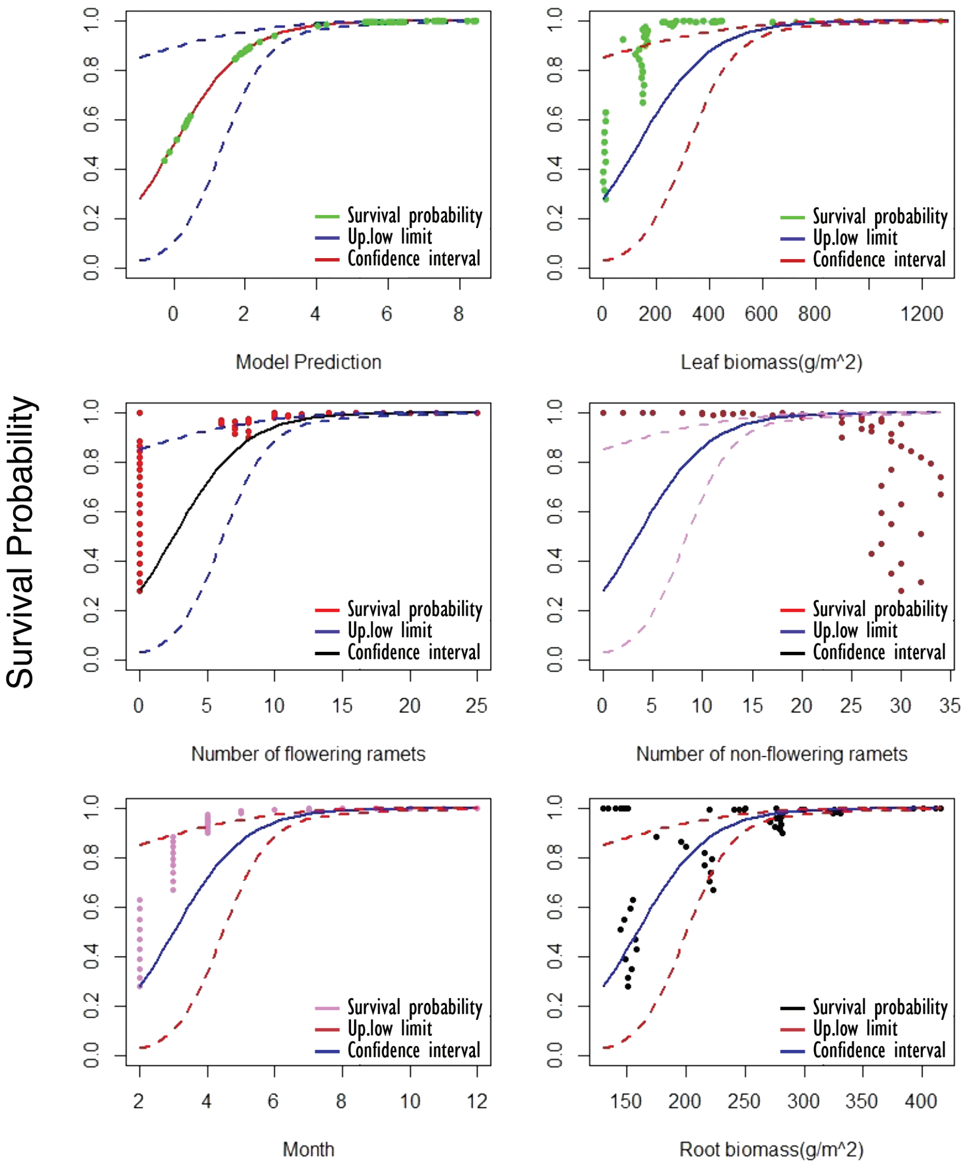

Figure 2. The relationship between survival probability and predictors from the top model for Canal bank habitat.

and soil PH for invaded areas. For roadsides, the best model (AW = 0.423, AIC = 111.1) included month, stem diameter, flowering ramets, non-flowering ramets and soil pH of invaded areas. These three top models revealed 97.5%, 42.9%, and 50.8% of the deviance explained in canal banks, wastelands and roadsides, respectively (Suppl. material 1).

For the abiotic variables, there was a positive significant interaction between the binomial response variable and sampling time in canal bank, while this interaction

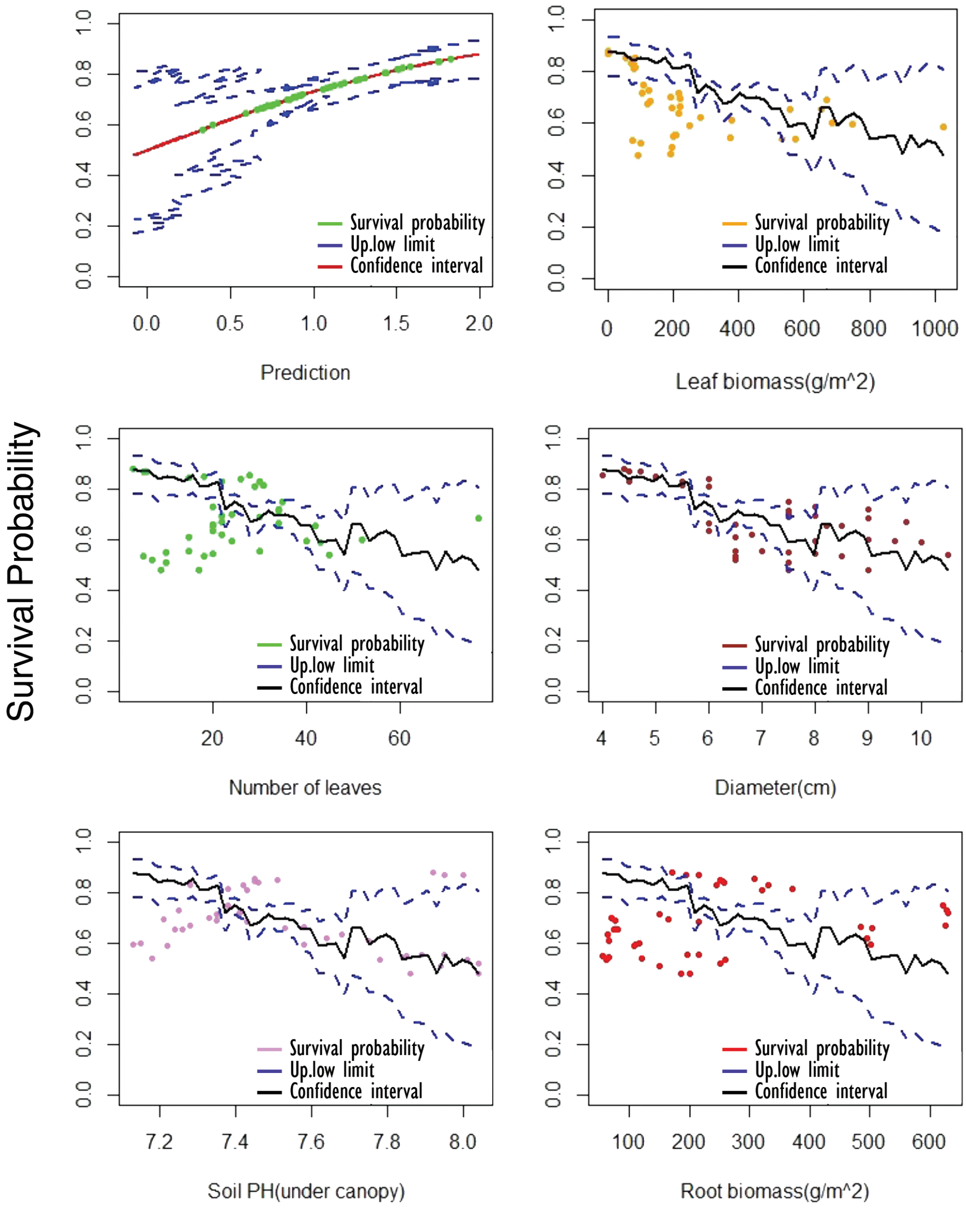

Figure 3. The relationship between survival probability and predictors from the top model for wasteland habitat.

showed a negative significant effect in road side habitats. Additionally, being in soil with high pH (>7) values resulted in lower *I. carnea* survival in wasteland habitat (Table 2).

All of the *I. carnea* biomass traits differed significantly between habitats. Higher values of leaf biomass had a strongly significant negative effect on the survival rate in canal bank and wasteland. Additionally, higher root biomass decreased survival rate in

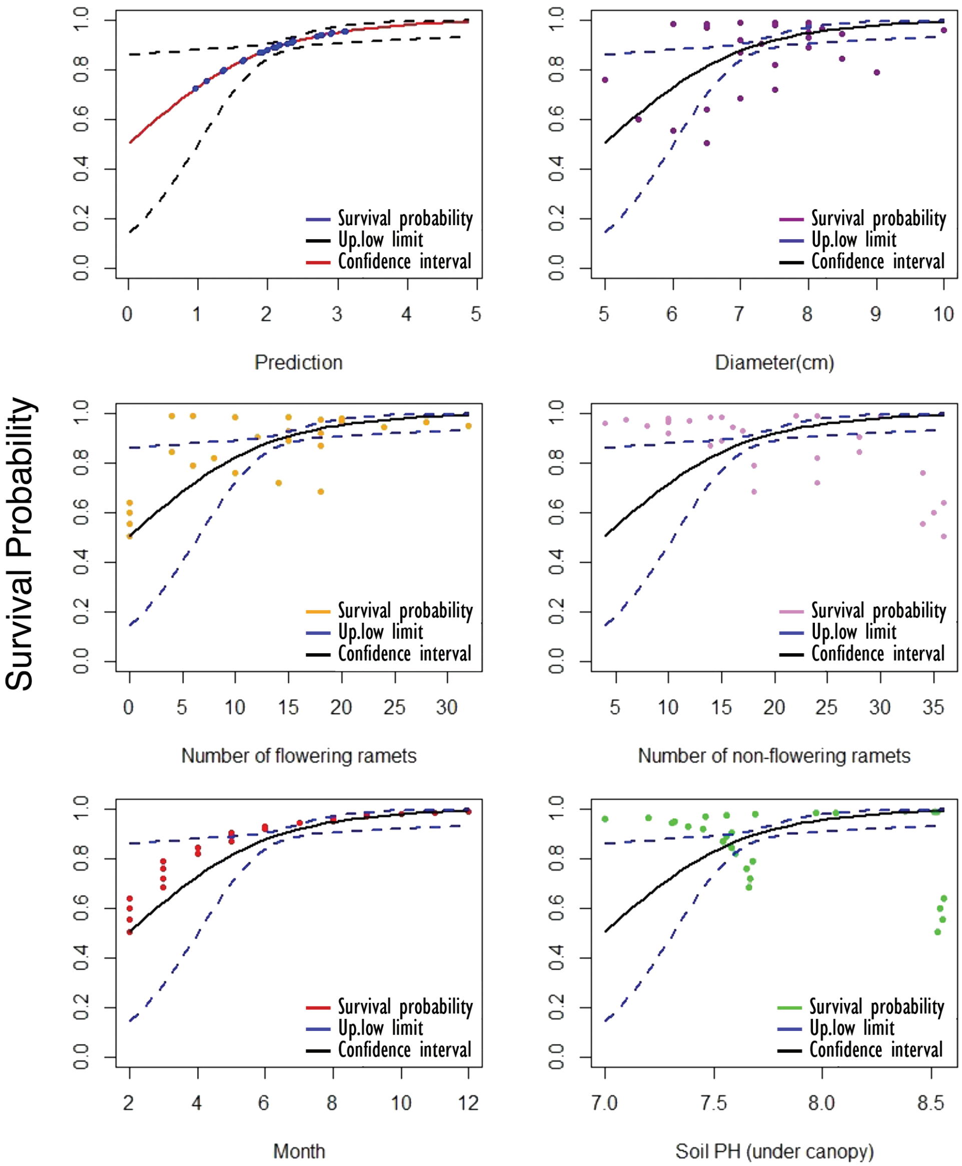

Figure 4. The relationship between survival probability and predictors from the top model for Roadside habitat.

wasteland but increased survival in canal bank. Other traits that significantly increased survival probability included the number of leaves in wasteland habitat, higher values of flowering ramets and non-flowering ramets in road sides, and the number of flowers in canal banks. Although declining stem diameter led to a significant reduction in survival rate in wasteland habitats, smaller stems were positively correlated with survival rate in roadside habitats (Table 2).

Table 2. Comparison of the top multivariable models from the stratified generalized linear models. The confidence interval (CI) with upper (U) and lower limit (L) and odds ratios (OR) for the modelled coefficients in the three habitats: canal banks (CB), roadsides (RS), waste lands (WL). (-) represents a variable that is excluded in the given top model.

Variables	Coefficients			CI (U,L)			Odds ratio (OR)			P-value		
	CB	WL	RS	CB	WL	RS	CB	WL	RS	CB	WL	RS
Month	0.79	-	-0.145	0.577, 1.025	-	-0.24, -0.05	2.2	-	0.86	0.00	-	0.003
Leaf biomass	-0.03	-0.001	-	-0.032, -0.018	-0.002, -2.9×10^{-4}	-	0.97	0.99	-	0.00	0.02	-
# Flowering ramets	0.46	-	0.13	0.276, 0.730	-	0.05,0.21	1.58	-	1.13	0.00	-	0.000
# Flowers	0.13	-	-	0.055, 0.190	-	-	1.14	-	-	0.00	-	-
# Non-flowering ramets	0.09	-	0.05	-3.2×10^{-4}, 0.200	-	0.001,0.11	1.09	-	1.05	0.05	-	0.05
Root biomass	0.02	-0.001	-	-8.5×10^{-5}, 0.030	-0.002, -1.7×10^{-6}	-	1.01	0.99		0.02	0.05	-
Diameter	-	-0.13	0.28	-	$-0.25,-1.25\times10^{-2}$	0.024, 0.54	-	0.87	1.32	-	0.03	0.03
Number of leaves	-	0.013	-	-	-0.002, 2.8×10^{-2}	-	-	1.01		-	0.10	-
Soil PH (under canopy)	-	-0.79	0.95	-	$-1.52,-7.3\times10^{2}$	-0.24,2.12	-	0.45	2.6	-	0.03	0.11

Furthermore, when we tested the difference between the observed survival probability from actual data and fitted survival probability from the three top models in different habitats, we found that the difference was very low compared to other models (Fig. 1b–d).

Odds ratio (OR)

The odds ratio and confidence interval for modelled variables were interpreted as the ratio of the probability of success (survival) over the probability of failure (mortality). For each top model, we used odds ratios as a measure of statistical significance of the association between each modelled traits and survival probability. Accordingly, all odds ratios were (>1 and <1) (Table 1), therefore the association between each modelled trait and survival probability was statistically significant (Figs 2–4). If we take leaf biomass as an example, we see that one unit increase in this predictor, led to a 9.7% and 9.9% increase in the odds of *I. carnea* survival in canal bank and wasteland respectively, assuming that other variables are fixed (see Table 2).

Discussion

In our study we showed that plant attributes associated with the survival of the invasive species *I. carnea* differed by urban habitat type. Confirming recent calls for the inclusion of intraspecific variation in ecological studies, we showed that growth and biomass allocation traits were indeed important for predicting species performance, but that the important traits differed among the habitats analyzed. Our results showed that using morphological plant traits provides a simple approach to understand invasive species survival in novel habitats. The critical conclusion is that while the measured traits did influence survival of *I. carnea*, the importance of specific traits was contingent on the local environment, meaning that local trait-environment interactions need to be understood in order to predict and plan for invasive species.

Our study showed a clear selection of traits in different habitats (Table 2, Figs 2–4). In canal banks habitat, the interaction among leaf biomass, root biomass, number of flowering ramets and non-flowering ramets has a significant effect on the survival rate of *I. carnea*. In waste lands, leaf biomass, root biomass, number of leaves and stem diameter, but in roadsides stem diameter, number of flowering ramets and non-flowering ramets. Consequently, growth and survival of this species was a function of measured traits, especially those reflecting size.

However, it should be noted that size-based traits were the best predictors for invader survival, which is in some ways not surprising. It is well known that larger plants have higher survival probabilities and greater reproduction (Horvitz and Schemske 2002). Larger plants are those individuals that have already experience successful growth and might reflect the fact that these individuals are in locations with optimal micro environmental conditions. Yet, what was unexpected was that different size traits predict survival in different habitats.

Traits linked to invader colonization in new environments are those most likely to predict invasion success. Trait-environment relationships were also consistent with general patterns observed along large ecological gradients (Ozenda 1985, Pornon et al. 2007). In a meta-analysis of trait comparisons related to invasiveness, shoot allocation, leaf-area allocation, physiology, size, growth rate, and fitness were found to be most important for plant invader success (Van Kleunen et al. 2010).

From the top models, our study showed a significant relationship between leaf traits and different habitats. For example, there was a positive significant effect of the number of leaves on the survival probability of *I. carnea* in wastelands, whereas survival probability decreased significantly with increasing leaf biomass in canal banks and wastelands habitat. Moodley et al. (2013) stated that for some plant traits there are clear mechanisms for the association of selected traits and invasion success, also some traits show differing responses at the different stages of invasion. Leaf traits in particular have been linked to invader success, including a large meta-analysis of local and global leaf traits predicting invasion (Leishman et al. 2007). Leaf growth and production is dependent upon the rate of supply of limiting resources (Shinozaki and Kira 1956). Both leaf area and leaf consistency are related to the moisture conditions prevailing in the habitat occupied by the plant. The moisture conditions are reflected by climatic and soil factors and it may be difficult to distinguish between the effects of either (Werger and Ellenbroek 1978).

It should be noted that the three habitat types were spatially segregated and thus the analyses would be pseudo replicated if included in single statistical models (Hurlbert 1984). We analyzed the three habitats separately and our expectation was that if trait-performance relationships were robust enough, we should see similar patterns in the different habitats. Yet trait-performance relationships were quite different at the different sites. Future studies should find more habitat replicates or design experiments to delve deeper into the trait-environment relationships.

This study concluded that trait-environment interactions are critical predictors of invader species survival and subsequent success in novel urban habitats. As invasive plant species continue to pose significant threat to natural areas, understanding how they interact in novel, urban habitats is often a first step to understand the dynamics of invasive species in more pristine and protected habitats. Our approach was able to predict the local abundance of *I. carnea* across a large ecological gradient. Also it can help to assess monitoring of invasive species in native Egyptian ecosystems. We gain a better insight on the rapid growth and adaptability of *I. carnea* from dry to aquatic habitats which may indicate that this plant is capable of rooting within a few days (Cook 1987, Chaudhuri et al. 1994, Shaltout et al. 2010). Due to the invasion of *I. carnea*, diversity of native Egyptian wetland flora and fauna is being reduced (Eid 2002). By understanding which traits are correlated to invasion success of *I. carnea*, what the mechanisms behind such correlations are, and under which conditions invasions are favoured can provide accurate predictive tool to reduce the impact of invasive species.

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Supplementary material 1

Table 1S. Comparison of stratified multivariable generalized linear models

Authors: Reham F. El-Barougy, Marc W. Cadotte, Abdel-Hameed A. Khedr, Reham M. Nada, J. Scott Maclvor

Data type: PDF file

Explanation note: Comparison of stratified multivariable generalized linear models that model the relationship between survival probability and different variables. The best model, selected by AIC, p-value of chi square, deviance explained (DE) and (AW). AW is the Akaikes weight which is the probability of the model being the best model explaining the relationship between survival probability and different variables. DE is the percentage of deviance explained (DE) as a measure of the model's goodness-of-fit.

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Small details of big importance: Carbon mass determination in the invasive cladoceran *Cercopagis pengoi* (Ostroumov, 1891) by the high temperature combustion method

Irena V. Telesh[1]

[1] *Zoological Institute of the Russian Academy of Sciences, Universitetskaya Embankment 1, 199034, St. Petersburg, Russian Federation*

Corresponding author: *Irena V. Telesh* (Irena.Telesh@zin.ru)

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Abstract

Carbon mass of the non-indigenous predatory fishhook water flea *Cercopagis pengoi* (Ostroumov, 1891) from the eastern Gulf of Finland, the Baltic Sea, was for the first time measured using the high temperature combustion method. Prior to the analysis, individual dry weight of *Cercopagis* was determined; altogether ca. 500 organisms were examined. Mean individual dry weight of *C. pengoi* for July-September was estimated as 34.0 µg; carbon mass averaged 15.8 µg; carbon content, calculated as percent of dry weight, averaged 43.4%. Those values varied over months, mainly because of different population structure of *C. pengoi* and variation in their diet due to seasonal dynamics of the food objects. However, relations between carbon mass and dry weight for different months did not differ statistically ($p<0.001$). Therefore, the general polynomial regressions (k=2), describing carbon mass-to-dry weight and carbon content-to-dry weight relationships, were calculated for the entire dataset of individual measurements of *C. pengoi* body metrics. These data will contribute to adequate evaluation of food web structure and ecosystem alterations in various water bodies invaded by *C. pengoi* which has got a strong potential to pelagic food web transformations that may impact the overall energy balance and decrease the size of fish stocks.

Keywords

Alien species, Baltic Sea, carbon content, *Cercopagis pengoi*, dry weight

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Introduction

In invasion biology, ecosystems vulnerability to non-indigenous species introductions, biodiversity of native communities and competitive resource utilization depending on the size of organisms are pervasive and closely linked to environmental changes (Holopainen et al. 2016). For the adequate food web structure evaluation and the appropriate energy balance calculations in aquatic ecosystems, determination of carbon mass of organisms as a biomass measure is an important prerequisite. Since decades, individual carbon mass has been a routine parameter known for many zooplankton organisms (Hessen et al. 2013, Kiørboe 2013, Walve and Larsson 1999), even the smallest meso- and microzooplankters such as rotifers (Telesh et al. 1998b). For a limited number of zooplankters, the relations between carbon mass and other size metrics were established (Telesh et al. 1998b, Vasama and Kankaala 1990). Precise knowledge of the individual carbon mass and carbon content of aquatic organisms is of exceptional value when assessment of the impacts of alien species invasions on the ecosystems, food webs, competitive interactions, and composition of native communities is in the research focus.

Among such hotspot research fields is the estimation of ecosystem impact of the opportunistic generalist predator – the Ponto-Caspian onychopod cladoceran *Cercopagis pengoi* (Ostroumov, 1891), one of the recent invaders to the Baltic Sea (Ojaveer and Lumberg 1995, Krylov et al. 1999, Leppäkoski et al. 2002, Telesh et al. 1999, 2001, 2008, Rowe et al. 2016) and to the Laurentian Great Lakes (MacIsaac et al. 1999, Therriault et al. 2002). This invader has got a strong potential to cause alterations in plankton communities, including population shifts (Ojaveer et al. 2004, Telesh and Ojaveer 2002), resource competition (Holliland et al. 2012, Lehtiniemi and Lindén 2006), depletion of prey populations (Kotta et al. 2006), or changes in energy fluxes (Laxson et al. 2003, Litvinchuk and Telesh 2006, Naumenko and Telesh 2008).

However, despite the fact that much is known about population dynamics, feeding behavior and the diet of *C. pengoi* (Holliland et al. 2012, and references therein), as well as its role in fish diet (Gorokhova et al. 2004) and competition of *C. pengoi* with 0-group fish for small prey (Vanderploeg et al. 2002), such a routine parameter as biomass of *C. pengoi* can only be roughly estimated so far. Most often it is assumed that the individual dry weight of *C. pengoi* is 20 µg (Uitto et al. 1999), or carbon content is calculated assuming the carbon to dry weight relation of 44% which is available for other cladocerans (Hessen 1990). Until now, preliminary data on the direct carbon mass determination in *C. pengoi* from the eastern Gulf of Finland was only available as a brief abstract publication (Telesh et al. 1998a); correlation between those parameters has never been established.

To fill in this gap, the present research aimed at direct measurement of carbon mass and dry weight of the invasive water flea *Cercopagis pengoi* from the eastern Gulf of Finland (the Baltic Sea), for (i) evaluating its average individual carbon mass, dry weight and carbon content, and (ii) for calculating the carbon mass-to-dry weight relationship during the period of maximum population development when the impact of *C. pengoi* on the native pelagic community is the greatest.

Materials and methods

Zooplankton samples were collected in July, August and September 1997 at three sampling stations in the eastern Gulf of Finland (EGF), the Baltic Sea: station P (St. P, sampling dates 22 August and 11 September) in the coastal zone near Primorsk, station F-2 (St. F-2, sampling date 22 July) in the open waters of the EGF, and station 21 (St. 21, sampling date 10 September) in the coastal waters of the EGF in the vicinity of Zelenogorsk (Fig. 1). All stations were located in the oligohaline waters with salinity 4-6 psu at the depth of 12 m (St. 21 and St. P) and 23 m (St. F-2).

Zooplankton at each station was sampled by several vertical tows from 1.5 m above the bottom to the surface using the Juday plankton net with the opening diameter 0.2 m and mesh size 138 µm. The composite samples from each location were preserved with formaldehyde (final concentration 4%) and frozen at -18 °C. This method is known to provide superior preservation for the purpose of carbon mass determination for many zooplankton species (Salonen and Sarvala 1980, Telesh et al. 1998b).

On the date of the analysis, samples were defrosted, ca. 120 individuals of *C. pengoi* were picked from each sample, rinsed 5 times in distilled water in Petri dishes and kept on ice at about -5 °C until processing. Prior to carbon mass determination, *Cercopagis* were placed in pre-weighed tin capsules individually and dried at 60 °C for 36 h. Dried organisms were kept in desiccator until carbon mass determination. Individual dry weight (DW) of each cladoceran was registered using Sartorius microbalance (± 0.0001 mg) immediately before carbon measurement. Altogether, ca. 500 individuals of *Cercopagis* were analyzed.

Carbon mass (CM) of each individual *Cercopagis* with the known dry weight was measured using the high temperature (+950 °C) combustion method (Salonen 1979) in the Universal Carbon Analyzer (UNICARB) at the Department of Biology, Faculty of Science and Forestry, University of Eastern Finland (Joensuu, Finland). The results of carbon mass determination and dry weight measurements of *C. pengoi* obtained in 1997 were statistically analyzed at the Zoological Institute of the Russian Academy of Sciences (St. Petersburg, Russia) in 2015-2016.

Carbon content (CC) was calculated as percent of dry weight for each individual. Mean dry weight, carbon mass, carbon content of *C. pengoi* and regressions for these parameters were calculated separately for each month (July, August and September) and for the entire study period using the complete dataset.

Variations in dry weight and carbon mass of *C. pengoi* at three stations during different months were compared statistically using the method of Multiple Comparisons (2-tailed) that allowed to assess the impacts of categorical independent variables, controlling for the effects of the continuous predictor variable, CM. The non-parametric Kruskal-Wallis ANOVA by Ranks test was also used for comparison of multiple independent samples (groups) to determine whether DW- and CM-frequency distribution varied over months. Dry weight dependency of carbon mass and carbon content was examined using the linear and polynomial (k=2) regressions based on individual measurements of body metrics and calculated CC-values. Statistical analyses were carried out using the program package Statistica 7.0.

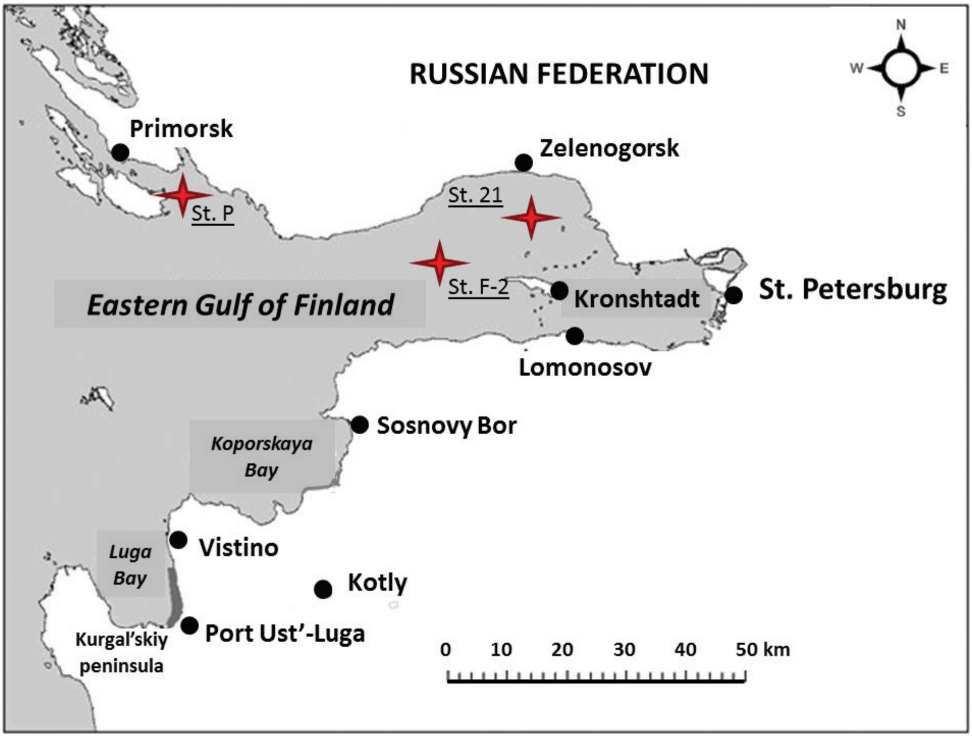

Figure 1. Scheme of the eastern Gulf of Finland (the Baltic Sea) showing the location of sampling stations: St. P, St. F-2 and St. 21 (asterisks).

Results

Dry weight of *C. pengoi* individuals collected in the eastern Gulf of Finland in July–September 1997 ranged one order of magnitude: from 9 to 94 µg; variation in carbon mass exceeded two orders of magnitude and ranged from 0.21 µg to 46.09 µg. The exceptionally low values of CM (< 1.0 µg) and the relevant DW and CC values were excluded from the analyses as possible results of methodological bias during CM-measurements in the smallest individuals of *C. pengoi*. The overall number of CM/DW measurements used for the further analyses was 432.

In July, the population of *C. pengoi* consisted mainly of rather small individuals with DW from 13 to 35 µg, while the organisms larger than 52 µg DW were absent, except for one individual of 88 µg (Fig. 2A). In August and September, the population of these cladocerans in the study area was represented by organisms with a broader DW range, and larger individuals of 53-73 µg DW were common in all sampling locations, particularly in September (Fig. 2B–D).

Mean DW of *C. pengoi* in the study area in July–September was 34.0 ± 14.2 µg, CM averaged 15.8 ± 8.8 µg; these parameters, however, varied between months; the highest average DW (39.6 µg) and CM (18.5 µg) values were registered in August (Table 1).

Table 1. Carbon mass, dry weight and carbon content (mean ± SD) of *Cercopagis pengoi* in the eastern Gulf of Finland (the Baltic Sea).

Parameter	July	August	September*	Average for July – September
Carbon mass (CM, μg)	10.8 ± 7.7	18.5 ± 8.4	17.1 ± 8.5	15.8 ± 8.8
Dry weight (DW, μg)	26.3 ± 11.4	39.6 ± 14.9	35.2 ± 13.4	34.0 ± 14.2
Carbon content (CC, %)	37.0 ± 12.3	44.9 ± 7.1	45.9 ± 10.7	43.4 ± 11.0
Number of individuals analyzed (*n*)	112	111	209	432

* Data from samples collected in September at two stations (St. 21 and St. P) were pooled because preliminary tests revealed high similarity of both data sets (p<0.001).

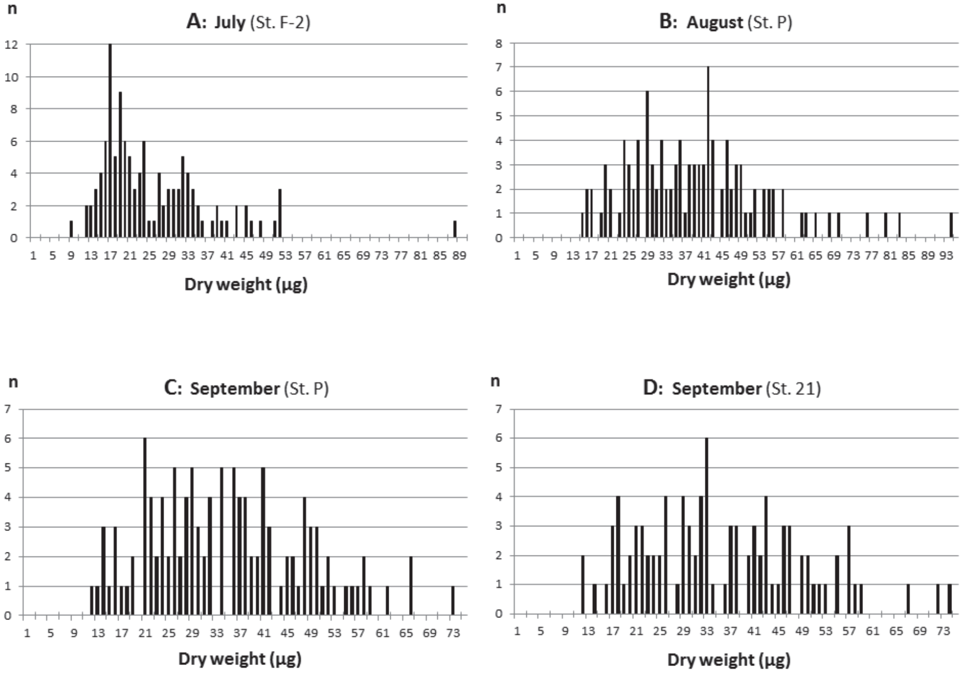

Figure 2. Frequency distribution (*n*) of *Cercopagis pengoi* individuals with different dry weight (μg) at three stations in the eastern Gulf of Finland in July (**A**), August (**B**) and September (**C, D**).

Variation in the data on *C. pengoi* DW- and CM-frequency distribution during three months was statistically significant (Kruskal-Wallis ANOVA by Ranks test for DW: H (3, N=432) =59.908; p<0.001; test for CM: H (3, N=432) =50.830; p<0.001). However, the Multiple Comparison (2-tailed) p values witnessed for the fact that only data for July were statistically different from the rest of the dataset (p<0.001), while the differences in data for August and September were statistically insignificant. Univariate test of significance for CM allowed concluding that DW was the major contributor to standard deviation of CM-values while the input of the factor "Month" was negligible (p<0.001).

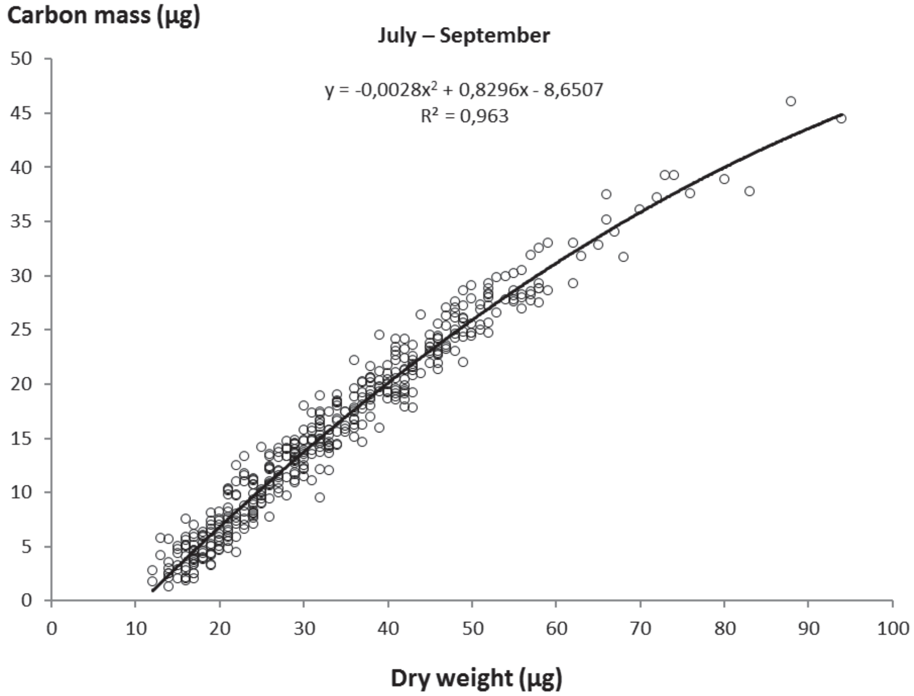

Figure 3. Relationship between carbon mass (µg) and dry weight (µg) of *Cercopagis pengoi* for July–September.

The CM-to-DW relationships for different months can be sufficiently well described by the linear regressions (r^2 = 0.951–0.969, $p<0.001$). However, the best approximation was achieved by applying the polynomial (quadratic) regression model (r^2 = 0.975–0.984, $p<0.001$); moreover, slopes and intercepts for these regressions for different months did not differ statistically ($p<0.001$). Therefore, the general polynomial regression (k=2), describing CM-to-DW relationship during July through September, was calculated for the entire dataset of individual measurements of *C. pengoi* body metrics (Fig. 3):

$$CM = -\,0.0028\ DW^2 + 0.8296\ DW - 8.6507 \qquad (1)$$

where CM is carbon mass (in µg), and DW is dry weight (in µg); r^2=0.96, $p<0.001$.

Average carbon content of *C. pengoi* in July-September was estimated as 43.4%. The highest mean CC (45.9%) was recorded in September; this value, however, was close to the one for August (44.9%); in July, CC of crustaceans was the lowest and averaged 37.0% (Table 1). Carbon content-to-DW relation was described by quadratic regression (Fig. 4):

$$CC = -\,0.0177\ DW^2 + 1.9507\ DW + 0.8942 \qquad (2)$$

where CC is carbon content (in percent of dry weight), and DW is dry weight (in µg); r^2=0.66, $p<0.001$.

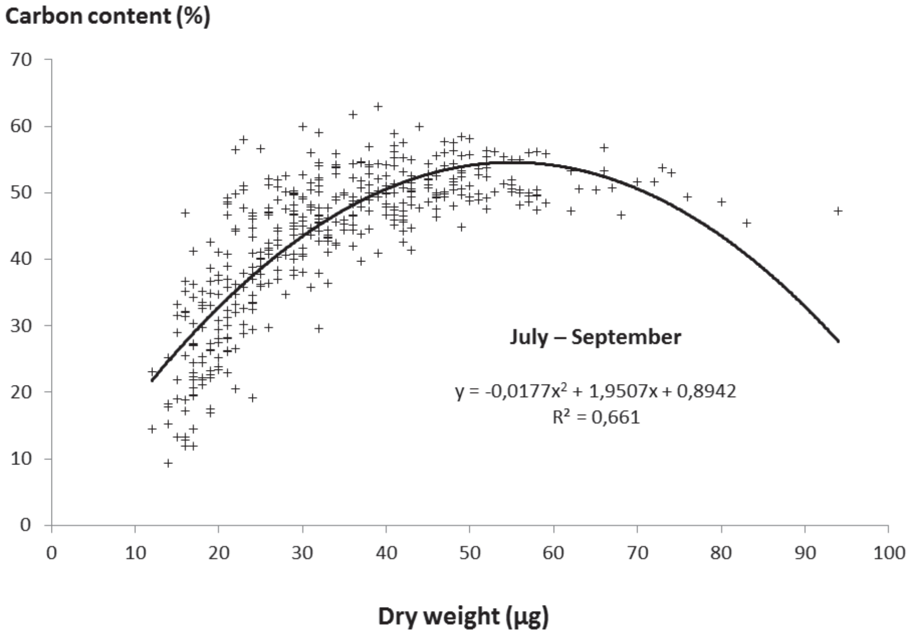

Figure 4. Relationship between carbon content (%) and dry weight (µg) of *Cercopagis pengoi* in July–September (*n*=432).

Discussion

The fishhook water flea *Cercopagis pengoi* (Ostroumov, 1891) has recently become an important component of the pelagic food web in the eastern Gulf of Finland. On the one hand, planktivorous pelagic fishes such as herring and sprat can feed on *Cercopagis* (Antsulevich and Välipakka 2000, Gorokhova et al. 2004); besides, these cladocerans are readily consumed by mysids (Gorokhova and Lehtiniemi 2007). On the other hand, *C. pengoi* significantly impacts the native zooplankton community by feeding on dominant native species such as podonid cladocerans and preferably copepods *Acartia* spp. and *Eurytemora affinis* (Lehtiniemi and Gorokhova 2008, Holliland et al. 2012). These water flees can also feed on *Bosmina* spp. (Gorokhova et al. 2005, Pollumäe and Väljataga 2004) and other planktonic filtrating crustaceans (Laxson et al. 2003) which are abundant during summer. These carnivorous planktonic invaders thus make the food chain longer by one level which allows additional energy losses during the energy flow through the pelagic ecosystem (Telesh et al. 2015b). This phenomenon can affect the overall energy balance and the size of pelagic fish stocks.

In general, the predator capture rates are known to scale positively with consumer mass (Barrios-O'Neill et al. 2016). Additionally, invasion success and spatial distribution of a planktonic predator can be restricted by a larger invasive competitor (Ptáčníková et al. 2015). Thus, body size of these organisms is recognized as a pivotal component of evolutionary fitness which provides a beneficial contribution to certain ecological patterns (Telesh et al. 2015a, 2016). Nevertheless, despite the long-recognized importance of body size in ecology, it is only recently that ecologists have begun to comprehensively resolve the body mass dependencies of consumer feeding rates, including the invasive predators (Barrios-O'Neill et al. 2016, and references therein). In particular, body mass of *C. pengoi* was accounted as part of the algorithm which allows evaluating its predation impact (Telesh et al. 2001, Laxson et al. 2003), and this assessment can be used for monitoring of the invasion range and its effect on the natural zooplankton community. However, exact knowledge of the body mass and particularly carbon content of the invader is essential for the precise calculations of matter turnover and energy balance, as well as for the consumer feeding rate evaluation.

Results of the current study for the first time allowed calculating the carbon mass-to-dry weight relationship based on the precise, direct carbon mass measurement by the high temperature combustion method (Salonen 1979) in a large number of *C. pengoi* individuals. In this research, the laboratory determination of carbon mass and dry weight of *C. pengoi* from the eastern Gulf of Finland were carried out and its average individual carbon mass, dry weight and carbon content were evaluated for July, August and September 1997 when *C. pengoi* was characterized by the maximum population density, as shown in our previous publications (Krylov et al. 1999, Litvinchuk and Telesh 2006, Telesh et al. 2001). The proposed polynomial (k=2) regression (Fig. 3) can describe perfectly well the carbon mass-to-dry weight relationship for *C. pengoi* individuals of 12-94 μg DW for the entire study area, which can be considered as a uniform shallow-water sampling site since it is characterized by the intensive wind-induced water mixing and the subsequent relative homogeneity of zooplankton community in the region (Telesh et al. 1999, 2008).

The discovered differences in averaged values of DW and CM of *C. pengoi* between July and August-September (Table 1) can be explained by several reasons. Firstly, they can be attributed to different population structure of these cladocerans in July and August-September: e.g., the changing abundance proportion of parthenogenetic and gametogenetic females and males (Litvinchuk and Telesh 2006). Moreover, major part of the *C. pengoi* population in July are often represented by the so-called 'spring form' (the first parthenogenetic generation, hatched from resting eggs) which are thereafter gradually substituted by the individuals of the 'summer form' – organisms with longer caudal spine, as shown for the Gulf of Riga of the Baltic Sea (Simm and Ojaveer 1999).

Other reasons can involve shifts in the diet of *C. pengoi* at different developmental stages (Holliland et al. 2012), also due to their diel vertical and spatial migrations (Krylov et al. 1999). Moreover, seasonal succession in dominant zooplankters from rotifers in spring to small cladocerans and juvenile copepods in summer to adult copepods in the fall in the eastern Gulf of Finland (Telesh et al. 1999, 2001) defines significant differences in composition of prey organisms for *C. pengoi*. Inputs of different carbon sources caused by varying stoichiometry of pelagic systems due to changing plankton community structure (Hessen et al. 2013) is largely responsible for the discovered variation in the carbon content of these crustaceans in different months, as well as for the lower CC in the smaller individuals of *C. pengoi*. This conclusion bases on the fact that the diet of the smaller *C. pengoi* differs substantially from the diet of the larger crustaceans, not only due to the inability of the smallest *C. pengoi* to catch larger prey but also due to different zooplankton community structure and, therefore, different elemental composition of food objects for the small vs. large individuals of *C. pengoi*.

Meanwhile, the obtained values of carbon content, calculated as percent of dry weight, averaged 43.4% for July-September which is in good correspondence with the 44% value obtained earlier for other cladocerans (Hessen 1990), especially for *Evadne* sampled in the Baltic Sea in 1997 (42.5%, Walve and Larsson 1999), and close to 46-49% for copepods *Acartia* and *Eurytemora* (Kiørboe 2013, Walve and Larsson 1999). However, these data differ substantially from the 5.2% carbon content of copepods, cladocerans and rotifers suggested by Mullin (1969), the latter value being presumably a percentage of wet weight (compare: Table 1 in Kiørboe 2013).

Interestingly, the mean CC values for *C. pengoi* in July were significantly lower than in August-September (Table 1), and calculations showed that the smallest individuals contained less carbon (Fig. 4). These surprising results were possibly recorded due to substantial morphological differences between the 'spring forms' of *C. pengoi* in July and 'summer forms' in the following months. The rigid, chitinous caudal process of the summer individuals is usually twice as long as that of the 'spring forms': in July the caudal process is as long as 225% of the total body length while in the 'summer forms' it constitutes 474% of the total body length (Simm and Ojaveer 1999). Therefore, the longer caudal process in the larger individuals in August-September is likely responsible for the higher proportion of carbon in these organisms if compared with the July forms.

Besides, the brood pouch of the instar III parthenogenetic females of *C. pengoi* is known to be 236% larger than that of instar I individuals of the smaller size (Grigorovich et al. 2000) which, therefore, contain relatively less carbon compared to larger individuals. At the same time, the brood pouch of females is filled with body fluids and embryos that have lower proportion of chitin and, respectively, lower carbon content compared to the brood pouch itself. This fact was additionally supported by the discovery of lower carbon content of *Evadne* compared to *Bosmina*, since *Evadne* contains more water due to its large egg sac (Walve and Larsson 1999). Similarly, carbon content was increasing with growth of mysids *Nyctiphanes couchi*: 33.41% in calyptopis stage CI, 36.02% in stage CII, and 37.60% in CIII (Lindley et al. 1999). Winter forms of *Meganyctiphanes norvegica* contained less carbon (39.4%) than spring forms (46.5%) (Lindley et al. 1999). These and other examples support our findings on carbon content of *C. pengoi* from the Baltic Sea.

According to our results, the assumed individual dry weight of 20 µg (Uitto et al. 1999) which is commonly used for *C. pengoi* biomass calculations (e.g., Gorokhova et al. 2004), is apparently largely underestimated. In our study, the lowest mean *C. pengoi* individual dry weight of 26.3 µg was registered in July, while in August and September these values were significantly higher: 39.6 and 35.2 µg DW, respectively (Table 1).

These data along with equations (1) and (2) for calculation of carbon mass-to-dry weight and carbon content-to-dry weight regressions reported in this study will allow avoiding miscalculations of *C. pengoi* biomass and favor adequate assessment of the food web structure and energy fluxes. These results may be applied also to *C. pengoi* from the Laurentian Great Lakes, albeit regional variations in the diet of these cladocerans likely exist (Lehtiniemi and Gorokhova 2008, Laxson et al. 2003, Ptáčníková et al. 2015), due to specific features of zooplankton community composition, diversity and environmental characteristics.

Conclusion

The research presents new data on the average individual carbon mass (15.8 μg), dry weight (34.0 μg) and carbon content (43.4%) of the invasive cladoceran *Cercopagis pengoi* from the eastern Gulf of Finland (the Baltic Sea), and suggests the polynomial (k=2) regressions for describing carbon mass-to-dry weight and carbon content-to-dry weight relationships during the period of maximum population development of *C. pengoi* when the invader's impact on the native community and food web is the greatest. This impact jointly with ecosystem vulnerability to invasions, food web structure and biodiversity are closely interrelated and tightly linked with the on-going environmental alterations (Vuorinen et al. 2015, Holopainen et al. 2016). New experimentally derived knowledge on carbon mass of the alien fishhook water flea *C. pengoi* will contribute to future development of methods for assessment of the ecosystem impacts of non-indigenous species and refining the invasibility criteria for successful species coexistence in the changing environment which might significantly enhance predictive ecology.

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RESEARCH ARTICLE

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Advancing research on alien species and biological invasions

Patterns of selectivity in introductions of mammal species worldwide

Tim M. Blackburn[1,2,3,4], Sally L. Scrivens[4], Sarah Heinrich[4], Phillip Cassey[4]

1 *Department of Genetics, Evolution & Environment, Centre for Biodiversity & Environment Research, Darwin Building, UCL, Gower Street, London WC1E 6BT, UK* **2** *Institute of Zoology, Zoological Society of London, Regent's Park, London NW1 4RY, United Kingdom* **3** *Centre for Invasion Biology, Department of Botany and Zoology, Stellenbosch University, South Africa* **4** *School of Biological Sciences and the Centre for Conservation Science and Technology, The University of Adelaide, South Australia 5005, Australia*

Corresponding author: *Tim M. Blackburn* (t.blackburn@ucl.ac.uk)

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Abstract

Humans have an extremely long history of transporting and introducing mammal species outside their native geographic ranges. The characteristics of the species introduced (taxonomy, life-history, ecology, environment) can all influence which traits are available (and selected) for establishment, and subsequent invasive spread. Understanding the non-randomness in species introductions is therefore key to understanding invasions by alien species. Here, we test for selectivity in the identities and traits of mammal species introduced worldwide. We compiled and analysed a comprehensive database of introduced mammal species, including information on a broad range of life history, ecological, distributional and environmental variables that we predicted to differ between introduced and non-introduced mammal species. Certain mammal taxa are much more likely to have been introduced than expected, such as Artiodactyls in the families Bovidae and Cervidae. Rodents and bats were much less likely to have been introduced than expected. Introduced mammal species have significantly larger body masses, longer lifespans and larger litter sizes than a random sample of all mammal species. They also have much larger native geographic ranges than expected, originate from significantly further north, from cooler areas, and from areas with higher human population densities, than mammal species with no recorded introductions. The traits and distributions of species help determine which have been introduced, and reflect how the evolutionary history of mammals has resulted in certain species with certain traits being located in the way of human histories of movement and demands for goods and services. The large amount of unexplained variation is likely to relate to the intrinsically stochastic nature of this human-driven process.

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Keywords

Acclimatisation Societies, alien species, geographic range, introduced mammals, phylogenetic logistic regression models, taxonomic bias

Introduction

Humans have deliberately (and accidentally) transported a large number of species beyond the limits of their native distributions, to areas where they have subsequently escaped, or been released, into environments where they do not naturally occur (here termed introductions or introduced). Yet, these species are only a small fraction of those that could potentially be introduced. Given that introductions occur during the earliest stages of a process that leads, in some cases, to alien invasions (Blackburn et al. 2011), two particularly important questions are how many, and which, species are introduced? Here, we set out to answer these questions for mammal introductions worldwide.

Many studies have examined what proportion of the species in a taxon have been introduced, largely as a result of the influential Tens Rule proposed by Mark Williamson (Williamson 1993, 1996; Williamson and Brown 1986). Examples include angiosperms and Pinaceae introduced in Britain (Williamson 1993, 1996), fish, bird and mammal species introduced from Europe to North America (Jeschke and Strayer 2005), bird species introduced from North America to Europe (Jeschke and Strayer 2005), and amphibians introduced to Australia (García-Díaz and Cassey 2014). At the global scale, around 15% of parrots (54 out of *c.*350 species; Cassey et al. 2004), 10% of birds (973 out of *c.*10,000 species; Blackburn et al. 2015) and 3% of amphibians (179 out of *c.*6,000 species; Tingley et al. 2010) are known to have been introduced. Long (2003) provides accounts of 337 mammal species moved around the world (around 6% of the global mammal fauna), but some of this number have been re-introduced rather than introduced, while other mammal species with known introductions (e.g. *Callosciurus finlaysonii*, Bertolino and Lurz 2013) are missing from the compilation. A recent study by Capellini et al. (2015) identified 232 mammal species as having been introduced (*c.*4% of the total mammal species richness) based on data in Long (2003) and other sources.

Introduced species tend not to be a random subset of the species in a taxon. This has been studied most extensively for birds (Blackburn et al. 2009). Among birds, species from taxa favoured as game and cage birds occur more often than expected by chance in lists of introduced species (Blackburn and Duncan 2001; Duncan et al. 2006; Blackburn and Cassey 2007; Blackburn et al. 2010). At the global scale, Nearctic and Palaearctic species are also over-represented, and this translates into a tendency for introduced species to derive from latitudes in the northern hemisphere (Blackburn et al. 2009). Introduced birds tend to be species affiliated with humans (e.g., commensals, cage-birds, and food species), widespread and abundant, and large-bodied and long-lived (Blackburn and Duncan 2001; Cassey et al. 2004; Jeschke and Strayer 2006; Blackburn and Cassey 2007; Blackburn et al. 2009, 2010). This suggests that introduction is an outcome of the interaction between human socio-economic pressures (e.g., for food and pets) and species availability for these uses (e.g., common species in areas where socio-economic demands have historically been high).

Similar patterns of selectivity have been shown in other taxa. For example, introduced fishes show a strong taxonomic bias towards game or forage fishes, or other species of human interest. They are also often piscivorous (Garcia-Berthou 2007). At the global scale, introduced amphibians tend to originate from the Northern hemisphere, to have broad geographic ranges, and to be sympatric with high densities of humans (Tingley et al. 2010). Amphibian introductions to Australia were more likely for species imported both accidentally and for trade (rather than by one or the other pathway), and for larger-bodied species (García-Díaz and Cassey 2014). Taxonomic non-randomness and large body size were features of reptiles introduced to South Africa (van Wilgen et al. 2010). Through analysis of fish, bird and mammal introductions between Europe and North America, Jeschke and Strayer (2006) found that introduction was more likely for widespread, human-affiliated fish with large eggs, and long-lived, herbivorous mammals. When fish, birds and mammals were analysed together, human affiliation, wide latitudinal range and body mass were all significant predictors of introduction (Jeschke and Strayer 2006). At the global scale, introductions have been shown to be more likely for mammal species with larger and more frequent litters, and longer reproductive lifespans (Capellini et al. 2015), although this study only analysed body size and life history traits related to reproduction.

Here, we build on these previous studies, exploring the number and characteristics of introduced species, using a global database of mammal introductions. First, we quantified and characterised the taxonomic distribution of introduced mammal species, to reveal which orders and families of mammals have more (or fewer) introduced species than expected by chance. As far as we are aware, this is the first study to identify non-randomness in the taxonomic distribution of introduced mammal species worldwide. We then tested for non-randomness in a range of characteristics that previous studies have shown to be associated with introduction selectivity, and which may help explain why certain taxa are over or under-represented in the list of introduced mammals. Specifically, we tested whether mammal species that have been introduced somewhere in the world differed in measures of (1) body size, (2) fecundity, (3) lifespan, (4) ecological generalism, (5) herbivory, (6) geographic extent, (7) human population density across their geographic ranges, and (8) location of their native geographic range, compared to mammal species that have not been introduced. The specific hypotheses tested are given in Table 1. Previous studies have considered subsets of these characteristics (e.g. Capellini et al. 2015) or regional introductions (Jeschke and Strayer 2006), whereas this is the first test of such a range of hypothesised associations at the global scale.

Table 1. The characteristics of species that we expected to influence whether or not mammal species have been introduced, based on patterns of selectivity shown in other taxa (see Introduction for more details), the specific hypotheses associated with those characteristics, the specific variables analysed (with sample size) and a description of that variable (see Methods and Jones et al. (2009) for more details).

Characteristic	Hypotheses	Variable (sample size)	Description
Body size	We expect utilitarian species (e.g., food and pack animals) to be more likely to have been transported and introduced, and therefore that introduced species will be larger than expected by chance.	Adult body mass (3,542 species)	Grams (log transformed)
Fecundity	Species with relatively slow life histories may be more likely to be utilitarian species (and so also have large body size) and better able to survive the introduction process. Alternatively, species with faster life histories may be more likely to maintain populations through the stresses of transport and introduction.	Litter size (2,502 species)	Number of offspring born per litter (log transformed)
Lifespan	Species with relatively slow life histories may be more likely to be utilitarian species (and so also have large body size and low fecundity) and better able to survive the introduction process.	Maximum Longevity (1,013 species)	Months (log transformed)
Ecological generalism	Generalist species may be more widespread and abundant, more easily kept in captivity, and more flexible in their ability to cope with the demands of transport and introduction. Thus, introduced species are more likely to have generalist diets.	Diet breadth (2,161 species)	Number of dietary categories used by a species
	Generalist species may be more widespread and abundant, more easily kept in captivity, and more flexible in their ability to cope with the demands of transport and introduction. Thus, introduced species are more likely to be habitat generalists.	Habitat breadth (2,724 species)	Number of habitat layers used by a species
Herbivory	We expect utilitarian species (e.g., food and pack animals) to be more likely to have been transported and introduced, and therefore that introduced species are more likely to be herbivores.	Trophic level (2,161 species)	1: herbivore (not vertebrate and/or invertebrate prey): 2: omnivore (vertebrate and/or invertebrate prey plus any of the other categories); 3: carnivore (vertebrate and/or invertebrate prey only)
Geographic extent	Species with a greater native distribution (which tend also to be abundant) will be more available for deliberate or accidental transport and introduction.	Geographic range size (4,668 species)	Area of the native range in km^2 (log transformed)
Human population density	Introduced species tend to be those affiliated with humans. Such species may be more likely to be found in areas with greater concentrations of humans and human activities, and will be more likely to be deliberately or accidentally transported and introduced as a result.	Human population density (4,668 species)	Average number of persons per km^2 within the native geographic range (log +1 transformed)
Location of the native geographic range	Many introductions have been associated with colonial expansion of European countries, primarily to Neo-European colonies at similarly high latitudes. We therefore expect introduced species to be more likely than expected by chance to derive from higher latitudes.	Latitudinal mid-point of the geographic range (4,668 species)	Degrees of latitude, with negative values indicating mid-points south of the equator
	Many introductions have been associated with colonial expansion of European countries. We therefore expect introduced species to be more likely than expected by chance to derive from European longitudes.	Longitudinal mid-point of the geographic range (4,668 species)	Degrees of longitude, with negative values indicating mid-points west of the Greenwich Meridian
	Rainfall tends to be higher in tropical areas that have been less associated with European colonial expansion. We therefore expect introduced species to be less likely than expected by chance to derive from high rainfall regions.	Mean precipitation (4,533 species)	Mean monthly precipitation (mm) within the geographic range (log transformed)
	For the same reasons as latitude, we expect introduced species to be more likely than expected by chance to derive from areas with lower mean temperatures.	Mean temperature (4,533 species)	Mean monthly temperature (°C) within the geographic range

Methods

Data

We compiled a comprehensive database of mammal species introduced to areas beyond the limits of their historically recognised native geographic ranges. The starting point for our database was the compilation of mammal introductions by Long (2003). Each species listed by Long (2003) was then subjected to a primary literature search to verify or update these classifications using Google Scholar, with the search terms 'introduced OR alien OR exotic OR invasive OR native' and the species' common and scientific names. We also conducted specific searches including the names of potential geographic locations of introduction identified in Long (2003). We searched the following online databases to determine the status of the species recorded in Long (2003): the International Union for Conservation of Nature (IUCN) Red List of Threatened Species, Delivering Alien Invasive Species Inventories for Europe (DAISIE) and the Invasive Species Specialist Group (ISSG). These online databases, together with general Google Scholar searches using the search terms 'introduced OR alien OR exotic OR invasive OR native AND mammal AND Country Name/Region', were used to identify introduced species omitted from Long (2003), either because he had missed the evidence or the introduction post-dates his work.

Species were considered to be introduced when there was evidence that individuals arrived into an environment via human mediation, except when there was evidence that the liberated or escaped populations were to sites within the historic range of the species (i.e., re-introductions). Native ranges were determined from a combination of IUCN distribution maps (IUCN 2014), the Handbook of Mammals of the World (Wilson and Mittermeier 2009, 2011; Mittermeier et al. 2013) and primary literature. There were a number of species in our database for which it was unclear whether or not introductions had actually taken place (e.g. *Leopardus tigrinus*; Long 2003). We excluded these species from further consideration. We cross-checked our compilation with that of Capellini et al. (2015), and in some cases amended our classifications to align with theirs; we did not always concur with their classifications, however (see Discussion). We also excluded species not considered to be valid according to the taxonomy we used (Wilson and Reeder 2005). A full list of introduced mammal species in our analysis is provided in Table S1 in Suppl. material 1, and the references used to build this list in Suppl. material 2.

We obtained data on a range of life history and geographic variables for a large sample of mammal species from the PanTheria database (Jones et al. 2009), where more details of sources and calculation are provided. We used the version of the database based on the taxonomy of Wilson and Reeder (2005). The geographic variables were all calculated from digital geographic range maps of all extant, non-marine mammals from Sechrest (2003), converted to this taxonomy. PanTheria sometimes includes multiple variables relating to the characteristics of interest in our analyses. In such cases, we selected variables that measured different facets of that trait (e.g. dietary and habitat generalism), but only if they were available for a reasonable number (at least 40%) of species. The only characteristic that did not meet this sample size criterion was lifespan: for this trait, we used the variable with the largest sample size instead (Maximum longevity: 18.7% of species). Excluding variables with few data may mean that some traits associated with introduction are missed by our analysis. On the other hand, ensuring that we have data for a high proportion of mammal species reduces the likelihood of spurious relationships based on small and biased samples. We have generally excluded variables that are correlated with those we included so that in most cases we should capture variation in the relevant characteristic. The 12 variables associated with the eight characteristics of interest (and associated sample sizes) are provided in Table 1. Correlation analysis shows that these variables are generally weakly related ($r < 0.34$ for 30/36 pairwise correlations); the exceptions are correlations of log litter size to log mass ($r = -0.43$), log lifespan to log litter size (–0.58) and log body mass (0.66), and of mean temperature to log litter size (–0.42), log precipitation (0.47) and latitudinal range mid-point (–0.61).

Analysis

We analysed introduction as a binary trait. We did not address variation in the number of introductions because it is difficult to get good data on the number of introductions, especially for species that have been accidentally translocated. We adopted both taxonomic and phylogenetic approaches to assess non-randomness in the characteristics of introduced mammal species. All analyses were conducted in R v. 3.1.1 (R Core Team 2014).

We used the permutation approach described in Blackburn and Cassey (2007) to test for differences between the observed number of introduced mammal species in each mammalian order, and the number that would be expected if mammals were selected at random for introduction. Each iteration of the simulation involved picking S species at random, and without replacement, from the global mammal fauna, using the *sample* function in R, and summing the number of these randomly chosen species in each order. S is the number of mammal species we recorded as having been introduced ($S = 306$; see Results). This was repeated 100,000 times, to produce 100,000 lists of randomly chosen species. The observed number of species actually introduced from any given mammal order was judged significantly greater than expected if at least 99.95% of the randomly derived values for that order were less than the observed (i.e., if there were fewer species from that order on 99.95% of the 100,000 random lists). Similarly, the observed number of introduced species was judged to be significantly less than expected if at least 99.95% of the randomly derived values for that order were greater than the observed (i.e., if there were more species from that order on 99.95% of the 100,000 random lists). These percentages were chosen to be conservative, being less than the Bonferroni corrected critical value of $a/n = 0.0017$; where $a = 0.05$ and $n = 29$ (the number of mammal orders). The same simulation approach was also used to assess taxonomic selectivity in terms of family membership. In this case, we used percentages of 99.995, given 153 mammal families.

We used phylogenetic logistic regression (Ives and Garland 2010) and the mammalian phylogeny in Fritz and Purvis (2010) to test whether or not introduced mammals differed from other mammal species in terms of the life history, ecological, distributional and environmental variables described above. We calculated the phylogenetic statistic *D* (Fritz and Purvis 2010), using the phylo.d function in the R package 'caper' (Orme et al. 2013), to test for phylogenetic signal in whether or not species in this sample had been introduced. *D* measures character dispersion on a phylogeny: a value of 0 indicates that the trait is clumped as if it had evolved through Brownian motion, and a value of 1 that the trait is randomly dispersed across the phylogeny (Fritz and Purvis 2010). We fitted univariate phylogenetic logistic regression models (Ives and Garland 2010) using the phylolm function in the 'phylolm' package, with the error term modelled on the basis of the estimated Pagel's λ (Ho and Ane 2014). We then fitted a full model for mammal species for which there were no missing data in the variables found to be significant in the univariate tests. We calculated Variance Inflation Factors for these variables using standard linear and PGLS models to test for collinearity amongst these predictors. Variable significance in the full model was assessed on the basis of full model estimates (beta) and their standard errors (Hegyi and Laczi 2015). The variance explained by this model was estimated using Nagelkerke's R^2 (Nagelkerke 1991). Adult mass, litter size, maximum longevity, geographic range size, and precipitation were all natural logarithmically transformed for this analysis, while human population density was natural log + 1 transformed.

Results

We identified a total of 306 mammal species that have been recorded as having been introduced to areas beyond the limits of their normal geographic distributions (Suppl. material 1). These represent 5.65% of all mammal species in the taxonomy used here.

Six mammalian orders have had more species introduced outside their native range limits than expected by chance (Table 2). Of these, Diprotodontia, Artiodactyla, Perissodactyla and Carnivora have had significantly more introduced than expected after Bonferroni correction for multiple tests. The order with the most introduced mammal species is Artiodactyla, with 83 (34.7%). Within this order, five families also have had more introduced species than expected (Table 3), and of these, the Bovidae and Cervidae remain significant after Bonferroni correction. The Bovidae has had the most species introduced of any mammalian family, with 49 (Table 3). The Carnivora, Diprotodontia and Perissodactyla each have one family that is significantly over-represented in the list of introduced mammals after Bonferroni correction (the Mustelidae, Macropodidae and Equidae, respectively; Table 3).

The mammalian order with second highest number of introduced species is the Rodentia, with 75 (Table 2). However, this is actually significantly fewer species than expected, even after Bonferroni correction, given the very high richness of this order (Table 2). Two Rodent families, the Cricetidae and Muridae, also have fewer intro-

Table 2. The distribution, across mammal orders, of all mammal species (No. species), introduced mammal species (No. introduced), and the expected number of introduced species per order (median and range, based on 100,000 iterations of the permutation test) assuming that mammal species were selected for introduction at random (Expectation). Species numbers are based on the taxonomy in Wilson & Reeder (2005). Orders with significantly more introduced species than expected by chance are shown in bold, while orders with significantly fewer introduced species are shown in italics.

Order	No. Species	No. Introduced	Expectation
Afrosoricida	51	1	3 (0–12)
Artiodactyla	239	**83*** **	**13 (2–32)**
Carnivora	286	**41*** **	**16 (3–34)**
Cetacea	84	*0**	*5 (0–17)*
Chiroptera	1116	*3****	*63 (33–98)*
Cingulata	21	2	1 (0–9)
Dasyuromorphia	71	1	4 (0–14)
Dermoptera	2	0	0 (0–2)
Didelphimorphia	87	3	5 (0–15)
Diprotodontia	143	**28*** **	**8 (0–22)**
Erinaceomorpha	24	2	1 (0–8)
Hyracoidea	4	0	0 (0–4)
Lagomorpha	92	**12***	**5 (0–17)**
Macroscelidea	15	0	1 (0–6)
Microbiotheria	1	0	0 (0–1)
Monotremata	5	2	0 (0–4)
Notoryctemorphia	2	0	0 (0–2)
Paucituberculata	6	0	0 (0–4)
Peramelemorphia	21	2	1 (0–8)
Perissodactyla	16	**6****	**1 (0–7)**
Pholidota	8	0	0 (0–5)
Pilosa	10	1	0 (0–5)
Primates	376	30	21 (6–41)
Proboscidea	3	**2***	**0 (0–3)**
Rodentia	2277	*75****	*129 (89–168)*
Scandentia	20	0	1 (0–9)
Sirenia	5	0	0 (0–4)
Soricomorpha	428	*12***	*24 (7–46)*
Tubulidentata	1	0	0 (0–1)

*P<0.05, **P<0.01, ***P<0.0001.

duced species than expected after Bonferroni correction (Table 3). Conversely, the Castoridae, Hystricidae and Sciuridae have had more species than expected introduced, albeit that these are not significant once corrected for multiple tests (Table 3). A further three mammalian orders have also had fewer than expected species introduced, of which Chiroptera and Soricomorpha remain significant after Bonferroni correction (Table 2). Five Chiropteran families have had fewer species introduced than expected

Table 3. The distribution, across mammal families, of all mammal species (No. species), introduced mammal species (No. introduced), and the expected number of introduced species per family (median and range, based on 100,000 iterations of the permutation test) assuming that mammal species were selected for introduction at random (Expectation). Species numbers are based on the taxonomy in Wilson and Reeder (2005). Only families with significantly more (in bold) or fewer (in italics) introduced species than expected by chance are shown.

Order	Family	No. species	No. Introduced	Expectation
Artiodactyla	__Bovidae__	143	__49***__	8 (0–21)
	__Camelidae__	4	__4***__	0 (0–4)
	__Cervidae__	50	__19***__	3 (0–13)
	__Suidae__	19	__5**__	1 (0–7)
	__Tayassuidae__	3	__2*__	0 (0–3)
Carnivora	__Canidae__	35	__8**__	2 (0–10)
	__Mustelidae__	59	__14***__	3 (0–12)
	__Viverridae__	35	__7**__	2 (0–10)
Chiroptera	_Hipposideridae_	81	_0*_	4 (0–16)
	Molossidae	100	_1*_	6 (0–19)
	Phyllostomidae	160	_0***_	9 (0–23)
	Pteropodidae	186	_1**_	10 (0–28)
	Vespertilionidae	407	_0***_	23 (6–45)
Diprotodontia	__Macropodidae__	65	__16***__	4 (0–13)
	__Potoroidae__	10	__3*__	0 (0–5)
	__Vombatidae__	3	__2*__	0 (0–3)
Lagomorpha	__Leporidae__	61	__12**__	3 (0–13)
Perissodactyla	__Equidae__	7	__5***__	0 (0–4)
Primates	__Cercopithecidae__	132	__14*__	7 (0–20)
	__Lemuridae__	19	__6**__	1 (0–8)
Proboscidea	__Elephantidae__	3	__2*__	0 (0–3)
Rodentia	__Castoridae__	2	__2**__	0 (0–2)
	Cricetidae	681	_12***_	38 (16–66)
	__Hystricidae__	11	__3*__	0 (0–6)
	Muridae	730	_17***_	41 (20–69)
	__Sciuridae__	278	__25*__	16 (2–33)
Soricomorpha	_Soricidae_	376	_10**_	21 (5–42)

*P<0.05, **P<0.01, ***P<0.0001

by chance, and the Phyllostomidae and Vespertilionidae remain significantly under-represented after Bonferroni correction (Table 3).

Introduced species are distributed across the mammal phylogeny with $D = 0.51$. This was significantly different from both phylogenetic randomness ($P < 0.0001$) and a strict Brownian motion model of evolution ($P < 0.0001$). Univariate phylogenetic logistic regressions show that introduced species have significantly larger body masses and litter sizes, longer lifespans and broader diet breadths than mammal species not introduced (Table 4). Introduced mammal species have much larger native geographic

Table 4. Univariate phylogenetic generalised logistic models of the relationship between mammal species introduction and the variables in the second column. Ch. = characteristic of interest with which each variable is associated (see Introduction, Methods, and Table 1). Negative values of latitude relate to latitudes in the southern hemisphere. Negative values of longitude relate to longitudes west of the Greenwich Meridian. Estimate ± s.e. = regression coefficient ± standard error, Log. = natural logarithmically transformed, Lat. = Latitude, Long. = Longitude, Pop. = Population. λ = maximum likelihood estimate of Pagel's lambda for the model.

Ch.	Variable	Estimate ± s.e.	t	N	P	λ
1	Log. Adult Body Mass	0.029 ± 0.004	7.44	3435	< 0.0001	0.44
2	Log. Litter Size	0.092 ± 0.016	5.62	2460	< 0.0001	0.43
3	Log. Maximum longevity	0.152 ± 0.023	6.63	1000	< 0.0001	0.53
4	Diet Breadth	0.013 ± 0.004	2.95	2114	0.003	0.46
4	Habitat Breadth	0.013 ± 0.012	1.12	2664	0.26	0.52
5	Trophic Level	–0.025 ± 0.013	–1.86	2114	0.06	0.43
6	Log. Geographic range size	0.014 ± 0.001	11.19	4457	< 0.0001	0.43
7	Log. (1+Human Pop. Density)	0.008 ± 0.003	2.80	4457	0.005	0.43
8	Lat. range mid-point	0.0017 ± 0.0002	7.70	4457	< 0.0001	0.42
8	Long. range mid-point	–0.0001 ± 0.00007	–1.47	4457	0.14	0.43
8	Log. Precipitation	–0.028 ± 0.005	–5.25	4336	< 0.0001	0.44
8	Temperature	–0.0005 ± 0.00006	–8.73	4336	< 0.0001	0.43

Table 5. The full phylogenetic generalised logistic model based on the significant variables in Table 4. The estimate and standard error for temperature are based on units of 0.1°C. Nagelkerke's $R^2 = 0.30$; N = 704, maximum likelihood estimate of Pagel's lambda = 0.32.

Variable	Estimate	Std. Error	t	P
Intercept	–1.08	0.238	–4.52	<0.0001
Log adult body mass	0.046	0.010	4.58	<0.0001
Log. Litter Size	0.140	0.040	3.50	0.0005
Log maximum longevity	0.099	0.031	3.21	0.0014
Diet Breadth	0.009	0.009	0.95	0.34
Log geographic range size	0.049	0.008	5.74	<0.0001
Log. (1+Human Pop. Density)	0.046	0.015	3.13	0.002
Lat. range mid-point	0.0009	0.001	1.01	0.31
Precipitation	–0.029	0.025	–1.16	0.24
Temperature (0.1°C)	–0.001	0.0003	–4.38	<0.0001

ranges (Table 4): the geometric mean range size of introduced mammals is 8.5 times larger than the mean of species that have no recorded introductions. Introduced mammal species also tend to originate from significantly further north, from cooler areas, from areas with lower precipitation, and from areas with higher human population densities, than mammal species with no recorded introductions (Table 4). Conversely, mammal species with or without recorded introductions showed no difference in their longitudes of origin, habitat breadths or trophic levels (Table 4).

The full phylogenetic logistic regression model, for the subset of 704 (of which 178 were introduced) species for which data on all nine significant variables in Table 4 were available, included strong positive effects of adult body mass and geographic range size, and a strong negative effect of temperature (Table 5). There were also positive effects of litter size, maximum longevity, and human population size. Variance inflation factors for these nine variables ranged from 1.06 to 2.27 using standard linear models (and were lower using PGLS models), indicating low levels of collinearity.

Discussion

The geographic distributions of species have always been dynamic, but in recent centuries the processes underlying these changes in distribution have been greatly accelerated. In particular, natural dispersal, which for most of the history of life has been the only way in which species expand their ranges, has been massively augmented by the global movement of organisms by human activities. The first recorded human-introduction relates to a mammal–the grey cuscus *Phalanger orientalis* introduced to New Ireland around 20,000 years ago (Grayson 2001)–and given the general interest in both biological invasions and mammals, it is surprising that only one previous study (Capellini et al. 2015) has attempted to quantify or characterise the world's introduced mammal fauna. The work reported here takes significant further steps in these regards. First, we identify a larger set of mammal species with introduced populations than in previous studies. Second, we characterise for the first time the taxonomic composition of introduced mammal species, and identify which orders and families have more introduced species than expected by chance. Third, we analyse a wide set of traits that may influence which species have been introduced at the global scale. These data reveal clear evidence of selectivity in the identities and traits of introduced mammal species worldwide, as has previously been demonstrated for birds and amphibians (Blackburn et al. 2009; Tingley et al. 2010).

Our database includes 306 species that we considered to have been introduced somewhere in the world, which is just under 6% of all mammal species. Mammals therefore sit between birds (c.10%; Blackburn et al. 2015) and amphibians (c.3%; Tingley et al. 2010) in terms of the proportion of their global richness species subject to human-mediated introduction. It is also 74 (32%) more species than in another recent global compilation (Capellini et al. 2015). These two compilations share 215 species in common, but each included some species not on the other list. The greater number of species on our list reflects in part the fact that our literature search identified species that we believe have unambiguously been introduced (e.g. *Callosciurus erythraeus*; Bertolino and Lurz 2013), but in part also differences of interpretation of the evidence for introduction, especially in terms of whether or not a population counted as an introduction versus a re-introduction. The temporal dynamics of native distributions means that this judgment is not always black-and-white.

For example, there is little doubt that the Barbary ape (*Macaca sylvanus*) population on Gibraltar derives from individuals liberated by humans (other individuals were released in Germany; Long 2003), but this species was widespread across Europe and North Africa in the Pleistocene. Its historic distribution spanned much of North Africa, though it persists in only a few parts of this former range. Capellini et al. (2015) did not include this species as having been introduced, but we followed the IUCN (http://www.iucnredlist.org/details/summary/12561/0) and included it. Arguably, this species is a "restored native" *sensu* Crees and Turvey (2015), rather than a non-native, but the degree to which the German introduction location in particular could be considered within the potential current distribution of the species (and hence a re-introduction) is open to debate. In other cases, it is not clear whether the introduction location was actually within the previous range of the species. For example, the individuals of the Black Capuchin (*Sapajus* (*Cebus*) *nigritus*) released on Anchieta Island (Bovendorp and Galetti 2007) are beyond this species' range limits as given by the IUCN (http://www.iucnredlist.org/details/136717/0). Nevertheless, Anchieta is offshore from that range, and so it is plausible that the Black Capuchin could once have been native there, although there is no evidence of this. As the population definitely derives from captive individuals and lacking evidence that the species had ever previously inhabited the island, we again included this species on our list of introductions. In sum, as noted earlier, we included species as introduced when individuals arrived into an environment via human mediation, unless there was evidence that the environment was within the historic range of the species.

The mammalian order with the most introduced species globally in our database is the Artiodactyla: this order includes less than 5% of all mammal species, but 27% of all introduced species (Table 2). This representation is much higher than expected by chance. Artiodactyls include deer (Cervidae), camels and their relatives (Camelidae), antelopes, buffaloes, sheep and goats (Bovidae), pigs (Suidae), and peccaries (Tayassuidae), and therefore the most important animals for most human societies in terms of meat, game, milk, fibres (wool and hair), hides and transport (Pattiselanno 2003; Geisser and Reyer 2004; Haenlein 2001; Haenlein 2007). It is unsurprising that humans should have desired to introduce such species to new areas, so that they could continue to benefit from the goods and services provided by them. Classic examples include: (i) the release of pigs and goats onto islands by European sailors, to ensure a supply of meat the next time they (or other people) made landfall there (Cheke 2010; Campbell and Donlan 2005; Robins et al. 2003); (ii) the introduction by Acclimatization Societies of a range of game species (e.g., deer) to provide hunting on naturally mammal-free New Zealand (McDowall 1994); and (iii) the introduction of camels to aid with the exploration and development of the newly colonised (by Europeans) desert continent of Australia (McKnight 1969; Long 2003). The Bovidae, Camelidae, Cervidae, Suidae and Tayassuidae are all significantly over-represented on the list of mammal introductions, and the Bovidae and Cervidae remain so when correcting for multiple comparisons (Table 3).

The mammalian order with the second highest number of introduced species globally is the Rodentia (75 species, 24.5%; Table 2). This order includes some of the most ubiquitous and notorious alien species, such as black and brown rats (*Rattus rattus* and *R. norvegicus*, respectively) and the house mouse (*Mus musculus*), which have been accidentally introduced to most ice-free land areas on the planet. However, not all rodent introductions are accidental: many species have been introduced deliberately for a variety of reasons, such as Pacific rats (*R. exulans*) for food (Roberts 1991; Matisoo-Smith et al. 1998), beavers (*Castor* sp.) for fur (Lizzaralde 1993), and the grey squirrel (*Sciurus carolinensis*) for ornamentation (Huxley 2003; Gurnell 1996). Nevertheless, given that Rodentia is the richest mammalian order, with more than 40% of all the world's mammal species, the 75 introduced species actually equates to significantly fewer than would be expected by chance (Table 2). The major families within the Rodentia (Cricetidae and Muridae) are also significantly under-represented (Table 3). Presumably, few rodents have qualities that would promote their deliberate introduction, or the opportunity for accidental introduction (see below). The second richest mammalian order (Chiroptera) is also significantly under-represented on the list of introduced species (Table 2), as are five of its families (Table 3), as only three (<1%) of the 1,116 bat species have recorded introductions.

Other mammalian orders well represented on the global list of alien species include Carnivora (41 species, 13%) and Diprotodontia (28 species, 9%) (Table 2). Amongst introduced Carnivora, the Mustelidae, Viverridae and Canidae figure prominently. The first of these includes a variety of stoat and weasel species often introduced for the purposes of pest control–sometimes as a misguided response to problems caused by introduced rodents (Uchida 1968; Uesugi et al. 1998). Introduced Diprotodontia include a number of translocations to offshore islands for the purposes of conservation, again largely in response to problems caused by other introduced species (Langford and Burbidge 2001; Miller et al. 2011), but also introductions for food (e.g. *P. orientalis* mentioned above), fur (*Trichosurus vulpecula* to New Zealand) and through escapes from private collections (e.g., *Macropus rufogriseus* in the UK) (Long 2003). The order Perissodactyla is also significantly over-represented amongst introduced species (Table 2), due to the introduction of most of the species in the family Equidae (Table 3), for similar reasons to the Artiodactyla (see above).

As well as exhibiting significant selectivity in terms of identity, introduced mammals are a non-random set in terms of their traits (Table 4). The relative over-representation of species introduced for game, pack, fur, or other goods and services, translates into a strong relationship between introduction and body size: the geometric mean mass of introduced mammals is 24 times that of species that have no recorded introductions. Introduced species also tend to be longer-lived and to have larger litters, as also shown by Capellini et al. (2015), which is not simply a consequence of allometry, as maximum longevity, litter size and body mass all explained variation in introduction status in a phylogenetic multivariate model (Table 5). Capellini et al. (2015) found an effect of number of litters per year but not body mass on introduction; we do not use the former measure as it lacks data relative to litter size, but a correlation between these two variables may explain the effect of body mass in our full model. Interestingly, running our phylogenetic models on Capellini et al.'s (2015) list of introduced mammals revealed a similarly strong univariate effect of body mass on introduction, but a much weaker effect in the full model (estimate ± standard error = 0.021 ± 0.009, t = 2.33, P = 0.02; c.f. Table 5). This suggests the weaker effect of mass in their analysis is not simply an effect of their inclusion of number of litters per year. Jeschke and Strayer (2006) found univariate effects of longevity and body size on a much smaller sample of mammal species introductions to Europe and North America, but only longevity (and trophic level) explained variation in their phylogenetic multivariate model. The benefits to humans of large body size and litter size in introduced species are obvious; the additional independent benefits of longevity are less so, although such species may be better able to survive the introduction process. Our global dataset also identifies a tendency for introduced species to have broader diet breadths than expected (Table 4), although there was no effect of diet breadth on introduction in the full model (Table 5).

Species traits help determine which mammals have been introduced, but so too do the characteristics of their geographic range: widespread species inhabiting cooler locations and areas with denser human populations are more likely to have been introduced (Tables 4, 5). These results identify an effect of species availability on selection. Widespread mammal species tend also to be abundant (Blackburn et al. 1997), and hence are likely to be more familiar to local inhabitants, and more available for deliberate or accidental translocation. Availability will also be higher for species that overlap areas with higher human population densities. Similar patterns have been observed for global bird (Blackburn et al. 2009) and amphibian (Tingley et al. 2010) introductions, and in multi-taxon models for mammal, bird and fish introductions to Europe and North America (Jeschke and Strayer 2006). The negative effect of temperature (and precipitation in univariate analysis) likely reflects the fact that much of the history of introductions has occurred alongside movements of species by Europeans to and from Europe and the neo-European colonies (e.g. especially North America, Australia, New Zealand, South Africa), which tend to lie at temperate latitudes. Peoples from these latitudes moved the species that were available to them. Translocations are still occurring at these latitudes, although increasingly they concern native species moved for conservation purposes (e.g. threatened marsupial species in Australia (Masters et al. 2004), declining game species in southern Africa (Matthee and Robinson 1999; Spear and Chown 2009), or on-going unplanned introductions as a result of releases or escapes of mammals from the pet trade (e.g., domestic cats (*Felis catus)* in several countries, including Australia (Abbott 2002) and New Zealand (Parkes and Murphy 2003).

Phylogenetic analysis revealed that there is significant phylogenetic signal in which mammal species have been introduced, albeit less than expected under a Brownian motion model of evolution. This reflects the clear non-randomness of introduction with respect to taxonomic affiliation, but that selection is not simply based around phylogenetic clumping of mammals. These models demonstrate that several variables explained independent variation in introduction (large-bodied, long-lived, widespread, temperate species), in line with findings from other taxa at the global or regional scale (Jeschke and Strayer 2006; Blackburn et al. 2009; Tingley et al. 2010; van Wilgen et al. 2010; García-Díaz and Cassey 2014). Nevertheless, these models also show that most of the variation in introduction is unaccounted for: the full model for our data explained c. 30%. We suspect that much of the unexplained variation relates to the intrinsically stochastic nature of the introduction process, driven as it is by historical contingency in the interaction between the evolutionary history of mammals that located certain species with certain traits in the way of human histories of movement and demands for goods and services.

Introduction is an early step on the invasion pathway (Blackburn et al. 2011), and the characteristics of the species that get introduced outside their normal distributions determine which traits are available to influence the subsequent stages of establishment and invasive spread. Our analyses show that the species selected by humans to face the challenges of these later invasion stages tend to be long-lived, large-bodied, and fecund; they also tend to be widespread and come from areas with higher human population densities (Tables 4, 5). Widespread species may be able to tolerate a broad range of environmental conditions (Gaston 2003), and the fact that they are likely to be moved to areas with high human population densities, as well as from such areas, increases the likelihood that they will find new locations to their liking (Blackburn et al. 2009). Large-bodied, long-lived species may be less susceptible to the negative effects of demographic and environmental stochasticity (Sæther et al. 2004), whereas rapidly reproducing species can quickly escape the demographic and environmental traps associated with small populations (Moulton and Pimm 1986). This suggests that, deliberately or inadvertently, people have chosen alien mammal species with characteristics that may predispose them to success in the later stages of invasion.

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Supplementary material 1

A list of introduced mammal species

Authors: Tim M. Blackburn, Sally L. Scrivens, Sarah Heinrich, Phillip Cassey

Data type: Text

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Supplementary material 2

References from which the database of introduced mammals was constructed

Authors: Tim M. Blackburn, Sally L. Scrivens, Sarah Heinrich, Phillip Cassey

Data type: Text

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RESEARCH ARTICLE

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Impact assessment with different scoring tools: How well do alien amphibian assessments match?

Sabrina Kumschick[1,2], Giovanni Vimercati[1], F. Andre de Villiers[1],
Mohlamatsane M. Mokhatla[1], Sarah J. Davies[1], Corey J. Thorp[1],
Alexander D. Rebelo[1], G. John Measey[1]

1 *Centre for Invasion Biology, Department of Botany & Zoology, Stellenbosch University, Private Bag X1, Matieland 7602, South Africa* **2** *Invasive Species Programme, South African National Biodiversity Institute, Kirstenbosch National Botanical Gardens, Claremont 7735, South Africa*

Corresponding author: *Sabrina Kumschick* (sabrina.kumschick@gmail.com)

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Abstract

Classification of alien species' impacts can aid policy making through evidence based listing and management recommendations. We highlight differences and a number of potential difficulties with two scoring tools, the Environmental Impact Classification of Alien Taxa (EICAT) and the Generic Impact Scoring System (GISS) using amphibians as a case study. Generally, GISS and EICAT assessments lead to very similar impact levels, but scores from the schemes are not equivalent. Small differences are attributable to discrepancies in the verbal descriptions for scores. Differences were found in several impact categories. While the issue of disease appears to be related to uncertainties in both schemes, hybridisation might be inflated in EICAT. We conclude that GISS scores cannot directly be translated into EICAT classifications, but they give very similar outcomes and the same literature base can be used for both schemes.

Keywords

Environmental Impact Classification for Alien Taxa (EICAT), Generic Impact Scoring System (GISS), prioritisation, listing, alien species, biological invasions

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Introduction

Alien species can cause a variety of changes to the areas in which they are introduced (Simberloff et al. 2013, Vilà et al. 2010, 2011). Impacts of invasive species can include changes to the environment, economy and social systems, they can vary in magnitude, and can include positive as well as negative effects (Jeschke et al. 2014). In its Strategic Plan for Biodiversity, the Convention on Biological Diversity includes the identification and prioritisation of harmful alien species in Aichi Target 9 (UNEP 2011, McGeoch et al. 2016). For prioritisation of actions, and to generally improve our understanding of alien species' impacts, we need ways to compare a multitude of variables measured on impacts caused through various mechanisms by species belonging to widely divergent taxonomic groups. Risk assessment tools in general, and impact assessments specifically are used to prioritise species for management action (e.g., Leung et al. 2012, Kumschick and Richardson 2013, Essl et al. 2011). Due to the importance of such tools in management prioritisation, policy making and regulation, it is crucial that they represent reality as accurately as possible. However, a systematic comparison between impact scoring tools is lacking. For this study we were interested in whether two impact scoring systems relying on published evidence, rather than expert opinion, would lead to the same classification of alien species, using amphibians as a case study. Alien amphibians are an interesting group as the total number of introduced species is relatively small and they can be assessed in their entirety (Kraus 2009), and the quantity and quality of literature reflects that of other taxa (Measey et al. 2016, Evans et al. 2016).

The two impact scoring schemes we chose for the comparison are the Generic Impact Scoring System GISS (Kumschick et al. 2015, Nentwig et al. 2016) and the Environmental Impact Classification for Alien Taxa (EICAT) scheme (Blackburn et al. 2014, Hawkins et al. 2015). While EICAT was formally adopted by the IUCN as an official system to classify the threat posed by alien species to the native environment (https://portals.iucn.org/congress/motion/014), to be used alongside the Red List for species conservation, to date it has only been systematically applied to one taxonomic group, namely birds (Evans et al. 2016). The GISS on the other hand is one of the most widely used and adopted impact scoring tools and has been applied to a wide variety of taxa ranging from plants (Kumschick et al. 2015, Novoa et al. 2016) to vertebrates (e.g., Evans et al. 2014, Martin-Albarracin et al. 2015) and invertebrates (Vaes-Petignat and Nentwig 2014, Nentwig 2015) and spanning many habitats (see Nentwig et al. 2016 for an overview of previous applications). A comparison between these impact scoring schemes can be useful in order to assess to what extent GISS scores can be "translated" into EICAT classifications, given the many GISS assessments which were performed before the adoption of EICAT by IUCN. If GISS scores and EICAT assessments consistently led to the same classification we suggest GISS scores could be adopted under IUCN as an interim measure before full EICAT assessments are made.

In this study, we use the same literature as source information to assess all alien amphibian species with EICAT and GISS. We ask (i) whether the two impact scoring schemes produce complementary maximum classifications, (ii) whether GISS total scores correlate with EICAT assessments, and (iii) under which conditions anomalies occur. Furthermore, it is well known that some taxa receive more research attention than others (e.g., Pyšek et al. 2008). Given that both scoring schemes rely solely on published evidence, it is possible that species reaching higher scores in any of the impact schemes only do so because more information is available on their impact. This would create a bias towards more "popular" species reaching higher impacts. To assess this issue, we ask whether the quantity of literature used to make an assessment correlates with a larger score (i.e., sum and maximum in GISS, and maximum in EICAT) in each of the scoring schemes, and if EICAT assessments with higher confidence ratings were underpinned with more references.

Methods

Species selection

We assessed all alien amphibians established anywhere outside of their native range. They comprised of a list provided by Kraus (2009) and additional searches for species with introduced distributions indicated in the IUCN Red List, and led to a selection of 105 alien amphibians (see Measey et al. 2016 for details).

Literature search

Both schemes applied here rely on published literature. We used the species' scientific (scientific binomial) name as search term on Web of Science and Google Scholar and subsequently manually filtered through the titles and abstracts to find publications relevant with regards to impacts of alien populations. We incorporated articles published until August 2015. In the case that the scientific species name had changed recently (since 2000; e.g. *Bufo marinus* changed to *Rhinella marina*), we also searched under the older name. In addition, we consulted the references in the relevant publications for suitable references.

GISS, EICAT and how they differ

GISS and EICAT both aim to produce a comparative score for different alien taxa based on published evidence. Both schemes have five levels of impact, and discriminate between no impact and a lack of available data which results in a Data Deficient status (in EICAT) and no score (in GISS), respectively. Table 1 outlines the impact levels of both schemes and the acronyms used for EICAT in this study. Both also specify that the maximum score in any one category should be the overall status for that species and category.

Table 1. Summary of GISS and EICAT scores applied across mechanisms (e.g., competition, hybridisation, etc.). See Hawkins et al. (2015) and Nentwig et al. (2016) for details of mechanisms.

EICAT/GISS score	Massive (MV)/5	Major (MR)/4	Moderate (MO)/3	Minor (MN)/2	Minimal concern (MC)/1
EICAT	Causes at least local extinction of native species, and irreversible changes in community composition; even if the alien taxon is removed the system does not recover its original state	Causes changes in community composition, which are reversible if the alien taxon is removed	Causes population declines in native species, but no changes in community composition	Causes reductions in individual fitness, but no declines in native population sizes.	No effect on fitness of individuals of native species
GISS	Major large-scale impact with high damage and complete destruction, threat to species including local extinctions	Major impact with high damage, major changes in ecosystem functions, decrease of species	Medium impacts, large-scale, several species concerned, relevant decline, relevant ecosystem modifications	Minor impacts, more widespread, also on rarer species	Minor impacts, only locally, only on common species

Although amphibian impacts have previously been assessed using EICAT (Kraus 2015), we have not considered these data as no detail on separate species' impact classifications were given, and only high impact amphibians were included in this study.

GISS and EICAT differ in (i) the number of categories (i.e., mechanisms) and (ii) the details of what is required to score a species in any category. The details of both schemes are published elsewhere (Hawkins et al. 2015, Nentwig et al. 2016) but have been summarised here in Table 1. GISS scores concentrate on the spatial scale at which an alien species is having an impact as well as the number of species that are impacted by the alien. EICAT has no intrinsic spatial scale, instead allowing the impact on the community invaded (however large or small) to dictate the level of threat. Furthermore, EICAT focuses on single species affected within a community and therefore does not take into account the number of native species affected by the alien species.

The schemes also differ in that GISS provides categories for economic as well as environmental impact assessments whereas EICAT only includes environmental impacts. Here we only use scores that relate to environmental assessments of both schemes, because economic assessments were poorly populated for amphibians (see Measey et al. 2016) and it was necessary to keep the results comparable between the two schemes.

In addition to the maximum GISS score (1 to 5), GISS gives sums which are totals of all scores across all categories (1 to 30), but EICAT uses only the maximum scores. However, EICAT assessments assign a confidence level to each assessment ranging from low to high as described in Hawkins et al. (2015). The latest guidelines on the GISS system published refers to the EICAT guidelines for confidence assessment (Nentwig et al. 2016). However, we did not include these in the analyses as previous publications of GISS did not include them (e.g., Nentwig et al. 2010, Kumschick et al. 2015).

Data analyses

We used a paired Wilcoxon signed rank test to assess how similar the maximum and total scores obtained in GISS were to those scored in EICAT. For this we assigned numerical values to EICAT assessments, namely 1 for MC to 5 for MV, respectively: we refer to this as nEICAT. We used a non-parametric (Kendall's tau) correlation test to assess the relationship between the number of publications found per species and (i) nEICAT, (ii) the maximum GISS score and (iii) the sum of all GISS scores for each species respectively. All analyses were performed in R v3.2.1 (R Core Team 2015). Furthermore, we were interested in whether species assessed using EICAT with higher confidence scores had more publications underpinning their impacts. Confidence limits (low, medium and high) were assigned scores 1, 2 and 3, respectively, and analysed with a Kendall's tau correlation test against the number of publications used for the species.

Results

We found that the maximum scores produced by the two impact scoring systems were not equivalent, but the paired Wilcoxon signed rank test was significant, suggesting that they are similar ($V = 25$; $P < 0.0001$; Figure 1a). Of the 40 species for which we found relevant literature and which had maximum scores in both systems, 40% had equivalent scores, while 55% scored higher in EICAT and 5% higher in GISS. Of those that scored higher in EICAT, all ($n = 22$) were a single category higher, while those where GISS scored higher ($n = 2$) were a single category lower in EICAT. This means that most EICAT scores span at least two maximum GISS scores, except MO which spans three and MC which is directly equivalent to maximum GISS scores for all four species (Table 2).

GISS total scores do not correlate with EICAT assessments ($V = 315.5$; $P = 0.315$; Figure 1b). Top total scores in GISS (>10) only reached MR in EICAT with a single exception, the tiger salamander *Ambystoma tigrinum* scoring in the highest category (MV). Other amphibians which scored MV under EICAT had very low total scores of 4 under GISS, which at the same time are the maximum scores for these species as they only scored under one mechanism. The anomalies (see Figure 1b) occur with high scores for hybridisation in EICAT compared to the comparatively low scores in GISS. It was also noteworthy that there was little difference in total GISS scores between MC and MN classes in EICAT.

In total, we found 242 relevant publications for 40 species, with an average of 5.9 publications per species (excluding the 65 species for which no data was available). A full reference list can be found in Measey et al. (2016). We found that both EICAT and GISS maximum score were not related to the number of publications found on the species' impacts (Kendall's tau = 0.24 and 0.25; $P = 0.059$ and 0.055 respectively; Figure 2). However, we found that the sum of environmental scores for GISS was more related to the number of publications, explaining nearly half of the variation in the data

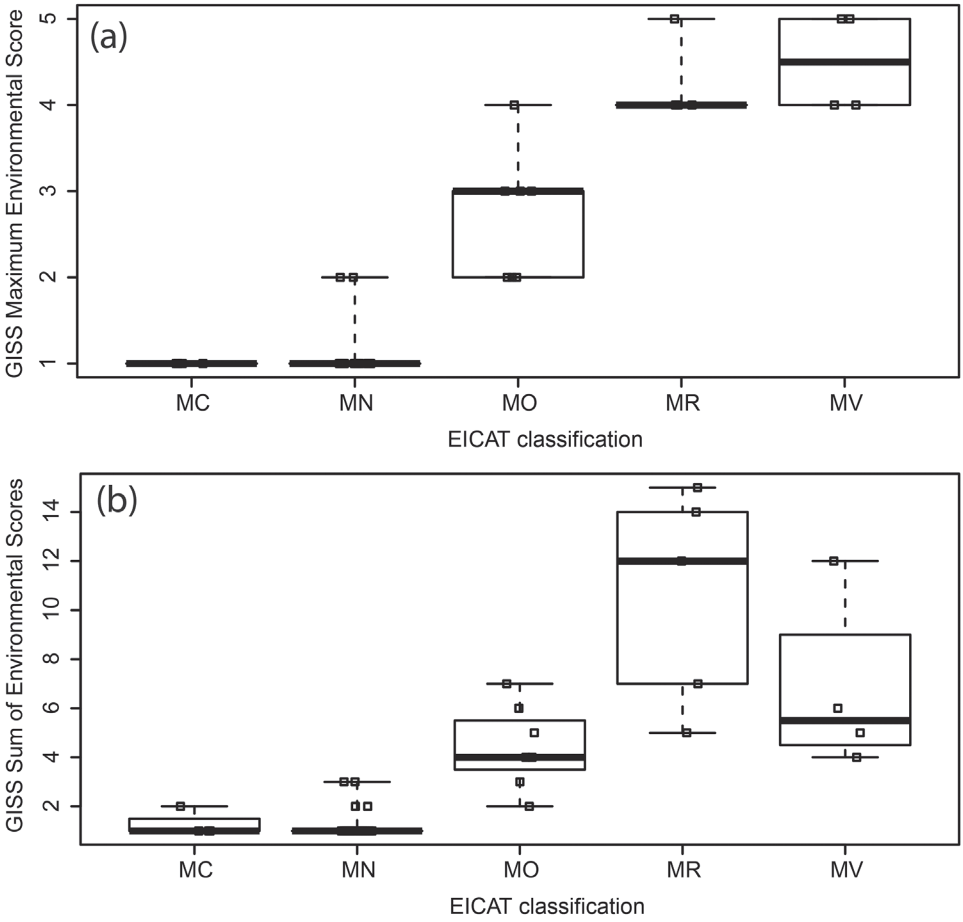

Figure 1. Boxplots showing how **a** GISS maximum scores and **b** the sum of all GISS environmental scores are related to EICAT classifications. Individual data points represent different species (with a jitter effect to prevent overlapping), and show the entire range of data in all groups.

(Kendall's tau = 0.41; P = 0.048; Figure 2c). Lastly, higher confidence EICAT classifications did not have more publications for that species (Kendall's tau = 0.21; P = 0.121).

Discussion

This paper presents the first systematic EICAT assessment for amphibians detailing species-specific classifications. Kraus (2015) assessed the impacts of selected amphibians using EICAT without however reporting on impact levels per species.

Our study shows that for alien amphibians, EICAT assessments are not equivalent to maximum or total scores under GISS. This means that we cannot simply adopt GISS assessments under IUCN instead of performing full EICAT assessments. However, we

Table 2. EICAT classification versus maximum environmental GISS scores for all 40 amphibian species for which data was available.

		EICAT				
		MV	**MR**	**MO**	**MN**	**MC**
GISS	**5**	*Ambystoma tigrinum* *Pelophylax bergeri*	*Rhinella marina*			
	4	*Pelophylax ridibundus* *Pelophylax bedriagae*	*Duttaphrynus melanostictus* *Lithobates catesbeianus* *Triturus carnifex* *Xenopus laevis*	*Sclerophrys gutturalis*		
	3			*Eleutherodactylus coqui* *Osteopilus septentrionalis* *Pelophylax nigromaculatus*		
	2			*Hyla meridionalis* *Pelophylax perezi* *Rana aurora*	*Hoplobatrachus rugulosus* *Scinax quinquefasciatus*	
	1				*Lithobates berlandieri* *Rhinella jimi* *Dendrobates auratus* *Discoglossus pictus* *Fejervarya cancrivora* *Fejervarya limnocharis* *Hoplobatrachus tigerinus* *Hylarana guentheri* *Lithobates clamitans* *Litoria ewingii* *Litoria fallax* *Microhyla pulchra* *Pelophylax lessonae* *Pipa parva* *Plethodon jordani* *Polypedates leucomystax* *Polypedates megacephalus* *Scinax ruber*	*Ichthyosaura alpestris* *Eleutherodactylus cystignathoides* *Eleutherodactylus planirostris* *Strongylopus grayii*

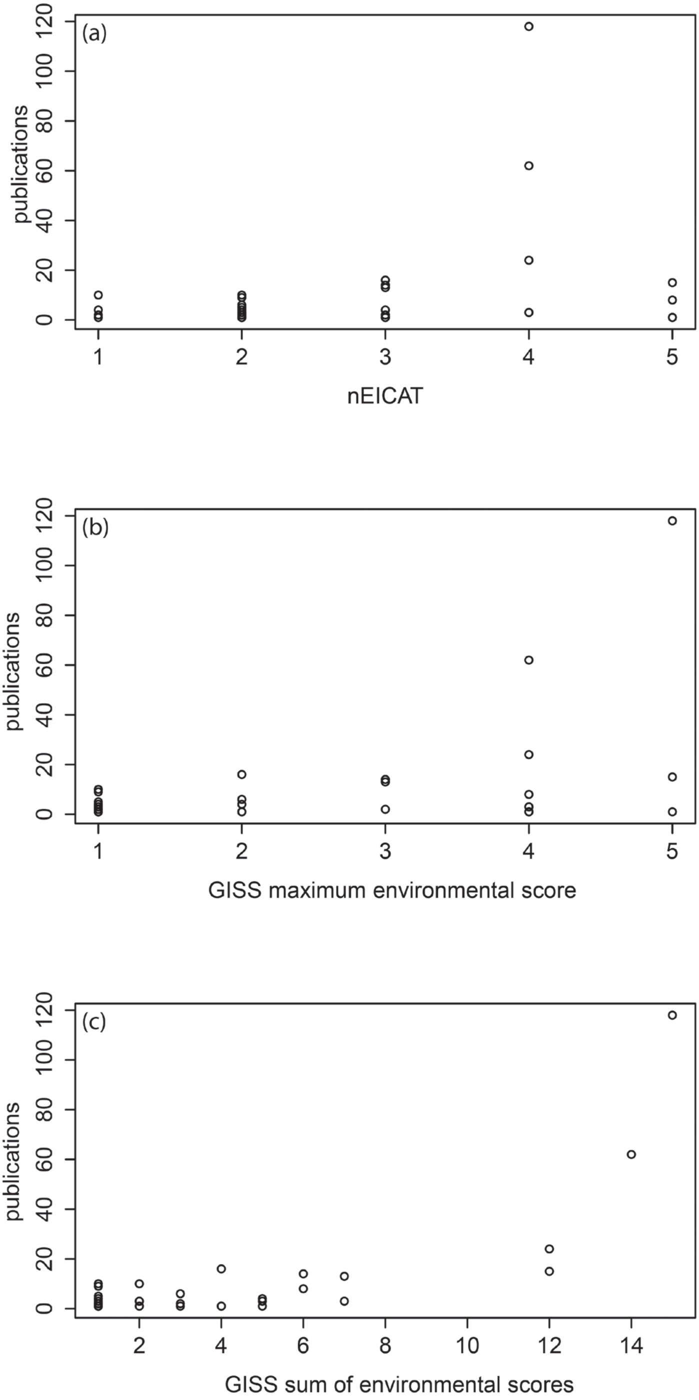

Figure 2. The relationship between the number of publications with data that can be used to assess impact for a species of alien amphibian and **a** its EICAT score **b** its GISS score and **c** the sum of environmental scores.

found that the scores were very similar, and, where they did differ, they differed by a single level of impact. The broad agreement between these two impact scoring schemes is encouraging as it suggests that each is managing to provide a comparative measure of impact, despite having different sets and numbers of criteria. Moreover, as both schemes rely on the same type of data, namely published evidence, once literature has been amassed for making a GISS score, the same data sources can be productively used for an EICAT assessment. The detailed EICAT assessments for each species will be externally reviewed and published under the IUCN umbrella on the Global Invasive Species Database (GISD; http://www.iucngisd.org/gisd/) after acceptance by the EICAT Unit (Hawkins et al. 2015).

Of particular note are species which score the highest possible in the one system but not the other: 5 in GISS but MR in EICAT, or MV in EICAT but 4 in GISS. This is the case for three species (Table 2). On the one hand, *Rhinella marina* reached GISS scores of 5 in two categories, namely "Impacts on animals through [...] intoxication" and "Impacts through transmission of diseases [...]". A local extinction of *Dasyurus hallucatus* occurred in Australia where quolls were poisoned when they preyed on *R. marina* (Oakwood and Foster 2008), however as the effect was considered reversible, it was given MR in EICAT. *R. marina* have also been shown to be the hosts of a parasite negatively affecting native Australian frogs, which was not present in the area before the toads arrived (Hartigan et al. 2010, 2011, 2012). The formulation in GISS of a maximum disease impact (see Nentwig et al. 2016) leaves room for different assessors to score different impacts, based on their interpretation, which might have led to a high score in GISS and a MO in EICAT. Given the severity of the effects of *Batrachochytrium dendrobatidis* and other diseases, both EICAT and GISS appear to highlight the difficulty of assigning the spread of disease through alien taxa and the transmission thereof to native species (see also Measey et al. 2016, Evans et al. 2016), although this is widely acknowledged in amphibians (Fisher and Garner 2007).

The two *Pelophylax* species scoring highest in EICAT but not in GISS had demonstrated impacts related to hybridisation, predation and competition with native species. The two schemes have in common that for low to medium impact levels of 1-3 (GISS) or MC to MO (EICAT) respectively, hybrids of the native and alien species need to be sterile. However, in the distinction of the two highest impact levels, EICAT and GISS differ. Higher impacts through hybridisation in GISS are determined by the relative quantity of hybrid populations (Nentwig et al. 2016). Given that EICAT scores have not been published before for amphibians, we would like to point out a feature of the scheme which could potentially be problematic for some taxa. According to Hawkins et al. (2015), the impact of an alien species on native species through hybridisation follows a slightly different logic than the remaining categories, insofar as fitness (and capacity to produce offspring) of the hybrids is also considered on top of fitness of the pure native species: EICAT distinguished the two highest classifications in terms of the vigor of F1 offspring - MV leading to fully vigorous and fertile offspring, MR with sterile F1 hybrids (Hawkins et al. 2015). Therefore, to reach the maximum score in EICAT (i.e. MV), a proportion of hybrids is not stipulated and consequently, for many amphibians where F1s are fertile, it does not appear to be possible to have an EICAT score lower than MV.

Hybridisation should be carefully considered in amphibians, especially frogs and salamanders, as some of these species readily hybridise through polyploidy and may have done so for many decades (e.g., Vorburger and Reyer 2003). To the best of our knowledge no native species have been lost from any specific location despite destabilising hybridisation favouring the alien taxon (e.g., Quilodrán et al. 2015, Leuenberger et al. 2014). If strictly following the guidelines by Hawkins et al. (2015), only species of which F1 parents produce sterile offspring could have MR impacts. However in cases where F1 hybrids can produce fertile offspring, it would be classified as MV, assuming that in all cases this would lead to genomic extinction of the native species. In the GISS hybridisation, impacts of level 4 and 5 are only distinguished through the size of the hybrid population (and remaining native population), which in the case of frogs might be a more sensible way to classify alien species' impacts through this mechanism. We feel that this would also be more in line with the impact levels of the remaining mechanisms in EICAT.

Furthermore, in some cases, species previously imbedded under the same species name were split into two species, which "creates" a hybridisation impact of one species on another which was previously unrecognised. An example thereof is the hybridisation of tiger salamanders (*Ambystoma tigrinum*) with the California tiger salamander (*Ambystoma californiense*) (e.g., Riley et al. 2003, Fitzpatrick et al. 2010). This issue is not restricted to amphibians, but could happen in every case where subspecies change to species status. Also, the impact mechanism is not restricted to hybridisation, but could for example include competition (e.g. Arntzen and Thorp 1999). This might lead to the need to revise assessments in certain cases when taxonomy is updated.

Summing impact scores can potentially be biased towards species with higher research efforts, as it is more likely for various mechanisms to be studied for these species. Our data on the number of publications to make an assessment are not atypical (Measey et al. 2016) and similar patterns should therefore be expected in other taxa. Using maximum scores not only for EICAT but also GISS assessments, as suggested previously (e.g. Kumschick et al. 2016), can reduce this bias. Still, alien species which affect the recipient communities through various mechanisms might be more problematic as the impacts are less specific and probably less context dependent. For example, species only impacting communities through hybridisation (e.g. *Pelophylax ridibundus* and *P. bedriagae* in our study; Arano et al. 1995, Pagano et al. 1997, Holsbeek et al. 2008, 2010) are less likely to cause such impacts in other areas where these native species are not present than species like *A. tigrinum* which also affect native communities through predation (Ryan et al. 2009). Furthermore, we show that high confidence for an assessed impact score might come from a single, well executed study, while many studies which are poor with respect to defining impact will not result in a higher level of confidence (but see Evans et al. 2016). Likewise, many good studies might result in a high confidence for a lesser impact level, but a single less rigorous study may result in a higher impact, but with poor confidence. Therefore, we emphasise the importance of reporting more detail than simply the highest score and its mechanisms for the classification of taxa, but also to include other high confidence findings, as well as information on different impact mechanisms (Hawkins et al. 2015).

Conclusion

The adoption of a single impact scoring scheme under an international umbrella such as IUCN is necessary, yet we show the potential pitfalls of converting scores between two widely used schemes: GISS and EICAT. These schemes are largely congruent, but do present some challenges where one might borrow from the other to resolve apparent discrepancies for amphibians which we feel are likely to manifest in time for other taxa. Levels of impact assigned in general, but specifically on disease transmission and hybridisation require detailed background information backing up the classification, and additional guidelines should be considered to make classifications more unified in this regard.

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RESEARCH ARTICLE

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Range expansion drives the evolution of alternate reproductive strategies in invasive fire ants

Jackson A. Helms IV[1], Eli S. Bridge[2]

1 *Department of Biology, University of Oklahoma, 730 Van Vleet Oval, Rm 314, Norman, OK USA 73019*
2 *Department of Biology and Oklahoma Biological Survey, University of Oklahoma, 111 E. Chesapeake St, Norman, OK USA 73019*

Corresponding author: *Jackson A. Helms IV* (jacksonhelmsiv@gmail.com)

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Abstract

Many species are expanding their ranges in response to climate changes or species introductions. Expansion-related selection likely drives the evolution of dispersal and reproductive traits, especially in invasive species introduced into novel habitats. We used an agent-based model to investigate these relationships in the red imported fire ant, *Solenopsis invicta*, by tracking simulated populations over 25 years. Most colonies of this invasive species produce two types of queens practicing alternate reproductive strategies. Claustral queens found new colonies in vacant habitats, while parasitic queens take over existing colonies whose queens have died. We investigated how relative investment in the two queen types affects population demography, habitat occupancy, and range expansion. We found that parasitic queens extend the ecological lifespan of colonies, thereby increasing a population's overall habitat occupancy as well as average colony size (number of workers) and territory size. At the same time, investment in parasitic queens slowed the rate of range expansion by diverting investment from claustral queens. Divergent selection regimes caused edge and interior populations to evolve different levels of reproductive investment, such that interior populations invested heavily in parasitic queens whereas those at the edge invested almost entirely in claustral queens. Our results highlight factors shaping ant life histories, including the evolution of social parasitism, and have implications for the response of species to range shifts.

Keywords

Agent-based Model, Dispersal Evolution, Dispersal Polymorphisms, Invasions, Reproductive Polymorphisms, Range Expansion, Social Parasitism, *Solenopsis invicta*

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Introduction

Many species throughout the world are shifting or expanding their ranges in response to climate changes or species introductions (Parmesan et al. 1999, Hickling et al. 2006, Chen et al. 2011). Range shifts may in turn drive evolutionary changes, as populations colonize vacant habitats and experience novel conditions (Thomas et al. 2001, Sexton et al. 2009). Populations at expanding range edges, in particular, are likely to evolve greater dispersal ability as a result of both selection and assortative mating (Cwynar and MacDonald 1987, Phillips et al. 2008, Hill et al. 2011). Other traits that are linked to dispersal, such as fecundity or mating system, may also evolve in response to range expansion (Burton et al. 2010, Hargreaves and Eckert 2014).

Ants present some of the world's most conspicuous recent range expansions. Many species are global invasives whose non-native ranges are expanding through natural and human-assisted dispersal (Holway et al. 2002). Colonies of most ant species reproduce and disperse by rearing winged queens that fly to locate mates and new nest sites (Hölldobler and Wilson 1990, Peeters and Ito 2001). There are countless variants of this life cycle (Heinze and Tsuji 1995, Heinze 2008), and many ants pursue multiple reproductive strategies (Ross and Keller 1995, Sundström 1995, Heinze and Keller 2000). In some species, for example, colonies can produce two different types of queens from the same genome—an independent one that founds new colonies and a parasitic one that joins existing colonies of the same species (Bourke and Franks 1991, Rüppell and Heinze 1999). These alternate strategies result in dispersal differences, since only one queen type can colonize vacant sites while the other can reproduce only in occupied areas. Reproductive polymorphisms have been documented in many invasive ants (Yamauchi and Ogata 1995, Holway et al. 2002, Tsutsui and Suarez 2003), and trait variability has been linked to invasion success in several other taxa (Richards et al. 2006, Davidson et al. 2011, Forsman 2014, González-Suárez et al. 2015). But it remains unclear how reproduction-dispersal polymorphisms in ants affect rates of range expansion, or how investment in different strategies responds to expansion-related selection.

The red imported fire ant (*Solenopsis invicta*), perhaps the best-known invasive ant, is an ideal organism for examining these relationships. It is native to South America but was accidentally introduced to the southeastern USA in the 1930s and to several other countries afterward (Tschinkel 2013). It has been expanding its non-native ranges ever since through human transport and natural dispersal during mating flights (Tschinkel 2013). Most populations of *S. invicta* are monogyne, with a single reproductive queen per colony (Porter et al. 1997). Mature monogyne colonies reproduce using both claustral and parasitic queens (Tschinkel 1996, DeHeer and Tschinkel 1998). Claustral queens fly in spring and summer and found new colonies independently. They dig nest cavities in unoccupied soil, lay eggs, and rear a first generation of workers from their own energy reserves. The parasitic queens, in contrast, fly in late winter and take over conspecific colonies whose queens have recently died, thereby inheriting an existing workforce. Parasitic queens make up a minority of a colony's reproductive effort (Morrill 1974), but are thought to provide a substantial return per investment due to the constant natural orphaning of colonies in mature populations (DeHeer and Tschinkel 1998).

Using *S. invicta* as a model, this study addresses two questions related to range expansion and alternative reproductive strategies. The first question, posed from the perspective of a population ecologist, asks how investment in parasitic queens affects the spatial distributions of fire ant populations with regard to colony size (number of workers in a colony), territory size (area controlled by a colony), and the propensity to expand into suitable habitats. The second question takes an evolutionary perspective and asks what the optimal relative investment in the two strategies is for colonies seeking to maximize their contribution to future generations.

The presence of parasitic queens in a population makes colonies potentially immortal. Genetic lineages within a colony are replaced over time as queens die and new ones take over. But the colony itself may remain on the landscape for generations, as long as it is successfully parasitized every time it is orphaned. This scenario prompted us to conceive the *Immortality Hypothesis*, which entails three predictions associated with extending the ecological lifespan of colonies. First, parasitic queens should increase the average colony size in a landscape. Second, parasitic queens should increase occupancy of the habitat by fire ant colonies (Korzukhin and Porter 1994). Third, in expanding ranges, investment in parasitic queens should slow range expansion by diverting investment from claustral queens that colonize vacant sites. Alternatively, investment in parasitic queens may speed up range expansion by increasing the average size and persistence of colonies, thereby increasing overall queen production.

From the perspective of a reproductive queen, the optimal investment in daughters practicing the two strategies probably varies with location. Colonies at an expanding edge should experience more reproductive success by investing heavily in claustral daughters that can colonize empty habitat. On the other hand, colonies in the saturated range interior should benefit more from investment in parasitic daughters, as empty habitat is scarce and there are plenty of established colonies with recently deceased queens. Under what we call the *Optimal Investment Hypothesis*, relative investment in claustral versus parasitic queens should evolve as populations expand. In particular, the average investment in claustral queens should increase from the core to the range edge.

We evaluate these hypotheses using an agent-based computer model to track dispersal and colony founding in expanding fire ant populations over 25 years. To examine the ecological effects of reproduction-dispersal polymorphisms, we compare demography, habitat occupancy, and range expansion among populations differing in relative investment in claustral versus parasitic queens. To examine fitness implications of the two strategies, we monitor changes in relative investment within a single variable population as it expands. While we focus on the dynamics of range shifts, our results also provide insight into factors shaping the evolution of reproductive strategies in ants.

Methods

Model design

We constructed an agent-based model in the program R (R Core Team 2012), which simulated the behavior of individual queens and colonies, and allowed us to examine properties of populations of interacting individuals. The inputs to our model determined colony growth and death, competitive territory growth, reproduction and dispersal through the production of new queens, and the relative amount of biomass invested in the production of claustral versus parasitic queens. With these first principles in place, we seeded hypothetical arenas with colonies possessing specified combinations of traits. The arenas were 50 meters wide and bounded on three sides, but unlimited on the upward edge, allowing populations to expand indefinitely. After seeding the arenas with starting populations of colonies, we then monitored how the populations behaved over time (Figure 1). Appendix A provides a detailed description of the model, and the R code can be accessed at the following Github repository: https://github.com/Eli-S-Bridge/RIFA_ABM.

Experimental design

We ran two sets of simulations, the first to examine the effects of reproductive polymorphisms on populations, and the second to examine the fitness implications for colonies investing in the two reproductive strategies. For the first set of simulations, we seeded arenas with 50 colonies that all invested the same amount of effort in claustral versus parasitic queens. We then ran each simulation for 300 months (25 years). Each simulation represented one of six treatments, wherein the proportion of effort that colonies invested in claustral queens was set to 1, 0.98, 0.95, 0.90, 0.75, or 0.50. We ran 72 simulations for each treatment using a C4.8xlarge virtual computer available through Amazon Web Services, which allowed us to run 36 simulations at a time. After accounting for failed simulations (see Appendix A), we ended up with 67 to 69 replicates of each treatment for a total of 407 simulations (n = 69 at relative claustral investment = 1; n = 68 at 0.98, 0.95, and 0.90; and n = 67 at 0.75 and 0.5). We then compared demography, habitat occupancy, and range expansion among the populations that emerged from the six treatments after 300 months.

For each simulation in this first set, we measured the average colony size, average territory size, percentage of available area occupied by all colonies, percentage of colonies headed by parasitic queens, and the maximum upward extent of the range. The upward extent was defined by the maximum y-coordinate among all the territory outlines. To examine spatial patterns we divided the occupied area into sampling windows that were 5 meters high in the up-down axis and extended across the 50-meter width of the arena. We focused on colony size rather than age, because in fire ants (and other social insects) a colony's size is a better indicator of its ecological impact and reproductive potential. Moreover, a colony's size at any age can vary over orders of magnitude due to environmental factors and competitive interactions (Tschinkel 2013).

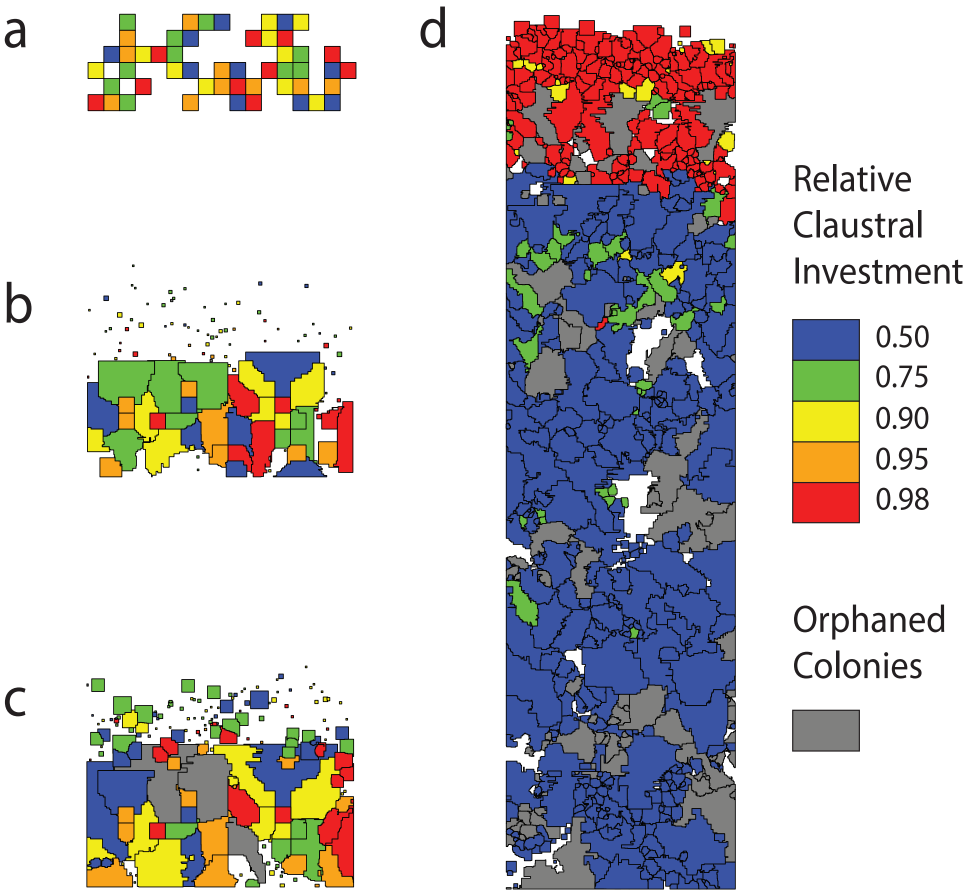

Figure 1. Example simulation of a mixed population consisting of several lineages. **a** Simulation after 0 months, showing starting conditions **b** after 22 months, after the first season of dispersal **c** after 34 months, showing orphaned colonies (gray); and **d** 300 months, at the end of the simulation. Simulation arenas are 50 meters wide. Colors represent lineages that invest different amounts of effort in claustral versus parasitic queens.

The second set of simulations investigated fitness and optimal investment of colonies producing the two queen types. For these simulations, we seeded each arena with 50 colonies varying in relative claustral investment. Each of five levels of investment—0.98, 0.95, 0.90, 0.75, and 0.5—was represented by 10 starting colonies, yielding an initial average claustral investment of 0.847. We then ran the simulation for 300 months (25 years), allowing average claustral investment to evolve through the differential survival and reproduction of colonies with different levels of claustral investment (Figure 1d). We ran 72 simulations using the virtual computer described above, resulting in 66 completed replicates. At the end of the simulation we measured the average claustral investment among colonies large enough to reproduce (≥30,000 workers, Appendix A) in 5 × 50 meter sampling windows.

Results

Population effects

Simulated colony size and territory distributions matched those observed in the field, such that populations consisted of many small colonies and few large ones (Tschinkel 2013), with territories closely packed and irregularly shaped (Adams 1998, Figure 1). As predicted by the Immortality Hypothesis, investing in parasitic queens increased average colony size by 23 to 92% over populations producing only claustral queens (ANOVA $F_{5, 401} = 723.4$, $P = 2 \times 10^{-16}$, Figure 2a). Every decrease in claustral investment below 0.98 increased average colony size in the population (Tukey's post-hoc tests, 1 to 0.98 comparison $P = 0.997$; all other Ps $< 10^{-7}$), from a low of 9,306 workers per colony at total claustral investment to 17,877 workers per colony at half claustral investment. The same results occur when comparing colony territory sizes (ANOVA $F_{5, 401} = 850.5$, $P = 2 \times 10^{-16}$, Figure 2b). Mean territory size in the population increased by up to 133% over populations producing only claustral queens. Every increase in parasitic investment increased average territory size (Tukey's post-hoc tests, all Ps $< 10^{-7}$), from a low of 7.2 m^2 at total claustral investment to 16.8 m^2 at half investment. Even a 2% decrease in claustral investment, from 1 to 0.98, caused a 15% increase in average territory size to 8.26 m^2.

Also as predicted, fire ant colonies occupied up to 12% more of the available habitat in populations that produced parasitic queens (Figure 3a). In all populations habitat occupancy fluctuated around consistently high values before dropping to zero at the expanding range margin. But fluctuations were dampened and habitat occupancy was usually higher in populations producing parasitic queens. Mean habitat occupancy over the whole range varied from 75.3% (±2.57) in populations that produced only claustral queens to 84.5% (±2.68) in those that invested half their effort in parasitic queens. These values correspond well with rough field estimates of fire ant territory coverage of available habitat (>90%, Korzukhin and Porter 1994).

The observed changes in demography and habitat occupancy were driven by the parasitic takeover of orphaned colonies. Even a slight increase in the production of parasites, from 0 to 2% of reproductive investment, led to an average of 43.1% (±20.2%) of colonies being headed by parasitic queens (Figure 3b). In populations investing a fourth to a half of their effort in parasites, there were regions where nearly 100% of colonies were headed by parasitic queens (range-wide average of 75.4 ±31.6% for 0.75 claustral investment, 74.8 ±33.7% for 0.5 claustral investment).

Despite its positive effects on average colony size and persistence, investment in parasitic queens decreased the rate of range expansion by up to 4% (ANOVA $F_{5, 401} = 43.593$, $P = 2 \times 10^{-16}$, Figure 4), from an average maximum of 196.2 (±3.1) meters per simulation in totally claustral populations to 188.8 (±3.2) meters in populations investing half their effort in parasitic queens. Decreasing investment in claustral queens from 1 to 0.9 had no effect (Tukey's post-hoc tests, $P > 0.137$), but further decreases

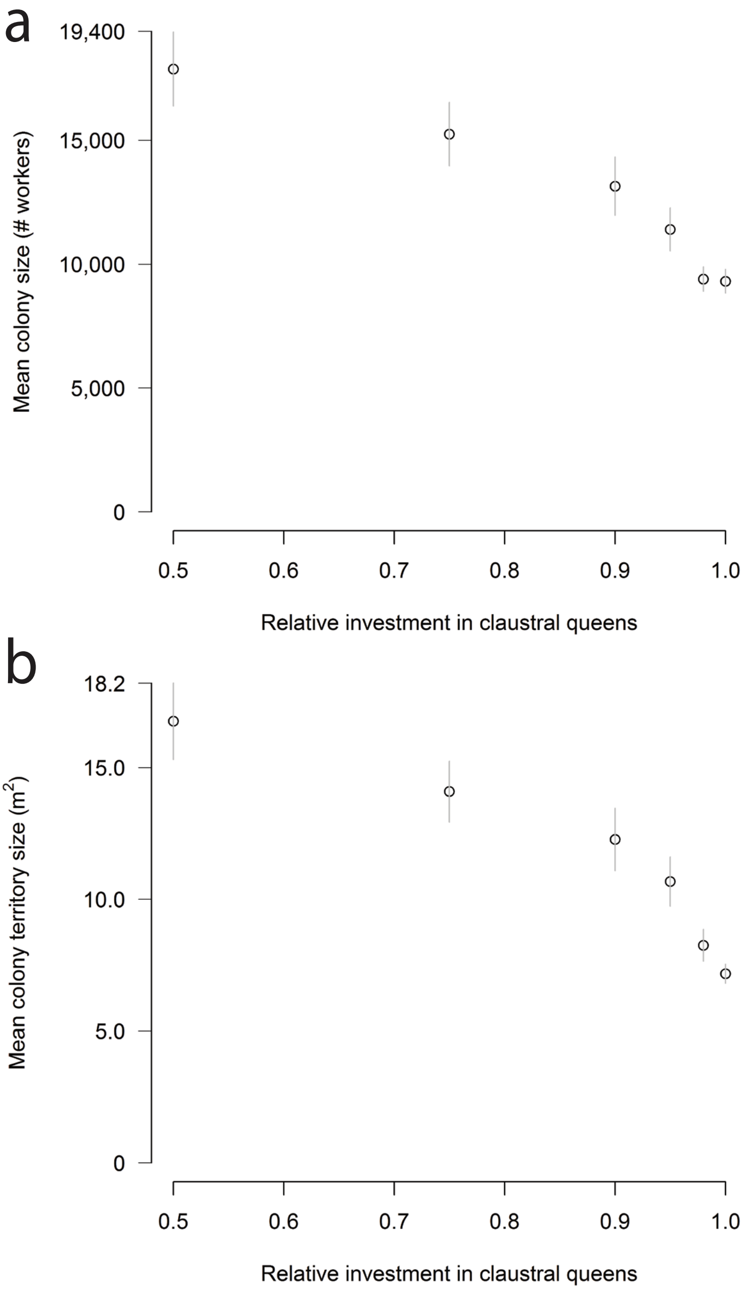

Figure 2. Colony and territory sizes versus reproductive investment. Because parasitic queens extend the ecological lifespan of colonies, populations that invest more in parasitic queens experience larger average colony sizes (**a**) and colony territory areas (**b**). Points show means over all simulations for a given reproductive investment, and error bars show standard deviations. In (a), all values differ ($P < 0.001$) except for those at 1 and 0.98 relative investment ($P = 0.997$); in **b** all values differ ($P < 0.001$).

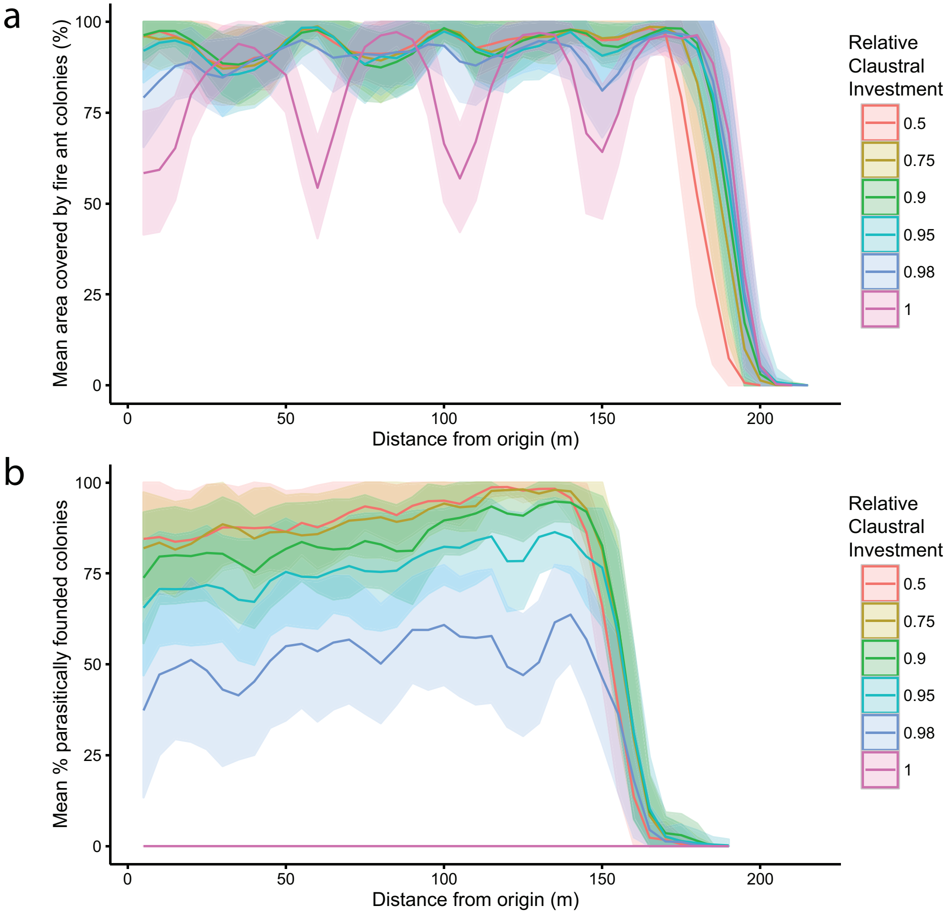

Figure 3. a Percentage of available habitat occupied by fire ant colonies versus distance from the origin (bottom) of a range. Investment in parasitic queens increases and stabilizes the amount of habitat occupied by fire ant colonies **b** The percentage of all colonies that are headed by a parasitic queen versus distance from the origin of a range. Even small investments in parasitic queens lead to high proportions of parasitically founded colonies in the range interior. In all simulations, only claustrally founded colonies occur at the extreme range edge. Colors denote different levels of reproductive investment, lines show averages over all simulations for a given investment, and shading shows standard deviations.

to 0.75 or 0.5 slowed range expansion ($P < 0.003$). Parasites thus appear to affect range expansion primarily by slowing it down through the diversion of investment from claustral queens that can colonize vacant sites, rather than speeding it up by stabilizing larger, more productive colonies.

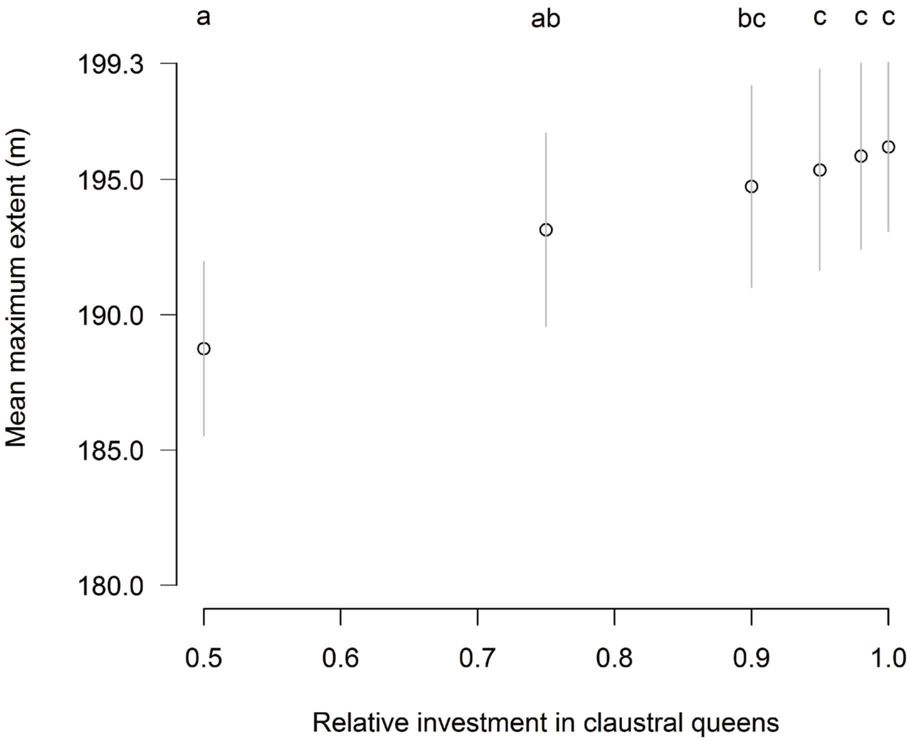

Figure 4. Range expansion versus reproductive investment. Investment in parasitic queens slows range expansion by diverting resources from the production of claustral queens. Points show mean maximum extents of spreading populations over all simulations for a given reproductive investment, and error bars show standard deviations. Points with different letters differ at $P < 0.003$.

Optimal investment

Mature colonies occurred at an average density of 323 ±119 colonies per hectare (n = 66), which is strikingly similar to field estimates from monogyne populations in the southern USA (300 ±240 colonies/ha, Porter et al. 1991). Core and edge populations experienced divergent selection regimes during range expansion. As predicted by the Optimal Investment Hypothesis, a pattern emerged over the course of every simulation wherein colonies in the range interior invested more heavily in parasitic queens and less in claustral queens (Figure 5). The innermost populations averaged slightly above 50% investment in claustral queens (minimum 0.51 ±0.028), which was the minimum allowed in our simulation. At the same time, edge populations retained a heavy investment in claustral queens, with average values approaching 100% (maximum claustral investment 0.96 ±0.015). In these simulations, expansion-related selection has created a geographic gradient in life history strategy within a single variable species.

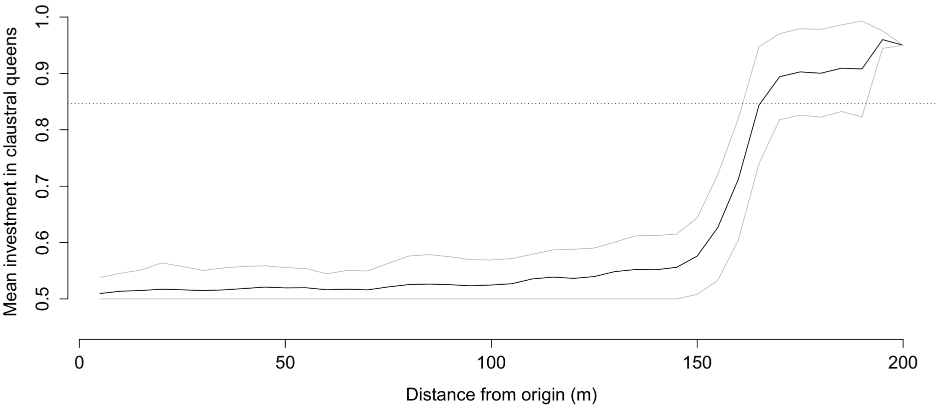

Figure 5. Mean reproductive investment of mature colonies from the range origin (bottom) to the top edge. Gray lines show standard deviations, dashed line shows starting average of 0.847. Populations in the saturated range interior evolve greater investment in parasitic queens, while those at the uninhabited range edge retain greater investment in dispersing claustral queens.

Discussion

Range expansion is a defining character of invasive ants. In species practicing alternate life histories, range dynamics are likely affected by relative investment in different strategies. In our simulations of red imported fire ants, the production of parasitic queens resulted in larger average colony and territory sizes and higher habitat occupancy. On the other hand, by diverting investment from claustral queens that can colonize vacant habitats, the production of parasitic queens slowed range expansion. Range expansion in turn affected the fitness of colonies producing the two queen types. Colonies at expanding range edges benefitted more by investing in claustral queens that could colonize the surrounding vacant habitat, whereas those in the crowded range interior profited from investing more in parasitic queens that could take over orphaned colonies. Divergent selection regimes appeared to drive the evolution of different levels of reproductive investment based on their distance from the range edge.

The effects of range expansion also shed light on other factors shaping the evolution of reproductive strategies in ants. Parasitic founding is thought to be more beneficial in stable saturated environments, and claustral founding to be more beneficial in vacant or disturbed habitats (DeHeer and Tschinkel 1998, Tschinkel 2013). The evolved population differences in our simulations support this notion and also parallel differences among co-occurring fire ant species in the field. Along the US Gulf Coast, *Solenopsis invicta* lives alongside the closely related tropical fire ant, *Solenopsis geminata*, which has a similar life cycle (McInnes and Tschinkel 1995). Within this range, the introduced *S. invicta* occurs primarily in highly disturbed anthropogenic habitats, while the native *S. geminata* occupies more stable natural habitats (Tschinkel 1988b). These habitat differences are mirrored by reproductive differences, with *S.*

geminata investing three to four times as much effort in parasitic queens than *S. invicta* (33% of investment versus <10%). Similarly, our results suggest that within a species older populations should evolve a more parasitic, less dispersive, lifestyle than recently established ones.

Our simulated populations generally behaved realistically, highlighting the model's value for investigating fire ant ecology. Our populations displayed near total occupancy of available habitat (Korzukhin and Porter 1994), closely packed irregularly shaped territories (Adams 1998), size distributions consisting of many small colonies and a few large ones (Tschinkel 2013), and population densities similar to those in the field (323 ±119 colonies/ha simulated versus 300 ±240 in the field, Porter et al. 1991). We note, on the other hand, that in our simulated populations, the observed frequency of parasitic founding and the optimal reproductive investment in interior colonies (>40% of colonies headed by parasites, 40–50% investment in parasitic queens) more accurately describe the native *S. geminata* (35% of colonies, 33% investment in parasites, McInnes and Tschinkel 1995) than *S. invicta* (3.5% of colonies, <10% investment in parasites, DeHeer and Tschinkel 1998). Our goal is not to make absolute predictions about fire ant biology, however, but rather to investigate the interplay between reproductive strategy and range dynamics within a given species.

We made several simplifying assumptions in constructing our model. We assumed, for example, that habitat is constant and homogeneous and that lineages do not interbreed. Incorporating disturbance—to better capture the ecological preferences of *S. invicta*—would shift optimal investment toward more claustral queens by providing a steady supply of vacant habitat in which to found colonies. Allowing gene flow among lineages would slow divergence between interior and edge populations, probably shifting investment toward more claustral queens in the interior. Programing farther dispersal distances (see Appendix A) would probably make the transition between interior and edge populations more gradual, and allowing claustral investment to drop below 50% may reveal upper limits to parasitic investment or shed light on the evolution of obligate parasitism. Furthermore, a substantial minority of fire ant populations in the field (≤20%, Porter et al. 1997) are polygyne and practice fundamentally different life histories in which colonies contain many unrelated queens and reproduce vegetatively by budding or splitting (Tschinkel 2013). Finally, introduced populations of *S. invicta* compete with (Porter et al. 1988, Tschinkel 1988b) or hybridize with (Ometto et al. 2012) other fire ant species, creating a complex network of interspecific interactions affecting dispersal, colony growth, and reproductive success. A complete model of fire ant invasions would incorporate all these variants, and is beyond the scope of our current study.

The rapid spread of several invasive ant species around the globe, through multiple introduction events, provides a valuable opportunity to investigate the interplay between range expansion, dispersal, and reproduction. Because small differences in reproductive strategy cause pervasive changes in demography, habitat occupancy, range expansion, and the response to expansion-related selection, founder effects may play a major role in determining the ecological impacts of introduced ants. Subsequent selection associated with rapid range expansion may further shape the evolution of introduced populations. For similar reasons, some native ant species may be unable to shift their ranges rapidly enough to track climatic changes, and those that do may experience changes in dispersal ability or reproductive ecology as a result. In a world where ant range shifts are increasingly likely (Colwell et al. 2008), predicting these outcomes has substantial practical importance. Agent-based models are a useful approach for addressing these issues, given sufficiently detailed life history inputs, and provide a relatively rapid and low-cost method of examining future scenarios.

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Supplementary material 1

Range expansion drives the evolution of alternate reproductive strategies in invasive fire ants

Authors: Jackson A. Helms IV, Eli S. Bridge

Data type: species data

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